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THE TREMATODE *PLAGIOPORUS SHAWI* (MCINTOSH, 1939) N. COMB. (OPECOELIDAE: PLAGIOPORINAE) FROM THE NORTH PACIFIC SOCKEYE SALMON, *ONCORHYNCHUS NERKA*

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ABSTRACT

Based on the presence of preacetabular vitellaria, *Podocotyle shawi* McIntosh, 1939 is transferred to *Plagioporus*. The species is redescribed from specimens collected from adult sockeye salmon, *Oncorhynchus nerka*, from the Columbia and Quinault rivers on the Pacific coast of the U.S.A. *P. shawi* is a freshwater species confined to salmonoid fishes in the northwestern part of the U.S.A. The source of the infections in adult sockeye salmon is discussed.

RESUMEN

Con base en la presencia de vitelaria preacetabulares. *Podocolyle shawi es transferido* a *Plagioporus*. Se redescribe la especie sobre ejemplares colectados en el salmón "sockeye" adulto, *Oncorhynchus nerka*, de los ríos Columbia y Quinault, en la costa pacífica de los Estados Unidos. *P. shawi* es una especie dulceacuícola confinada a peces salmonoides en la parte noroccidental de los Estados Unidos. Se discute el origen de las infecciones del salmón "sockeye" adulto.

INTRODUCTION

During a survey of the parasites of the North Pacific anadromous sockeye salmon, *Oncorhynchus nerka*, covering almost the entire range of the species (Margolis, 1963), the trematode formerly known as *Podocotyle shawi* was found a number of times in the intestine of adult *O. nerka* from only two rivers in the northwestern United States. In individual samples of 17-25 fish from the Columbia and Quinault rivers, the incidence of infection varied from 8%-84% and the mean number of trematodes per infected fish varied from 1-9.6 (Table I). The maximum number of specimens in a single fish was 31.

While studying this trematode material some difference were noted from the original description of *P. shawi*, which prompted a re-examination of the holotype, the only available specimen of the type series.

In the present paper the species will be redescribed, its systematic position reassessed, its range of hosts and geographical distribution reviewed, and the source of the adult sockeye salmon infections discussed.

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TABLE I

INCIDENCE AND INTENSITY OF INFECTION OF *PLAGIOPOURS SHAWI* (MCINTOSH, 1939) N. COMB. IN ADULT SOCKEYE SALMON FROM THE COLUMBIA AND QUINAULT RIVERS

	Date collected	No. examined	*Incidence* no.	*Incidence* %	*Intensity* range	*Intensity* mean *
Columbia River						
Celilo Falls	26-VII-1955	25	12	48	1-23	4.7
Astoria, Oregon	28-VI-1956	25	12	48	1-7	3.6
Bonneville Dam	11-VII-1957	25	21	84	1-31	9.6
Astoria, Oregon	22 to 28-VI-1958	23	7	30	1-2	1.4
Astoria, Oregon	24-VI-1959	25	2	8	1-4	2.5
Quinault R., Washington	30-V-1957	17	3	18	1	1

* Based on infected fish.

MATERIAL AND METHODS

The infected fish were all caught in the lower reaches of the Columbia and Quinault rivers during their upstream spawning migration after having spent approximately two years at sea. There were three collection sites on the Columbia River (Table I). Celilo Falls, inundated in 1957 by a hydroelectric dam development, is about 180 miles (290 km) from the mouth of the river; Bonneville Dam is about 140 miles (225 km) from the mouth; and Astoria is near the mouth. The samples obtained at Astoria were from landings from a commercial fishery operating between the mouth of the river and Bonneville Dam. The exact locations of catch of the Astoria samples are unknown.

The trematodes collected in the survey were killed *in situ* by freezing the host fish which were transported to the Nanaimo Biological Station in the frozen state. After retrieval from the thawed fish, the parasites were fixed in 10% commercial formalin (i.e., ca. 4% formaldehyde) and later transferred through water and a graded series of alcohols to 70% ethanol in which they were stored.

In addition to the material collected from frozen salmon, the holotype and four freshly fixed specimens collected from an adult Columbia River sockeye salmon were also examined. The latter were alive when removed from the host and were immediately killed and fixed in Bouin's fluid, two under slight pressure and two by dropping into hot fixative.

Whole specimens were stained with Gower's alumn carmine or Delafield's haematoxylin and mounted in Canada balsam. Serial transverse sections of one specimen were cut at 10μ and stained with Delafield's haematoxylin and eosin. All figures were drawn with the aid of a camera lucida.

DESCRIPTION
(Figures 1-4)

Based on examination of 54 specimens. Measurements are from 13 whole mounts in Canada balsam of mature specimens killed *in situ* by freezing and are in mm except for eggs which are in μ. The specimens measured were selected to include the smallest and largest.

Body length 2.77 - 5.25; maximum width 0.88 - 1.46. (Immature specimens, i.e., without eggs, measured 2.19 - 2.40 by 0.73 - 0.80.)

Oral sucker length 0.26 - 0.47; width 0.26-0.40. Prepharynx length 0.036-0.071. Pharynx length 0.13-0.25; width 0.15-0.24. Esophagus length 0.18-0.53. Caecal bifurcation about mid-way between pharynx and acetabulum. Caeca lateral, terminating near posterior end of body. Acetabulum anterior to mid-body, circular, or transversely or longitudinally oval in outline, 0.37-0.62 in length by 0.42-0.66 in width. Ratio of transverse diameters of suckers 1:1.29-1:1.76.

Genital pore to left of posterior portion of esophagus, about mid-way between mid-line and left body margin. Cirrus sac 1.34-2.98 in length by 0.067-0.20 in maximum diameter near its posterior end; may reach posteriorly as far as ovary and always reaching more than one-half distance between acetabulum and ovary; postacetabular portion usually sinuous, occasionally straight (in 4 of 54 whole mounts studied), remaining portion straight or slightly curved. Cirrus non-spinous, up to 1.53 in length when everted. Seminal vesicle long, occupying approximately posterior two-thirds to three-quarters of cirrus sac when cirrus everted, about 1.0-2.0; divided into two portions, of which anterior is more slender and longer than posterior and possesses a thicker wall (Fig. 2); division between two portions of seminal vesicle usually in postacetabular part of cirrus sac, occasionally slightly anterior to posterior margin of acetabulum; posterior portion may or may not be constricted or folded back on itself at one or two places along its length; anterior portion sometimes sinuous near its proximal end; sperm more densely packed in posterior than anterior portion, resulting in posterior portion staining more intensely; anterior portion surrounded by prostatic cells. No distinct pars prostatica.

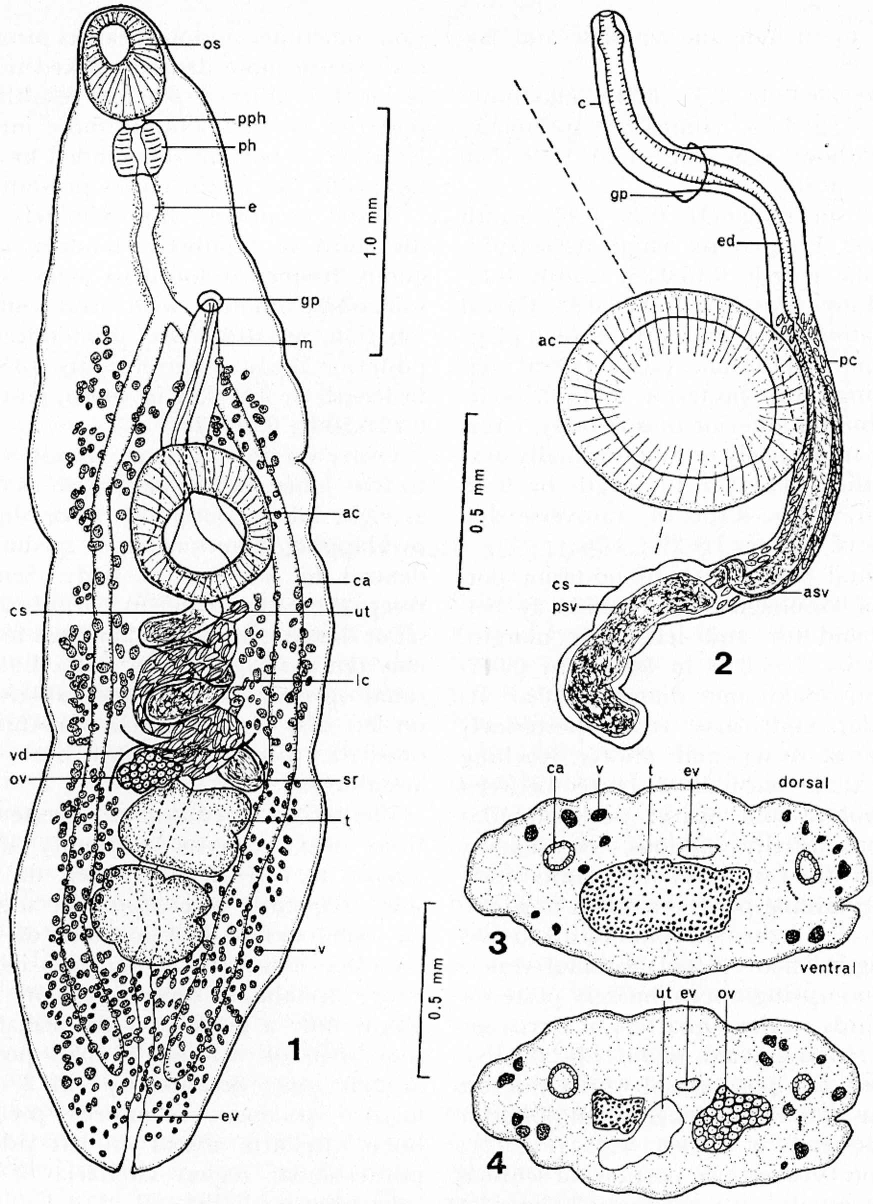
Testes occupying approximately middle third of hindbody, tandem, contiguous, frequently lobed to some extent, sometimes smooth with oval outline; lobation usually more pronounced in posterior testis; anterior testis 0.18-0.39 in length by 0.31-0.71 in width, posterior 0.22-0.50 by 0.22-0.71.

Ovary variable in shape, usually three- to five- lobed, occasionally with as many as eight lobes, contiguous to or slightly overlapping anterior testis, median or dextral to mid-line of body. Seminal receptacle large, ovoid to pyriform, dorsal or dorsosinistral to ovary, base may or may not overlap anterior testis. Laurer's canal opening dorsallly and sublaterally on left side of body, about one-third to one-halft distance between ovary and acetabulum.

Vitellaria circumcaecal, extending from near posterior extremity to, or almost to, caecal bifurcation on each side, frequently interrupted in acetabular zone; extent and location of vitellaria-free zone variable and may include entire acetabular zone, but more commonly only a portion of the acetabular zone with or without a small postacetabular zone; occasionally (in 2 of 49 mature specimens examined) preacetabular vitellaria absent on left side; in posttesticular region vitellaria of both sides meet medially.

Uterus pretesticular. Eggs 62-83 by 36-57.

Excretory pore terminal; excretory vesicle tubular, dorsal to testes, reaching to ovary.



Plagioporus shawi (McIntosh, 1939) n. comb.
Fig. 1. Ventral view, entire specimen killed *in situ* by freezing.
Fig. 2. Cirrus sac, ventral view of flattened specimen in which forebody is bent to the right. Broken lines represent longitudinal axes of fore-and hindbody.
Fig. 3. Transverse section at level of anterior region of anterior testis.
Fig. 4. Transverse section at level of posterior region of ovary.
ac = acetabulum; asv = anterior seminal vesicle; c = cirrus; ca = caecum; cs = cirrus sac; e = esophagus; ed = ejaculatory duct; ev = excretory vesicle; gp = genital pore; lc = Laurer's canal; m = metraterm; os = oral sucker; ov = ovary; pc = prostatic cell; ph = pharynx; pph = prepharynx; psv = posterior seminal vesicle; sr = seminal receptacle; t = testis; ut = uterus; v = vitellaria; vd = vitelline duct.

DISCUSSION

Anatomy

McIntosh (1939) described the cirrus as spinous but there is no evidence of spines in the specimens I examined, including the holotype. This absence of spines on the cirrus is not the result of loss due to possible maceration in the "freeze-killed" specimens, since none were observed in the specimens collected alive and killed and fixed immediately. Pratt and McCauley (1961) also failed to detect spines on the cirrus of *P. shawi*.

The anterior extent of the excretory vesicle was not mentioned by McIntosh (1939). His figure 1A shows only post-testicular portion of the vesicle which, it seems, led Yamaguti (1954, 1958) to believe that it did not reach anterior to the posterior border of the posterior testis. That the excretory vesicle reaches to the ovary is clearly evident in some whole mounts I examined and has been verified by study of serial transverse sections of an entire specimen (Fig. 3, 4).

The testes were described as "ovoid to almost spherical" by McIntosh, but in the specimens examined in the present study they frequently showed some degree of lobation or indentation.

The anterior portion of the seminal vesicle is probably the structure which Park (1937) called an ejaculatory seminal vesicle in several species of *Podocotyle*.

Systematics

Manter (1947) was the first to remark that *P. shawi* should be excluded from *Podocotyle*, but he did not assign it to any other genus. He considered the presence of preacetabular vitellaria, the very long cirrus sac, and the spined cirrus (as described by McIntosh, 1939) to be at variance with the concept of *Podocotyle* and felt that the long cirrus sac suggested affinities with *Peracreadium*.

Yamaguti (1954) transferred *P. shawi* to *Peracreadium*, which he reduced to a subgenus of *Allocreadium*, and later he (Yamaguti, 1958) placed it in *Cainocreadium*, of which *Peracreadium* was considered a synonym. Winter (1959) referred the species to *Peracreadium*, giving the latter full generic status. These generic allocations of *P. shawi* are not acceptable because in *Allocreadium*, *Peracreadium* and *Cainocreadium* the genital pore is median and the excretory vesicle does not extend anterior to the testes, whereas in *P. shawi* the genital pore is distinctly sinistral, lying about mid-way between the mid-line and the left body margin, and the excretory vesicle extends to the ovary. Schell (1970) retained the species in *Cainocreadium*, broadening the limits of this genus to include species with a sinistral genital pore.

In compiling a list of parasites of North Pacific salmonids, Fukui (1958) followed Yamaguti (1954) in listing this parasite as *Allocreadium shawi* (Mc Intosh, 1939) on page 615, but he listed it as *Podocotyle shawi* on page 617. In a later paper (Fukui, 1961, pp. 4, 8, 9) he again listed this species under both names.

In their reviews of *Podocotyle*, neither Skrjabin and Koval (1958) nor Pritchard (1966) mentioned *P. shawi*.

Since the cirrus in *P. shawi* is actually non-spinous, it is evident from its other anatomical features that it belongs to the *Podocotyle - Plagioporus* complex. The characters on which to base a separation of these two genera have been cause for concern for a number of years. When few species were known the distinction seemed clear. The absence of preacetabular vitellaria, the presence of a lobed ovary, and a cirrus sac extending into the postacetabular region characterized *Podocotyle* (see Odhner, 1905), whereas the presence of preacetabular vitellaria, a smooth ovary, and a cirrus sac not extending beyond the acetabulum were features of *Plagioporus serotinus*, the type species of its genus (Stafford, 1904). Dawes (1946, 1947) used these combinations of characters in a key to separate British representatives of *Plagioporus* and *Podocotyle*, although he (Dawes, 1947) recognized that in one British species of *Podocotyle*, *P. syngnathi* Nicoll, 1913, the cirrus sac did not reach beyond the acetabulum. Hoffman (1967) used the same key to separate these genera, as represented in North American freshwater fishes, but he accepted *P. shawi* as a member of *Podocotyle* despite its preacetabular vitellaria.

As more and more species of *Plagioporus* and *Podocotyle* were described, various combinations of the three original distinguishing characters were uncovered. This presumably led Yamaguti (1954, 1958) and Skrjabin and Koval (1958) to resort to using a single character to separate the two genera, namely the presence of preacetabular vitellaria in *Plagioporus* and their absence in *Podocotyle*. As a practical means of assigning species to one or the other genus this proposal generally has been accepted.[1] Thus, because of its preacetabular vitellaria, *Podocotyle shawi* is renamed *Plagioporus shawi* (McIntosh, 1939) n. comb. The termination of the caeca posterior to the testes places it in the subgenus *Plagioporus* (see Manter, 1954).

In transferring *Podocotyle shawi* to *Plagioporus* it becomes the only species of this genus that has both a lobed ovary and a cirrus sac reaching posterior to the acetabulum. A lobed ovary occurs in about one-quarter of the approximately 65 species currently recognized as members of *Plagioporus*, but in only seven species, including *P. shawi*, does the cirrus sac extend behind the acetabulum. Thus the extension of the cirrus sac into the postacetabular region may be considered the character least typical of *Plagioporus*. The six previously known species possessing this character are *P. angusticolle* (Hausmann, 1896) Dobrovolny, 1939; *P. synagris* Yamaguti, 1952; *P. longicirratus* Manter, 1963; *P. longisaccus* Fischthal and Kuntz, 1964; *P. pontica* Koval, 1966; and *P. gerridis* Fischthal and Thomas, 1970. *Plagioporus trematichtys* (Vaz, 1932) Yamaguti, 1958 also has a cirrus sac extending into the postacetabular region, but is median genital pore and apparently papillose oral sucker (Vaz, 1932) do not support Yamaguti's (1958) decision to assign this species to *Plagioporus*. Two other unnamed species assigned to *Plagioporus* by their describers (Shulman and Shulman-Albova, 1953; Ichihara *et al.*, 1965) have the cirrus sac extending into the postacetabular region. However in both species preacetabular vitellaria are lacking; therefore they should be excluded from *Plagioporus*. Because of their smooth ovaries, they apparently belong to the group of species for which Pritchard (1966) created the genus *Allopodocotyle*.

Distinguishing between *Podocotyle* and *Plagioporus* solely on the basis of vitellarian distribution is not as clear-cut as one would like. The extension of the vitellaria into the forebody in some individuals of the type species of *Podocotyle*, *P. atomon* (Rudolphi, 1802), has been reported by Odhner (1905), Nicoll (1909), Savina (1927), Shulman-Albova

[1] Pritchard (1966) recently partitioned the genus *Podocotyle*, distributing its species among five genera, all of which lack preacetabular vitellaria.

(1952), [2] and Polyansky (1955). [3] Nicoll (1909) even created for his specimens a separate variety, *P. atomon* var. *dispar,* based on the presence of a separate preacetabular group of vitellaria on the right side. Also, in *P. lanceolata* Price, 1934 and *P. endophrysi* Park, 1937 a few vitellarian follicles on the right side of the body occur immediately anterior to the acetabulum.

The variability ascribed to *P. atomon* tends to discredit the value of preacetabular vitellaria as the distinguishing feature of *Plagioporus,* nevertheless the remaining approximately 110 species in the *Plagioporus-Podocotyle* complex can be readily segregated into two groups based on presence or absence of this character. Perhaps on further study better grounds will be found for generic segregation within this large group of species but at the moment it seems convenient to accept the consistent presence of preacetabular vitellaria as the identifying character of *Plagioporus.* Mehra's (1966) proposal, as indicated in his key to the genera of Plagioporinae, to differentiate *Podocotyle* from a number of other genera including *Plagioporus* by the presence of a short acetabular peduncle compared to absence of a peduncle requires further examination.

Host and Geographical Distribution

Plagioporus shawi is known only from salmonoid fishes from northwestern U. S. A. (Oregon, Washington and Idaho) and most likely does not occur outside this area. Reported hosts are *Oncorhynchus kisutch, O. nerka, O. nerka kennerlyi* (kokanee, a land-locked form of the sockeye salmon), *Salmo clarki, Salmo gairdneri, Prosopium williamsoni,* and *P. williamsoni cismontanus* (McIntosh, 1939; Shaw, 1947; Griffith, 1953; Fritts, 1959; Pratt and McCauley, 1961; Weatherly and Canaris, 1961).

Source of Infections in Adult Sockeye Salmon

Previous records of *P. shawi* from such strictly freshwater salmonoids as *P. williamsoni* and *O. nerka kennerlyi* dictate that this trematode has a freshwater life cycle, precluding the possibility of fish becoming infected at sea. Like some other freshwater parasites (Polyansky, 1958) *P. shawi* may also be able to complete its life cycle in waters of low salinity such as may be encountered in estuaries.

The trematodes observed in adult sockeye salmon may represent a carryover of infections acquired by the young salmon during their first year of life prior to leaving fresh water for the sea (sockeye salmon have a very strongly expressed homing instinct, returning to the spawning grounds of their birth) or they may represent new infections acquired by the adult fish after re-entry into fresh water.

The following evidence favours the latter alternative. First, *P. shawi* was not found in any of 145 seaward migrant sockeye salmon examined from northwestern USA watersheds, including 73 from the Columbia River system, and secondly, immature and yound adult *P. shawi* were found in the Columbia River adult sockeye salmon, indicating recent infections.

The life cycle of *P. shawi,* although unknown, presumably involves two intermediate hosts, the first being as in almost all other trematodes a mollusc

[2] MacKenzie and Gibson (1970) implied that *P. atomon* may not be as variable a species as believed by Shulman-Albova (1952) and others.

[3] Pritchard (1966) stated that the three specimens figured by Polyansky (1955) do not agree with the diagnosis of *Podocotyle* and she doubted that they were even conspecific. She made no reference to the work of Shulman-Albova (1952) on the variability of *P. atomon.*

and the second also an invertebrate, probably an aquatic arthropod. Infection of the salmonoid host occurs when second intermediate hosts harbouring the metacercariae are eaten. This implies that contrary to generally accepted opinion (Foerster, 1968), some sockeye salmon may feed after entering rivers on their spawning migration, at least in the lower reaches of the rivers. Other parasitological evidence, namely the presence of the freshwater trematode *Crepidostomum farionis* in an adult sockeye salmon taken in a stream, was previously used (Margolis, 1965) to arrive at a similar conclusion.

ACKNOWLEDGMENT

I am grateful to Miss Martha L. Walker (National Animal Parasite Laboratory, U. S. Department of Agriculture, Beltsville, Maryland) for loan of the holotype of *Podocotyle shaw* Mc Intosh, 1939 and to Dr. H. W. Manter from University of Nebraska, for reviewing the manuscript.

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* The book shows the year of publication as 1953, but the U. S. Dept. of Agriculture Index-Catalogue of Medical and Veterinary Zoology, Supplement 6 (1956), indicates that it was issued January 10, 1954.

ADDENDUM

Two recent books by S. Yamaguti contain information relevant to the present paper. These are "Digenetic trematodes of Hawaiian fishes" (1970. Keigaku Publishing Co., Tokyo) and "Synopsis of digenetic trematodes of vertebrates" (1971. Keigaku Publishing Co., Tokyo).

In contrast to his earlier views, Yamaguti (1971) accepted *Peracreadium* as an independent genus and, although a median genital pore was listed as a generic character, he retained ***P. shawi*** in this genus.

Yamaguti (1971) continued to use the presence of vitellaria in the forebody as the character distinguishing *Plagioporus* from *Podocotyle.* However, his definition of the forebody as that region anterior to the *midlevel* of the acetabulum (rather than the region *entirely* anterior to the acetabulum) accounts for his (Yamaguti, 1970) inclusion in *Plagioporus* species in which the vitellaria extend anteriorly only to about the level of the anterior margin of the acetabulum. Of six new species described from Hawaii, well-developed preacetabular vitellaria are distinctly present in only two.