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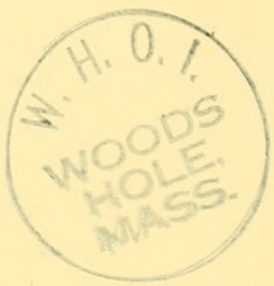
CESTODES OF WHALES AND DOLPHINS FROM THE DISCOVERY COLLECTIONS

By

S. MARKOWSKI



CONTENTS

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By S. Markowski

(Plates XX, XXI and Text-figs. 1–45)

MATERIAL AND METHODS

THE material for this study was collected mainly at whaling stations and on board factory ships by various members of the staff of the Discovery Investigations.[1] It consists of eighty-eight samples taken from the intestines and blubber of forty-six Blue Whales (*Balaenoptera musculus*), eight Fin Whales (*B. physalus*), thirteen Sei Whales (*B. borealis*), fourteen Sperm Whales (*Physeter catodon*) and seven dolphins, namely: two *Globicephala edwardi*, two *Lagenorhynchus obscurus*, one *L. australis* and two *Steno bredanensis*. Of these, four samples of *Tetrabothrius affinis* from Blue Whales belong to the collections of the British Museum (Natural History).

The material comprises intestinal forms of cestodes, as well as several examples of larval stages encysted in the blubber. The specimens are on the whole in very good condition, except for a few cases where slight maceration has occurred. In some samples the cestodes have been fixed and preserved attached to portions of the gut.

The bulk of the collection was preserved in 4% formalin, although some of the worms were fixed in Bouin's solution.

About 600 slides of serial sections and whole mounts have been made, stained in Ehrlichs' haematoxylin and counter-stained with erythrosin. The whole mounts, stained in Mayer's paracarmine were cleared in benzyl-alcohol with very good results, even for the larger portions of the strobila. The serial sections have been cut at 10–15 μ thick.

The hosts were caught in South Africa (Saldanha Bay, Durban, Cape Town and Simon's Town), the Azores, the Falkland Islands, South Georgia, the South Shetlands and at various positions in the Southern Ocean. The localities are given with the description of each species.

I have the greatest pleasure in expressing my gratitude to The Royal Society for advancing me a grant from the Browne Research Fund which enabled me to complete this investigation.

I also take this opportunity of expressing my thanks to Dr N. A. Mackintosh, C.B.E., of the National Institute of Oceanography and to Dr H. E. Bargmann of the same Institute for their kind assistance in the course of this work, and to Mr S. Prudhoe of the British Museum (Natural History). My thanks are also extended to Dr Gwendolen Rees who kindly lent whole mounts of *Tetrabothrius* from whales.

ABBREVIATIONS USED IN THE FIGURES

c.s., cirrus-sac.
e., excretory system.
l.m., longitudinal muscles.
o.v., ovary.
t., testis.
u., uterus.
u.o., uterine opening.
v., vagina.
v.d., vas deferens.
v.g., vitelline gland.

[1] Now incorporated with the National Institute of Oceanography.

GENERAL DISCUSSION

The cestodes collected represent ten different species belonging to six genera. Of these species, two appear to be new to science and two represent larval stages, the specific identification of which does not seem possible at present, although it can be seen that they belong to two different genera. The list given below shows the names of the cestodes examined and Table 2 (p. 394) their occurrence in particular hosts.

LIST OF CESTODES EXAMINED

1. *Tetrabothrius affinis* (Loennberg, 1891).
2. *T. wilsoni* (Leiper & Atkinson, 1914).
3. *T. ruudi* Nybelin, 1928.
4. *T. schaeferi* sp.n.
5. *Trigonocotyle globicephalae* Baer, 1954.
6. *Tr. prudhoei* sp.n.
7. *Priapocephalus grandis* Nybelin, 1922.
8. *Diplogonoporus balaenopterae* Loennberg, 1892.
9. *Phyllobothrium* larva.
10. Tetraphyllidean larva.

With the exception of the two larval forms and *Diplogonoporus balaenopterae*, the rest of the above mentioned cestodes belong to the family Tetrabothriidae, which appears to contain the bulk of the cestodes found in Cetacean hosts.

Because of their great similarity the identification of certain species presents certain difficulties.

The scolex in the majority of these cestodes bears four suckers, which are variable in shape and size. These suckers are usually provided with modifications called 'epaulettes' or with fleshy protuberances such as occur in the Genus *Trigonocotyle*. The scolex is subject to contraction and consequently its size and shape give no help in specific determination. In the genus *Priapocephalus*, however, this organ is acorn-like and easy to distinguish, though some variations in its contour do occur, as was mentioned by Nybelin (1928) for *P. minor*.

The strobila in the Tetrabothriids is either cylindrical and worm-like, or flattened, as in the other groups of cestodes. The cylindrical strobila appears to be typical of *Tetrabothrius affinis*, though in some cases, a short portion showing flattened segments occurs in the hind part of the body (Pl. XX, fig. 1). In *Trigonocotyle globicephalae* a short anterior portion of the body is cylindrical, while the remainder of the strobila is flattened.

Modifications of the anterior part of the body have also been noticed in the only example of the Pseudophyllidea, present in this collection, namely *Diplogonoporus balaenopterae*, where that portion of the strobila is markedly undulate dorso-ventrally (Pl. XXI, fig. 6). It is difficult to prove at the moment whether these modifications represent natural features or are caused by fixation.

The genital organs in Tetrabothriids are also very similar and uniform in structure. Although there is much variation in the number of the testes in immature proglottids and their size and arrangement in the medullary parenchyma is difficult to determine, in the fully mature segments where egg production has not yet begun, it is possible to ascertain their number and arrangement.

In some forms, as in *Trigonocotyle globicephalae*, the testes, when examined in the cylindrical part of the body, are distributed in many layers. In the flattened portion of the body, however, they are arranged in a single layer.

In the species of *Tetrabothrius* examined during the present work, the testes are situated dorsally, except in *T. affinis*, where they are distributed dorso-ventrally. This arrangement, however, may be altered and affected by the growth of the uterus, particularly when filled with eggs.

The testes seem also to decrease rapidly in number in the gravid segments, being either partially spent or else crowded nearer to the surface of the medullary parenchyma by the uterus. Some differences in the size of the testes in mature segments (measured in transverse sections of the body) are noticeable, and this may be regarded as a valuable feature in specific differentiation (Table 1, p. 387).

The cirrus-sac, although similar in structure, is also subject to much contraction and its size and shape depend greatly on this factor. In some cases, as in *Trigonocotyle globicephalae*, and *Tr. prudhoei* sp.n., some muscular modification occurs in the area of the genital atrium, forming a kind of sucker. This, however, is also met with in other species of Tetrabothriids not found in whales.

In cetacean Tetrabothriids, the ovary and vitelline glands are situated in the ventral half of the segment. In some of the species examined, the ovary contains fairly large egg-cells. The full development of the ovary is reached in the portion of the strobila occupied by the mature proglottids. From this point onwards towards the posterior end, the ovary gradually undergoes a process of deterioration, caused by the overgrowth of the uterus.

In fully gravid segments the uterus is so strongly developed that it practically replaces the rest of the genital system. It is a centrally situated, sac-shaped organ extending laterally and gradually occupying the whole of the medullary parenchyma.

There is no proper uterine pore in cetacean Tetrabothriids. Instead, the uterus opens through the body-wall, when the eggs are ready to be discharged from the segment. The rupture through which the eggs are passed appears on the dorsal surface of the body, at one definite point, and the path in the cortical parenchyma, along which the distending uterus is pushed, is surrounded by a distinct mass of eosinophil tissue. In *Priapocephalus grandis*, however, many such ruptures on the dorsal surface have been observed. No uterine openings or ducts have been found in the two species of *Trigonocotyle* from the present collection.

It seems that a kind of 'cement'[1] protects the newly formed uterine opening from the effects of the gastric juices in the host's intestine and which closes the opening after the eggs have been discharged.

It is well known that the eggs of cestodes lose much of their characteristic structure after fixation and extraction from the uterus. Nevertheless, specific differences seem to occur between the eggs of particular species found in the Discovery Collection. Their size appears to be related to the thickness of the outer and inner membranes in the various species, and in some cases to the number of membranes as well.

The embryos also seem to vary in size with species, and, with the exception of *Tetrabothrius ruudi* (Fig. 15), the three pairs of hooks with which they are all provided exhibit specific differences (Table 1).

The vagina runs ventrally to the cirrus-sac in all examined species of *Tetrabothrius*.

The most striking differences among particular species seem to occur in the structure and arrangement of longitudinal muscles, as seen in transverse section.

In the present material, the longitudinal muscles of Tetrabothriids undergo morphological changes within the individual strobila itself. These changes are associated with the development of the genital organs and it appears that in the immature portion of the strobila, where the genital organs are either non-existent or rudimentary, the longitudinal muscles are differentiated into bundles, but in the mature portion of the strobila, these bundles have taken on a very definite arrangement. As the mature proglottids ripen, and the uterus becomes increasingly distended, the muscle bundles tend to atrophy, although their characteristic arrangement can still be distinguished. This series of changes is shown in sections of *Trigonocotyle globicephalae* (Figs. 24, 25) and *Priapocephalus grandis* (Figs. 34–36).

[1] This 'cement' is probably produced by gland-cells in the modified tissue.

SUMMARY OF DISCUSSION

To sum up: Specific differences are to be found in the size and the arrangement of testes, in the size and structure of eggs, embryos and embryonic hooks, and in the arrangement and shape of the longitudinal muscles in the fully mature, but not gravid segments.

SYNONYMY

The history and the nomenclature of some of the Tetrabothriids occurring in Cetacea have been given by Rees (1953).

Recently, Baer (1954) has published a list of synonymous names of Tetrabothriids and their specific classification. From the present work it seems, however, that *Tetrabothrius wilsoni*, which he considers to be synonymous with *T. affinis*, actually represents a distinct species (Table 1, p. 387).

Baer's (1954) criticism of Baylis's (1926) description of *T. affinis* appears to be justified, as the material examined by Baylis seems to represent another species, described in this paper as *T. schaeferi* sp.n. The form mentioned by Rees (1953) as *Tetrabothrius* sp. also appears to represent the same species.

The two new species described in this paper, namely *T. schaeferi* and *Trigonocotyle prudhoei* have been named after Miss F. H. A. Schaefer who, during my recent illness nursed me in hospital, and after my friend Mr S. Prudhoe of the British Museum (Natural History).

SYSTEMATIC NOTES

Genus Tetrabothrius Rudolphi, 1819

This genus is represented in the present material by four species. Of these, one seems to be new.

Tetrabothrius affinis (Loennberg, 1892). (Figs. 1–6, Pl. XX, figs. 1–2.)

Diplobothrium affine Loennberg, in Jägerskiöld, 1891.
Tetrabothrium (*Diplobothrium*) *affine*. Loennberg, 1892.

HOSTS: Blue Whale (*Balaenoptera musculus*); Sperm Whale (*Physeter catodon*).
LOCALITIES: Saldanha Bay and Durban (South Africa); South Georgia; and 58° 32′ S, 34° 52′ E.

The specimens examined are about 20 cm. long and about 5 mm. wide. The strobila is cylindrical with very short segments. In some specimens the posterior end of the body is modified into flattened segments, markedly separated from each other (Pl. XX, fig. 1).

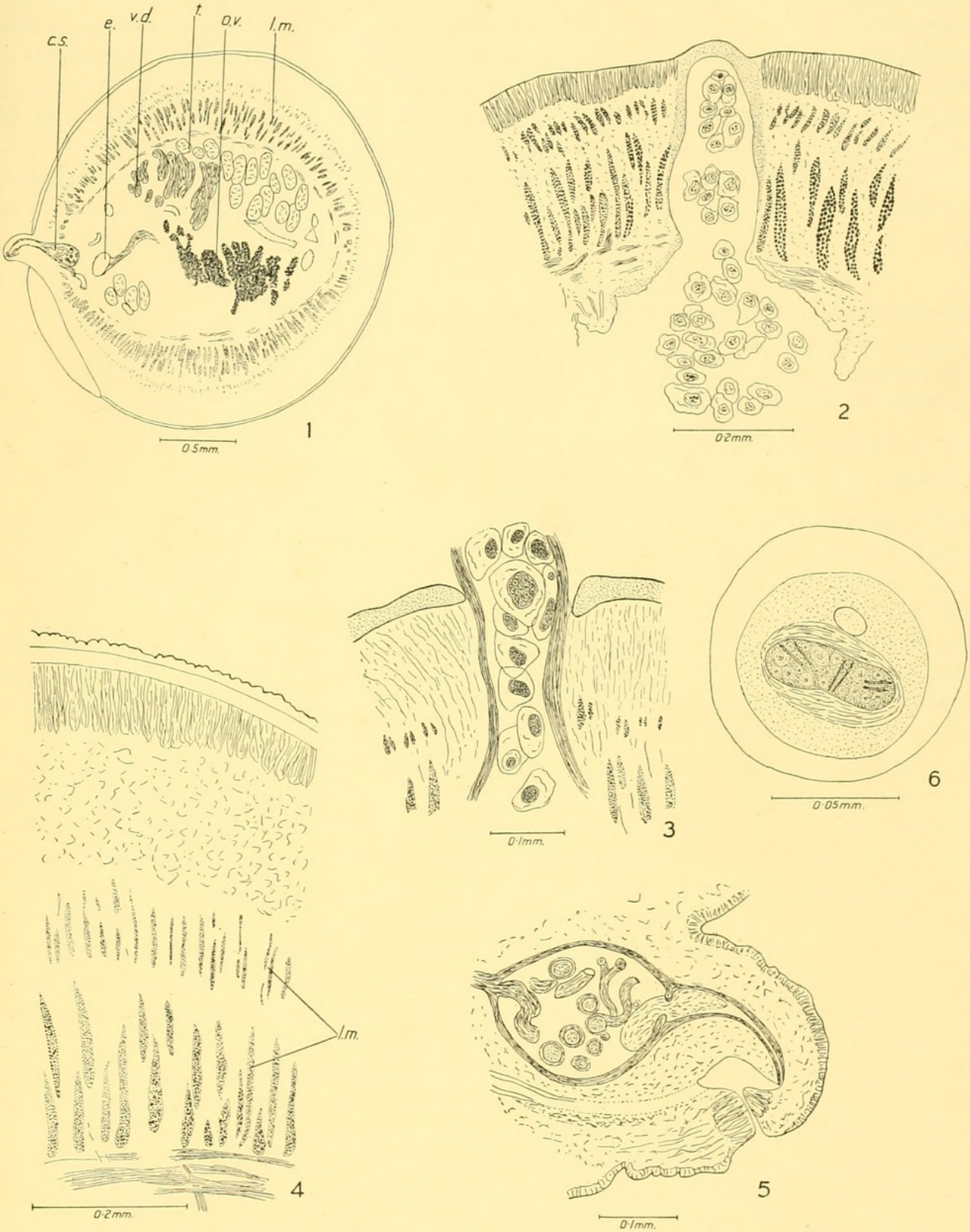
This region is the spent part of the body containing the degenerate genital organs.

The scolex, about 2 mm. long and 2 mm. broad, is variable in shape and bears typical 'epaulettes'. A neck does not seem to be present.

The musculature is strongly developed in this species. Cross-sections of the body show that the longitudinal muscles form two distinct rings. The internal ring is composed of strongly developed bundles of a very characteristic shape shown in Fig. 4. The circular and dorso-ventral muscles are also very well developed.

The testes are dorso-ventrally elongate in younger segments and about $90 \times 53 \mu$ in diameter, but in the more developed segments they are irregularly spherical and seem to be arranged in several layers, which are distributed dorso-ventrally. The thick-walled, coiled vas deferens is well developed. The pear-shaped or rounded cirrus-sac possesses thick muscular walls and a strongly developed cirrus.

The lobate ovary extends transversely in the ventral part of the segment and is composed of distinct egg-cells. The vitelline gland is situated ventrally to the ovary.



Figs. 1–6. *Tetrabothrius affinis* from Blue Whale. 1, cross-section through mature segment; 2, formation of uterine opening and mode of discharging eggs; 3, eggs being discharged from uterus; 4, transverse section of a portion of longitudinal muscle; 5, transverse section of segment showing cirrus-sac and vagina; 6, egg.

The uterus is a well-developed sac. There is no special uterine pore, but dorsally in the central part of the segment, the parenchyma undergoes some modification. Transverse sections of this part of the segment show differentiated tissues which appear to form a cone. Gradually the distending uterus, filled with eggs, breaks through this part of the segment and the eggs are discharged through the rupture in the body-wall. The diameter of the egg is about (66–106 × 33–83)μ with the embryonic membrane measuring 51 × 66μ. The embryo measures about 52 × 26μ and is provided with three pairs of hooks, of which the lateral pairs measure 17μ in length, and the central pair 20μ.

The excretory system, composed of two main canals with transverse vessels, is very well developed. The ventral canal is relatively wider in diameter than the dorsal one, but the latter possesses thick walls.

Tetrabothrius wilsoni (Leiper & Atkinson, 1914). (Figs. 7–10.)

Oriana wilsoni Leiper & Atkinson, 1914.
Tetrabothrius wilsoni Baylis, 1926.
Tetrabothrius affinis Baer, 1954.

HOSTS: Sei Whale (*Balaenoptera borealis*); Blue whale (*B. musculus*).
LOCALITIES: Durban; South Africa; South Georgia.

Of the thirty-four specimens examined several appear to be gravid, a condition not hitherto reported. The length of the worms varies from 6 to 14 cm. and the width from 2 to 3 mm. The body is dorso-ventrally flattened. The scolex bearing four suckers with weakly developed 'epaulettes' is about 3 mm. broad.

The longitudinal muscles are arranged in two very indistinct rings, as shown in Fig. 9. Individual bundles are not well defined and are composed of rather thick muscle fibres. Their arrangement appears diffuse and differs considerably from that found in *Tetrabothrius affinis*. The circular muscles, though present, are poorly developed.

The testes are situated in the dorsal part of the segment, being 99 × 120μ in transverse section. They seem to be arranged in an irregular layer. The vas deferens is not very strongly developed, while the cirrus-sac is pear-shaped or more or less spherical in transverse sections of the strobila.

The ovary is extremely well developed, lobate, extending transversely in the ventral part of the segment, and occupying a considerable area of the proglottid.

The egg-cells are fairly large, being about 15μ in diameter.

The vitelline gland, situated ventrally beneath the ovary, is well developed.

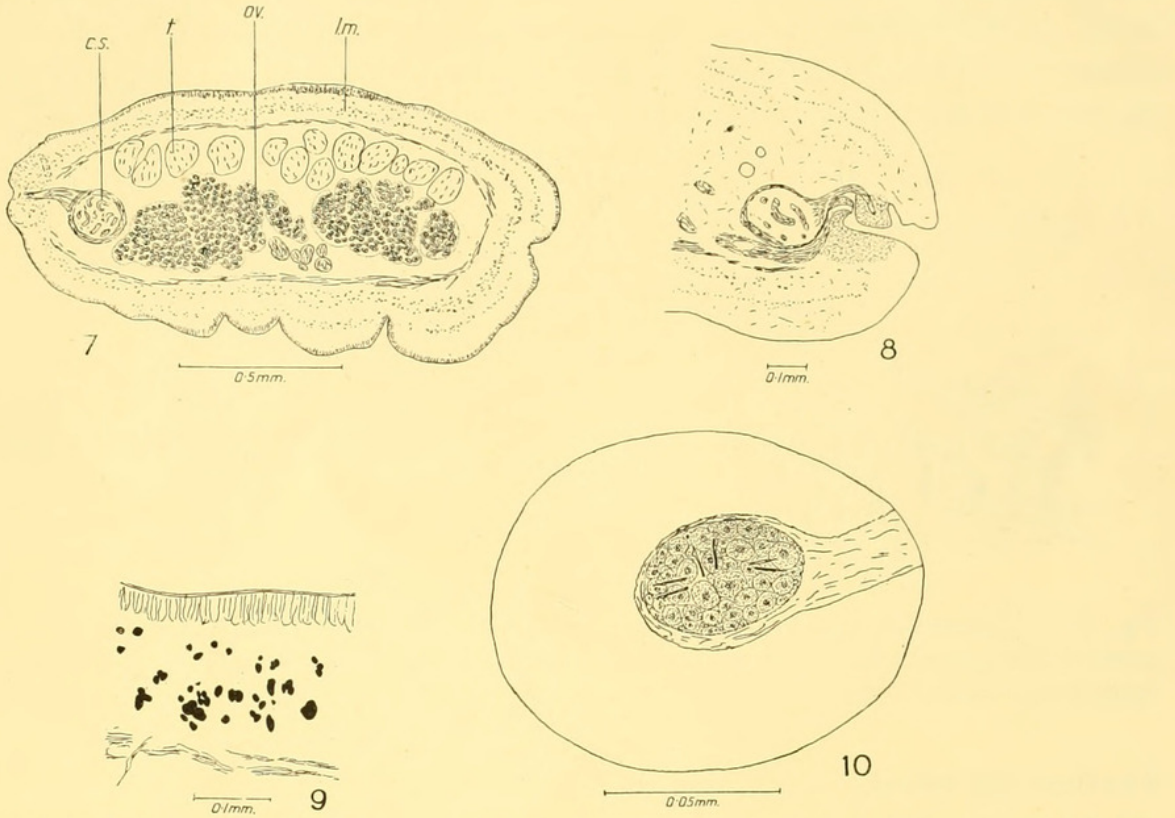
The uterus, in fully gravid segments, occupies the whole of the medullary parenchyma of the segment, considerably displacing the internal organs. The walls of the segments are much thinner than in *T. affinis*.

The eggs are discharged through a small opening in the dorsal face of the segment. They measure about 90 × 60μ. The embryonic membrane is about 45 × 30μ and the embryo 36 × 21μ in diameter. It seems that the latter is attached by its membrane to the external egg-capsule, as shown in Fig. 10. The external and internal pairs of embryonic hooks are of similar length, i.e. about 12μ.

The excretory system appears to be weakly developed and both the ventral and the dorsal trunks are of similar diameter. In the younger segments, as well as in the gravid, the ventral trunk of the excretory system seems to have a greater diameter. This, however, may be caused by the fixation and contraction of the tissues.

This form, described by Leiper & Atkinson in 1914, by Baylis in 1926 and recently by Baer (1954), represents a valid species, distinguished by differences in the arrangement and structure of the longi-

tudinal muscles, the arrangement of the testes, the development of the ovary, and the structure of the eggs. The above-mentioned authors appear to have dealt only with immature specimens, which of course are not satisfactory for comparative purposes.



Figs. 7–10. *Tetrabothrius wilsoni* from Sei Whale. 7, cross section through mature segment; 8, transverse section of segment showing cirrus-sac and vagina; 9, cross-section through portion of longitudinal muscle; 10, egg.

Tetrabothrius ruudi Nybelin, 1928. (Figs. 11–15.)

HOST: Fin Whale (*Balaenoptera physalus*).

LOCALITY: South Georgia.

The length of the specimens examined is about 9 cm. and the width about 2 mm. The scolex, provided with four suckers and 'epaulettes' is about 2 mm. broad.

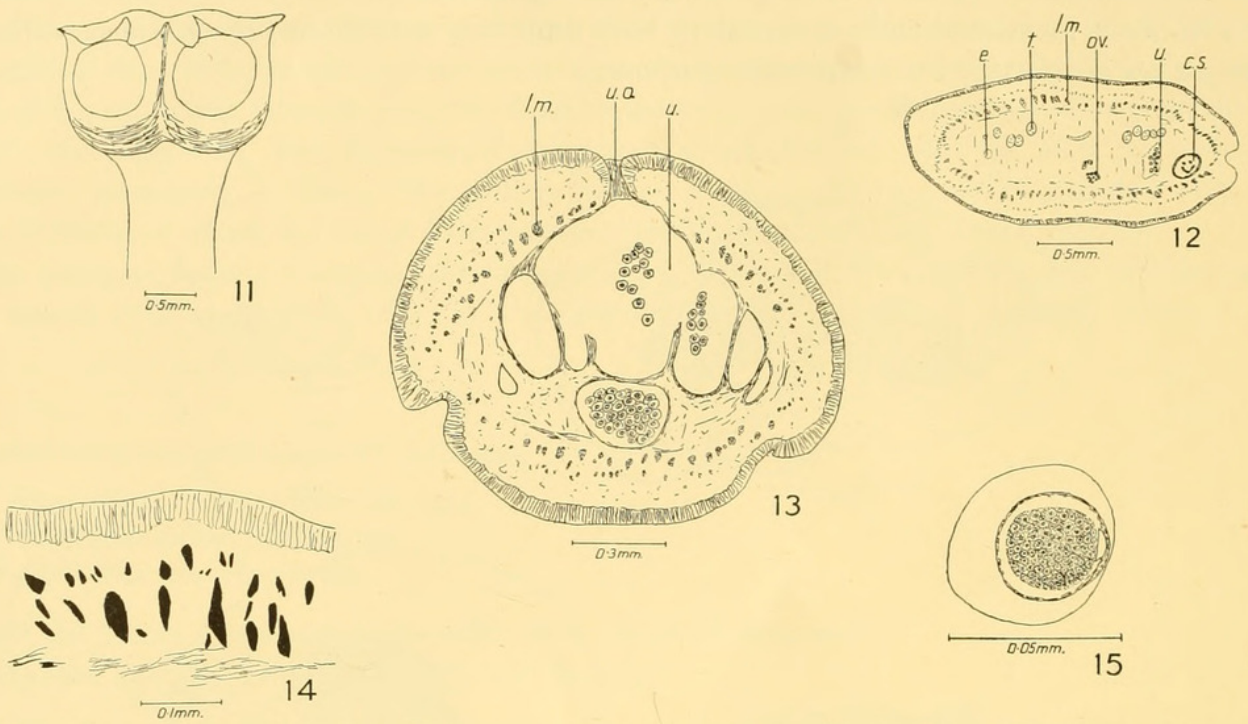
The longitudinal muscles form two more or less distinct rings. The inner one is formed by well accentuated bundles, composed of well developed fibres. The circular muscles are not well developed.

The testes, situated dorsally, are about $42 \times 45\mu$ in transverse section. They are not very numerous. The vas deferens is well developed. The cirrus-sac is pear-shaped, as depicted by Nybelin (1928).

The ovary, extending horizontally in the ventral part of the segment is well developed. The vitelline gland lies ventrally to the ovary.

The very well developed uterus possesses the same kind of opening as in previous forms and similar modified parenchymatous tissue. The formation of the uterine duct commences in the mature segments where the uterus has not yet reached full development. In the early stages the modified tissue surrounding the duct is markedly visible. The eggs are $40–50\mu$ in diameter, the embryonic membrane $30 \times 30\mu$ and the embryo $17 \times 18\mu$. In eggs cleared in glycerine, embryonic hooks have not been observed.

The excretory system shows the ventral vessel to be relatively greater in diameter than the dorsal one, the latter possessing thick muscular walls.



Figs. 11–15. *Tetrabothrius ruudi* from Fin Whale. 11, scolex in lateral view; 12, cross-section of mature segment; 13, cross-section through gravid segment showing uterus and uterine opening situated dorsally; 14, cross-section through portion of longitudinal muscle; 15, egg.

Tetrabothrius schaeferi sp.n. (Figs. 16–20).

Tetrabothrius affine. Baylis, 1926.
Tetrabothrius sp. Rees, 1953.

Host: Blue Whale (*Balaenoptera musculus*).
Localities: South Georgia, Southern Ocean.

The body is rather slender and flattened, varying from about 7 to 14 cm. in length and about 2 to 3 mm. in breadth. The segmentation is distinct. The scolex, provided with four suckers and 'epaulettes' is 3 mm. broad. A neck is present and well defined.

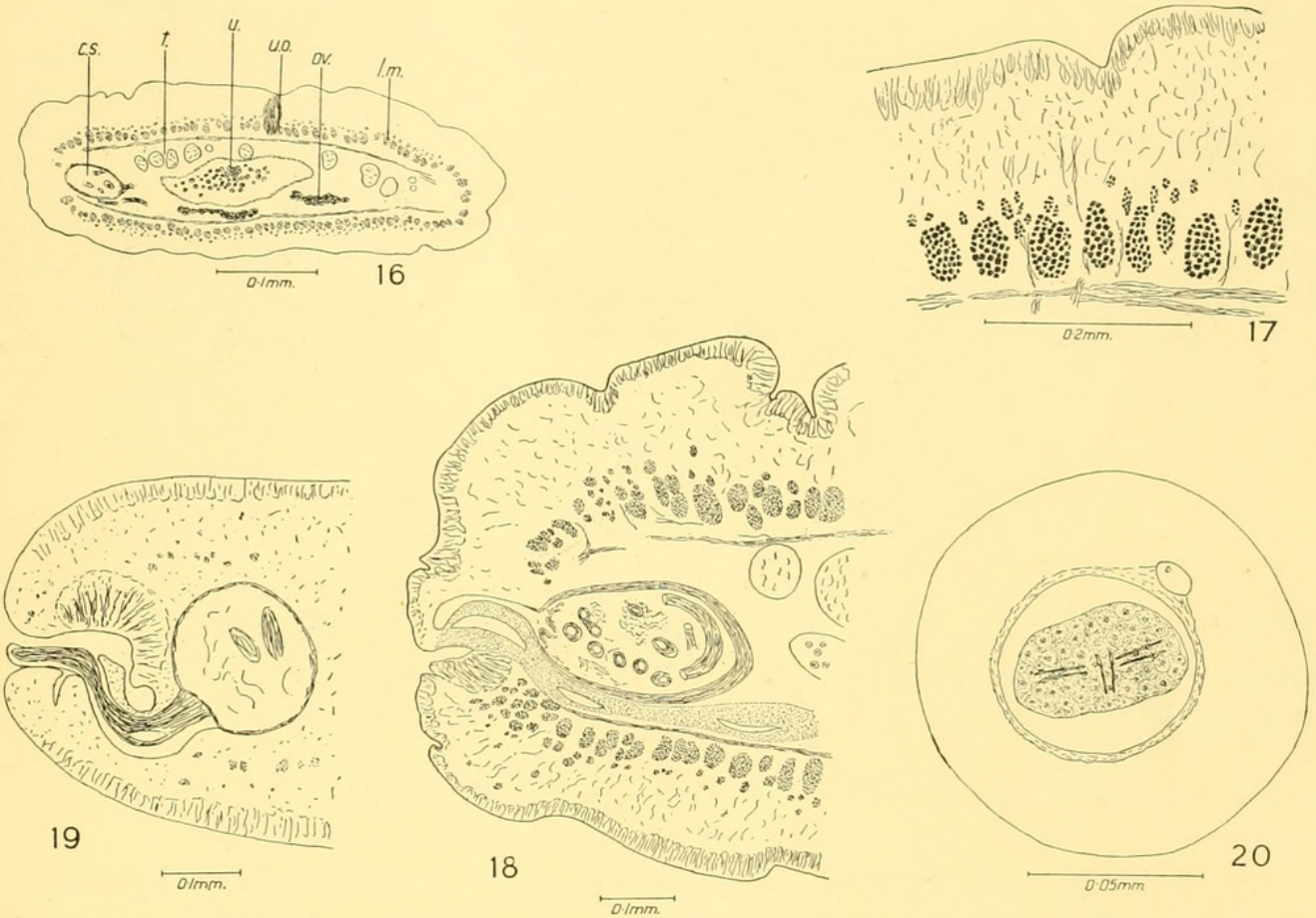
The longitudinal muscles are seen to form two rings, if the segment is examined in cross-section. The inner ring is composed of distinctly separated bundles, irregularly oval in outline and well developed. Immediately, above the inner ring lies the external ring of longitudinal muscles which are weakly developed, as are the circular and dorso-ventral muscles.

The testes, about fifty in number, are about $90 \times 90 \mu$ when measured in transverse section. They occupy the dorsal part of the segment, being arranged in a single or many layers in fields extending laterally and antero-posteriorly. The cirrus-sac, spherical or pear-shaped is about 30μ long and 150μ wide. The vas deferens is a much coiled, fairly well-developed organ. The well-developed ovary lies in the ventral parenchyma. It is lobate and in transverse section more or less oval in outline. The egg-cells are fairly large, about 21μ in diameter. The vitelline gland is ventral to the ovary. The uterus is a sac-like organ which as it matures gradually fills the medullary parenchyma. The uterine duct appears fairly early in the strobila as a differentiation of parenchymatous tissue. The uterine opening is spherical when observed in horizontal section. It is well marked, and surrounded with modified cells which appear to absorb more haematoxylin than the counter-stain erythrosin.

The egg is about $90 \times 75 \mu$ in diameter, or more or less spherical. The inner membrane containing

an embryo is about $45 \times 36\mu$ in diameter, while the embryo is about $24 \times 45\mu$. The lateral pairs of hooks are 12μ in length and the central pair 18μ. The proportions of these hooks is not represented accurately in Fig. 20.

The ventral and dorsal trunks of the excretory system differ in diameter and have rather thin walls. The differences between this new form and *Tetrabothrius affinis* lie in the shape of the body and in the arrangement of the longitudinal muscles. These characters also differ from those found in other species of *Tetrabothrius*. Further differences in structure and in the eggs and the embryos have been given in Table 1.



Figs. 16–20. *Tetrabothrius schaeferi* sp.n. from Blue Whale. 16, Cross-section of semi-gravid segment with eggs; 17, cross-section through longitudinal muscle; 18, cross-section of segment showing cirrus-sac and vagina; 19, cross-section showing cirrus-sac and everted cirrus; 20, egg.

Table 1. *Measurements of Tetrabothriids occurring in the Cetacea from the Discovery Collections*

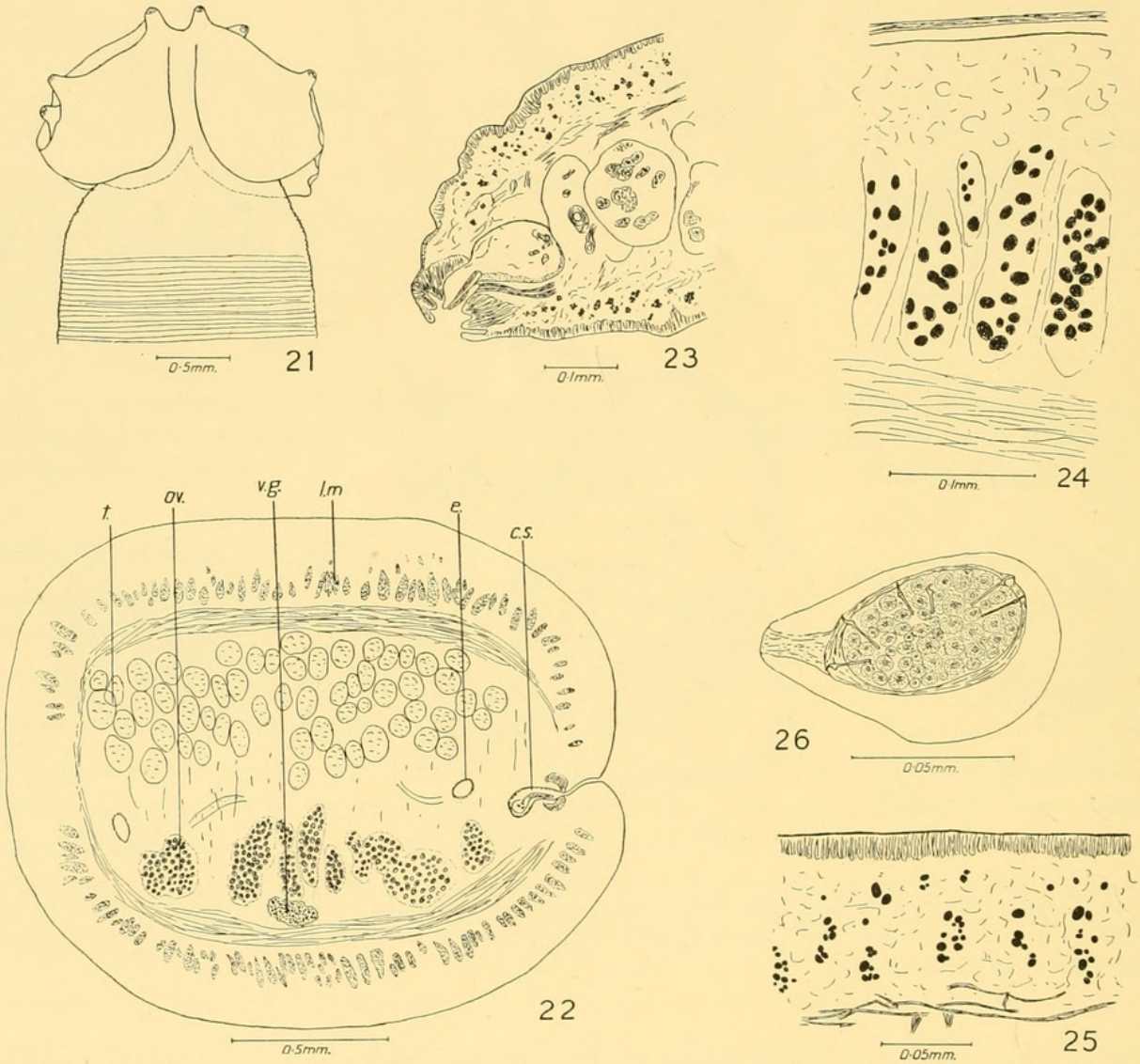
Species	Body length	Body width	Testis diameter	Egg	Embryonic shell	Embryo diameter	Lateral hooks	Central hooks
Tetrabothrius affinis	20 cm.	5 mm.	$90 \times 53\mu$	$106 \times 83\mu$	$51 \times 66\mu$	$52 \times 26\mu$	17μ	20μ
T. wilsoni	14 cm.	3 mm.	$99 \times 120\mu$	$90 \times 60\mu$	$45 \times 30\mu$	$36 \times 21\mu$	12μ	12μ
T. ruudi	9 cm.	2 mm.	$42 \times 45\mu$	$40 \times 50\mu$	$30 \times 30\mu$	$17 \times 18\mu$	—	—
T. schaeferi sp.n.	14 cm.	3 mm.	$90 \times 90\mu$	$90 \times 75\mu$	$45 \times 36\mu$	$24 \times 45\mu$	12μ	18μ
Trigonocotyle globicephalae	21 cm.	3/2 mm.	$120 \times 135\mu$	$75 \times 45\mu$	$60 \times 40\mu$	$54 \times 36\mu$	18μ	12μ
Tr. prudhoei sp.n.	14·5 cm.	1 mm.	$120 \times 60\mu$	$60 \times 84\mu$	$45 \times 30\mu$	$27 \times 30\mu$	9μ	6μ
Priapocephalus grandis	15 m. 24 cm.	12 mm.	$68 \times 60\mu$	$99 \times 66\mu$	—	$33 \times 50\mu$	17μ	17μ

Trigonocotyle Baer, 1932

Trigonocotyle globicephalae Baer, 1954. (Figs. 21–26.)

Prosthecocotyle monticelli Linton 1923; nec Furhmann, 1899.
Trigonocotyle monticelli Linton, 1923; Baer 1932.
Trigonocotyle lintoni Yamaguti, 1942; nec Guiart, 1935.

HOST: *Globicephala edwardi*.
LOCALITY: Off Cape Town (South Africa).



Figs. 21–26. *Trigonocotyle globicephalae* from *Globicephala edwardi*. 21, scolex in lateral view; 22, cross-section through mature segment in anterior cylindrical part of strobila; 23, cross-section through segment in flattened part of strobila, showing cirrus-sac, vagina and longitudinal muscles; 24, cross-section through mature segment in anterior cylindrical part of strobila showing longitudinal muscles; 25, cross-section through gravid, flattened part of strobila showing longitudinal muscles; 26, egg.

The length of the body in the specimens examined is about 21 cm. The strobila appears to be divided into two portions; the anterior part is cylindrical and about 2 cm. in length, composed of very short segments, while the rest of the body is flattened. It seems that the anterior portion, which bears a resemblance to the cylindrical strobila in *Tetrabothrius affinis*, contains mature segments and the flattened part gravid segments with eggs. The scolex, 1·5 mm. broad is provided with four suckers, bearing fleshy protuberances in the form of horns.

The longitudinal muscles are well developed and composed of thick fibres. In transverse section they are collected in elongate bundles, separated from each other by muscular septa. The longitudinal muscles in the cylindrical portion of the strobila are far better developed than those in the gravid segments.

The bundles in the anterior portion are thicker than in the gravid segments as shown in Figs. 24 and 25. This is probably owing to the pressure of the uterus as it becomes distended with eggs. The circular muscles are exceedingly well developed, noticeably in the anterior portion of the body.

The testes are about $120 \times 135\mu$ in transverse diameter and arranged in many layers in the cylindrical part of the body. In the flattened portion they seem to be arranged in a single layer. The vas deferens is well developed. The pear-shaped cirrus-sac is about $186 \times 90\mu$ in diameter.

The genital atrium possesses a muscular modification in the form of a sucker.

The ovary extends ventrally in the medullary parenchyma and is well developed. The vitelline gland situated ventrally under the ovary is composed of compactly arranged cells. Neither the uterine opening nor the rudiment of its duct has been found. The uterus is very well developed and gradually pushes away other parts of the genital complex. The eggs are $75 \times 45\mu$ in diameter and the embryo $54 \times 36\mu$. The lateral hooks measure 18μ and the central 12μ. Yamaguti (1942) could not find any hooks in his material.

The excretory system is well developed and has transverse vessels connecting the two main trunks.

Trigonocotyle prudhoei sp.n. (Figs. 27–32).

HOSTS: *Steno bredanensis*, *Lagenorhynchus obscurus*, *L. australis*.

LOCALITY: 14° 45′ N, 18° 34′ W; East Falkland Islands (southernmost point of Bay of Harbours).

The body is about 14·5 cm. in length and 1 mm. in width and composed of slightly overlapping segments. The scolex, measuring from 1·5–2 mm. in width, is provided with four suckers bearing fleshy protuberances.

The longitudinal muscles are collected into bundles, with some indication of two layers dorsally, when examined in transverse section. They seem to be separated by muscular septa. The circular muscles are well developed. There are also dorso-ventral muscle fibres.

The testes are not very numerous and occur mainly in the dorsal part of the segment. They are about $120 \times 60\mu$ in transverse section, the longer axis being in the dorso-ventral plane. The cirrus-sac is flask-shaped, about $32 \times 15\mu$ in diameter, with thick muscular walls and a well-developed cirrus. The vas deferens is well developed. Radiate muscles forming a sucker occur in the genital atrium.

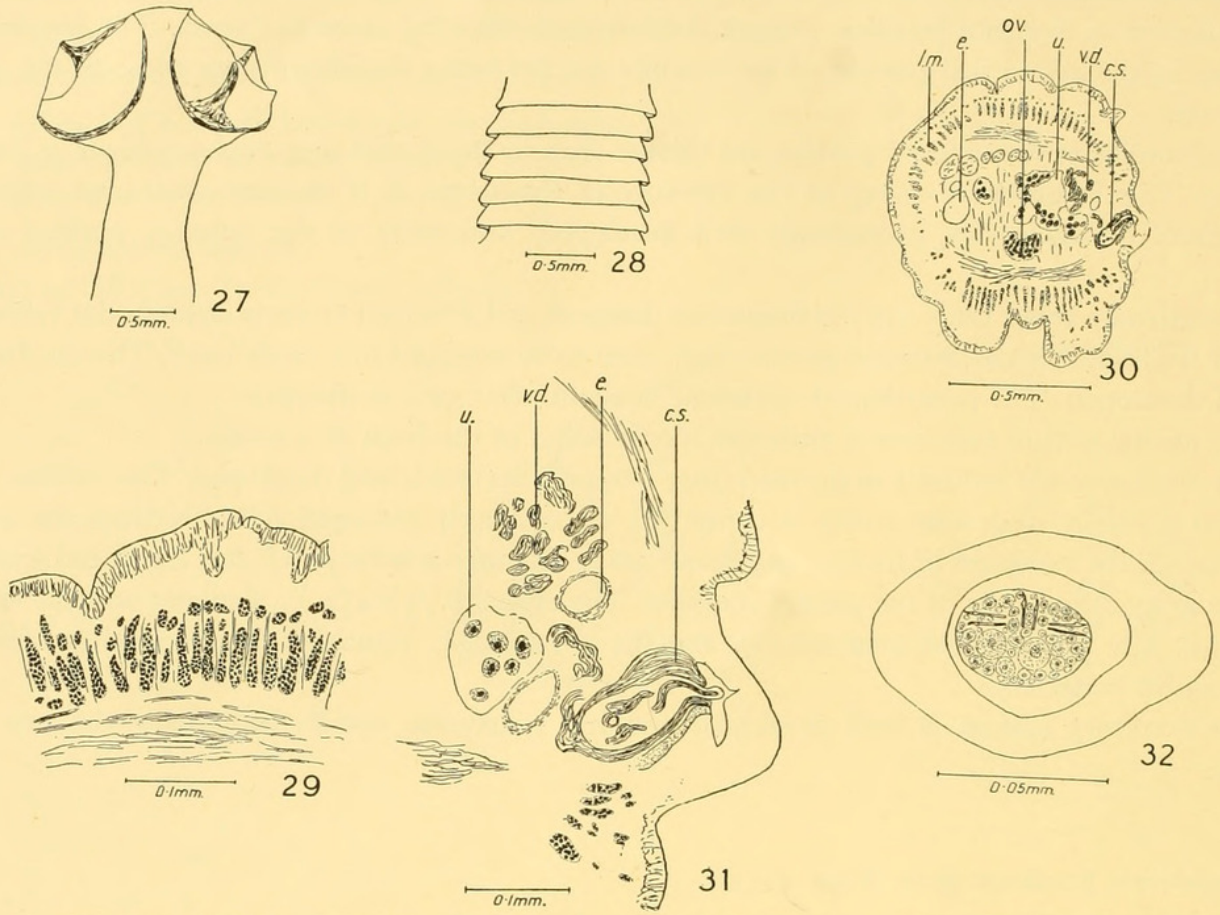
The ovary is situated ventrally and extends laterally on both sides of the median line. The well-developed vitelline gland is situated ventrally beneath the ovary.

Neither a uterine pore nor the rudiment of a uterine duct have been observed.

The eggs are $60 \times 84\mu$. The inner membrane is $45 \times 30\mu$ and the embryo $27 \times 30\mu$. The lateral pairs of embryonic hooks measure 9μ and the central 6μ in length.

The excretory system is well developed.

This species differs mainly from other species of *Trigonocotyle* occurring in Cetacea in the form of the serrate strobila and in the arrangement of the longitudinal muscles. It also differs in the number and arrangement of the testes, these being less numerous and distributed dorsally. There are also differences in the size of the eggs and in the length of the embryonic hooks as shown in Table 1.



Figs. 27–32. *Trigonocotyle prudhoei* sp.n. from *Lagenorhynchus obscurus*. 27, the scolex; 28, part of the strobila; 29, cross-section through part of longitudinal muscles; 30, cross-section through mature segment; 31, cross-section showing cirrus-sac and vagina; 32, egg.

Priapocephalus grandis Nybelin, 1922. (Figs. 33–41; Pl. XX, 3–4).

Hosts: Blue Whale (*Balaenoptera musculus*), Sei Whale (*B. borealis*), Fin Whale (*B. physalus*), Sperm Whale (*Physeter catodon*).

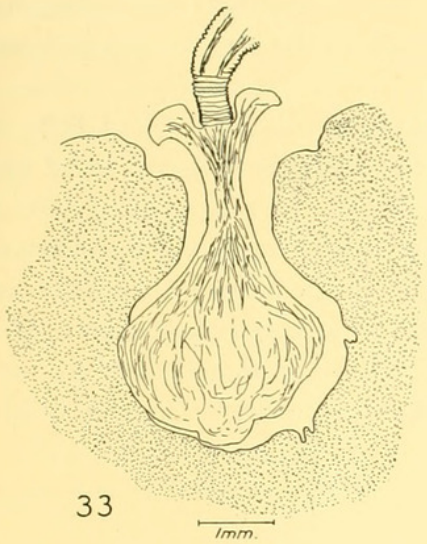
Localities: Saldanha Bay and Durban (South Africa); South Georgia; Southern Ocean (56° 40′ 32′ S, 24° 33′ W); Porto Pim, Azores.

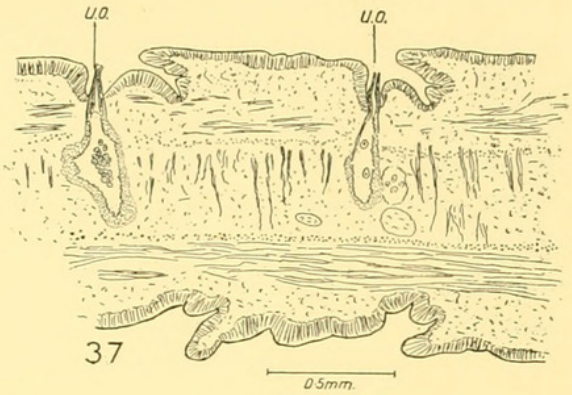
The size of the specimens examined varies from 4 cm to 15 m. 24 cm. in length with a width varying from 2 to 12 mm. The worms are in various stages of development, from immature to full-grown individuals. There are also fragments of worms, measuring from 12 cm. to 5 m. 75 cm. in length and 2–12 mm. in width; some of these have scolices intact. These are typically acorn-like and are deeply embedded in the mucous which exudes from the gut of the host.

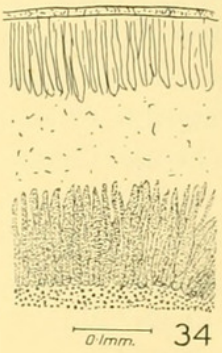
Fig. 33 shows the mode of attachment. It seems that there is a free space between the scolex and the surrounding intestinal tissues of the host. The scolex bears a kind of collar, which possibly serves as a supplementary organ of attachment. The maximum length of the scolex amounts to 7 mm., including the collar; the corresponding width is 4 mm.

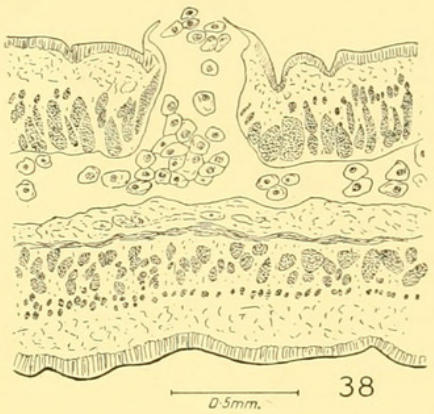
The segments are wider than long (the length being about 1·5 mm.), and not craspedote. The body is ivory white or yellowish in preserved specimens.

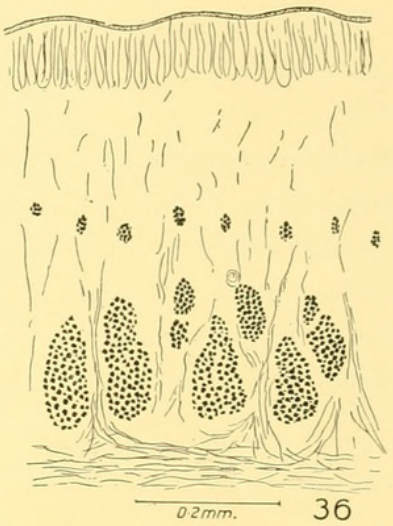
The longitudinal muscles are very well developed. They are arranged in two rings, the outer one being the less well developed. The inner one is composed of strong bundles, oval in transverse section. The longitudinal muscles are variously developed in the same individual. In the juvenile forms or in

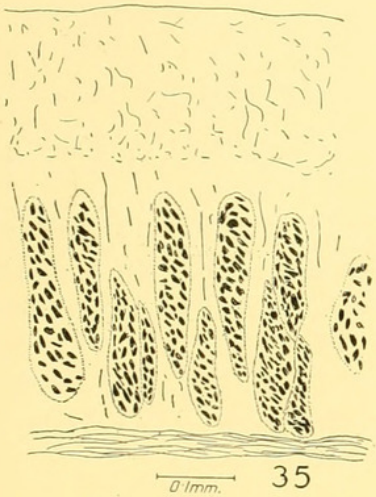


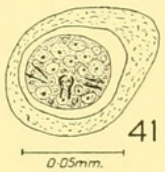


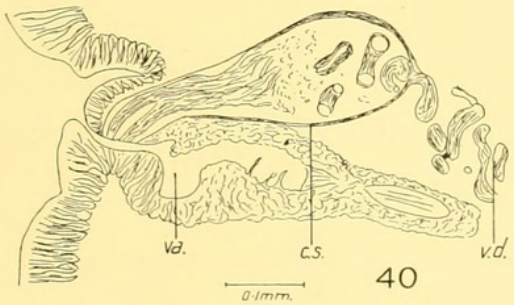


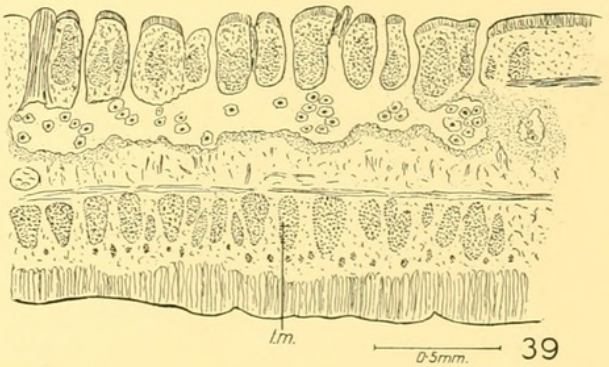












Figs. 33–41. *Priapocephalus grandis* from Blue Whale. 33, longitudinal section through scolex of immature specimen embedded in mucous; 34, cross-section through part of longitudinal muscles; 35, cross-section through part of longitudinal muscles; in segment with rudimentary genital organs; 36, cross-section of longitudinal muscles in mature segment; 37, sagittal section of body showing uterine ducts and openings for discharge of eggs; 38, mode of egg-discharge; 39, cross-section of segment showing uterine pores; 40, cross-section of cirrus-sac and vagina; 41, egg.

the anterior portion of the body the bundles are arranged very densely. They seem to form definitely shaped bundles in the mature and gravid segments. In the young specimens their arrangement is radiate. The differences in the arrangement of the longitudinal muscles in the various segments are shown in Figs. 34–6. The circular muscles are well developed.

The testes are numerous and arranged in many layers. They measure about $\times 68(53–60)\mu$ in transverse section and about $45 \times 53\mu$ in horizontal section. The vas deferens is well developed and arranged in coils. The cirrus-sac is about 135μ long and about 60μ wide.

The fairly large ovary is composed of large egg-cells. The uterus, filled with eggs, occupies most of the medullary parenchyma. The eggs, after the uterus has broken through the cuticle, are discharged by numerous pores situated in the dorsal part of the segment. No specially defined uterine pore is present, as in the species of *Tetrabothrius* described above. There is no difference in the formation of the uterine ducts, but instead of one, several openings are formed. Figs. 37–39 show the mode of discharging the eggs.

The egg is about $(83–99 \times 66)\mu$ and contains the embryo, $33 \times 50\mu$ in diameter. The embryonic hooks are about 17μ in length.

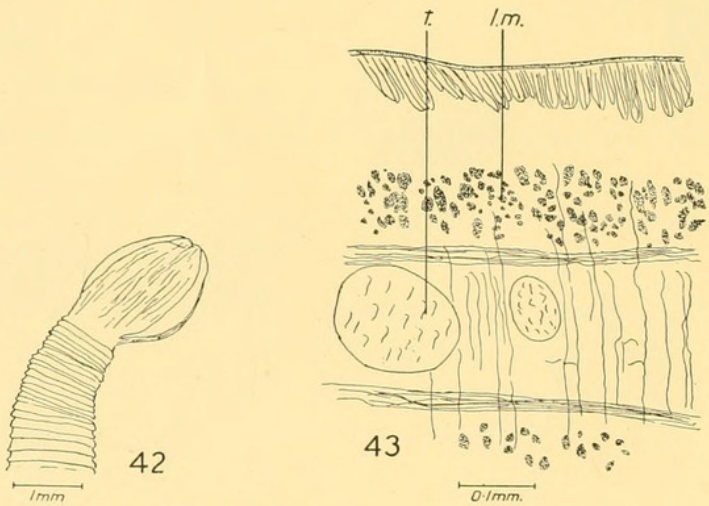
The excretory system is well marked.

Genus Diplogonoporus Loennberg, 1892

Diplogonoporus balaenopterae Loennberg, 1892. (Figs. 42–43; Pl. XXI, figs. 5–7.)

Hosts: Blue Whale (*Balaenoptera musculus*); Fin Whale (*B. physalus*); Sei Whale (*B. borealis*).
Locality: South Georgia.

The body is flat and tape-like. In all the specimens with a scolex, irrespective of size, the anterior part of the body is undulate, as shown in Pl. XXI, fig. 6. Though this modification of the body may be caused by fixation, it seems nevertheless to be constant. Although the only complete worms occurring



Figs. 42, 43. *Diplogonoporus balaenopterae* from Sei Whale. 42, scolex; 43, transverse section showing arrangement of longitudinal muscles.

in the collection measure up to about 13 cm. in length, there are many fragments, one of which is over 8 m. long. The scolex is typical, with two grooves from 1 to 1·5 mm. broad and from 1 to 2 mm. long. The bothria are deep and well pronounced. There is no neck.

The longitudinal muscles, as examined in transverse section, form irregular groups of muscle bundles composed of loosely arranged fibres. Individual groups are separated by muscle fibres, running dorso-ventrally. The circular muscles are well developed.

The genital organs occur as separate units in both lateral fields of the segment. In some specimens, however, there are three sets of organs on one side, and two on the other. Two parallel furrows run along the strobila, marking the position of the genital organs. The testes are about $120 \times 150\mu$ in transverse diameter and are arranged in a single layer. Their number between the right and left genital sets seems to be from about thirty-seven to forty. It seems also that the number of testes occurring in each of the genital sets varies greatly when examined in transverse sections, the left-hand side of the segment may possess a few testes or none, while on the right side sixteen or more testes may occur. The cirrus-sac is about $345 \times 300\mu$. The vas deferens is well developed and much coiled. The cirrus is fairly large.

The ovary forms an arch in the ventral half of the segment. The uterus, forming a 'rosette' is filled with operculate eggs of about $66 \times 48\mu$ in diameter. The egg-shell is 3μ thick.

The vitelline glands are situated dorsally and ventrally, in the cortical parenchyma, leaving a free field around the genital organs. They are more or less spherical in transverse section.

LARVAE

Two types of larval stages have been found in the present material.

All specimens examined seem to belong to the Genus *Phyllobothrium*, except one specimen which probably belongs to the Tetraphyllidea. Specific identification is not possible owing to the complete lack of any morphological characters.

Phyllobothrium (*sensu lato*) sp. larva. (Fig. 44; Pl. XXI, fig. 8.)

HOSTS: Sperm Whale (*Physeter catodon*) and (*Lagenorhynchus obscurus*).
LOCALITIES: Durban, Simon's Town, South Africa and South Georgia.

This larval stage is found in cysts in the blubber and may be regarded as a cysticercus. The body is composed of a bladder with an invaginated scolex and neck. The size of the cyst is variable, measuring from 3–20 × 2–9 mm. The scolex is about 2 mm. broad and is similar to that of *Phyllobothrium*. The evaginated neck is 6 mm. long and 3 mm. wide in the larger specimens.

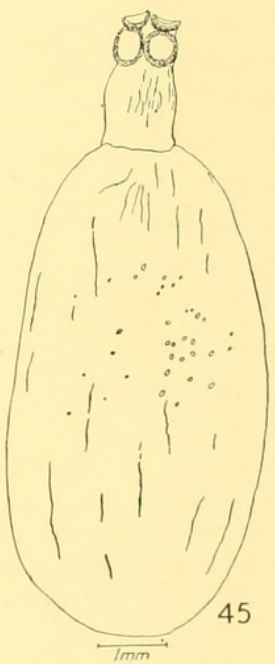


Fig. 44. *Phyllobothrium* sp. from Sperm Whale. 44. larval stage extracted from blubber.
Fig. 45. Tetraphyllidean larva from blubber of Sperm Whale.

Tetraphyllidean larva. (Fig. 45.)

HOST: Sperm Whale (*Physeter catodon*).

LOCALITY: South Georgia.

Only one specimen has been found; it occurred in the same host together with the previously described form.

The total length of the evaginated cyst is about 9 × 3 mm. The scolex is 1 mm. wide, provided with four discoid suckers, which measure about 420 × 525 μ in diameter.

RELATIONSHIPS BETWEEN THE HOST AND THE PARASITE

From the material examined it seems that host-specificity does not exist. The only exception is *Tetrabothrius ruudi*, which at present has been recorded only in the Fin Whale. This, however, does not mean that this species may not occur in other species of whales, and it is probably a matter of the number of the hosts examined. This appears to be true as far as the present material is concerned.

Table 2. *Infection of hosts with particular species of cestodes*

Host	No. of hosts examined	*Tetrabothrius affinis*	*T. wilsoni*	Species of cestodes		*Trigonocotyle globicephalae*	*T. prudhoei* sp.n.	*Priapocephalus grandis*	*Diplogonoporus balaenopterae*	*Phyllobothrium* sp. larva	Tetraphyllidean larva
				T. ruudi	*T. schaeferi* sp.n.						
Balaenoptera musculus	46	11	2	—	15	—	—	31	1	—	—
B. borealis	13	—	10	—	—	—	—	1	3	—	—
B. physalus	8	—	—	4	—	—	—	2	2	—	—
Physeter catodon	14	1	—	—	—	—	—	1	—	12	—
Lagenorhynchus obscurus	2	—	—	—	—	—	1	—	—	1	1
L. australis	1	—	—	—	—	—	1	—	—	—	—
Steno bredanensis	2	—	—	—	—	—	2	—	—	—	—
Globicephala edwardi	2	—	—	—	—	1	—	—	—	—	—

The Blue Whale has been found to harbour five different species of Cestodes, while in the seven other hosts only one to three different species occurred. Blue Whales formed by far the greater number of the hosts examined (Table 2) and this undoubtedly accounts for the greater variety of worms from this species of whale. Hitherto *Diplogonoporus balaenopterae* has been found only in the Sei Whale. In the present material this cestode has been found in two other hosts, the Fin Whale and the Blue Whale. The latter appears also to be a new host for *Tetrabothrius wilsoni*. The Fin Whale is a new host for *Priapocephalus grandis* and *Tetrabothrius affinis*.

Two species of tapeworms may occur together in the same gut, for in Blue Whale, *Priapocephalus grandis* was found either with *Diplogonoporus balaenopterae* or with *Tetrabothrius affinis*, or with *T. schaeferi* sp.n. Triple infestation has not, however, been noted in any of the hosts examined.

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