

DIGENETIC TREMATODES FROM MARINE FISHES

IN THE SAN JUAN ARCHIPELAGO

by

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INTRODUCTION

Except for the pioneering work of Lloyd and Guberlet (32) in 1932 and Lloyd (31) in 1938, little is known concerning the digenetic trematode parasites of the fishes of the San Juan Island region of North Puget Sound, Washington.

Prior to the collection reported herein, made during the summer of 1957, only members of the genus Podocotyle had been known from this general area of North America. These were P. atomon, P. abitionis and P. reflexa which were taken from Departure Bay, British Columbia, Canada, by McFarlane in 1936 (42). Species belonging to Fellodistomum and Zoogonus have not been previously reported from this area, nor from the coastal waters of Oregon and California.

In 1937, Park (65) collected and described as new species, Podocotyle enophrysi, P. apodichthysi, P. blennicottusi, P. californica, P. kofoidi, P. elongata, P. pedunculata and P. pacifica from the marine waters in the vicinity of Dillon's Beach, California. His publication included a revision of the genus and a key to most of the species, based upon the newly recognised separation characters of the shape of the seminal vesicle and the location of the testes. Subsequent additions to the genus have been made by McIntosh (43) who in 1939, described P. shawi from the silver salmon of Oregon waters, and in 1949 Johnson (19) added P. gibbonsiae, taken in

Monterey Bay, California.

Stafford (75, p. 486) erected the genus Fellodistomum in 1904 with the single species incisum (Rudolphi). His material came from marine fishes from Eastern Canada. Subsequently Nicoll (50, p. 469-472) described F. agnotum from British waters; F. sebastodis was described by Yamaguti and Matumura (90, p. 117-122) from Japan; Cabellero et al. (3, p. 167-171) described F. preovaricum from Panama; Sogandares-Bernal (73, p. 589-590) described F. mendezi from Panama and Aldrich (1) found F. phrissovum n. sp. in the waters of Puget Sound, Washington. The other species included in the genus were formerly in the genus Steringophorus, but were transferred to Fellodistomum by Yamaguti in 1953 (88, p. 18). These species were: F. furcigerum (Olsson, 1868) which has been reported from fishes from Scandinavia, the British coast, Greenland, the Sea of Japan (Toyama Bay), Woods Hole and Northern Siberia; F. magnum (Manter, 1934) and F. profundum (Manter, 1934) from the deep waters at Tortugas, Florida.

The family Zoogonidae was established in 1911 by Odhner (60). The genus Zoogonus had been established by Looss in 1901 (34, p. 439-442) with the species mirus as the type. The type specimens were from marine fish from the Bay of Trieste in the Mediterranean Sea. Other species described in the genus have been: Z. rubellus (Olsson, 1868) Odhner, 1902 (58, p. 58-61), collected from the west coast of Sweden, Z. pagrosomi which was described by Yamaguti (85, p. 223-225) from the Inland Sea of Japan and Z.

dextrocirrus n. sp. from Puget Sound, Washington. Goldschmidt (12, p. 870-873) did embryological and comparative studies on Z. mirus and Z. rubellus at Trieste. Nicoll (49, p. 17-18) reported that he found numerous examples of Z. rubellus in every specimen of Anarrhichas lupus he examined from St. Andrews Bay in Scotland. Stunkard (79, p. 308-334; 80, p. 33-34; 81, p. 205-214) has done considerable work on the genus, with his studies of the larval stages and life history, as well as work on the specificity and host relationships of the genus.

Podocotyle was established by Dujardin (11, p. 401) in 1845, as a sub-genus. Stossich (77, p. 11) raised it to generic rank in 1892. In his 1898 review of the helminth fauna of the area of Trieste, Stossich (78, p. 24-27) included in addition to his species pedicellatum, all the then known species of Podocotyle including contortum and fractum of Rudolphi, macrocotyle of Diesing, furcatum of Bremser, retroflexum of Molin and pachysomum of Eysenhardt. Additional early records of species, collected from various areas of Europe, were recorded by Olsson (64) in Scandinavia, Molin (45) and Linstow (25) from central Europe and Stossich (76) and Rudolphi (69) from Trieste. In 1905, Odhner (59, p. 320-327) redescribed the genus, clarified the synonymy, and established P. atomon Rudolphi, 1802) as the type species. He added only P. reflexa (Creplin, 1825) and a new species, olssoni to the genus. Thirty-seven species are considered valid.

Nicoll (50, 51, 53) described three new species of Podocotyle

from the waters of the British Isles, but none of these has been reported from the west coast of North America. Nicoll (54) in his 1915 paper gave a comprehensive list of all the species of Podocotyle and their hosts, which were in the literature up to that time.

Linton (26, 27, 28, 29, 30) added the collection records of Podocotyle simplex and P. olssoni taken at Woods Hole and Beaufort, North Carolina, to the literature.

Lieper and Atkinson (23, 24) described a new species from the waters of Antarctica, which has not been reported from other areas.

Isaitschikov (17) described two new species from the Russian Arctic. Podocotyle olssoni has been previously reported from the east coast of North America and P. levenseni is reported in this paper from Puget Sound.

Takahashi (82) reported a new species, Podocotyle ayu from the waters of Japan, but it has not been subsequently mentioned.

Yamaguti (84, 86, 89) described five new species, also from the waters of Japan. None of these species has been reported from the Eastern Pacific.

Yamaguti (87) described two new species from Macassar, Celebes, neither of which have been reported from any other area. He lists (89) thirty-eight species, in his account of the genus, from all over the world.

Price (66) described a new species from Puerto Rico and Sogandares-Bernal (74) a new one from Bimini, in the West Indies. These have not been reported from other waters.

Timon-David (83) reported Podocotyle fracta from the fishes of the gulf of Marseille, France.

In 1939, Nigrelli (55) described a new species of Podocotyle from fish taken in deep water off the Madeira Islands. This species has not been reported since this original record.

Miller (44) described a new species from material in Stafford's collection, from the eastern Canadian shore. This species has not subsequently been reported.

Manter (38, 39, 40) described a new species from the deep waters off Tortugas, Florida, two from the vicinity of the Galapagos Islands and one from New Zealand. Bravo-Hollis and Manter (2) described a new species of Podocotyle from Mexican waters. None of these new species has been reported from other areas. Manter (36, 37) listed both P. atomon and P. olssoni from marine waters of Maine.

In 1950, Dayal (9) described a new species from fresh-water fishes at Lucknow, India. This species has not since been reported.

With the previous permission of the Graduate Council of Oregon State College, a new species of Fellodistomum and a new species of Zoogonus have been described and accepted for publication in The Journal of Parasitology, in connection with the preparation of this thesis.

The general plan for the thesis is a survey of the hosts and incidence of the trematode genera Podocotyle, Zoogonus and Fellodistomum in the area of the San Juan Archipelago, Washington.

Keys have been prepared for the species of Podocotyle and Fellodistomum, taking into consideration new characteristics which appear to be more usable in the separation of species.

## MATERIALS AND METHODS

The host fishes were collected during the months of July and August, 1957, in the marine waters of the San Juan Archipelago area. Of the one hundred ninety-three fishes examined for intestinal parasites, one hundred fifty belonging to thirty-two different species were found to be infected with digenetic trematodes. All host fish were identified by the author with the help of the keys, illustrations and descriptions of fishes of this region in Clemens and Wilby (4), and Schultz (70).

The areas of procurement and approximate depths at which collections were made, are as follows:

1. San Juan Channel	20 fathoms
2. Firday Harbor	10 "
3. Lopez Sound	20 "
4. Argyle Lagoon of North Bay	5 "
5. Haro Strait (off Smallpox Bay)	10 "
6. Bellingham Bay	10 "
7. East Sound	14 "
8. North Bay	10 "
9. West Sound	16 "
10. Deer Harbor	5 "
11. Salmon Bank	4 "

In all the collection areas the bottom was covered with mud, except in San Juan Channel, Haro Strait and Salmon Bank where it was

rocky. In these three latter areas the tide flow and rips are quite severe during the tidal changes, which necessitated the making of collection tows during the period of the slack tide. Extra care had to be taken in these areas to prevent the trawl from hitting bottom and fouling or ripping and destroying the bag on the rocks.

The majority of the hosts were collected by means of an 8 foot beam trawl having a 15 foot bag of heavy,  $1\frac{1}{2}$  inch mesh, which was towed near the bottom in the collecting areas, by the M. V. Hydah. The Hydah is 55 feet in length and has a diesel motor of 100 horsepower. This vessel is utilized for the collection of marine materials for teaching and research at the Friday Harbor Laboratories of the University of Washington. Tows were made for fifteen minutes at the designated depth. The total elapsed time from the lowering of the trawl and putting out the required amount of cable to place the trawl at the proper depth in relation to the speed of the Hydah, and the presence or lack of a running tide, to the time when the trawl was brought alongside and lifted out of the water was 25-30 minutes. The variability was generally due to the amount of cable put out, or the lack of maneuverability in the collection area which inhibited the bringing of the trawl over the deck until the Captain had placed the vessel in a safer position. The time and speed of the tow, which was necessary to keep the trawl and bag off the bottom, caused some mortality among the smaller and more fragile fishes due to the pressure of the water flowing



through the net bag which forced them against the net and killed them by pressure, or drowned them. In general this mortality was low. On two tows in East Sound and the one tow in Deer Harbor, primarily due to confined quarters which called for slower towing speeds and shallow water, the trawl touched bottom and picked up a considerable load of mud on top of its already contained collection of fish. It was found however that most of this mud could be washed out of the net by slowly towing it alongside the boat while it was suspended from the crane boom, which prevented it from fouling the propeller, before swinging it out of the water and over the after-deck. The contents of the trawl were, in all cases, released over two collecting boxes filled with sea water and placed side by side in the center of the after-deck. The collecting boxes were made from  $3/4$  inch plywood with outside dimensions of 4 feet by 1 foot by 1 foot. A row of 1 inch holes spaced at 3 inch intervals, 2 inches from the top along one side, acted as overflow outlets. These were covered on the outside of the box with  $1/2$  inch hardware cloth to prevent escape of the contained animals. A number of the fish overflowed onto the deck when the trawl was emptied, but were collected as soon as possible and placed in collecting boxes, into which constantly flowing fresh sea water was being injected under pressure for aeration. Those remaining in the collecting boxes were sorted from the debris of the haul and placed in boxes of clean water for a few minutes to allow them to free their gills of debris and then transferred to fresh tanks to await transport

back to the Laboratories. On arrival at the Laboratories, the fish were removed from the boat boxes into either dockside holding boxes or aquaria in the laboratory building, through which fresh sea water was continuously flowing. Collections were generally made once a week, although more frequent collections were at times possible.

The trematode parasites were removed from the intestine of the fish immediately after it was taken from the tank and killed. The entire intestine was removed from the rest of the viscera and placed in a dissection tray made from a 150 mm. diameter, glass Petri dish in which the bottom was covered with black wax to a depth of 3 cm. It was found that this made a very satisfactory dissection tray, as it fitted well on the stage of a dissection microscope; was large enough to conveniently hold the entire intestine of all but the larger fish, while it was being searched for parasites; and the black wax bottom did not reflect glare under the intense illumination necessary, as well as serving as an excellent contrast background for finding any trematodes which were in the mucus or intestinal contents which were scraped out onto it for examination during the final stage of examining for trematodes.

Upon removal from the intestine, the parasites were placed on slides in 5% Ethyl Urethane (Ethyl Carbamate) solution made with filtered sea water, which was used as a relaxing solution. The trematodes were arbitrarily sorted, as to relative size, into two or three groups on different slides when placed in the relaxing

solution. This separation allowed for the larger ones to be left in the solution for a longer time until they were completely relaxed. The time for relaxation varied considerably, and appeared to depend upon the size of the parasite and the amount of cuticle present on the body. When the trematodes appeared to be relaxed, they were covered with a glass cover-slip and as the relaxing solution was drawn out on one side, Lavdowsky's solution (A.F.A.) for fixation was put in on the other side until the cuticle appeared white and opaque. In general no pressure, other than the weight of the cover-slip and the capillary pressure of the fluid between the two glass surfaces was used or found necessary to flatten the specimens. After the trematodes were completely fixed, they were carefully transferred to "micro-vials" made from 4 mm. soft glass tubing cut in 27 mm. lengths and heat fused on one end to form a small vial. These were filled with Lavdowsky's solution; stoppered with rolled lens tissue which was found to be much easier and more satisfactory to use than cotton, and placed in standard  $2\frac{1}{2}$  inch vials of the fixing solution for storage. The parasites were stained with Delafield's Hematoxylin, cleared in clove oil and mounted on slides in Canadian Balsam.

## Family Fellodistomidae

Genus Fellodistomum Stafford

Stafford established the genus Fellodistomum in 1904, using Distomum incisum Rudolphi, 1809, as the type species. The genus consists of smooth bodied animals having a large ventral sucker located in the midbody region. The oral sucker is ventral and at or near the anterior end. The intestinal ceca are sacular and terminate in the area of the testes. The ovate to round testes are situated laterally in the posterior part of the body, behind the ventral sucker. The ovary is pretesticular. The genital pore is median or to the left of the midline, anterior to the ventral sucker. The vitellaria are follicular and are located laterally in zones either beside the ventral sucker or anterior or posterior to it. The uterus, which is filled with numerous eggs in mature specimens, reaches to the posterior end of the body. The excretory vesicle is Y- or V-shaped, with a terminal pore. (75, p. 486; 88, p. 18; 44, p. 43)

The following species have been placed in the genus:

Fellodistomum incisum (Rudolphi, 1809) Stafford, 1904 (75, p. 486; 44, p. 43); F. fellis (Olsson, 1868) Nicoll, 1909 (50, p. 459-469); F. agnotum Nicoll, 1909 (50, p. 469-472); F. furcigerum (Olsson, 1868) Yamaguti, 1953 (88, p. 18); F. magnum (Manter, 1934) Yamaguti, 1953 (88, p. 18); F. profundum (Manter, 1934) Yamaguti, 1953 (88, p. 18); F. sebastodis Yamaguti and Matumura, 1942 (90, p. 120-122);

F. preovaricum Caballero, Bravo and Grocott, 1952 (3, p. 167-171);  
F. mendezi Sogandares-Bernal, 1955 (73, p. 589-590) and F. phrissovum  
n. sp. Aldrich, 1960 (1).

The genus Fellodistomum was established by Stafford (75, p. 486) in 1904. The type species F. incisum (Rudolphi, 1809) Stafford, 1904, was placed in questionable synonymy by Nicoll (50, p. 459-460) with Distoma fellis Olsson, 1868. Miller in 1941 (44, p. 43) in his study and review of Stafford's materials and report, placed F. incisum in positive synonymy with F. fellis. According to Miller (44, p. 43-44) there were three specimens of F. agnotum Nicoll, 1909 in Stafford's collection, which he undoubtedly included in F. incisum, but since none of the slides was labeled, one can only conjecture as to their original designations. Dawes (8, p. 242-244) placed F. agnotum Nicoll, 1909 with the synonyms of F. fellis, on the basis that it would be unlikely for two different species of trematodes to be so specific as to occur in the same location in the same host, in various parts of the world. On the basis of Miller's (44, p. 43-44) descriptions and illustrations, and Nicoll's (50, p. 459-472) descriptions, as well as their acceptance by both Yamaguti (89, p. 27) and Skrjabin (72, p. 185-186) as valid species, it would appear that this synonymy is of doubtful validity.

Yamaguti (89, p. 27) considers the genus Steringophorus Odhner, 1905 to be a synonym of Fellodistomum Stafford, 1904 and has therefore transferred S. furciger Olsson, 1868; S. magnum Manter, 1934

and S. profundum Manter, 1934 to the new combinations of F. furcigerum (Olsson, 1868) Yamaguti, 1959 (originally F. furciger [Olsson, 1868] Yamaguti, 1953); F. magnum (Manter, 1934) Yamaguti, 1953 and F. profundum (Manter, 1934) Yamaguti, 1953. Manter (38, p. 274) includes two Steringophorus (?) species inquirende with his descriptions of S. magnum and S. profundum, but Yamaguti (89, p. 27-28) has chosen to ignore them. This would appear to be the correct procedure in view of the lack of any species designation for these two specimens by Manter. Skrjabin in 1957 (72, p. 273-295) apparently did not accept the placing of Steringophorus Odhner, 1905 in synonymy with Fellodistomum Stafford, 1904, as established by Yamaguti in 1953 (88, p. 18), since he still retained the genus in his 1957 publications. It would seem that since Manter (38, p. 271-274), who described 2 of the 3 species in the genus Steringophorus, has not contested the synonymy, it should remain valid as given in Yamaguti (89, p. 27-28). It should be noted that when Nicoll (52, p. 192) established the family Fellodistomidae in 1914, he placed Steringophoridae of Odhner, 1911 (61, p. 98) in synonymy.

Skrjabin (72, p. 173) says, (my translation) "To (our) regret, in our opinion the disposition is not present in the literature in the species F. sebastodis Yamaguti et Matamura, 1942 and F. preovarum (sic) Caballero, Bravo et Grocott, 1952". Although he makes this statement which seems to infer that he does not feel that these two species are placed correctly as to genus, or perhaps

even to family, he includes them in his key to the species of the genus Fellodistomum. The writer agrees that several of the outstanding internal morphological characters are quite different from those of all other members of the genus, but feels that at present no other designation can be made for them and so retains them in the genus as valid species.

The following are considered valid species of Fellodistomum:  
F. fellis (Olsson, 1868) Nicoll, 1909; F. agnotum Nicoll, 1909;  
F. furcigerum (Olsson, 1868) Yamaguti, 1953; F. magnum (Manter, 1934) Yamaguti, 1953; F. profundum (Manter, 1934) Yamaguti, 1953;  
F. sebastodis Yamaguti and Matumura, 1942; F. preovaricum Caballero, Bravo and Grocott, 1952; F. mendezi Sogandares-Bernal, 1955 and F. phrissovum n. sp. Aldrich, 1960.

Only Fellodistomum phrissovum was found in the course of this investigation.

Fellodistomum phrissovum n. sp.

See fig. 1.

The following description is based on 101 specimens taken from the lemon sole Parophrys vetulus Girard, 1854, from Bellingham Bay and East Sound of Orcas Island, Washington.

Extrenal features. Digenetic trematodes having an ovate body, tapering toward the ends and flattened dorso-ventrally. The type specimen measured 1.27 mm. in length, while the range of ten specimens selected at random from all size ranges and from all hosts, was from 0.86-1.88 mm. Maximum width at the level of the center of the ventral sucker was 0.74 mm. in the type (0.53-0.96 mm.). The skin is smooth and unspined. The oral sucker is well developed and is located at the anterior end of the body, slightly subterminally, on the ventral surface. In the type specimen it measured 0.19 mm. in diameter (0.20-0.33 mm.). The oral opening is antero-ventral in the oral sucker and leads directly into the prepharynx. The ventral sucker measures 0.41 mm. in diameter in the type (0.30-0.58 mm.). It is located in the center of the body and has a large circular opening for attachment. The genital pore is median or slightly to the left, anterior to the ventral sucker, in the area of the cecal bifurcation. The pore opens into a large genital atrium.

Digestive system. The prepharynx, which is one-half the diameter of the oral sucker in length, leads from the mouth,



posteriorly to the border of the oral sucker where it joins the oval, muscular pharynx. An esophagus, the length of the pharynx, leads posteriorly to a point midway between the oral and ventral suckers at the midline, where it bifurcates, forming the two ceca which pass posteriorly along the sides of the body, ending blindly just anterior to the testes.

Genital systems. The paired, ovoid testes are located in the posterior one-third of the body, laterally, opposite one another. The testes in the type specimen measured 0.18 by 0.31 mm., while the range was 0.13 by 0.17 to 0.24 by 0.30 mm. The elongate, ovoid cirrus sac is situated just anterior to the ventral sucker and contains the bipartite seminal vesicle as well as the non-reversible cirrus. The prostatic tissue completely surrounds the cirrus and seminal vesicles, and compactly fills the remaining space within the membranous wall of the cirrus sac. In the type, the cirrus sac measured 0.34 mm. in length (0.20-0.38 mm.). A vas efferens runs from the lateral side of each testis, forward to the base of the cirrus sac where the two enter the first of the two seminal vesicles.

The ovary is lobate and is located postero-laterally between the ventral sucker and the right testis. It measured 0.12 by 0.20 mm. in the type specimen (0.07 by 0.13 to 0.15 by 0.26 mm.). The vitelline glands which are composed of discrete, but compactly-placed vitelline cells, are located laterally in the area between the sides of the body and the lateral side of the intestinal crura.

They begin anteriorly at the line of the intestinal bifurcation and continue posteriorly to the center of the ventral sucker. A single vitelline duct originates from the medial, central edge of each vitelline mass and runs posteriorly to the point where it joins the vitelline reservoir. The uterus has several loops in the posterior part of the body and in the testicular area, while one portion is directed anteriorly, running dorsal to the ventral sucker and continuing forward to the genital pore. The eggs are spiny and measure 0.026 by 0.031 mm. in the type (0.019 by 0.034 to 0.026 by 0.037 mm.).

Excretory system. The only portion of the excretory system visible, is the excretory bladder which is V-shaped. Its two anteriorly directed arms terminate laterally at the line of the pharynx. The two arms join together at the posterior part of the body just anterior to the excretory pore which is located at the posterior extremity of the body.

The V-shaped excretory bladder is in direct contrast to the Y-shaped bladder, which Yamaguti (89, p. 26-27) stated is present in the subfamily and genus in which this specimen has been placed, but in complete agreement with his key separation characteristic to the family (89, p. 22-25). It would seem that this tends to give emphasis to the complete inadequacy and unreliability, of the shape of the excretory bladder, for use as an important key characteristic for separation of the trematodes of this and many other families, especially on generic level. The form of the

excretory bladder undoubtedly varies considerably, depending on whether it contains excretory products or is partially or completely empty at the time the animal is fixed, and the amount of flattening used in the fixation or preparation processes. It is therefore submitted, that this character should not be used in the classification of digenetic trematodes due to its high variability, which makes it unreliable, and the difficulty of observing the character at all in many preserved specimens.

Key to the species of Fellodistomum

1. Vitellaria completely anterior to posterior margin  
of ventral sucker - - - - - 3
- Vitellaria otherwise - - - - - 2
2. Vitellaria completely posterior to ventral sucker - - - - - 6
- Vitellaria lateral to ventral sucker - - - - - 8
3. Ovary anterior to ventral sucker - - - - - F. preovaricum
- Ovary posterior to ventral sucker - - - - - 4
4. Sucker ratio 1:2 - - - - - F. fellis
- Sucker ratio 1:1.5 - - - - - 5
5. Eggs spiny, esophagus present - - - - - F. phrissovum
- Eggs smooth; no esophagus - - - - - F. agnotum
6. Uterus with one coil posterior to ovary - - - - - F. furciger
- Uterus with more than one coil posterior to ovary - - - - - 7
7. Sucker ratio 1:2; body length 6 to 7 mm. - - - - - F. magnum
- Sucker ratio 1:1.5; body length 1.7 to 2 mm. - - F. profundum
8. Uterus with one coil posterior to ovary - - - - - F. mendezi
- Uterus with numerous coils posterior to ovary - - F. sebastodis

## Family Zoogonidae

Genus Zoogonus Looss

The genus Zoogonus was established in 1901 by Looss in describing a new digenetic trematode from Labrus merula, taken in the harbor of Trieste in the Mediterranean Sea. The type species was Z. mirus Looss, 1901. The members of the genus are small trematodes having spiny skin and a subterminal oral sucker. The prepharynx may be either long or short. The esophagus is comparatively long, while the ceca are short and end blindly toward the posterior. The ventral sucker is located in the midbody, usually slightly anterior to the midline. The testes are symmetrical, laterally placed at the midline just posterior to the ventral sucker. The cirrus pouch is located in the area of the ventral sucker and contains a bipartite seminal vesicle and well developed prostatic complex. The genital pore is marginal to submarginal, on a level with the ventral sucker. The ovary is median, between the two cecal ends, and the single, compact vitellarium is located in close proximity to the ovary. The uterine coils occupy the entire posterior body behind the testes. The excretory vesicle is saccular, with a terminal pore. (89, p. 50; 88, p. 36; 7, p. 247; 34, p. 439-442; 79, p. 308-334; 49, p. 1-25; 72, p. 12-33)

The following species have been named in the genus: Zoogonus mirus Looss, 1901 (34, p. 439-442); Z. rubellus (Olsson, 1868) Odhner, 1902 (58, p. 58-61); Z. pagrosomi Yamaguti, 1939 (85, p.

223-225); Z. dextrocirrus n. sp. Aldrich, 1960 (1).

Looss (34, p. 439-442) established the genus Zoogonus in 1901 and described the species mirus as the type. In 1902, Odhner (58, p. 58-61) redescribed Distoma rubellum Olsson, 1868 and transferred it to the genus Zoogonus. The host, Labrus berggylta (syn. L. maculatus) was from the west coast of Sweden, as had been the earlier collections of Olsson. Odhner used the size of the suckers and the length of the miracidia as the primary separation characteristics for the two species. During that same year, Goldschmidt (12, p. 870-873) in his paper on the form and embryological development of Z. mirus, took specimens from Labrus merula at Trieste and compared them with the earlier descriptions of Z. mirus and Z. rubellus of Looss and Odhner and reported that he could discern no morphological differences. In a later paper, Goldschmidt (13, p. 607-609) again expressed the opinion that the two species were identical and that the characters used by Odhner to separate them were subject to variation and therefore could not serve for separation of species.

Nicoll (49, p. 17-18) reported in his 1909 study of the entozoa of British marine fishes, that he found numerous examples of Zoogonus rubellus in every specimen of Anarrhichas lupus he examined from St. Andrew Bay. The parasites were located in the rectum and lower part of the intestine of the host. He noted that some doubt remained as to whether Z. rubellus and Z. mirus were identical and stated that "my specimens agree best with Goldschmidt's description."

(49, p. 17). It should be noted that although Nicoll felt that his specimens were most like Z. mirus of Goldschmidt, in the shape and location of the digestive system, he apparently overlooked the variation in the location of the vitellarium. In Goldschmidt's description of his specimens, he says, "Der Dotterstock ist unpaar und liegt als kleines birnförmiges Organ in der Nähe des Keimstockes. (In Fig. 1, die nach einem gepressten Tiere gezeichnet wurde, ist ein wenig zur Seite gedrängt.)" (12, p. 872). In his illustration it is clearly shown that the vitellarium lies posterior to the ovary and not anterior to the ovary as in Z. rubellus of Nicoll, which seems to indicate that they are definitely separate species. On close examination and comparison of the illustrations of Z. rubellus in the papers of Nicoll (49) and Looss (34) it is noted that the location of the vitellarium is anterior to the ovary in both cases, which would seem to indicate that Z. rubellus of Nicoll is probably more closely related to the type species, than it is to Z. mirus of Goldschmidt. Stunkard states that, "It is significant that the worms studied by Nicoll and Odhner came from the same region, whereas Goldschmidt's material was collected in the Mediterranean and presumably was identical with that of Looss." (79, p. 313). However, if we consider the various locations of the vitellarium as significant morphological criteria for species separation, the two Mediterranean forms are not the same species even though they came from the same host from the same area. It would seem also, that Nicoll assumed that his specimens were like

those of Odhner which were also taken in Northeastern Atlantic waters, and placed them in the species rubellus even though by his own statement he considered them to be more like the Mediterranean species. In Z. mirus of Looss (the type genus and species), the vitellarium is anterior to the ovary and in Z. mirus of Goldschmidt it is posterior to the ovary. In Z. rubellus of Odhner, the vitellarium appears to be located to the right of the ovary and slightly toward the anterior, while in Z. rubellus of Nicoll, the vitellarium is anterior to the ovary at the midline. In his paper establishing the family Zoogonidae, Odhner (60, p. 237-253) described a comparative study of specimens of Zoogonus from North Atlantic and the Mediterranean, and stated that although the two forms are very similar, they are separate species. On comparison of size ranges of various organs of his specimens, with those of the original descriptions, sufficient discrepancies appear to leave considerable doubt as to the use of his paper as a positive criterion for arbitrarily placing all the northern specimens in one species and all the southern specimens in another species. In a continuation of earlier life cycle studies (80, p. 33-34), Stunkard reported in 1941 that "there is no basis for a positive distinction between species of Zoogonus from the North Sea and the Mediterranean, but it appears probable that the European and American forms are specifically distinct. If this proves to be true, the American species is Z. lasius (Leidy, 1891) Stunkard, 1940." (81, p. 213). On the basis of study of these papers and



the comparison of their illustrations, it would appear that there are at least two species of Zoogonus in the Eastern Atlantic and Eastern Mediterranean areas, with a possible additional species in the Western Atlantic (22, p. 415-416). It is suggested that Z. mirus Looss, 1901 and Z. rubellus (Olsson, 1868) Odhner, 1902 stand as valid species and that Z. rubellus as figured and discussed by Nicoll be considered rather as belonging to Z. mirus. It is further proposed that the trematode which Goldschmidt discussed and figured as belonging to Z. mirus, be considered as another and undescribed species of the genus, although it must be retained in the literature until it can be redescribed from specimens.

The following are considered valid species of Zoogonus:

Z. mirus Looss, 1901; Z. rubellus (Olsson, 1868) Odhner, 1902; Z. pagrosomi Yamaguti, 1939 and Z. dextrocirrus n. sp. Aldrich, 1960.

Only Zoogonus dextrocirrus n. sp. was found in the course of this investigation.

Zoogonus dextrocirrus n. sp.

See fig. 2.

The following description is based on 168 specimens taken from Lepidopsetta bilineata (Ayres), 1855, the rock sole; Microstomus pacificus (Lockington), 1879, the Dover sole; Lycodopsis pacificus (Collett), 1879, the black-bellied eel-pout; Lycodes brevipes Bean, 1890, the short-finned eel-pout; Parophrys vetulus Girard, 1854, the lemon sole; Lumpenus anguillaris (Pallas), 1811, the eel-blenny and Isopsetta isolepis (Lockington), 1880, the butter sole. The host animals were collected from the waters of East Sound and West Sound of Orcas Island and Bellingham Bay, Washington.

External features. Trematodes belonging to the Digenea, with elongate bodies which taper slightly toward the rounded ends, and are flattened dorso-ventrally. The length of the type specimen was 1.409 mm., while the range of nine specimens selected at random from all size ranges from different hosts was 1.427 to 0.924 mm. Maximum width of the body at the level of the gonopore and the center of the ventral sucker was 0.462 mm. in the type (0.511 to 0.280 mm.). The cuticle contains rows of spines running around the body, from the area of the oral sucker, posteriorly to the area of the ceca. The numbers of spines per row, decrease from anterior to posterior and the rows are farther apart. Specimens from fifteen of the twenty hosts were without cuticle and were therefore unspined. Seventy-two of the specimens had a

heavy cuticle containing the normal spination pattern. One specimen was only partially spined, in that cuticle and spines occurred only in a small area of the mid-section of the body. In all cases except one, the parasites collected from any single host possessed a cuticle with spines or lacked the cuticle and were therefore unspined. In the exception, eleven parasites were collected from the host and of these, five appeared to be normally spined, while two had lost small amounts of cuticle, one had only a small area of cuticle in the mid-body region and three had no cuticle, so appeared to be unspined. No explanation is offered for the lack of cuticle and spines in those specimens in this condition. No correlation could be made between the time which elapsed between capture of the host animals and their being examined, as to whether their parasites possessed cuticle or not. The oral sucker is well developed and is located ventrally at the anterior end of the body. It measured 0.173 mm. in diameter in the type specimen (0.206 to 0.149 mm.). The oral opening is antero-ventral in the oral sucker and opens directly into the short prepharynx. The genital pore is lateral and is located on the right side of the body at the level of the center of the ventral sucker. The ventral sucker, 0.190 mm. in diameter in the type (0.198 to 0.132 mm.) is slightly anterior to the center of the body on the midline.

Digestive system. The prepharynx, which is 0.132 mm. in length in the type (0.132 to 0.083 mm.), joins the heavy, muscular pharynx 0.149 mm. (0.149 to 0.066 mm.) just posterior to the oral sucker.

The esophagus, which is 0.528 mm. in length in the type specimen (0.528 to 0.314 mm.) runs toward the posterior from the pharynx, along the midline, to the posterior part of the body where it bifurcates just behind the testes to form two short, sacculate ceca.

Gential systems. The testes, which are paired and vary from round to slightly irregular in shape, are located toward the sides in the midbody region between the posterior border of the ventral sucker and the anterior border of the ceca. They measure 0.099 by 0.132 mm. in the type specimen (0.083 by 0.116 to 0.116 by 0.116 mm.). A vas efferens runs from the median edge of each testis to the posterior end of the cirrus sac where the two join and enter the bipartite seminal vesicle, which communicates directly with the cirrus. The elongate, ovoid cirrus sac, which measured 0.182 mm. in length in the type (0.149 to 0.231 mm.) lies on the right side of the body, in the area from the midline to the gonopore with the posterior portion between the right testis and the ventral sucker. It is filled with the large, glandular cells of the prostatic tissue, which completely surrounds the non-reversible cirrus and the bipartite seminal vesicle.

The ovary, which measured 0.099 by 0.099 mm. in the type specimen (0.066 by 0.132 to 0.116 by 0.116 mm.), is round to lobate and is situated in the midline area between the ends of the ceca. The vitellarium is compact and is a single gland, which is about one-half the size of the ovary and situated just posterior

to that organ, at the midline. The seminal receptacle is about one-fourth the size of the ovary and is located to the right of the vitelline gland, just posterior to the ovary. A Laurer's canal is present. The uterus, which has several loops in the posterior portion of the body, is filled with miracidia in various stages of development inside the egg membranes. The uterine loops extend forward to the area of the vitellaria, from which point the terminal portion runs anteriorly between the testes, then between the right testis and the cirrus sac toward the side of the body, where it loops over the lateral portion of the cirrus sac and joins the common atrium at the gonopore.

Excretory system. The excretory bladder, which was the only part of the system observed, is a small, membranous sac located at the posterior extremity of the body and ends in a posterior terminal pore.

The new species is readily separated from all other species of the genus by the dextral location of the cirrus sac. Zoogonus dextrocirrus resembles Z. pagrosomi in that the gonopore is dextral, but differs from Z. mirus and Z. rubellus in which it is sinistral. The cirrus sac is also dextral in the new species, while it is sinistral in Z. pagrosomi, Z. mirus and Z. rubellus. In Z. dextrocirrus the prepharynx is short as in Z. rubellus of Nicoll and of Odhner, but wider. In Z. pagrosomi and Z. mirus of Goldschmidt and of Looss, the prepharynx is several times longer. The testes in Z. dextrocirrus are of the shape and size ratio of

Z. rubellus of Odhner, but smaller and of different shape than those of Z. pagrosomi and Z. mirus of Goldschmidt and of Looss. In Z. dextrocirrus the intestinal ceca are generally as in Z. rubellus of Nicoll, Z. mirus of Goldschmidt and Z. pagrosomi, but not so elongate nor bifurcating so far anteriorly as in Z. mirus of Looss and Z. rubellus of Odhner. The location of the vitellaria in Z. dextrocirrus is posterior to the ovary as in Z. mirus of Goldschmidt and Z. pagrosomi, while in Z. rubellus of Nicoll and Z. mirus of Looss it is located anterior to the ovary, but on the right side of the ovary in Z. rubellus of Odhner. The uterus in Z. dextrocirrus extends into and fills the most posterior portion of the body as it does in all the other species with the exception of Z. rubellus of Nicoll. The number and distribution of eggs and miricidia in the uterus in Z. dextrocirrus closely resembles all descriptions of Z. mirus and Z. rubellus but varies considerably from Z. pagrosomi.

## Family Opecoelidae

Genus Podocotyle (Dujardin, 1845) Odhner, 1905Syn: Sinistroporus Stafford, 1904

Dujardin established the genus Podocotyle in 1845. Odhner redescribed it in 1905 and clarified the synonymy. The type species was P. atomon (Rudolphi, 1802) Odhner, 1905, from Pleuronectes flesus. Members of the genus have an unarmed, rather elongate body. The ventral sucker is located in the anterior half of the body and is sometimes slightly pedunculate. The oral sucker, which is generally terminal, is well developed, as is the pharynx. The prepharynx is short to very short and the esophagus varies from short to comparatively long. The ceca terminate at or near the posterior end of the body. The testes are tandem, generally located in the midportion of the hindbody. They are rounded bodies having either smooth or indented edges, and may be touching one another or separated some distance, with the intervening area filled by vitellaria or not. The cirrus pouch may be either long and slender, or of medium length and claviform. The long and medium length cirrus pouches may be either nearly straight or sinuous and generally extend some distance beyond the posterior border of the ventral sucker. No external seminal vesicle is present. The genital pore is located to the left of the midline in the area of the intestinal bifurcation or slightly anterior to

it. The ovary is usually three lobed, occasionally rounded, and is located just anterior to the testes at the midline or to the right. A seminal receptacle and Laurer's canal are present. The vitellaria are located in the area posterior to the anterior edge of the ventral sucker and may either be lateral and separated posterior to the testes or may completely fill all the posterior body spaces. The uterine folds are in the space between the ovary and the ventral sucker, with a straight portion running forward to the genital pore. The excretory vesicle is sac-like and generally reaches forward to the vicinity of the ovary. (59, p. 320-327; 88, p. 72-73; 89, p. 119-120; 11, p. 401)

The following species of Podocotyle have been described: P. abitionis McFarlane, 1936 (42, p. 339-341); P. aeglefini (Müller, 1776) (46, p. 224); P. apodichthysi Park, 1937 (65, p. 407-409); P. atherinae sp. inq. Nicoll, 1914 (53, p. 474-475); P. atomon (Rudolphi, 1802) Odhner, 1905 (59, p. 320-326); P. atzi Nigrelli, 1939 (55, p. 156); P. ayu Takahashi, 1928 (82, p. 51-56); P. blennicottusi Park, 1937 (65, p. 409-411); P. breviformis Manter, 1940 (39, p. 384-386); P. caithnessi Manter, 1954 (40, p. 517-518); P. californica Park, 1937 (65, p. 411-412); P. contortum (Rudolphi, 1819) Stossich, 1898 (78, p. 24-25); P. atomon var. dispar Nicoll, 1909 (50, p. 451-452); P. elongata Park, 1937 (56, p. 413-414); P. enophrysi Park, 1937 (65, p. 406-407); P. epinepheli Yamaguti, 1942 (86, p. 339-340); P. fracta (Rudolphi, 1819) Stossich, 1898 (78, p. 26); P. furcata (Bremser in Rudolphi, 1819) Odhner, 1928 (63,



p. 1-6); P. gibbonsiae Johnson, 1949 (19, p. 107-109); P. gracilis Yamaguti, 1952 (87, p. 156-157); P. indica (Dayal, 1950) (9, p. 5-7); P. kofoidi Park, 1937 (65, p. 412-413); P. lanceolata Price, 1934 (66, p. 6-7); P. lepomis (Dobrovolsky, 1939) Yamaguti, 1958 (89, p. 121); P. lethrini Yamaguti, 1942 (86, p. 341-343); P. levenseni Isaitschikov, 1928 (17, p. 37-39); P. macrocotyle (Diesing, 1858) Stossich, 1898 (78, p. 25); P. mecopera Manter, 1940 (39, p. 383); P. musculometra Bravo-Hollis and Manter, 1957 (2, p. 42-44); P. mycteropercae Sogandares-Bernal, 1959 (74, p. 95 and 97); P. odhneri Isaitschikov, 1928 (17, p. 39-43); P. olssoni Odhner, 1905 (59, p. 327); P. pachysomum (Eysenhardt, 1829) Stossich, 1898 (78, p. 27); P. pacifica Park, 1937 (65, p. 415-416); P. pearsei Manter, 1934 (38, p. 289-290); P. pedicellata (Stossich, 1887) Stossich, 1898 (78, p. 25); P. pedunculata Park, 1937 (65, p. 414-415); P. pennelli Leiper and Atkinson, 1914 (23, p. 224); P. petalophallus Yamaguti, 1934 (84, p. 295-298); P. reflexa (Creplin, 1825) Odhner, 1905 (59, p. 326-327); P. retroflexum (Molin, 1859) Stossich, 1898 (78, p. 26-27); P. serrani Yamaguti, 1952 (87, p. 157-159); P. shawi McIntosh, 1939 (43, p. 379-381); P. simplex (Rudolphi, 1809) Yamaguti, 1953 (88, p. 74); P. staffordi Miller, 1941 (44, p. 37-38); P. synnathi Nicoll, 1913 (51, p. 238-240) and P. tamame Yamaguti, 1942 (86, p. 340-341).

Podocotyle aeglefini is made a synonym of P. atomon since both Yamaguti (89, p. 120) and Dawes (8, p. 200) consider Sinistroporus

simplex (Rudolphi, 1809) Stafford, 1904 to be a synonym of P. aeglefini and Miller (44, p. 35-38) considers S. simplex to be a synonym of P. atomon. P. angulatum was made a synonym of P. atomon by Odhner (59, p. 320-322). P. breviformis was made a synonym of Hamacreadium oscitans Linton, 1910 by Manter (39a, p. 300). P. contortum was transferred to the genus Accacoelium by Looss (33, (33, p. 632). In 1928, Odhner (63, p. 1-6) transferred P. furcata to Opecoeloides and made it the genotype. Odhner (62, p. 172) that same year also transferred P. macrocotyle to the genus Accaclado-coelium. P. pachysomum was transferred to the genus Haplosplanchnus by Looss (35, p. 129). P. pennelli is transferred in this paper to Plagioporus. P. retroflexum was transferred to Lecithostaphylus by Odhner in 1911 (61, p. 115-116). Cainocreadium shawi is in this paper, transferred back to its original genus Podocotyle. P. simplex of Yamaguti, 1953 (88, p. 74) is herein made a synonym of P. atomon in accordance with the synonymy established by Odhner in 1905 (59, p. 320).

In a complete consideration of a genus as large and with as many species synonymies as Podocotyle, it is necessary to discuss at length a number of these synonyms as well as other problems which have arisen in the literature during the past one hundred fifteen years. The following section is for this purpose.

In considering the rather complex synonymy of Podocotyle atomon, it should be noted that "Stafford created the genus Sinistroporus for Distomum simplex Rudolphi. Odhner (1905) has

pointed out that D. simplex is a synonym of both D. angulatum and D. atoman (sic). He further states that D. angulatum which was made the type species of the genus Podocotyle by Stiles and Hassall (20) cannot be retained because it was inadequately described, and because the type material has been lost. Thus P. atoman (sic) becomes the proper name of this species and the type of the genus." (44, p. 35).

Since Yamaguti (89, p. 120) and Dawes (8, p. 200) considered Sinistroporus simplex (Rudolphi, 1809) Stafford, 1904 to be a synonym of P. aeglefini, this species of Podocotyle also becomes a synonym of P. atomon.

Nicoll (48, p. 73; 50, p. 452-453) early noted the diversity of form and distribution as well as the large numbers of hosts in which this species seemed to occur. His reservations about all these various specimens being identical probably were well founded, in view of the large numbers of species which have been described for the genus since that time. It would seem that a great deal of the confusion by the early workers was due to their use of characters which did not truly separate species. This resulted in the description of a number of "species" which possessed only minor anatomical variations. Many synonymies thereby accumulated.

The separation characters, as established by Park (65, p. 405-406), which include the form of the seminal vesicle, the extension of the cirrus sac and the position of the testes and their relationship to each other, seem to be more useable and sound characters for

the determination of species than the prime character of the extent of the vitellaria only, as was used previously. The form of the seminal vesicle is sometimes rather hard to determine, but seems to be the best useable character for separation of species.

Little is known of the life cycle of Podocotyle atomon, but Shulman (71, p. 275-278) reported that "The life-history of Podocotyle atomon in the White Sea was shown to be cyclic. Infection of the first intermediate host, Littorina saxatilis, occurred in the spring and almost disappeared toward autumn. At that time the infection of the second intermediate host, a crustacean named 'bokoplav', rose to 80% - 100% while the infection of the definitive host (fish) dropped. Podocotyle atomon parasitized many species of fish and in some induced characteristic modifications of the internal organs."

It should be noted that in Miller (44) the specific name of Podocotyle atomon is repeatedly spelled atoman which is incorrect according to the spelling given the species name by Rudolphi (67, p. 70) in his original description.

P. atherinae was described by Nicoll (53, p. 474-475) as a species inquirende, from a single specimen obtained from Atherina presbyter (sand smelt) from Plymouth. He referred it to the genus Podocotyle with reservations, but from the lobed ovary and other outstanding anatomical characters brought out in his description and illustration, it seems to be a valid reference to the genus. The species was not included by Park (65) in his review of the

genus, but was accepted by Dawes (7, p. 176) and Yamaguti (89, p. 120) as valid, and is recognised as such in this paper.

In discussing the relationships of Hamacreadium to Podocotyle, with special reference to P. breviformis Manter, 1940, Manter (39a, p. 297) says that "Restudy of cotype material shows that this species can not only be transferred to Hamacreadium on the basis of the diagonal testes but that thereupon it agrees very well with Hamacreadium oscitans from related hosts at Tortugas.". On this basis, even though the species has been retained by Yamaguti (89, p. 120), P. breviformis is made a synonym of Hamacreadium oscitans Linton, 1910.

Podocotyle atomon var. dispar is considered a valid species and must be retained in the literature under the laws of nomenclature. Its validity in the present paper is based on its acceptance by Park (65, p. 417) and the definite variation from P. atomon in the form of "an asymmetrical group of follicles in front of the ventral sucker on the right side. This had not the linear arrangement of the other follicles, but was more dendritic, and from it a separate duct passed down to join the longitudinal duct. This asymmetrical group was never observed on the left side.", as noted by Nicoll (50, p. 452). Since Nicoll collected a number of specimens of this variety and compared them with specimens of P. atomon in his collection and concluded that the variety existed and named it in the literature, it must be retained until it is proven to be a synonym. Yamaguti (89, p. 119-122) in his monograph on the

trematodes, has not included this variety in his section on the genus.

Nigrelli (55, p. 156) described Podocotyle atzi in a paper given before the American Society of Zoologists in 1939. The following year he published the description (56, p. 265-267) with appropriate illustrations. Although the original description was only mentioned in a published abstract of the paper given before the Society, and since no precedent is known for the disposition in such a case, I am assuming that the 1939 paper and abstract do not serve as a valid description. Therefore the correct designation is P. atzi Nigrelli, 1940.

Due to a misspelling of the generic name of the host fish Enophrys bison (Girard), 1854, for which the new species enophrysi was named, the name given to the new species and the generic name of the host were given incorrectly as Endophrys and endophrysi in Park's review of the genus Podocotyle (65, p. 406-407). The correct spelling of the new species name was given as enophrysi in Park's key to the species of Podocotyle (65, p. 416-417), and as this is also correct for the spelling of the host genus (4, p. 258), it should be placed in the literature with this correct spelling.

In his 1954 paper on the digenetic trematodes from fishes of New Zealand, Manter (40, p. 518) stated that "Another closely related species is P. gibbsoniae Johnson, 1949\* from Gibbsonia elegans in California.". In the footnote indicated by the

asterisk, he said "The original spelling of this name was 'gibbsonia' but the genitive case must have been intended." (40, p. 518). His changing the species name is incorrect, since the correct spelling of the host genus is Gibbonsia Cooper, 1863 (5, p. 103) which can be further verified in the official check list of the U. S. Bureau of Fisheries, where it is listed as genus 1294 Gibbonsia Cooper (21, p. 458) and in the works of Hubbs who described several of the species in the genus (14, p. 353; 15, p. 15). In view of this, the specific name of Podocotyle gibbonsiae is correct and should remain thus in the literature.

Yamaguti, in 1953 (88, p.73) transferred Plagioporus lepomis Dobrovolny, 1939 to Podocotyle, making the new combination Podocotyle lepomis. The new combination and the resulting synonymy is accepted here on the basis of the extent of the vitellaria, which reaches only to the posterior edge of the ventral sucker, as is the case in many Podocotyle, and not into the area anterior to the ventral sucker as it does in Plagioporus. However, the orbiculate shape of the ovary is unusual, as the ovary in Podocotyle is commonly lobate, but smooth in Plagioporus. This would seem to be of somewhat questionable validity in determining this species, however on the basis of other characteristics, specimens from my collection are referred to Podocotyle lepomis. Considerable work needs to be done on a clarification of the relationships and separation of these genera and others which seem to be very similar to them. When one considers the cercarial types and their flame-cell

formulae, for these two genera, it is found that in species where the cercaria has been identified, that they have the microcercous type of cercariae with the flame cell formula  $2 \left[ (2 + 2) + (2 + 2) \right]$  (8, p. 443 and 10, p. 465). Dobrovolny stated that at least 5 species of Plagioporus have cercariae which "definitely belong to the cotylocercous group." (10, p. 463). This cercarial type is also found in Podocotyle atomon (16, p. 12) as well as in several species of Hamacreadium (41, p. 220).

Podocotyle lanceolata Price, 1934, was considered by Park (65, p. 417) in his 1937 paper on the revision of the genus, to possess a coiled seminal vesicle. Examination of the original species description and illustration of the species, in the judgment of the author, indicates that the seminal vesicle is sinuous rather than coiled.

Podocotyle pearsei Manter, 1934, is not considered to be a synonym of P. levenseni Isaitschikov, 1928, as proposed by Park, who stated that "The size of eggs is the only reliable difference between P. levenseni Isaitschikov (1928) and P. pearsei (1934).", and since the slight variation is not considered to be sufficient for separation "the validity of P. pearsei as a different species from P. levenseni can scarcely be established only by a difference in the size of their respective eggs." (65, p. 411). I consider the egg size variation (96 to 105 by 39 to 45 microns in P. pearsei as compared to 80 to 95 by 40 to 58 microns in P. levenseni) to be significant, when added to the variation of the anterior extent of



the vitellaria, for separation of the two species and retention of P. pearsei as a valid species. It is agreed however, that small variations in the anterior extent of the vitellaria should not be considered as a good separation characteristic, unless this variation is consistent through a reasonable series of specimens.

Yamaguti (89, p. 121) does not include Podocotyle musculometra Bravo-Hollis and Manter, 1957, in his species list of the genus, nor does he include it in the index to the genera and species in his monograph of the digenetic trematodes. One can only assume that this was an oversight in the compilation of the species list. Since this is a valid species of the genus, it must be restored to the literature as such.

When Odhner described Podocotyle olssoni, he apparently placed Distomum simplex of Olsson, 1868, in synonymy with his new genus and species, as he notes that (my translation) "Besides the type of Olsson's Distomum simplex from Gadus melanostomus (= G. poutassou) I have seen only two examples of this species, which were found by myself in Lumprenus (sic) maculatus on the Swedish West coast." (59, p. 327). Odhner, in his same publication, placed Distoma simplex of Rudolphi, 1809, in synonymy with P. atomon, which poses an interesting problem since it would appear that both Rudolphi and Olsson used the same species name for two different animals. In view of this, D. simplex of Olsson must become a synonym of P. olssoni and D. simplex, Rudolphi, 1809, remains a synonym of P. atomon. Thus the synonymies given for P. olssoni by Linton

(26, p. 525-526; 30, p. 67) must stand corrected by deletion of D. simplex of Rudolphi and the addition of D. simplex of Olsson as the correct synonym of P. olssoni.

Stossich (76, p. 6) described Distomum pedicellatum in 1887 and then transferred it to Podocotyle in 1898 (78, p. 25). Since the description is very meager and no illustration appears in the 1898 paper, and the 1887 paper has not been available to me, I have determined the validity of this species and placed it in my key through the use of the excellent description and illustration in the 1953 publication of Janiszewska (18, p. 23-26).

In a note at the end of his key to the species of Podocotyle, Park says that "P. pennelli Leiper and Atkinson (1914) is not placed in the key due to incomplete description." (65, p. 417), and includes only the 1914 paper of Leiper and Atkinson (23) in his list of literature cited. This apparently was a case of oversight on the part of Park, since it is clearly stated in the above cited paper of Leiper and Atkinson that this publication is only an annotated list of the parasitic worms collected on the British Antarctic Expedition of 1910, which was presented to the trustees of the British Museum, and that complete descriptions and illustrations of these worms would be published in the complete reports of the expedition. This was accomplished the following year (1915) (24, p. 36). It should be noted that the species name is incorrectly spelled (pennelii) in both the 1953 and 1958 checklists to the species of Podocotyle of Yamaguti (88, p. 74 and 89, p. 121).

The correct spelling of the specific name is pennelli, as given in Leiper and Atkinson in their description of the species (23, p. 224; 24, p. 36).

From the description given and the illustration of the new species, one is immediately aware that the outstanding characteristics of Podocotyle pennelli are not those of this genus but of Plagioporus. According to the description of Leiper and Atkinson (24, p. 36), the vitellaria range "from the level of the genital pore to the posterior extremity."; the ceca "end on a level with the posterior limit of the testes."; there is an "armed cirrus" present; the ovary "may be pear-shaped to very slightly lobate." and the eggs have "a distinct knob-like protrusion of the shell-substance at one pole.". These characters are typical of Plagioporus and for this reason Podocotyle pennelli is transferred to this genus and the new combination becomes Plagioporus pennelli (Leiper and Atkinson, 1914).

Although Miller (44, p. 35 and 37) in his 1941 review of Stafford's report and collection of trematodes, placed Sinistroporus productus of Stafford in synonymy with Podocotyle reflexa, Yamaguti has persisted in placing P. producta in his lists of the valid species of Podocotyle (88, p. 74; 89, p. 121). I feel that the synonymy as established by Miller is valid and therefore P. producta must remain a synonym of P. reflexa and P. producta (Stafford, 1904) Yamaguti, 1953, also becomes a synonym of P. reflexa. Miller also placed S. simplex, in part, of Stafford, in

synonymy with P. reflexa (44, p. 35 and 37).

Podocotyle shawi is considered a valid genus and species and as such should be returned to this, its original name, in the literature. Yamaguti (88, p. 70) transferred this animal to the subgenus Peracreadium Nicoll, 1909, of the genus Allocreadium Looss, 1900. In 1958 (89, p. 103) he again transferred it to another genus, this time to Cainocreadium. After examining specimens of Podocotyle shawi in the Oregon State College helminthological collection and finding that they are identical in all major respects with the original description of McIntosh (43, p. 379-381), I find no reason for transferring this parasite out of its original genus. Further emphasis is placed on the incorrectness of its transfer to Cainocreadium by the fact that the genital pore in P. shawi is on the left, as is characteristic for Podocotyle and not median as is characteristic for Cainocreadium. McIntosh (43, p. 380) said that the cirrus in P. shawi is spined, however he did not show any spines in his large illustration of the new species, nor have I been able to observe spines on the cirrus of any of the specimens examined. Manter (39a, p. 297) stated that the anterior extent of the vitellaria, the long cirrus sac and the spined cirrus "seem sufficient to exclude it from Podocotyle.", however I do not consider these to be necessarily valid objections since an elongate cirrus sac is quite common in Podocotyle; no spines could be observed on the cirrus and although the anterior extent of the vitellaria is not common throughout the genus, it does occur in

a few of the recognised species. In view of this, I feel that this species should remain in its original genus until further work is done.

In spite of the fact that Distoma simplex Rudolphi, 1809, was made a synonym of Sinistroporus simplex by Stafford (75, p. 484-485), and both were made synonyms of Podocotyle atomon by Odhner (59, p. 321) and Miller (44, p. 35), as well as S. simplex (in part) being a synonym of P. reflexa (44, p. 35), and D. simplex of Olsson being a synonym of P. olssoni (59, p. 327), Yamaguti has persisted in retaining P. simplex (Rudolphi, 1809) Stafford, 1904, through both editions of his *Systema Helminthum* (88, p. 74; 89, p. 121). There seems to be no basis for the retention of P. simplex in the literature, except as a synonym as mentioned previously. All the hosts listed for P. simplex have been assigned to their proper places as follows: To P. atomon; Acanthocottus scorpius (44, p. 35; 54, p. 354), Salmo salar (54, p. 369), Sebastes marinus (44, p. 35), Gasterosteus aculeatus (54, p. 356), Scomber scombrus (44, p. 35; 54, p. 364) and Gadus aeglefinus (54, p. 367); to P. reflexa; Salmo salar (54, p. 369), Hemitripterus americanus (44, p. 35); to P. olssoni; Urophycis chuss (30, p. 68).

Park (65, p. 417) has stated without reservation, in his key to the species of Podocotyle, that P. syngnathi Nicoll, 1913, has a coiled seminal vesicle. This is an obvious mistake, if one carefully observed the illustration of the cirrus pouch and its contents as shown in Fig. 2, Plate XI of Nicoll's description and

illustration of the new species (51, p. 238-240). The seminal vesicle must be considered sinuous, if one is to follow the criteria established by Park for species separation.

Yamaguti (89, p. 120-122) has, without explanation, divided the genus Podocotyle into three subgenera; Podocotyle, Neopodocotyle and Podocotyloides. I find no justification for this division which has erected two new subgenera, each for a single species. In view of this, Podocotyle (N.) indica (Dayal, 1950) Yamaguti, 1958 (89, p. 121-122), which was originally described as Neopodocotyle indica Dayal, 1950 (9, p. 5-7), becomes Podocotyle indica (Dayal, 1950) Yamaguti, 1958. Podocotyle (Podocotyloides) petalophallus (Yamaguti, 1934) Yamaguti, 1958 (89, p. 122), described originally as Podocotyloides petalophallus Yamaguti, 1934 (84, p. 295-298) reverts back to Podocotyle petalophallus (Yamaguti, 1934) Park, 1937.

The following are considered valid species of Podocotyle: P. abitionis McFarlane, 1936; P. apodichthysi Park, 1937; P. atherinae sp. inq. Nicoll, 1914; P. atomon (Rudolphi, 1802) Odhner, 1905; P. atzi Nigrelli, 1940; P. ayu Takahashi, 1928; P. blennicottusi Park, 1937; P. caithnessi Manter, 1954; P. californica Park, 1937; P. atomon var. dispar Nicoll, 1909; P. elongata Park, 1937; P. enophrysi Park, 1937; P. epinepheli Yamaguti, 1942; P. fracta (Rudolphi, 1819) Stossich, 1898; P. gibbonsiae Johnson, 1949; P. gracilis Yamaguti, 1952; P. indica (Dayal, 1950) Yamaguti, 1958; P. kofoidi Park, 1937; P. lanceolata Price, 1934; P. lepomis (Dobrovolny, 1939) Yamaguti, 1958; P. lethrini Yamaguti, 1942; P.

levenseni Isaitschikov, 1928; P. mecopera Manter, 1940; P. musculo-  
metra Bravo-Hollis and Manter, 1957; P. mycteropercae Sogandares-  
Bernal, 1959; P. odhneri Isaitschikov, 1928; P. olssoni Odhner,  
1905; P. pacifica Park, 1937; P. pearsei Manter, 1934; P. pedicel-  
lata (Stossich, 1887) Stossich 1898; P. pedunculata Park, 1937; P.  
petalophallus Yamaguti, 1934; P. reflexa (Creplin, 1825) Odhner,  
1905; P. serrani Yamaguti, 1952; P. shawi McIntosh, 1939; P.  
staffordi Miller, 1941; P. syngnathi Nicoll, 1913 and P. tamame  
Yamaguti, 1942.

Podocotyle atomon, P. blennycottusi, P. enophrysi, P. gibbonsiae,  
P. lepomis, P. levenseni, P. pacifica and P. reflexa were found in  
this investigation.

Podocotyle atomon (Rudolphi, 1802) Odhner, 1905 (59, p. 320-326).

See figs. 3 and 4.

Synonyms:

Fasciola atomon Rudolphi, 1802 (67, p. 70)

Distoma atomon Rudolphi, 1809 (68, p. 362-363)

Distoma simplex Rudolphi, 1809 of Olsson 1868 (64, p. 34)

Distoma angulatum Dujardin, 1845 (11, p. 401-402)

Allocreadium atomon (Rudolphi, 1802) Odhner, 1901  
(57, p. 506-513)

Sinistroporus simplex (Stafford, 1904, in part)  
(75, p. 484-485)

Psilostomum redactum Nicoll, 1906 (47, p. 525-526)

Distomum vitellosum Linton of Johnstone, 1907  
(20, p. 282-285)

? Fasciola aeglefini Müller, 1776, in part (46, p. 224)

The following description is based on twenty-one specimens; eleven specimens from six Juan de Fuca liparids Liparis fucensis Gilbert, 1895, two specimens from a Denny's liparid Liparis dennyi Jordan and Starks, 1895, and five specimens from two of Gunther's liparids Liparis cyclopus Gunther, 1861, all taken in Lopez Sound. In addition, two specimens were collected from a Midshipman Porichthys notatus Girard, 1854, from Bellingham Bay and one specimen from a Wilson's rock-fish Sebastodes wilsoni Gilbert, 1915, taken in Friday Harbor, Washington.

External features. Trematodes with elongate, straight sided bodies with short, tapering ends. They measure 2.09-2.84 mm. in length



by 0.70-0.97 mm. in width at the level of the ventral sucker. The terminal oral sucker is slightly ovate and measures 0.17-0.31 mm. in length by 0.14-0.32 mm. in width. The ovate ventral sucker is located in the anterior third of the body and measures 0.22-0.37 mm. in length by 0.25-0.47 mm. in width. The genital pore is situated to the left of the esophagus about midway between it and the side of the body. The excretory pore is postero-terminal. The cuticle is smooth and unarmed.

Digestive system. The oral opening is located in the ventral surface of the oral sucker and communicates directly through that organ, with the digestive tract. This system continues on through the elongate to rounded, muscular pharynx to the esophagus which bifurcates forming the two posteriorly directed ceca. The ceca are located laterally and continue nearly to the posterior end of the body. The pharynx measures 0.11-0.16 mm. in length by 0.09-0.16 mm. in width. The esophagus is equal to or longer than the pharynx.

Genital systems. The ovary is situated in the center of the body with the two testes in tandem behind it. The testes are separated some distance from one another. Short extensions of the vitellaria lie at the edges of this space but do not extend to the midline. The testes measure 0.21-0.30 mm. in length by 0.24-0.45 mm. in width. The clavate to round seminal receptacle is located in the middle of the body to the left of the midline and dorsal to the vitelline reservoir and ovary. Laurer's canal is a posteriorly directed sinuous tube with the pore located laterally from the

posterior portion of the seminal receptacle, in the area of the left cecum. A vas efferens runs anteriorly from each testis and separately go through the posterior wall of the cirrus sac to the seminal vesicle. The seminal vesicle and enclosing cirrus sac extend well beyond the posterior border of the ventral sucker. The vesicle has one large, clavate posterior portion and two smaller ones, one going posteriorly and the other toward the anterior. All the portions are connected by short, sinuous tubes. The ejaculatory duct leads to the common genital pore. The anterior half of the cirrus sac contains the muscular cirrus and associated prostatic cells.

The ovary has three lobes on the posterior side, and measures 0.14-0.25 mm. long by 0.25-0.45 mm. wide. The ovate to rounded vitelline reservoir is located near the midline, dorsal to the ovary and ventral to the seminal receptacle. The vitellaria extend forward from the center to the anterior edge of the ventral sucker. They form lateral bands which continue nearly to the posterior end of the body without interruptions. There are slight extensions of the vitellaria in the area just posterior to the ventral sucker and between the testes. Behind the posterior testis the vitellaria fill the area except for the separation at the midline. The egg-filled uterine loops are contained in an area bounded by the ceca laterally, the ovary posteriorly and the ventral sucker anteriorly. The anterior extension of the uterus passes to the left of the ventral sucker and follows along the

left side of the cirrus sac to the genital pore. A muscular metaterm is present. The eggs are thin-shelled, elongate, three sided and operculate and measure 0.070-0.080 mm. in length by 0.035-0.040 mm. in width.

Excretory system. The membranous, finger-like excretory bladder extends forward to the level of the ovary just in front of the anterior testis and terminates posteriorly at the terminal excretory pore.

In addition to the hosts reported for Podocotyle atomon in this paper, it has been reported from the following hosts. Pleuronectes flesus (59, p. 320), P. linanda Linnaeus (54, p. 360), P. microcephalus Donovan (54, p. 368), P. platessa Linnaeus (54, p. 360), Acanthocottus scorpius Linnaeus (= Cottus scorpius L.) (59, p. 323; 21, p. 386; 44, p. 35), A. bubalis (Euphrasen) (= Cottus bubalis Euphrasen) (59, p. 323; 21, p. 386), A. octodecemspinosus (Mitchill) (30, p. 65), A. aeneus (Mitchill) (30, p. 65), Pollachius virens (Linnaeus) (= Gadus virens L.) (54, p. 358; 21, p. 209), Gadus pollachius Linnaeus (54, p. 358), G. merlangus (54, p. 358), Melanogrammus aeglefinus (Linnaeus) (= Gadus aeglefinus L.) (54, p. 357-367; 21, p. 211), Gadus morrhua Linnaeus (= Gadus callarias L.) (54, p. 367; 21, p. 210), Salmo salar Linnaeus (54, p. 369), Conger conger (Linnaeus) (54, p. 370), Gaidropsarus mustela (Linnaeus) (= Onos mustela L.) (54, p. 359; 21, p. 208), Onos tricirratus (54, p. 359), Spinachia spinachia (Linnaeus) (= Gastrea spinachia L.) (54, p. 357; 21, p. 239), Gasterosteus

aculeatus Linnaeus (54, p. 356), Pholis gunnellus (Linnaeus) (= Centronotus gunnellus L.) (37, p. 81; 54, p. 467), Enchelyopus viviparus (54, p. 356), Gobius ruthensparri (54, p. 355), Neoliparis atlanticus Jordan and Evermann (= Liparis montagui) (54, p. 355; 21, p. 399), Zeugopterus norvegicus (54, p. 361), Anguilla vulgaris (59, p. 323), Acus aequoreus (Linnaeus) (= Nerophis aequoreus L.) (54, p. 362; 21, p. 243), Scomber scombrus Linnaeus (54, p. 364; 44, p. 35), Anarhichas lupus Linnaeus (54, p. 365), Sebastes marinus (Linnaeus) (= Sebastes norvegicus [Ascanius]) (54, p. 366; 21, p. 363; 44, p. 35), Raniceps raninus (59, p. 323), Bothus maximus (54, p. 368), Solea vulgaris (54, p. 368), Leptocottus armatus Girard (42, p. 341), Syngnathus griseo-lineatus Ayres (42, p. 341), Epigeichthys atropurpureus (Kittlitz) (42, p. 341), Gladiunculus bispinosus (Walbaum) (30, p. 65), Hemitripterus americanus (Gmelin) (30, p. 65), Limanda ferruginea (Storer) (30, p. 65), Microgadus tomcod (Walbaum) (30, p. 65), Merulinus carolinus (Linnaeus) (30, p. 65), Pseudopleuronectes americanus (Walbaum) (30, p. 65), Tautoga onitis (Linnaeus) (30, p. 65) and Hexagrammos stelleri Tilesius (42, p. 341).

The specimens of Podocotyle atomon reported in this paper are in all respects comparable to the description given by Odhner (59, p. 323-325) when he used the species as the type for his new genus. In addition to their conformation to the size ranges, my specimens have the same primary morphological characteristics of vitellaria distribution, separation of testes and size and conformity of the

seminal vesicle as described and figured for the type. Although the testes in most of my specimens have irregularly indented edges, while those of the type are figured as smooth, this is not considered to be a variation, but as a possible artifact of preparation technique. This also gives added evidence for my contention that use of the degree of smoothness, ~~or lack of it~~, of the testes is not feasible as a separation characteristic as established by Park (65, p. 416-417). In establishing a host list for P. atomon one must rely quite heavily on the work of Nicoll (48, 50, 54) and Odhner (59), with the reservation in mind that undoubtedly some of these early records listed for this species, have since become synonyms without proper transfer of the hosts. A number of the hosts listed in the early literature have also been placed in synonymy which further complicates the matter. With these points in mind, the host list for P. atomon is presented and with the records of this paper bring the total host records to forty-eight.

Podocotyle blennycottusi Park, 1937 (65, p. 409-411).

See figs. 5 and 6.

The following description is based on twelve specimens; nine of the specimens were collected from four Juan de Fuca liparids Liparis fucensis Gilbert, 1895 and three specimens were from a Denny's liparid Liparis dennyi Jordan and Starks, 1895. All host fish were taken in Lopez Sound, Washington.

External features. Trematodes with rather rectangular bodies which are rounded at the posterior and somewhat tapered at the anterior end from the area of the ventral sucker to the terminal to subterminal oral sucker. The bodies measure from 1.67-2.39 mm. in length and 0.41-0.76 mm. in width. The oral sucker is round to ovate and measures 0.15-0.19 mm. in length by 0.13-0.19 mm. in width at the level of the testes. The ovate ventral sucker is located in the anterior fourth of the body and measures 0.21-0.25 mm. in length by 0.24-0.31 mm. in width. The common genital pore is located about halfway between the esophagus and the lateral side of the body, on the left. The excretory pore is terminal at the posterior end of the body. The cuticle is unarmed and has tiny ridges in it which are apparent only along the sides of the body. Rudimentary spines in the region of the ventral sucker were reported by Park (65, p. 409), but could not be found in any of my specimens.

Digestive system. The oral opening is located in the antero-

ventral surface of the ventral sucker. The digestive tract leads from the oral opening through the oral sucker and muscular pharynx to the esophagus which bifurcates anterior to the ventral sucker, forming the two posteriorly directed, unbranched, lateral ceca. The ceca end blindly near the posterior end of the body. The pharynx measures 0.10-0.11 mm. in length by 0.09-0.11 mm. in width. The esophagus measures 0.085-0.090 mm. in length.

Genital systems. The ovary is located in the middle of the body, to the right of the midline, with the two testes immediately behind it in tandem and touching one another. The testes are rather ovate, being compressed antero-posteriorly and have irregularly indented edges. They measure 0.21-0.27 mm. in length by 0.21-0.35 mm. in width. The seminal receptacle, which is pear-shaped, is located at the midline or slightly to the right, at the level of and dorsal to the ovary. The sinuous Laurer's canal leads toward the posterior, from the anterior end of the seminal receptacle, to the pore which opens in the area of the cecum just in front of the anterior testis. A vas efferens leads forward from each testis and the two pass through the posterior wall of the cirrus sac side by side, and enter the seminal vesicle without joining. The seminal vesicle, which extends some distance posterior to the ventral sucker, is composed of three portions, all of which are in the posterior portion of the cirrus sac. The largest is most posterior while the two smaller portions lie on its ventral surface and are formed by two constricted sinuities. The second

portion is directed toward the posterior and the third portion is directed anteriorly. This latter part continues forward as the ejaculatory duct to the common genital pore. A muscular cirrus and prostatic cells fill the anterior portion of the cirrus sac. The cirrus may or may not be extended.

The ovary which has three posteriorly directed lobes, measures 0.11-0.21 mm. in length by 0.15-0.25 mm. in width. The small ovate vitelline reservoir is located near the midline in the area of the ovary and dorsal to it. The vitellaria extend forward to the center of the ventral sucker, from the area of the anterior testis, as lateral bands with a few follicles extending into the area immediately posterior to the ventral sucker but not to the midline. The vitellaria fill the areas lateral to the testes and extend somewhat between their postero-lateral edges. It forms four, rather loosely arranged bands in the body behind the posterior testis. These bands are somewhat separated by the excretory bladder at the midline and the ceca laterally. The vitellaria extend nearly to the posterior end of the body. The uterine loops, containing eggs, nearly fill the area bounded laterally by the ceca and vitellaria, the ovary posteriorly and the posterior border of the ventral sucker anteriorly. The anterior extension of the uterus is straight and passes dorsal to the ventral sucker to the sinistral genital pore. The eggs are thin-shelled, elongate, three-sided and operculate and measure 0.060-0.075 mm. in length by 0.025-0.040 mm. in width.

Excretory system. The clavate, membranous excretory bladder



is the only portion of the system observed. The diverticula mentioned by Park (65, p. 409) could not be defined in any of my specimens. The bladder terminates anteriorly at the level of the ovary and posteriorly at the terminal excretory pore.

Only Blennicottus globiceps Girard, 1858, the host of the original species, has been reported prior to this time. The original description of the species was from a host taken at Dillon's Beach, California.

The specimens of Podocotyle blennycottusi reported in this paper vary from the original description of Park (65, p. 409-411) only in respect to lengths and widths of the body. These are not considered significant, since he described the new species from only four specimens. The body size ranges for the twelve specimens reported here increase both the upper and lower ranges for the species. In all other respects they come well within the size ranges for structures and organs as reported for the type. The anterior diverticula of the excretory bladder, as reported for the type, were not observed in my specimens. The distribution of the vitellaria, the shape and extent of the excretory bladder (except as noted above), the shape and location to one another of the testes and ovary and the size and conformity of the seminal vesicle are as in the type species. This record increases the host species to three for this species of Podocotyle, which has been recorded only from the Eastern Pacific.

Podocotyle enophrysi Park, 1937 (65, p. 406-407).

See figs. 7 and 8.

The following description is based on four specimens; three of the specimens were collected from two Juan de Fuca liparids Liparis fucensis Gilbert, 1895, taken in Lopez Sound, and one specimen from a Pink salmon Oncorhynchus gorbuscha (Walbaum), 1792, from the waters of Haro Strait off Smallpox Bay, Washington.

External features. Rather elongate trematodes having smooth bodies which taper slightly at the ends, especially at the anterior end from the area of the ventral sucker forward to the terminal oral sucker. Body lengths measured 1.29-1.78 mm. and widths at the level of the ventral sucker from 0.39-0.48 mm. The oral sucker is slightly ovate to round and measures 0.12-0.17 mm. in length by 0.12-0.15 mm. in width. The ovate ventral sucker is located in the anterior one-third of the body and measures 0.19-0.22 mm. in length by 0.25-0.28 mm. in width. The genital pore is sinistral, between the posterior portion of the esophagus and the side of the body. The excretory pore is terminal at the posterior end of the body. The cuticle is smooth and unarmed.

Digestive system. The oral opening is antero-ventral in the oral sucker and communicates directly with the digestive tract which passes through the rounded, muscular pharynx, the esophagus and into the two posteriorly directed ceca which end blindly near the posterior end of the body. The pharynx measures 0.08-0.10 mm.

in length by 0.08-0.10 mm. in width. The short esophagus, which measures 0.05 mm. in length, bifurcates just anterior to the ventral sucker and forms the two unbranched intestinal ceca.

Genital systems. The ovary and testes are located in the posterior half of the body, with the ovary near the center and the two testes in tandem posterior to the ovary. The rounded testes have indented edges and are in contact. They measure 0.166-0.260 mm. in length and 0.186-0.287 mm. in width. The clavate seminal receptacle is located to the left and dorsal to the ovary. The pore of the sinuous Laurer's canal is located to the left of the seminal receptacle, near the cecum. A vas efferens runs anteriorly from each testis to a point near the posterior end of the cirrus sac, where the two join to form a single tube before entering the cirrus sac and seminal vesicle. The seminal vesicle is composed of four portions, which are formed by constrictions at the sinuosities. Three of the portions lie superimposed, in a ventral view, in the posterior part of the cirrus sac, while the fourth portion lies anterior to them and leads directly to the ejaculatory duct. The most posterior portion is the largest with the second and third portions being about one-half as wide and one-half to two-thirds as long respectively. The anterior portion is relatively long and slender, with its anterior part being modified to form the muscular ejaculatory seminal vesicle. The cirrus is muscular and is frequently protruded.

The ovary, which has three posteriorly directed lobes, is

situated in the middle of the body, to the right of the midline, just in front of the anterior testis and measures 0.11-0.13 mm. in length by 0.12-0.20 mm. in width. The ovate to round vitelline reservoir is located to the left of the ovary and dorsal to it. The vitellaria form two lateral bands anterior to the anterior testis, which run forward to the area of the ventral sucker. The left lateral band goes to the level of the center of the ventral sucker, and the right lateral band extends to the anterior edge, or slightly in front of the ventral sucker. The vitellaria fill the area lateral to the testes and have extensions between them, but these do not come together, thus leaving a separation at the midline. Behind the posterior testis the vitellaria form four bands, two lateral and two median, which are separated at the midline by the excretory bladder and laterally by the ceca. The vitellaria extend to the posterior end of the body. The loops of the uterus fill the center of the body between the ceca, the ovary and the posterior edge of the ventral sucker. It is filled with elongate, three-sided, operculate eggs, which measure 0.060-0.076 mm. in length by 0.025-0.040 mm. in width, and it has a straight portion leading forward, to the left and dorsal to the ventral sucker, to the common genital pore.

Excretory system. The membranous excretory bladder extends forward as an elongate tube, from the posterior terminal excretory pore to the level of the ovary just anterior to the edge of the anterior testis. The two diverticula, mentioned by Park (65,

p. 406) as occurring in this species, could not be identified in my specimens.

In addition to the hosts of the specimens described in this paper, the only previous host was Enophrys bison Girard, 1854, collected by Park (65, p. 406-407) at Dillon's Beach, California.

The specimens of Podocotyle enophrysi reported in this paper come well within the range of all measurements given for the species in the original description. In addition, the conformity of the vitellaria, the location of the seminal receptacle, the vitelline reservoir and the size and conformity of the seminal vesicle are as in the type. The main excretory bladder is also as in the type but the anterior diverticula could not be observed in any of my specimens. With the addition of the two new host species reported in this paper the host list has been increased to three for this species of Podocotyle which has been reported only from the Eastern Pacific.

Podocotyle gibbonsiae Johnson, 1949 (19, p. 107-109).

See figs. 9 and 10.

Synonym:

Podocotyle gibbsoniae (Johnson, 1949) Manter, 1954  
(40, p. 518)

The following description is based on eleven specimens; four from one host and two from another of the Brill, Eopsetta jordani (Lockington), 1879, from West Sound, two from a Window-tailed sea-poacher Averuncus emmelane Jordan and Starks, 1895, taken in Lopez Sound, and one each from a Pink salmon, Oncorhynchus gorbuscha (Walbaum), 1792, from Haro Strait, a Black-bellied eel-pout Lycodopsis pacificus (Collett), 1879 from East Sound and a Rock sole Lepidopsetta bilineata (Ayres), 1855 from West Sound, Washington.

External features. Trematodes with elongate, smooth-sided bodies which are rounded at the posterior end and tapering from the area of the ventral sucker to the terminal oral sucker. The bodies measure 2.61-2.91 mm. in length and 0.61-0.64 mm. in width at the level of the testes. The oral sucker is round and measures 0.17-0.23 mm. in diameter. The ventral sucker is located in the anterior fourth of the body and measures 0.26-0.32 mm. in length and 0.32-0.40 mm. in width. The genital pore is located to the left of the esophagus, about midway between it and the lateral side of the body. The excretory pore is located at the posterior extremity of the body. The cuticle is smooth and unarmed.

Digestive system. The oral opening is located in the antero-ventral portion of the oral sucker. The digestive tract leads directly from the oral opening through the oral sucker and the nearly round, muscular pharynx to the esophagus. It then bifurcates, about 0.10 mm. in front of the ventral sucker, to form the two unbranched ceca which run latero-posteriorly nearly to the posterior end of the body. The pharynx measures 0.11-0.15 mm. in width and 0.11-0.16 mm. in length. The esophagus is 0.10 mm. long.

Genital systems. The ovary is located in the center of the body with the two testes posterior to it in tandem. The testes which are separated from one another by vitellaria, are rounded structures having irregularly indented edges. They measure 0.32-0.40 mm. in width and 0.23-0.27 mm. in length. The pear-shaped seminal receptacle is located in the center of the body, either dorsal to the ovary or just anterior and dorsal to it. The pore of the Laurer's canal is located toward the left in the area of the cecum. A vas efferens leads anteriorly from each testis to a point just outside the wall of the cirrus sac, where they join forming a single tube leading through the wall and into the posterior end of the seminal vesicle. This vesicle has a large, clavate posterior portion bisected by a median, sinuous loop and a small, short, posteriorly directed sinuosity which again loops anteriorly and continues to the genital pore. The posterior portion of this anteriorly directed tube forms the ejaculatory seminal vesicle. No muscular cirrus or prostatic cells were

observed in any of the specimens.

The three lobes of the ovary are directed posteriorly and the ovary measures 0.28-0.36 mm. in width and 0.13-0.23 mm. in length. The small, ovate to round vitelline reservoir measures 0.070-0.091 mm. wide by 0.055-0.085 mm. long and is located near the center of the body, ventral to the seminal receptacle and dorsal to the ovary. The vitellaria extend forward to the posterior area of the ventral sucker. They form a lateral band on each side of the body from anterior to posterior, which has extensions into the area between the testes, but separated at the midline by the forward extension of the excretory bladder. In the posterior body the vitellaria form, in addition to the lateral bands, two additional bands which terminate anteriorly at the posterior testis and are separated laterally by the ceca and at the midline by the excretory bladder. The egg-filled uterine loops are enclosed in the area between the ceca laterally and the seminal receptacle and the posterior edge of the ventral sucker. The unlooped anterior portion goes behind the ventral sucker to the common genital pore. The eggs are thin-shelled, elongate and three-sided, having opercula and measuring 0.035-0.040 mm. in width by 0.066-0.076 mm. in length.

Excretory system. The membranous excretory bladder is the only portion of the system observed. It is a simple elongated, finger-like bag which terminates anteriorly just in front of the ovary and posteriorly at the terminal excretory pore.

In addition to the hosts reported in this paper, there are



only the hosts of the original description (19, p. 107). These hosts were Gibbonsia elegans and Caularchus meandricus from Pacific Grove, California.

The specimens of Podocotyle gibbonsiae reported in this paper vary somewhat from the type material, but these variations are considered to be insignificant in view of the fact that the species was erected from only two specimens which probably do not represent the range of sizes found in the species. My specimens had smaller mean measurements in body length (1-2 mm.), size of oral sucker (3 mm. in width) and size of ventral sucker (9 mm. in width and 8 mm. in length). The shape and location, as well as the size ranges of the pharynx, testes, ovary, seminal receptacle, vitelline reservoir, seminal vesicle, cirrus sac and eggs of my specimens are well within the ranges given for the type. The general body shape, the distribution of the vitellaria and the shape and extent of the excretory bladder also are as in the original species description, as is the primary characteristic demonstrated by the exact conformity of the seminal vesicle. Although the posterior extent of the cirrus sac in the type specimen is not beyond the anterior edge of the ventral sucker and while it is to the center or slightly posterior in my specimens, this is not considered to be a species variation. This record increases the host species to seven for this species of Podocotyle which has been recorded only from the Eastern Pacific.

Podocotyle lepomis (Dobrovolny, 1939) Yamaguti, 1958 (89, p. 121). See figs. 11 and 12.

Synonym:

Plagioporus lepomis Dobrovolny, 1939 (10, p. 461-470)

The following description is based on seven specimens; three from three Juan de Fuca liparids Liparis fucensis Gilbert, 1895, of which two were collected in Lopez Sound and the other from Deer Harbor and four specimens from two Denny's liparids Liparis denny Jordan and Starks, 1895, collected in Lopez Sound, Washington.

External features. Trematodes having rather short, stocky bodies which taper slightly from the center toward the rounded ends. The bodies measure 1.09-1.52 mm. in length by 0.50-0.72 mm. in width at the level of the testes. The terminal to sub-terminal oral sucker is slightly elongate and measures 0.13-0.18 mm. in length by 0.16-0.21 mm. in width. The ovate to round ventral sucker is in the anterior third of the body and measures 0.21-0.25 mm. in length by 0.26-0.32 mm. in width. The genital pore is located to the left of the esophagus, about midway between it and the side of the body. The excretory pore is portero-terminal. The cuticle is smooth and unarmed.

Digestive system. The oral opening is located in the mid-ventral area of the oral sucker and communicates directly through that organ with the digestive tract. This system passes through the rounded, muscular pharynx and the esophagus to the ceca. These are formed by a bifurcation of the esophagus just anterior

to the ventral sucker and run postero-laterally nearly to the end of the body, where they end blindly. The pharynx measures 0.10-0.14 mm. in length by 0.11-0.12 mm. in width. The esophagus is about of equal length.

Genital systems. The ovary is located in the center of the body with the two testes in tandem immediately behind it and touching one another. The testes measure 0.11-0.16 mm. in length by 0.13-0.28 mm. in width. The rounded to clavate seminal receptacle is located near the center of the body in the area of the ovary and lies dorsal to that organ and ventral to the vitelline reservoir. Laurer's canal is a sinuous tube leading from the seminal receptacle to the pore located laterally from the receptacle, on the left, in the area of the cecum. A vas efferens runs anteriorly from each testis to the posterior area of the cirrus sac, where the two join to form a single tube which goes through the wall of the cirrus sac to the posterior end of the seminal vesicle. This vesicle, which does not extend posteriorly beyond the center of the ventral sucker, is made up of two rather short, clavate portions one in front of the other, connected by a short sinuous tube. The anterior portion also has a short sinuous tube at the anterior end connecting it to the short ejaculatory duct. This latter has its opening at the common genital pore. A short, muscular cirrus and prostatic cells fill the anterior portion of the cirrus sac.

The ovary measures 0.08-0.12 mm. in length by 0.18-0.28 mm.

in width and is rounded to ovate in shape with only a slight indication of lobing. The small, ovate to round vitelline reservoir is located dorsally to the seminal receptacle and ovary in the center of the body. The vitellaria extend to the posterior area of the ventral sucker, but never forward beyond the center of the sucker. There are extensions from the lateral aggregation of vitellaria, in the area postero-lateral to the ventral sucker and in the area lateral to the testes. Dorsally the vitellaria are separated behind the posterior testis into four bands by the ceca and the excretory bladder, but ventrally the vitellaria extend completely across the posterior body without interruptions. The follicles of the vitellaria are large and discrete. The two uterine loops are confined to the area between the ovary and ventral sucker antero-posteriorly and the ceca and vitellaria laterally. The loops are either partially or completely filled with relatively large, thin-shelled, three-sided, operculate eggs. The first egg in the loop in front of the ovary is ovate with smooth sides and appears to be filled with cellular material. The uterine eggs measure 0.066-0.080 mm. in length by 0.030-0.040 mm. in width.

Excretory system. The membranous, clavate excretory bladder extends forward to the posterior testis and terminates posteriorly at the excretory pore.

In addition to the hosts reported for Podocotyle leporis in this paper, it has been reported from Lepomis megalotis peltastes,

Lepomis gibbosus and Lepomis macrochirus, the hosts discussed in the description of the species (10, p. 467).

I have assigned the specimens from my collection to this species with some reservation in respect to their having come from marine hosts from a strictly marine habitat, while those of the original description were from fresh water hosts. However when they are compared as to specific morphological characteristics, they appear to be the same species. Measurements of suckers, testes and eggs, which are considered to be the most valid characteristics, in my specimens fall well within the range given for the original species. The seminal vesicle has a comparable conformity and size, as does the vitellaria. The small number of uterine loops and eggs also are similar. On this basis these specimens are assigned to P. leponis until further work on and comparison of life cycles can be accomplished.

Podocotyle levenseni Isaitschikov, 1928 (17, p. 37-39).

See figs. 13 and 14.

The following description is based on three specimens; two from a Juan de Fuca liparid Liparis fucensis Gilbert, 1895, and one from a Denny's liparid Liparis dennyi Jordan and Starks, 1895, from Lopez Sound, Washington.

External features. Trematodes with rather short, stout bodies which are rounded at the ends and measure 1.28-1.37 mm. in length and 0.65-0.76 mm. in width at the level of the testes. The ventral sucker is broadly ovate in shape and measures 0.24-0.25 by 0.31-0.33 mm. The subterminal oral sucker is somewhat triangular in shape and measures 0.16 mm. wide by 0.17-0.19 mm. long. The genital pore is located to the left of the esophagus, about midway between it and the left side of the body. The excretory pore is located at the posterior end of the body. The cuticle is unarmed.

Digestive system. The oral opening is located in the center of the oral sucker and leads directly from it through the rounded, muscular pharynx to the short esophagus. The pharynx measures 0.12 by 0.13 mm. The esophagus is 0.10 mm. long and bifurcates just anterior to the ventral sucker, forming the two posteriorly directed ceca. The ceca are unbranched and continue nearly to the posterior end of the body.

Genital systems. The ovary is located in the center of the body with the two testes immediately behind it. The testes, which

are somewhat antero-posteriorly compressed, are elongate ovate in shape with irregular edges and measure 0.15 mm. long by 0.29 mm. wide. They lie in immediate proximity, one in front of the other, with their broad axis directed laterally. Their lateral ends extend outward to the area of the ceca. The clavate seminal receptacle is located in the center of the body, slightly anterior and dorsal to the ovary. A Laurer's canal is present and the pore is located toward the left in the area of the cecum. A vas efferens leads directly from each testis to the posterior end of the seminal vesicle. Here the two vasa efferentia join to form a single tube leading through the wall of the cirrus sac to the seminal vesicle. The cirrus sac is posteriorly directed from the genital pore to the center or posterior edge of the ventral sucker. The seminal vesicle is coiled at the anterior end where the large, clavate, posterior portion constricts to form a tube which runs anteriorly forming the ejaculatory seminal vesicle and the muscular cirrus. Prostatic cells surround the cirrus, filling the anterior third of the cirrus sac.

The three-lobed ovary, which measures 0.14 mm. long by 0.23 mm. wide, is also somewhat antero-posteriorly compressed and like the testes has its axis extended laterally. Although the large vitelline ducts could be readily observed coming to the center of the body from the laterally located vitelline follicles and joining together, no vitelline reservoir could be differentiated. The vitellaria which extend forward to the center of the ventral sucker,

form a lateral band along each side of the body which has slight extensions toward the midline at the levels of the uterine loops and the testes. In the body behind the posterior testis, the vitellaria form four bands by the addition of two short bands near the midline behind the testes. The uterine loops fill the area between the ceca laterally and the anterior edge of the ovary and the posterior edge of the ventral sucker, with the final portion leading directly behind the ventral sucker and ventral to the left cecum, to the common genital pore. The eggs are thin-shelled, elongate, triangular-shaped, operculate bodies, measuring 0.033-0.035 mm. wide by 0.069-0.074 mm. long.

Excretory system. Although details could not be clearly defined, the membranous excretory bladder appears to be an elongate, narrow structure terminating anteriorly at the level of the posterior testis and posteriorly at the terminal excretory pore.

In addition to the host fish of these specimens, an additional genus and one additional species of host has been reported. Issaitschikov (17, p. 37-39) found the parasite in Cyclopterus lumpus Linnaeus, from the White Sea, and in Liparis liparis (L.) from the Kara Sea. Yamaguti (89, p. 121) also listed Pleuronectes platessa from the White Sea as a host of this parasite. Exhaustive search of the literature fails however to provide a record of this host and so it is looked upon as a dubious entry. It should also be noted that in this same citation, Liparis liparis is listed, in error, as having been taken from the White Sea, in contrast to the



original records of Isaitschikov as listed above.

My specimens of Podocotyle levenseni vary slightly from the type in having a slightly smaller egg (1 micron smaller), a slightly longer cirrus sac (extends to posterior border rather than to center of ventral sucker in one specimen) and a slightly narrower ovary. The overall length and width of my specimens is slightly less than the type, which may account for the smaller proportions noted above. The shape and general conformity of the ovary and testes; extent and size of the ceca; distribution of the vitellaria; sucker ratio (1:2); location (subterminal) of the oral sucker; location of the oral opening; lack of a prepharynx; length of the esophagus; location of the genital pore and location of the uterine loops are the same as in the type specimen. It is of interest to note that Jordan et al. (21, p. 400) list Cyclopterus liparis from the White Sea as a synonym of Liparis liparis.

Since these two genera are apparently very closely related, and since my specimens were also collected from Liparis, it would seem that this parasite is quite host specific. The present record increases the host species to four and are the first hosts from the Eastern Pacific.

Podocotyle pacifica Park, 1937 (65, p. 415-416).

See figs. 15 and 16.

The following description is based on thirty-seven specimens collected from eight species of fish hosts. These hosts and parasite frequencies were: eight specimens from four Juan de Fuca liparids Liparis fucensis Gilbert, 1895, collected in Lopez Sound; one specimen from a Continuous-finned liparid Liparis pulchellus Ayres, 1855, collected in Lopez Sound; one specimen from a Spiny-headed sculpin Dasycottus setiger Bean, 1890, collected in Bellingham Bay; one specimen from a Cabezon Leptocottus armatus Girard, 1854, collected in Friday Harbor; two specimens from a Northern sculpin Icelinus borealis Gilbert, 1895, collected in Lopez Sound; one specimen from a Black-bellied eel-pout Lycodopsis pacificus (Collett), 1879, collected in Bellingham Bay; and twenty-one specimens from five Three-spined sticklebacks Gasterosteus aculeatus Linnaeus, 1758, collected in Argyle Lagoon of North Bay, Washington.

External features. Trematodes with rather elongate bodies which are somewhat tapering and rounded at the ends. The bodies measure from 2.14-3.36 mm. in length and from 0.50-0.87 mm. in width at the level of the testes. The oral sucker is slightly oblong in shape and measures 0.18-0.22 mm. in length by 0.16-0.19 mm. in width, and is terminal. The broadly ovate ventral sucker is located in the anterior one-fourth of the body and

measures 0.22-0.26 mm. in length by 0.26-0.37 mm. in width. The genital pore is located to the left of the posterior portion of the pharynx, about midway between it and the lateral edge of the body. The excretory pore is terminal at the posterior end of the body. The cuticle is unarmed and smooth.

Digestive system. The oral opening is located in the anterior portion of the oral sucker and leads through it to the rounded, muscular pharynx, from where the digestive tract continues posteriorly as a short esophagus which bifurcates just anterior to the ventral sucker, forming two unbranched ceca which terminate near the posterior end of the body. The pharynx measures 0.10-0.13 mm. in length by 0.10-0.11 mm. in width. The esophagus is about the same length as the pharynx.

Genital systems. The ovary is located in the center of the body and the two testes, which are separated, are in tandem posterior to the ovary. The testes have indented margins which gives them a slightly irregular, rounded appearance and they measure 0.23-0.35 mm. long by 0.26-0.41 mm. wide. The clavate seminal receptacle is dorsal to the ovary in the center of the body. Laurer's canal leads to the left and posteriorly from the anterior end of the seminal receptacle to the pore located in the cecal area. A vas efferens leads forward from each testis to the posterior end of the cirrus sac where the two join forming a single tube leading through the sac wall to the seminal vesicle. The seminal vesicle is composed of three clavate portions

interconnected by two smaller tubelike sinuosities. The most posterior portion is the largest, and the portion leading to the ejaculatory duct mainly consists of a muscular, ejaculatory seminal vesicle. The slightly muscular cirrus may be everted through the gonopore.

The ovary has three posteriorly directed lobes and measures 0.16-0.25 mm. in length and 0.23-0.35 mm. in width. The vitelline reservoir, which lies just to the left and anterior to the ovary, is generally one-half to equal in size to one of the lobes of the ovary. The vitellaria which are in large, discrete follicles, extend forward into the area from the posterior edge to the middle of the ventral sucker. The main portion is in the form of lateral bands which have extensions into the area posterior to the ventral sucker and in the area between the testes. These do not however join at the midline or fill these areas. The area posterior to the posterior testis is completely filled with vitelline follicles except for the narrow separation band at the midline. The loops of the uterus fill the area bounded by the ceca laterally, posteriorly by the anterior end of the ovary and anteriorly by the posterior border of the ventral sucker. An unlooped portion leads forward, behind the ventral sucker, along the anterior portion of the cirrus sac to the common gonopore. The eggs are elongate, thin-shelled and generally three-sided. They are operculate and measure 0.060-0.081 mm. in length by 0.030-0.040 mm. in width.

Excretory system. The anterior extent of the membranous excretory bladder could not be positively determined, but it appears to extend into the area of the ovary. The more apparent portion separates the vitellaria at the midline in the body, posterior to the posterior testis. The posterior termination of the system is at the excretory pore.

In addition to the hosts listed in this paper, only Blennicottus globiceps Girard, 1858, collected at Dillon's Beach, California, the host of the type, has been reported in the literature.

Since Park (56, p. 415-416) described the new species Podocotyle pacifica from a single specimen, no range of sizes or variability within the species is available. However in the present collection and discussion in this paper, such a range is presented. The mean size ranges of my specimens compare almost exactly with the various measurements given by Park, except in the case of body length where he gives the size as 3.55 mm. as compared to my range of 2.14-3.33 mm. This is not considered significant since he apparently had a specimen which was at the upper level of the size range. The general morphological characteristics such as type and size of seminal vesicle, distribution of the vitellaria, and testes being separated from one another verify these records and add to the hosts and distribution records for this parasite which has been reported only from the Eastern Pacific.

Podocotyle reflexa (Creplin, 1825) Odhner, 1905 (59, p. 326-327). See figs. 17 and 18.

Synonyms:

Distoma reflexum Creplin, 1825 (6, p. 54)

Sinistroporus productus Stafford, 1904, in part (75, p. 485)

Sinistroporus simplex (Rudolphi, 1809) Stafford, 1904, in part (75, p. 484-485)

Podocotyle producta (Stafford, 1904) Yamaguti, 1953 (88, p. 74)

The following description is based on forty-five specimens; thirty-nine specimens were collected from seven Three-spined sticklebacks Gasterosteus aculeatus Linnaeus, 1758, taken from Argyle Lagoon of North Bay, three specimens from a Cabezon Leptocottus armatus Girard, 1854, collected in Friday Harbor, two specimens from a Sturgeon-like sea-poacher Agonus acipenserinus Tilesius, 1811, taken in West Sound and one specimen from a Gray star-snout Asterotheca alascana (Gilbert), 1895, taken in Lopez Sound, Washington.

External features. Trematodes having elongate slender, smooth-sided bodies which are attenuated, but rounded at the ends. The anterior end tapers from the level of the somewhat pedunculate ventral sucker to the terminal oral sucker. The bodies measure from 1.19-3.34 mm. in length and from 0.24-0.43 mm. in width at the level of the testes. The slightly ovate to rounded oral sucker measures 0.13-0.18 mm. in length by 0.12-0.18 mm. in width.

The ovate ventral sucker which is pedunculate, is situated in the anterior fourth of the body and measures 0.20-0.30 mm. in length by 0.24-0.33 mm. in width. The genital pore is located to the left of the esophagus between it and the lateral side of the body, midway between the pharynx and ventral sucker. The excretory pore is postero-terminal. The cuticle is smooth and unarmed.

Digestive system. The oral opening is located in the ventral side of the oral sucker. The digestive tract leads directly through it to the ovate to round, muscular pharynx then through the esophagus to the two posteriorly directed lateral ceca, which extend nearly to the posterior end of the body. The bifurcation of the esophagus, forming the ceca, is just anterior to the base of the ventral sucker. The pharynx measures 0.06-0.12 mm. in length by 0.06-0.12 mm. in width.

Genital systems. The ovary is located in the center of the body with the two testes posterior to it in tandem. The testes which are widely separated by a horizontal band of vitellaria, are somewhat attenuated, ovate bodies with smooth margins. They measure 0.13-0.32 mm. in length by 0.15-0.25 mm. in width. The clavate seminal receptacle is located in the area of the ovary and dorsal to it. The pore of Laurer's canal is located to the right of the seminal receptacle in the area of the lateral vitellaria and is connected to the receptacle by a coiled and sinuous tube. A vas efferens runs anteriorly from each testis to a point near the posterior end of the cirrus sac where the two vasa

efferentia unite to form a single tube which then passes through the cirrus sac wall to the seminal vesicle. This vesicle, which extends some distance posterior to the ventral sucker, has three portions of different sizes but of similar lengths, interconnected by sinuosities. The third portion is the muscular ejaculatory seminal vesicle which connects directly with the ejaculatory duct. A muscular cirrus is present and is frequently extended through the genital pore.

The ovary measures 0.08-0.18 mm. in length by 0.13-0.22 mm. in width and has three posteriorly directed lobes. The small, ovate to round vitelline reservoir is in the center of the body, generally situated ventral to the seminal receptacle and dorsal to the ovary. The vitellaria in the forebody extends forward from the front of the anterior testis as two lateral bands, which end in the area posterior to the ventral sucker. In the area of the testes the vitellaria are completely divided laterally, but completely fill the area between the testes and the area behind the posterior testis. The uterine loops, which are filled with thin-shelled, three-sided operculate eggs, are located in the mid-body area between the ovary and the posterior end of the cirrus sac, with a straight portion directed anteriorly beside the cirrus sac and ending at the common genital pore. The eggs measure 0.060-0.080 mm. in length by 0.020-0.035 mm. in width.

Excretory system. The anterior extent of the membranous excretory bladder cannot be definitely determined beyond the



posterior testis. The posterior termination is at the terminal excretory pore.

In addition to the hosts reported for Podocotyle reflexa in this paper, it has been reported from the following hosts: Hemitripterus americanus (Gmelin) (75, p. 485; 44, p. 35), Urophycis chuss (Walbaum) (75, p. 485; 44, p. 35), Cyclopterus lumpus Linnaeus (6, p. 54; 59, p. 326), Spinachia spinachia (Linnaeus) (= S. vulgaris Fleming and = Gastrea spinachia L.) (59, p. 327; 54, p. 357; 21, p. 239), Gaidropsarus mustela (Linnaeus) (= Onus mustela L.) (54, p. 359; 21, p. 208), Trigla gurnardus Linnaeus (54, p. 365), Salmo salar Linnaeus (54, p. 369), Syngnathus griseolineatus Ayres and Leptocottus armatus Girard (42, p. 343).

The specimens of Podocotyle reflexa reported in this paper vary from the measurements given for Stafford's specimens by Miller, which were for "one of the larger specimens" (44, p. 37), except for egg size. My specimens however compare in all respects with the description of the general morphological characteristics as given for the type species by Creplin (6, p. 54) and in the description of characters and egg sizes given by Odhner (59, p. 326-327) when he placed the species of Creplin in Podocotyle. Since my specimens do conform to the morphological characteristics established for separation of the species of this genus, I consider that my specimens are valid members of the species and that the generally lower scale of measurements demonstrated by my specimens only gives added emphasis to the necessity of using

characters other than size alone for separation of species. It should be noted that Miller (44, p. 35) lists Urophycis tenuis as a host for P. reflexa in his study of Stafford's collection and report. Study of the paper of Stafford (75, p. 484-485) however, discloses that he reported his specimens from Phycis chuss which is a synonym of Urophycis chuss. Since these two species of Urophycis are considered as distinct species by Jordan et al. (21, p. 213) it would seem that Miller has placed the wrong species of this genus in the host list of P. reflexa. The present record increases the host species to twelve.

Key to the species of Podocotyle

1. Seminal vesicle straight (with no coils,  
sinuosities or constrictions) - - - - - 2
1. Seminal vesicle otherwise - - - - - 7
2. Testes separated, by distance or vitellaria  
or both - - - - - 3
2. Testes touching one another; vitellaria  
extending only to anterior edge of  
ovary - - - - - P. mycteropercae
3. Cirrus adorned with petal-like extensions  
at terminal end - - - - - P. petalophallus
3. Cirrus unadorned - - - - - 4
4. Vitellaria divided lateral to testes - - - - - 5
4. Vitellaria not divided lateral to testes - - - - - 6
5. Ventral sucker pedunculate; esophagus  
equal to pharynx in length - - - - - P. pedunculata
5. Ventral sucker not pedunculate; esophagus  
twice as long as pharynx - - - - - P. kofoidi
6. Cirrus sac extending some distance posterior  
to ventral sucker; uterine loops extending  
anteriorly from area of ovary - - - - - P. serrani
6. Cirrus sac not extending beyond posterior  
edge of ventral sucker; uterine loops  
extend posteriorly to front of anterior  
testis - - - - - P. indica
7. Seminal vesicle with one or more ring-like  
constrictions - - - - - 8
7. Seminal vesicle otherwise - - - - - 14
8. Testes separated, by distance or vitellaria  
or both - - - - - 9
8. Testes touching one another - - - - - 11
9. Vitellaria divided lateral to the testes - - - - - P. elongata
9. Vitellaria not divided lateral to the testes - - - - - 10
10. Ovary in front of anterior testis; eggs  
operculate; testes tandem - - - - - P. atzi
10. Ovary lateral to anterior testis; eggs  
not operculate; testes oblique - - - - - P. tamame

11. Testes tandem; cirrus sac extending posteriorly beyond anterior edge of ventral sucker - - - - - 12
11. Testes oblique; cirrus sac not extending posteriorly beyond anterior edge of ventral sucker - - - - - P. lethrini
12. Ventral sucker pedunculate; ovary smooth - - - - - P. gracilis
12. Ventral sucker not pedunculate; ovary lobed - - - - - 13
13. Cirrus sac extends to posterior edge of ventral sucker; vitellaria separated into four bands behind posterior testis; excretory bladder to center of posterior testis - - - - - P. ayu
13. Cirrus sac does not extend beyond center of ventral sucker; vitellaria separated only at the midline behind posterior testis; excretory bladder to level of ovary - - - - - P. californica
14. Seminal vesicle coiled - - - - - 15
14. Seminal vesicle sinuous - - - - - 21
15. Testes separated, by distance or vitellaria or both - - - - - 16
15. Testes touching one another - - - - - 18
16. Vitellaria divided lateral to testes - - - - - 17
16. Vitellaria not divided lateral to testes - - - - - P. abitionis
17. Cirrus sac short; not extending beyond center of ventral sucker - - - - - P. apodichthysi
17. Cirrus sac long; extending some distance beyond posterior edge of ventral sucker - - - - - P. olssoni
18. Ceca extend nearly to posterior end of body - - - - - 19
18. Ceca extend only to level of posterior testis - - - - - P. odhneri
19. Cirrus sac extending to center of ventral sucker - - - - - 20
19. Cirrus sac extending posterior to ventral sucker - - - - - P. epinepheli
20. Vitellaria extends to anterior edge of ventral sucker; divided at the midline behind the posterior testis - - - - - P. levenseni
20. Vitellaria extends to posterior edge of ventral sucker; not divided at midline but fills body behind posterior testis - - - - - P. pearsei

21. Testes separated, by distance or vitellaria  
or both - - - - - 22
21. Testes touching one another - - - - - 30
22. First sinuous curvature is at anterior end  
of primary portion of seminal vesicle - - - - - 23
22. First sinuous curvature is in center of  
primary portion of seminal vesicle - - - - - P. gibbonsiae
23. Vitellaria extending to area between ovary  
and anterior edge of ventral sucker - - - - - 24
23. A group of isolated vitelline follicles  
on the right, anterior to ventral  
sucker - - - - - P. atomon var. dispar
24. Vitellaria extending from center to  
anterior edge of ventral sucker; not  
divided lateral to testes - - - - - P. atomon
24. Vitellaria not extending beyond center  
of ventral sucker - - - - - 25
25. Vitellaria extending to area from posterior  
edge to middle of ventral sucker; divided  
lateral to testes and at midline posterior  
to the testes - - - - - P. pacifica
25. Vitellaria extending to area posterior to  
ventral sucker - - - - - 26
26. Vitellaria extending to posterior edge of  
ventral sucker; not divided lateral to  
testes or at midline between the testes - - - - P. staffordi
26. Vitellaria extending to area posterior  
to ventral sucker - - - - - 27
27. Vitellaria extending to a point in the  
area between the ovary and the area  
posterior to ventral sucker - - - - - 28
27. Vitellaria extending to level of ovary - - - - - P. mecopera
28. Vitellaria in lateral bands, the length of  
the body; without extensions toward mid-  
line in area of testes - - - - - 29
28. Vitellaria not in lateral bands, the length  
of the body; fills area between testes and  
posterior body; divided lateral to testes - - - - P. reflexa
29. Vitellaria divided at midline in posterior  
body; ova 0.092 X 0.047 mm. - - - - - P. syngnathi
29. Vitellaria not divided at midline in posterior  
body; ova 0.068-0.088 X 0.038-0.057 - - - - - P. caithnessi

30. Vitellaria as lateral bands; extending forward to area of middle of ventral sucker; divided at midline in area posterior to posterior testis - - - - - P. atherinae
30. Vitellaria not as lateral bands; extensions in area of testes and in posterior body - - - - - 31
31. Vitellaria divided at midline in posterior body; cirrus sac extending beyond posterior edge of ventral sucker - - - - - 32
31. Vitellaria not divided at midline in posterior body; cirrus sac not extending beyond posterior edge of ventral sucker - - - - - 33
32. Esophagus twice as long as pharynx - - - - - P. lanceolata
32. Esophagus about same length as pharynx - - - - - 35
33. Ventral sucker pedunculate; pharynx elongate; esophagus very short - - - - - P. pedicellata
33. Ventral sucker not pedunculate; pharynx nearly round; esophagus as long as or longer than pharynx - - - - - 34
34. Metraterm with sphincter muscle in center; excretory bladder extends to area of ventral sucker; eggs 0.05-0.06 X 0.04-0.06 mm. - - - - - P. musculometra
34. Metraterm without sphincter muscle; excretory bladder extends to area of posterior testis; eggs 0.07-0.08 X 0.04-0.06 mm. - - - - - P. lepomis
35. Seminal vesicle of four portions, connected by short sinuous tubes - - - - - P. enophrysi
35. Seminal vesicle of three portions, connected by short sinuous tubes - - - - - P. blennycottusi

Although it is considered a valid species, Podocotyle fracta (Rudolphi, 1819) Stossich, 1898 (78, p. 26) has not been included in my key to the species of Podocotyle, since the description available does not give sufficient information, and there is no illustration, to allow separation characters to be formulated.

It has been presumed that Podocotyle pearsei, P. odhneri, P. levenseni, P. olssoni and P. abitionis have a coiled seminal vesicle. This assumption, which follows Park (65) in part, is necessary to place them in the key.

## HOST LIST

The following is a list of the host fishes in which adult digenetic trematodes belonging to the genera Podocotyle, Fellodistomum and Zoogonus were found. The parasites found in each host are listed. The number of hosts examined is shown by the number in parenthesis. New host records are marked with an asterisk.

Agonus acipenserinus Tilesius, 1811, Sturgeon-like sea-poacher (1)

Podocotyle reflexa (Creplin, 1825) Odhner, 1905\*

Asterotheca alascana (Gilbert), 1895, Gray star-snout (1)

Podocotyle reflexa (Creplin, 1825) Odhner, 1905\*

Averuncus emmelane Jordan and Starks, 1895, Window-tailed sea-poacher (1)

Podocotyle gibbonsiae Johnson, 1949\*

Dasycottus setiger Bean, 1890, Spiny-headed sculpin (1)

Podocotyle pacifica Park, 1937\*

Eopsetta jordani (Lockington), 1879, Brill (2)

Podocotyle gibbonsiae Johnson, 1949\*

Gasterosteus aculeatus Linnaeus, 1758, Three-spined stickleback (12)

Podocotyle pacifica Park, 1937\*

P. reflexa (Creplin, 1825) Odhner, 1905\*

Icelinus borealis Gilbert, 1895, Northern sculpin (1)

Podocotyle pacifica Park, 1937\*

Isopsetta isolepis (Lockington), 1880, Butter sole (1)

Zoogonus dextrocirrus n. sp.\*

Lepidopsetta bilineata (Ayres), 1855, Rock sole (2)

Zoogonus dextrocirrus n. sp.\*

Podocotyle gibbonsiae Johnson, 1949\*

Leptocottus armatus Girard, 1854, Cabezon (2)

Podocotyle pacifica Park, 1937\*

P. reflexa (Creplin, 1825) Odhner, 1905

- Liparis cyclopus Günther, 1861, Günther's liparid (2)  
Podocotyle atomon (Rudolphi, 1802) Odhner, 1905\*
- Liparis dennyi Jordan and Starks, 1895, Denny's liparid (8)  
Podocotyle atomon (Rudolphi, 1802) Odhner, 1905\*  
P. blennycottusi Park, 1937\*  
P. lepomis (Dobrovolny, 1939) Yamaguti, 1958\*  
P. levenseni Isaitschikov, 1928\*  
P. pacifica Park, 1937\*
- Liparis fucensis Gilbert, 1895, Juan de Fuca liparid (20)  
Podocotyle atomon (Rudolphi, 1802) Odhner, 1905\*  
P. blennycottusi Park, 1937\*  
P. enophrysi Park, 1937\*  
P. lepomis (Dobrovolny, 1939) Yamaguti, 1958\*  
P. levenseni Isaitschikov, 1928\*  
P. pacifica Park, 1937\*
- Liparis pulchellus Ayres, 1855, Continuous-finned liparid (1)  
Podocotyle pacifica Park, 1937\*
- Lumpenus anguillaris (Pallas), 1811, Eel-blenny (1)  
Zoogonus dextrocirrus n. sp.\*
- Lycodes brevipes Bean, 1890, Short-finned eel-pout (5)  
Zoogonus dextrocirrus n. sp.\*
- Lycodopsis pacificus (Collett), 1879, Black-bellied eel-pout (8)  
Zoogonus dextrocirrus n. sp.\*  
Podocotyle gibbonsiae Johnson, 1949\*  
P. pacifica Park, 1937\*
- Microstomus pacificus (Lockington), 1879, Dover sole (1)  
Zoogonus dextrocirrus n. sp.\*
- Oncorhynchus gorbuscha (Walbaum), 1792, Pink salmon (2)  
Podocotyle enophrysi Park, 1937\*  
P. gibbonsiae Johnson, 1949\*
- Parophrys vetulus Girard, 1854, Lemon sole (8)  
Fellodistomum phrissovum n. sp.\*  
Zoogonus dextrocirrus n. sp.\*
- Porichthys notatus Girard, 1854, Midshipman (1)  
Podocotyle atomon (Rudolphi, 1802) Odhner, 1905\*
- Sebastodes wilsoni Gilbert, 1915, Wilson's rock-fish (1)  
Podocotyle atomon (Rudolphi, 1802) Odhner, 1905\*



The following fish collected incidentally to the main problem of this thesis, harbored adult digenetic trematodes belonging to genera other than those covered by this thesis.

- Asterotheca infraspinata (Gilbert), 1904, Spiny-cheeked star-snout (2)  
Hexagrammos stelleri Tilesius, 1809, White-spotted greenling (1)  
Hippoglossoides elassodon Jordan and Gilbert, 1880, Flat-headed sole (5)  
Hypsagonus quadricornis (Cuvier and Valenciennes), 1829, Four-horned sea-poacher (1)  
Lepidogobius lepidus (Girard), 1854, Fine-scaled goby (3)  
Ophiodon elongatus Girard, 1854, Lingcod (2)  
Sebastodes melanops Girard, 1856, Black rock-fish (1)  
Sebastodes zacentrus (Gilbert), 1890, Big-eyed rock-fish (1)  
Syngnathus griseo-lineatus Ayres, 1854, Pipe-fish (1)  
Theragra chalcogramma (Pallas), 1811, Whiting (4)

Fish collected from the areas indicated by the code letters in parenthesis following the name, contained no digenetic trematodes. (A-Friday Harbor, B-Lopez Sound, C-East Sound, D-West Sound, E-False Bay, F-Deer Harbor, G-Bellingham Bay, H-San Juan Channel).

- Averruncus emmelane Jordan and Starks, 1895 (G)  
Chitonotus pugetensis (Steindachner), 1877 (F)  
Dasycottus setiger Bean, 1890 (G)  
Gadus macrocephalus Tilesius, 1810 (C)  
Hemilepidotus hemilepidotus (Tilesius), 1810 (A)  
Hydrolagus colliei (Lay and Bennett), 1839 (C)  
Icelinus borealis Gilbert, 1895 (B, F, H)  
Lepidogobius lepidus (Girard), 1854 (D)  
Lepidopsetta bilineata (Ayres), 1855 (B)  
Liparis fucensis Gilbert, 1895 (F)  
Lycodes brevipes Bean, 1890 (C, G)  
Lycodopsis pacificus (Collett), 1879 (C, D)  
Microstomus pacificus (Lockington), 1879 (F)  
Ophiodon elongatus Girard, 1854 (C)  
Porichthys notatus Girard, 1854 (C, G)  
Raja rhina Jordan and Gilbert, 1880 (C)  
Ronquillus jordani (Gilbert), 1888 (C)  
Sebastodes wilsoni Gilbert, 1915 (A)

Sicyogaster meandricus (Girard), 1858 (E)  
Theragra chalcogramma (Pallas), 1811 (B)  
Triglops beanii Gilbert, 1895 (B)

## SUMMARY

Of the one hundred ninety-three fishes examined for intestinal parasites in the course of this research, one hundred fifty belonging to thirty-two different species were found to be infected with digenetic trematodes. From this collection of trematodes, ten species belonging to three different genera are included in this thesis. These species are: Fellodistomum phrissovum n. sp., Zoogonus dextrocirrus n. sp., Podocotyle atomon (Rudolphi, 1802) Odhner, 1905, P. blennycottusi Park, 1937, P. enophrysi Park, 1937, P. gibbonsiae Johnson, 1949, P. lepomis (Dobrovolny, 1939) Yamaguti, 1958, P. levenseni Isaitschikov, 1928, P. pacifica Park, 1937 and P. reflexa (Creplin, 1825) Odhner, 1905.

Zoogonus rubellus (Olsson, 1868) Odhner, 1902, was placed in synonymy with Z. mirus Looss, 1901.

Podocotyle aeglefini (Müller, 1776) and P. simplex (Rudolphi, 1809) Yamaguti, 1953, were placed in synonymy with P. atomon (Rudolphi, 1802) Odhner, 1905.

Podocotyle pennelli Leiper and Atkinson, 1914, became Plagioporus pennelli (Leiper and Atkinson, 1914) n. comb.

Cainocreadium shawi (McIntosh, 1939) Yamaguti, 1958, has been returned to its original genus, and as such is recognised as a valid species of Podocotyle.

Podocotyle pearsei Manter, 1934 and P. musculometra Bravo-Hollis and Manter, 1957 are considered valid species.

Distoma simplex Rudolphi, 1809, of Olsson, 1868, became a synonym of Podocotyle olssoni Odhner, 1905.

Podocotyle producta (Stafford, 1904) Yamaguti, 1953, has again been made a synonym of P. reflexa (Creplin, 1825) Odhner, 1905.

The three subgenera erected by Yamaguti in 1958 for Podocotyle are not recognised, and their assigned species were returned to Podocotyle.

The orthography of Podocotyle enophrysi Park, 1937, P. gibbonsiae Johnson, 1949, and Plagioporus pennelli (Leiper and Atkinson, 1914) has been clarified.

Keys to the species of Fellodistomum and Podocotyle are included.

New host records are listed for all parasites reported.

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## PLATE I

All figures were drawn with the aid of a Leitz Zeichenokular.

Figure 1. Fellodistomum phrissovum n. sp.  
Whole mount; dorsal view.

Figure 2. Zoogonus dextrocirrus n. sp.  
Whole mount; ventral view.

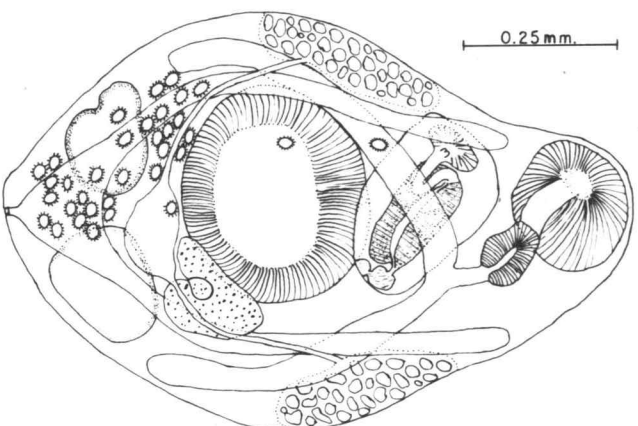


FIG. 1

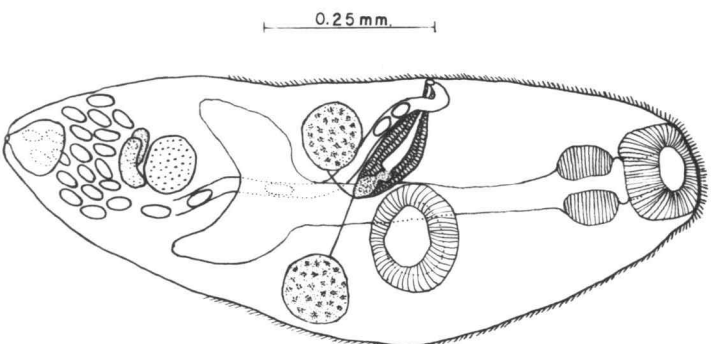


FIG. 2

## PLATE II

All figures were drawn with the aid of a Leitz Zeichenokular.

Figure 3. Podocotyle atomon (Rudolphi, 1802) Odhner, 1905.  
Whole mount; ventral view.

Figure 4. Cirrus sac of P. atomon.

Figure 5. Podocotyle blennycottusi Park 1937.  
Whole mount; dorsal view.

Figure 6. Cirrus sac of P. blennycottusi.

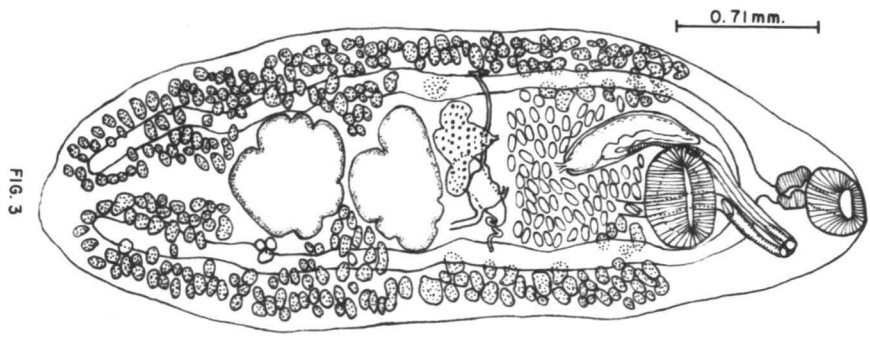


FIG. 3

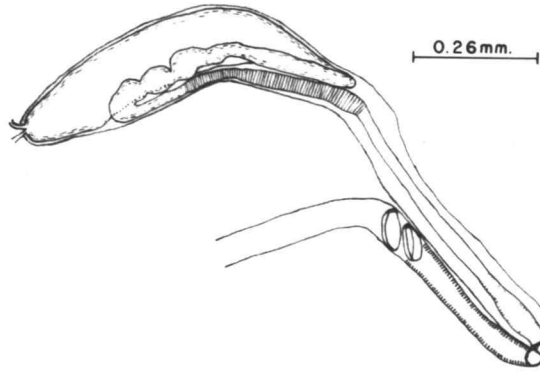


FIG. 4

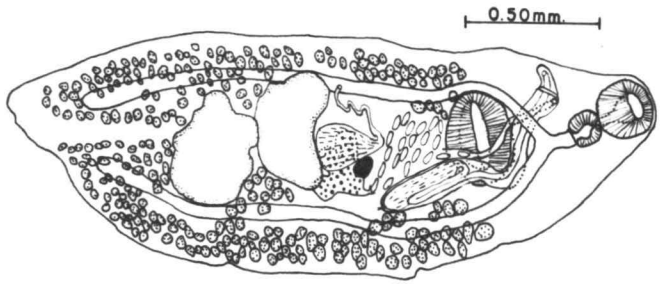


FIG. 5

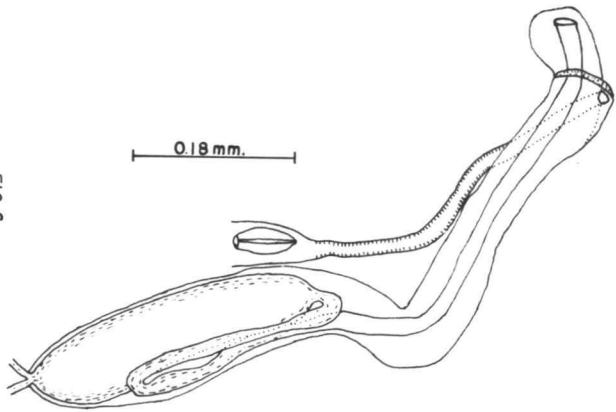


FIG. 6



## PLATE III

All figures were drawn with the aid of a Leitz Zeichenokular.

Figure 7. Podocotyle enophrysi Park, 1937.  
Whole mount; dorsal view.

Figure 8. Cirrus sac of P. enophrysi.

Figure 9. Podocotyle gibbonsia Johnson, 1949.  
Whole mount; ventral view.

Figure 10. Cirrus sac of P. gibbonsia.

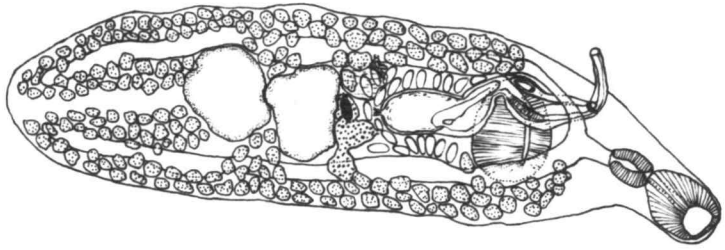


FIG. 7

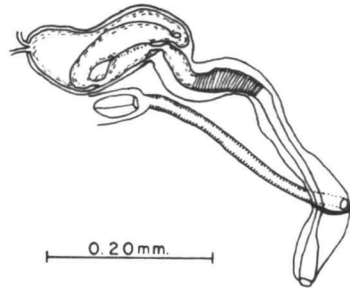


FIG. 8

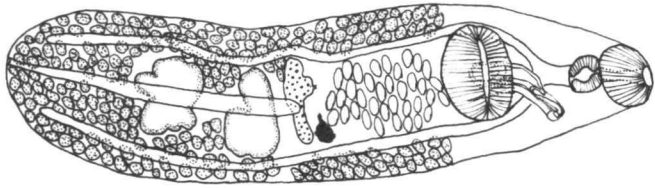


FIG. 9

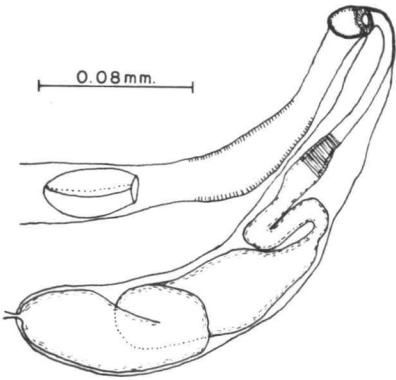


FIG. 10

## PLATE IV

All figures were drawn with the aid of a Leitz Zeichenokular.

Figure 11. Podocotyle leponis (Dobrevolny, 1939)  
Yamaguti, 1958.  
Whole mount; ventral view.

Figure 12. Cirrus sac of P. leponis.

Figure 13. Podocotyle levenseni Isaitschikov, 1928.  
Whole mount; ventral view.

Figure 14. Cirrus sac of P. levenseni.

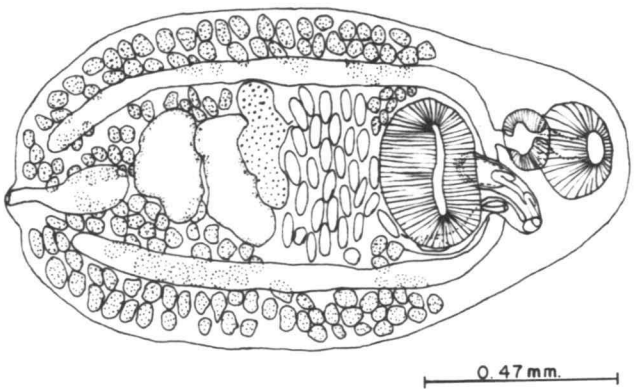


FIG. 11

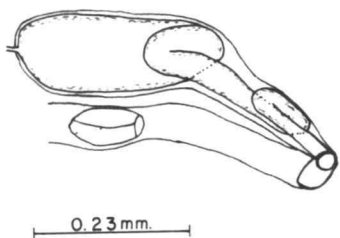


FIG. 12

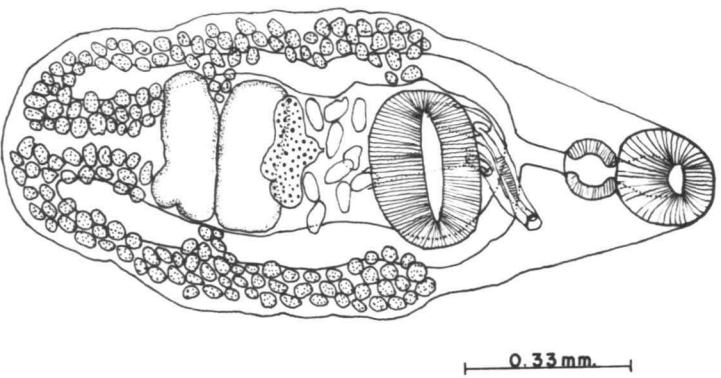


FIG. 13

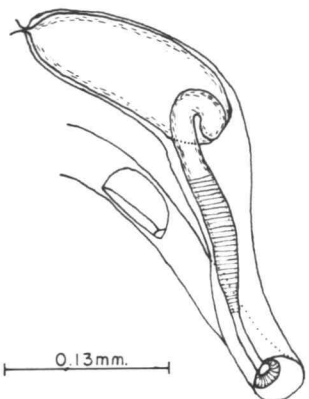


FIG. 14

## PLATE V

All figures were drawn with the aid of a Leitz Zeichenokular.

Figure 15. Podocotyle pacifica Park, 1937.  
Whole mount; ventral view.

Figure 16. Cirrus sac of P. pacifica.

Figure 17. Podocotyle reflexa (Creplin, 1825) Odhner, 1905.  
Whole mount; dorsal view.

Figure 18. Cirrus sac of P. reflexa.

