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Parasites of Lake Sturgeon, *Acipenser fulvescens* (Chondrostei: Acipenseridae), with Special Reference to the Coelenterate Parasite, *Polypodium hydriforme*, in Acipenseriform Fishes: an Annotated Bibliography

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PARASITES OF LAKE STURGEON, Acipenser fulvescens (CHONDROSTEI: ACIPENSERIDAE), WITH SPECIAL REFERENCE TO THE COELENTERATE PARASITE, Polypodium hydriforme, IN ACIPENSERIFORM FISHES: AN ANNOTATED BIBLIOGRAPHY

by

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Literature references on lake sturgeon parasites are annotated (Part I, 32 references) and a bibliography on Polypodium hydriforme (Cnidaria) dating from 1871 to 1990 follows (Part II, 67 references). There are two common references on Polypodium infection in A. fulvescens, the abstract of which appears in the section on Polypodium. Only four of the 67 references on Polypodium deal with North American acipenseriforms, the rest are studies on material obtained from Eurasian sturgeon. Sources of reference include Cambridge Life Sciences Compact Disc for 1986-1989, Science Citation Index Compact Disc for 1987-1989, Biological Abstracts, Zoological Record and cross-references from other publications. For some of the references cited in publications, titles were not available and could not be traced in the abstract sources used. Summaries where not original have been acknowledged as such along with their sources.

Key words: bibliographies; parasites.

RÉSUMÉ

Choudhury, A., and T.A. Dick. 1991. Parasites of lake sturgeon, Acipenser fulvescens (Chondrostei: Acipenseridae), with a special reference to the coelenterate parasite, Polypodium hydriforme, in acipenseriform fishes: an annotated bibliography. Can. Tech. Rep. Fish. Aquat. Sci. 1772: v + 15 p.

Les références tirées de la documentation scientifique sur les parasites de l'esturgeon de lac (ou esturgeon jaune) sont annotées (Partie I, 32 références) et une bibliographie sur Polypodium hydriforme (Cnidaria) portant sur la période de 1871 à 1990 suit (Partie II, 67 références). Il existe deux références courantes sur l'infection à Polypodium chez A. fulvescens, dont les résumés apparaissent dans la section sur Polypodium. Seules quatre des 67 références sur Polypodium traitent des acipenseriformes d'Amérique du Nord, le reste portant sur du matériel ayant trait à l'esturgeon eurasien. Les sources de référence comprennent le Cambridge Life Sciences Compact Disc de 1986-1989, le Science Citation Index Compact Disc de 1987-1989, les Biological Abstracts, le Zoological Record ainsi que des références croisées provenant d'autres publications. Dans le cas de certaines des références citées dans les publications, les titres n'étaient pas connus et ne pouvaient pas être retracés dans les sources de résumés utilisées. Les résumés qui n'étaient pas originaux ont été reconnus comme tels, de même que leurs sources.

Mots-clés: bibliographies; parasites.

INTRODUCTION

The lake sturgeon Acipenser fulvescens is one of the largest and evolutionarily ancient freshwater fishes of North America. Once common throughout its wide geographical range, lake sturgeon populations have been declining rapidly since the turn of this century due to overfishing and the loss of prime spawning grounds to pollution and the construction of dams and waterways. The lake sturgeon is fast developing an important commercial value due to its highly regarded flesh, which is at present one of the most expensive fish on the market. Its economic importance in Canada is beginning to be realized through the enhancement of natural stocks and aquaculture initiatives. Although there are some published reports on the parasites of lake sturgeon, as the following bibliography will show, they are largely restricted to reports on a particular parasite species or anecdotal information. The only major survey is unpublished, relatively restricted in terms of geography and reports only five species of parasites. This contrasts with the better studied freshwater sturgeon of Eurasia, and the recent report of twelve species of parasites from lake sturgeon of the Canadian prairies. This paucity of information on lake sturgeon is further illustrated by the lack of any published reports on diseases and information on its immunological and other blood parameters.

Polypodium hydriforme, the only known endoparasitic coelenterate of fishes, is an egg-parasite of acipenseriform fishes. It was first discovered in sterlet eggs in 1871 (Owsjannikow, 1872) from Russia and given its present scientific name by Ussov in 1885. It was not until 1970, nearly a hundred years after its first discovery, that this parasite was found in North American chondrosteans. It has been found in lake sturgeon (Acipenser fulvescens) eggs from the Black River, Michigan and in paddlefish (Polyodon spathula) from the Osage River in Missouri. Since then, the geographical range of this parasite has been extended to include the upper reaches of the Missouri in North Dakota and the Little Yellowstone River in Montana, having been found in paddlefish eggs in those locations. Most aspects of the biology of this parasite are unique. While it has been proposed that transmission could occur by gonads filled with binucleate pre-gametes deposited on the skin of sturgeon larvae, thereby indicating a long latent period, the evidence is entirely circumstantial and the actual mode of infection still remains a mystery. The earliest stages of the parasitic phase of the life cycle are found in young oocytes of sturgeon and the parasite develops with its germ layers inverted; the ectoderm is on the inside while the endoderm is on the outside in direct contact with the yolk from which the parasite draws its nourishment. The development of Polypodium is synchronized with the developmental cycle of oocyte maturation.

Immediately prior to spawning, the parasite stolon with its linearly arranged buds develop tentacles and the germ layers are reversed to occupy the normal position. The infected eggs are two to three times larger than normal eggs and have a pale, mottled or banded appearance. The fully developed stolon within the egg emerges as soon as the infected egg contacts water. In water the stolon breaks up into its component buds, each developing into two individuals with twelve tentacles, by longitudinal cleavage. The polyps have been kept alive till sexual maturity, but fertilisation has not been observed or established. Free living polyps have also been collected from the wild.

The actual extent of the damage caused by Polypodium infections in paddlefish or in lake sturgeon remains to be ascertained. Investigations are underway to determine the extent of this parasite's range in waterways of the Hudson Bay drainage and the prevalence and intensity of infection in lake sturgeon from these waters. The coelenterate parasite Polypodium hydriforme has important implications for lake sturgeon in Canada due to its predilection to infect sturgeon eggs. This annotated bibliography brings together for the first time, the published information on the occurrence of parasites in this fish species and the literature on one of the most enigmatic of chondrostean parasites.

ACKNOWLEDGMENTS

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The authors wish to thank Mr. Mike Papst, Freshwater Institute, DFO, Winnipeg for his interest and help in publishing this manuscript. The authors also thank the estate of the late Drs. George Lubinsky and Irene Lubinsky, for the donation of many of the original papers on Polypodium to the Department of Zoology, University of Manitoba.

BIBLIOGRAPHY

PART I

ACIPENSER FULVESCENS: PARASITES

ANTHONY, D. D. 1974. Helminth parasites of sturgeon (Acipenser fulvescens) from Lake Nipissing, Ontario, Canada. Abstract. Proc. 3rd. Int. Congr. Parasitol. 3: 1642-1643.

The heads and viscera of one hundred lake sturgeon were collected from Lake Nipissing, Ontario, Canada, between June, 1969 and October, 1973, and examined for parasites. Five species of helminths were found: Diclybothrium armatum was found on the gills (range= 1-100 worms with a "median" intensity of 40.5 and 100% prevalence); Skrjabinopsolus manteri from the stomach (mean intensity 0.48, range= 0-8); Crepidostomum lintoni from the intestine (range= 0-200, "median" intensity= 61); Cucullanus clitellarius from the intestine (range= 0-22, mean intensity= 3.4); Spinitectus from the stomach (range= 0-115, mean intensity= 11.3). Two forms of the monogeneans are reported; one fitting the description of Diclybothrium and another type resembling Paradiclybothrium. A variant of the typical Crepidostomum lintoni was also suggested as a different species. All the fish were infected with Diclybothrium and 12% of the sturgeon were infected with all five species of parasite. All species are first records for Lake Nipissing, S. manteri and C. clitellarius are the only records from Canadian sturgeon and Spinitectus is claimed to be the first record of this parasite from sturgeons.

ANTHONY, D. D. 1977. A new species of Spinitectus (Nematoda: Rhabdochonidae) from lake sturgeon (Acipenser fulvescens) from Lake Nipissing, Ontario. Program Abstr., 52nd Annu. Meet. Am. Soc. Parasitol. Abstr. 178: 70-71.

A form of Spinitectus is reported from lake sturgeon that is sufficiently different from the existing species to be considered a new species. Cuticular spination extends over the entire length of the body of females but is present only in the anterior third of males. Gravid females are 8.0-10.2 mm long, males between 5.5 and 6.6mm. The ratio of the muscular oesophagus to the glandular portion (1:3), the ratio of the oesophagus to the entire body length (1:6), the position of the vulva, 10 pairs of pedunculated papillae and the spiralled form of the posterior end of the male, and spination are considered distinctive characters. No name is given to "new species" but it was considered morphologically closest to S. gracilis.

BANGHAM, R. V. 1955. Studies on fish parasites of Lake Huron and Manitoulin Island. Am. Midl. Nat. 53(1): 184-194.

One adult specimen of "rock sturgeon"- Acipenser fulvescens was examined from South Bay. The following parasites were recovered: Crepidostomum lintoni, Cucullanus clitellarius, Diplobothrium hammulatum, Diplostomum sp., Echinorhynchus salmonis. The author cites Banghams (unpublished data) investigations of four rock sturgeons from Upper Lake Pepin. All were infected with C. lintoni, one with Rhabdochona cascadilla and two with a species of Spinitectus. Another "large" sturgeon captured in 1944 was infected with forty C. lintoni and hundreds of D. hammulatum.

BANGHAM, R. V., and G. W. HUNTER. 1939. Studies on fish parasites of Lake Erie. Distribution Studies. Zoologica (N. Y.) 24(4): 334-339.

Two specimens of Acipenser fulvescens were examined from pound nets near Peele Isle. Both were infected with a small number of Crepidostomum lintoni and Cucullanus clitellarius, and one was infected with a species of Allocreadium.

CABLE, R. M. 1952. On the systematic position of the genus Deropristis, of Dihemistephanus sturionis Little, 1930, and of a new digenetic trematode from a sturgeon. Parasitology 42: 85-91.

Cable erects a new genus Pristotrema, for digeneans from two specimens of Scaphirhynchus platorhynchus (shovel-nosed sturgeon), and Pristotrema manteri is described with diagrams as the type and only species. The lake sturgeon "Acipenser rubicundus" is listed as a possible definitive host. This is suggested by Ward's (1938) reference to trematodes which Stafford (1904) reported as Deropristis hispidus. Based on the descriptions of Stafford for this trematode, Cable agrees with Ward that Stafford was dealing with a species not even belonging to the genus Deropristis. Ward possessed a trematode specimen from lake sturgeon similar to Stafford's but never described it. An incomplete search through Wards collection did not yield this specimen. A re-study of Staffords collection by Miller (1941) does not add to the information. Since Staffords brief description agrees with that of Pristotrema by Cable, it is considered possibly as being Cable's P. manteri.

CABLE, R. M. 1955. Taxonomy of some digenetic trematodes from sturgeons. J. Parasitol. 42: 441.

The confusion arising from two generic names erected for the same type of sturgeon trematode is clarified. The genus Skrjabinopsolus was erected in Russia (authority considered uncertain but probably Ivanov, in Ivanov and Murygin, 1937), while Pristotrema was proposed in North

America by Cable (1952). Since Skrjabinopsolus has priority over Pristotrema, Pristotrema manteri becomes Skrjabinopsolus manteri (Cable, 1952).

COOPER, A. R. 1915. Trematodes from marine and fresh-water fishes, including one species of ectoparasitic turbellarian. Trans. R. Soc. Can. 4,3: 181-205.

As far as the author is aware, Acrodactyla petalosa whose original description was unavailable, has been reported from lake sturgeon only. As a footnote on p.195 is a brief description and comments on A. petalosa. Numerous specimens of this species were recovered from lake sturgeon from the St. Lawrence River, near Iroquois, Ontario, and examined, and it confirms Staffords description of the species. The position of the genital opening and the size of the cirrus-sac is considered to be distinctive of the genus, while the arrangement and size of the oral papillae are considered distinctive of the species. A typical specimen measured 2.44 X 0.61mm (maximum width), the oral sucker 0.38 X 0.33 mm, and ventral sucker 0.27mm in diameter.

CHOUDHURY, A., T. A. DICK, H. HOLLOWAY and C. OTTINGER. 1990. The lake sturgeon- Acipenser fulvescens in Canada: preliminary studies on parasitofauna and immunological parameters. Proc. N. Dak. Water Qual. Symp. 1990: 310-321.

Twelve species of parasites have been recovered from lake sturgeon (Acipenser fulvescens) of the waterways of Manitoba and Saskatchewan, seven of which are new host records for this species. A new form of Spinitectus has been found from sturgeon and has been given subspecies designation; S. gracilis acipenseri. The study also reports for the first time a precipitating antibody response against an antigen common to parasites and fungi.

DECHTIAR, A. O. 1972a. New parasite records for Lake Erie fish. Tech. Rep. Great Lakes Fish. Comm. 17. 20p.

Ten specimens of Acipenser fulvescens (lake sturgeon) were taken from the Port Dover area and examined. All fish were infected. Rhabdochona cascadilla was found in seven fish and Diclybothrium armatum in three.

DECHTIAR, A. O. 1972b. Parasites of fish from the Lake of the Woods, Ontario. J. Fish. Res. Board Can. 29: 275-283.

One specimen of lake sturgeon (Acipenser fulvescens) from the Lake of Woods, Ontario, was examined for parasites. The following species were recovered: Diplostomulum sp. from the eye, Diclybothrium armatum from the gills, and Crepidostomum lintoni from the intestine.

DICK, T. A., H. L. HOLLOWAY and A. CHOUDHURY. 1990. Polypodium sp. (Coelenterata) from lake sturgeon (Acipenser fulvescens, Rafinesque) in the prairie region of Canada. J. Parasit. (Accepted).

Please see this reference in Part II for summary.

FAUST, E. C. 1918. Studies on American Stephanophialinae. Trans. Am. Microsc. Soc. 37: 183-198.

Faust describes Acrolichanus petalosa (Lander), based on specimens from a variety of sources, including Cooper's (1915) specimens collected from lake sturgeon. Material from Ambloplites rupestris is also included in the description. Morphometrics include: Body= 1.5-2.5 X 0.32-0.54mm; oral sucker= 0.27-0.45mm; acetabulum= 0.16 X 0.32mm in cross section; eggs= 70-72 X 40-50um. Other morphological features are also described. A key is provided for the Stephanophialinae.

HOFFMAN, G. L. 1970. Parasites of North American Freshwater species. University of California Press, Berkley and Los Angeles. 486p.

The following species are listed from lake sturgeon: Allocreadium sp., Crepidostomum lintoni, Diclybothrium armatum, D. hammulatum, Diplostomulum sp., Skrjabinopsolus manteri, Cucullanus clitellarius, Rhabdochona cascadilla, Echinorhynchus salmonis, Argulus canadensis and A. stizostethi.

HOFFMAN, G. L., E. V. RAIKOVA and W. G. YODER. 1974. Polypodium sp. (Coelenterata) found in North American sturgeon. J. Parasitol. 60: 548-550.

See this reference in Part II for summary.

HOPKINS, S. H. 1934. The papillose Allocreadidae. Ill. Biol. Monogr. 13: 45-124.

A detailed description of the morphology and an account of the taxonomic history of Crepidostomum lintoni is provided. This parasite is reported from lake sturgeon of the Great Lakes and St. Lawrence River. The differences between Acrolichanus and Crepidostomum do not merit the status of separate genera. Acrolichanus petalosa is synonymized with C. lintoni. The inclusion of specimens from Ambloplites rupestris by Faust (1918) is considered "almost certainly erroneous". The descriptions are based on material from Acipenser fulvescens; Landers original specimens from near Detroit Michigan, specimens

collected by Cooper near Ogden Island and Iroquois, Ontario, and Wards collection from Lake St. Clair, Michigan. Sexually mature specimens measure 1.3-3.0 mm, with 1-30 ovoid/ellipsoid eggs measuring 50-72 X 25-40 um, and all morphological features are described. The life cycle is reported as unknown and Landers report of metacercariae from crayfish Cambarus is considered erroneous since Landers figure is thought to be metacercariae of C. cornutum.

LINTON, E. 1898. Notes on the trematode parasites of fishes. Proc. U.S. Natl Mus. 20: 507-548.

Distomum auriculatum from the lake sturgeon is reported for the first time and briefly described, based on the study of actual specimens from lake sturgeon.

LINTON, E. 1901. Parasites of fishes of the Woods Hole region. Bull. U. S. Fish Comm. 19: 405-492.

Echinorhynchus globulosus Rudolphi and Distomum auriculatum are listed as parasites of Acipenser fulvescens. The name Bunodera lintoni is proposed by Pratt for this species.

LOOS, A. 1902.Uber neue und bekannte Trematoden aus Seeschildkroten. Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere 16: 411-899, 32 pl.

A trematode is briefly described under the name Distomum petalosum C.H. Lander, labelled and sent to him by Lander from the intestine of a lake sturgeon. This species is considered to be the same as the one described by Linton as "Distomum auriculatum Wedl" but different from the true D. auriculatum Wedl.

LYSTER, L. L. 1939. Parasites of freshwater fish. I. Internal trematodes of commercial fish in the central St. Lawrence watershed. Can. J. Res. 17: 154-168.

Crepidostomum lintoni is described briefly, having been recovered from Acipenser fulvescens. Morphological features described include: size- 1 mm X 0.3 mm; prominent oral papillae, large oral sucker, pharynx one fifth of oral sucker, genital pore median close behind caecal fork, ventral sucker in anterior half of body and smaller than oral sucker, ovary lobed and pear shaped, lobed testes tandem or oblique and posterior to ovary, vitellaria lateral or dorsal meeting at terminal midline, broad flat muscular cirrus sac reaching posterior margin of acetabulum and uterus reaches upto the testes. Number of fish examined or the locality of collection is not given, although the various species of fish hosts examined in this survey were from Quebec. The trematodes were present in large numbers. A figure is provided.

MacCALLUM, W.G. 1895. On the anatomy of two distome parasites of freshwater fish. Vet. Mag. 2: 401-412.

Two distome digeneans; Bunodera luciopercae (Muller, 1776) Luhe, 1909, and Homalometron armatum are described from the intestines of some freshwater fish in Ontario, including lake sturgeon Acipenser fulvescens.

MEYER, A. 1933. Acanthocephala (concluded), p.333-582 In Bronn's Klassen und Ordnungen des Tierreichs, 4 Abteilung 2, Buch 2, Lief 2.

Tanaorhamphus ambiguus Van Cleave 1921 is described with Anguilla chryspa as the type host. In the host parasite list that follows on page 341, this parasite is listed under Acipenser rubicundus (lake sturgeon).

MOORE, J. P. 1924. The leeches (Hirudinea) of Lake Nipigon. Univ. Toronto Stud. Biol. 25: 17-31. (Ont. Fish. Res. Lab. Publ. 23)

Macrobdella decora is reported from the lake sturgeon Acipenser fulvescens from Ontario for the first time.

PEARSE, A. S. 1924. The parasites of lake fishes. Trans. Wis. Acad. Sci. Arts Lett. 21: 161-194.

Crepidostomum lintoni is briefly described based on collections made from the intestine of Acipenser fulvescens.

PRICE, E. W. 1942. North American monogenetic trematodes. V. The family Hexabothridae, n.n. (Polystomatoidea). Proc. Helminthol. Soc. Wash. 9: 39-56.

A new family of monogenean trematodes is erected - Hexabothridae with Diclybothrinae as a new subfamiliy. Diclybothrium armatum is described with the following morphometrics: body= 2.5-13 mm X 225 um- 1.1 mm; anterior oval bothria= 80-150 um; posterior haptor= 320 um-1 mm X 320 um-800 um; 6 muscular suckers with hook 400-470 um; posterior appendix 225-320 X 120-240 um; haptoral suckers striated, sucker of haptoral appendix 60 um, with 3 pairs of hooks, oral aperture 136-400 um from anterior end of body; pharynx 64-100 X 64-96 um; 2 pairs of eyes present; muscular cirrus = 160-320 X 50-160 um; median genital aperture 240-680 um from anterior end; eggs = 208-224 X 88-140 um.

RISER, N. W. 1948. Amphilina bipunctata, n. sp. A North American cestodarian. J. Parasitol. 6:

479-485.

Specimens of a hitherto undescribed species of cestodarian were recovered from a jar labelled Trematoda with a label that stated that these were collected from the coelom of a "sturgeon" from Dodson, Oregon, in 1923. The cestodarian is named Amphilina bipunctata and described as having the following salient morphological features; length of larger specimens > 50 mm, small apical organ, 350-400 testes between vitellaria and uterine coils, anastomosing vasa efferentia, coiled vas deferens, pyriform bulbus propulsorius 0.97-1.05 mm long; divided lateral vitellaria, small compact and lobed ovary, posteriorly attenuated well developed Mehlis gland, uterus dorsally arising from the Mehlis gland with ascending and descending loops on the same side, uterine pore terminal, seminal receptacle 0.51-0.79 mm long X 0.36-0.150 mm diameter, vaginal pore 0.04-0.07 mm lateral to the male papilla, eggs oval 0.112- 0.150 mm long X 0.059-0.075 mm maximum diameter. It is compared to existing species A. foliacea and A. japonica and found to be morphologically closer to A. japonica.

SKRYABINA, E. S. 1974. Gel'minty osetrovykh ryb (Acipenseridae Bonaparte, 1831). Izd. Nauka, Moskva. 167 p.

This is a monograph on the helminths found in acipenserids. Each species of helminth is discussed separately in the first section of the monograph. In the second section, the species of acipenserids are considered separately. The following parasites are listed under Acipenser fulvescens; Diclybothrium armatum, D. hammulatum, Acrolichanus auriculatus, Allocreadium sp., Skrjabinopsolus manteri, Diplostomum sp. metacercariae, Cucullanus clitellarius, Rhabdochona cascadilla, Spinitectus sp., Metechinorhynchus salmonis, and Tanaorhamphus ambiguus.

STAFFORD, J. 1904. Trematodes from Canadian fishes. Zool. Anz. 27: 481-495.

Parasites recovered from Acipenser fulvescens that were obtained from Montreal fish markets, are reported. Diplobothrium armatum is reported from the gills , 20 X 1 mm in size. Acrodactyla is erected as a new genus and Wed'ls Distomum auriculatum becomes Acrodactyla auriculatum. The trematodes measure 1.92 X 0.54 mm, oral sucker measures 0.325 mm and ventral sucker 0.275 mm. Other morphological characters are described. The size and arrangement of the ventral papillae is considered distinctive for Acrodactyla. Deropristis hispidus is reported from the posterior part of the intestine. The size reported is 11 X 1 mm and the species is described.

TIDD, W. M. 1931. A list of parasitic copepods and their fish hosts from Lake Erie. Ohio J. Sci. 31: 453-454.

Argulus stizostethi is reported from the lake sturgeon (A. fulvescens) in Lake Erie for the first time.

VLADYKOV, V. D. 1985. Record of 61 parasitic lampreys (Ichthyomyzon unicuspis) on a single sturgeon (Acipenser fulvescens) netted in the St. Lawrence River (Quebec). Nat. Can.(Que.) 112: 435-436.

A lake sturgeon (A. fulvescens) from Saint-Pierre-les-Becquets (Quebec), weighing 16 kg, was found to have 61 parasitic silver lampreys (Ichthyomyzon unicuspis).The average length of the lampreys was 104 mm (range: 89-130 mm). The total weight of the 61 individuals was 120 g.

WARD, H. B. 1917. On the structure and classification of North American Parasitic worms. J. Parasitol. 4: 1-12.

Ward considers the forms described by Linton (Distomum auriculatum) as being different from those of Lander (Distomum petalosum Lander in Loos, 1902). Acrolichanus was erected as a new generic name and differentiated from Crepidostomum.

WARD, H. B., and T. B. MAGATH. 1917. Notes on some nematodes from fresh-water fishes. J. Parasitol. 3: 57-64.

Cucullanus clitellarius is erected and described as a new species from the intestine of lake sturgeon (Acipenser rubicundus) in Lake St. Clair. Morphological characters include: males= 10-11 X 0.38 mm; females= 12-17 mm X 0.5 mm; head bent dorsad 60-90 degrees; clitellar like swelling 1.5 mm from anterior tip; three papillae on each oral margin; oral valves= 0.45 X 0.32 mm in males and 0.33 X 0.24 mm in females; eosophagus= 1.45 X 0.12-0.22 mm in males, 1.6 X 0.13-0.32 mm in females; caudal region of males bent in a single turn; ventral sucker 0.51 mm anterior to anus, diameter= 0.1 mm; male spicules= 1.62 X 0.035 mm and "gouge" shaped, accessory piece= 0.06 X 0.015 mm; 2 preanal and 4 postanal papillae; uterus and ovary double; ova= 63 X 46 um; distance of vulva from the anterior end = 5/9 - 2/3 of total body length.

WILSON, C. B. 1916. Copepod parasites of freshwater fishes and their economic relations to mussel glochidia. Bull. U. S. Bur. Fish. 34: 331-374.

Argulus canadensis is reported on the skin and fins of Acipenser fulvescens (from the Lake of the Woods, Ontario) for the first time.

PART II

POLYPODIUM HYDRIFORME

ANDREEV, V. V. and G. S. MARKOV. 1971. Copper, zinc and manganese content in the bodies of parasites of Acipenseridae. Dokl. Akad. Nauk SSSR. 196: 82-84.

Polypodium contained significantly less copper, cobalt, and manganese than in unparasitized sturgeon roe, but 2.1 times more zinc. Amphilina contained 7-10 times more manganese, and 22-54% more zinc, than in blood of caspian sturgeon and sterlet, but less zinc in the Russian and giant sturgeons. Contracaecum and Leptorhynchoides contain 30-40 times more copper than their host intestine, and exceeds Polypodium in the content of the trace elements except zinc. The high concentration of zinc in Polypodium may be an adaptation to the zinc requirements for enzymes and deoxynucleoproteids at the time of redistribution of DNA that takes place in the final stages of the endoparasitic existence of Polypodium.

BEHNING, A. 1913. Freilebendes Polypodium hydriforme Uss. in der Wolga bei Saratow. Zool. Anz. 41: 172- 173.

Free living polyps of Polypodium were found near Saratow, in a side arm of the stream Tschapowka. The single specimen of a free-living polyp of Polypodium was collected from seven metre deep waters along with a few specimens of Hydra. The Polypodium had twelve tentacles.

BEHNING, A. L. 1924. Zur Erforschung der am Flussboden der Wolga lebenden Organismen. Monogr. Biol. Wolga Stat. Saratov. pp ix + 398, 16 pls. 11 charts.

BERRIL, N. J. 1950. Development and medusa bud formation in Hydromedusae. Q. Rev. Biol. 25: 292-316.

Development and budding are described in 4 orders of the hydromedusae. The section on Narcomedusae contains a review of the developmental cycle of Polypodium hydriforme. Lipin's work of 1911 and 1926 is reviewed, along with figures. The parasitic stolon lies coiled within the acipenserid eggs and has an everted structure so that the endodermis is external and in contact with the yolk. Buds form on the stolon and twelve tentacles develop subsequently on each bud. When the sturgeon eggs are laid, the stolons exit the eggs and form free living polyps with 12 to 24 tentacles, that develop saccular gonads. It is suggested that the polyp stage is itself a medusa and a better developed medusa may not exist for this organism.

BYKHOVSKAYA-PAVLOVSKAYA, I. E., A. V. GUSEV, M. N. DUBININA, N. A. IZYUMOVA, T. S. SMIRNOVA, I. L. SKOLOVSKAYA, G. A. SHTEIN, S. S. SHUL'MAN, and V. M. EPSHTEIN. (Ed. E.N. Pavlovskii). 1962. Key to the parasites of freshwater fish of the U.S.S.R. Academy of Sciences of the U.S.S.R. Zoology Institute.(see p.237-238 and 240) Israel Program of Scientific Translation, Jerusalem,1964, Cat. No. 1136.) 919 p.

The work contains a section on coelenterates with a brief summary of the life cycle of Polypodium hydriforme, the only coelenterate parasite reported in the book. The exact taxonomic position is not clarified. A schematic figure of the life cycle is provided.

BOGATU, D. 1961. Un caz de infestatie cu Polypodium hydriforme Ussov, 1885, la cega (Acipenser ruthenus L.) din Dunare. Bul. Inst. Cercet. Proiect. Piscic. 20(1): 54-59.

This is the first case of Polypodium in Romanian waters. A female Acipenser ruthenus, 5 years old and 29.5 cm long, caught in the Danube, close to Piscia, was found to be heavily infected with P. hydriforme. The infected eggs were twice the diameter (4.5 mm) of normal ones and mottled in appearance. On breaking open an infected egg, a 13 mm long stolon with polyps, was released. Control measures suggested for this parasite include intensive fishing in contaminated areas and ensuring that infected eggs collected during commercial processing are not thrown back into the water. (Abstract of the tranlation by Dr. G. Lubinsky, 1976).

DERSHAVIN, A. 1910. Zwei beachtenswarten Funde, Hypania und Polypodium in Wolga-Delta. Zool. Anz. 36, 24: 408.

Cited in Smol'yanov and Raikova (1961); collected free living polyps and found sexually mature polyps from the Volga delta.

DICK, T. A., H. L. HOLLOWAY AND A. CHOUDHURY. 1990. Polypodium sp. (Coelenterata) in lake sturgeon (Acipenser fulvescens Rafinesque) from prairie region of Canada. J. Parasit. (Accepted)

Polypodium sp. is reported in eggs of lake sturgeon, Acipenser fulvescens, from the Nelson River (Hudson Bay drainage) in Canada for the first time. Infections were found only in sturgeon with eggs of 3 mm diameter or more and ranged from 1-179 infected eggs per set of gonads. All specimens of Polypodium recovered were in the stolon stage with a chain of buds, with or without tentacles.

DOGIEL, V. A. 1940. New finding places and new

hosts of Polypodium hydriforme. Zool. Zh. 19: 321-323. [In Russian]

The range of Polypodium hydriforme is considerably extended, and is reported from Acipenser gueldenstaedti and A. stellatus from River Sulak (west of Caspian Sea) and from A. gueldensatdti from River Don.

DOGIEL, V. A. 1954. Investigations into parasito logical problems in connection with reconstruction of fish farm. Vopr. Ikhtiol. 2: 57-68. [In Russian]

Various parasites of commercial importance to fish are discussed including, Diplostomum, Diphyllobothrium, Dactylogyrus, Contracaecum, etc. One paragraph on p. 65 deals with the problems of Polypodium infection.

DROZDOWSKI, A. 1972. Polypodium hydriforme (Coelenterata): a parasite of the Acipenseridae fishes. Prezgl. Zool. 16: 20-25. [In Polish]

The history and morphological features of the stages of the life-cycle of Polypodium are reviewed and described with diagrams. The present state of knowledge on this parasite is covered and the species is found to exhibit many unique characteristics.

DUDICH, N. J. 1967. Systematisches Verzeichnis der Tierwelt der Donau mit einer zusammenfassenden Erlauterung. Limnol. Donau, 3: 41-69.

GUSEV, A. V., M. N. DUBININA, O. N. PUGACHEV, E.V. RAIKOVA, I. A. KHOTENOVEKIJ and R. ERGENS. 1985. A Guide to the parasites of the freshwater fish of the USSR, Vol. 2. Parasitic Metazoa (Part 1). Opredeliteli Faune SSSR No. 143: 418 p. [In Russian]

GUDGER, E. W. 1928. Association between sessile colonioal hydroids and fishes. Ann. Mag. Nat. Hist. 1: 17-48.

Ten cases are cited of relationships between fishes and coelenterates, ranging from symbiosis in South African fishes to parasitism by Polypodium of the eggs of the Volga sterlet. Eight hydroids are listed in association with 10 fishes, with one hydroid parasitizing three different fishes. (From Biological Abstracts)

HOFFMAN, G. L., E. V. RAIKOVA and W. G. YODER. 1974. Polypodium sp. (Coelenterata) found in North American sturgeon. J. Parasitol. 60: 548-550.

Polypodium is reported for the first time in North America, in the eggs of a ripe lake sturgeon Acipenser fulvescens, taken from the Black River near Cheboygan, Michigan, on 27 May, 1970. Abnormal eggs contained the stolon stage of Polypodium with characteristic fingerlike tentacles.

ISKOV, M.P. 1978. Results of studies in fish parasite fauna from the Dneper till the regulation of the flow by the hydroelectric power station dam. p. 34-44. In A.P. Markevich (ed.) Problems of Hydroparasitology, Naukova Dumka, Kiev, [In Russian]

KOWALEVSKY, A.O. 1871. Sitzungsberichte der zoologischen Abtheilung der III. Versammlung russischer Naturforscher in Kiew. Z. wiss. Zool. 22: 292.

Professor Kowalesky presents personal communications from scientists on various topics. Pertinent is the communication by Ph. Owsjannikoff (p. 292) "on a new parasite which he found in the eggs (roe) of the sterlet (Acipenser ruthenus)". The parasite stolon within the egg is described, and the changes in the polyps after eggs contact the water is followed. Visible polyp structures are briefly described; six tentacles per polyp, ectoderm, endoderm and a middle muscle-layer, the mouth opening and the gastral cavity.

LIPIN, A.N. 1908. Brief outline of the morphologic and histologic structure of the freshwater form of Coelenterata, Polypodium hydriforme. Appendix to the protocol of the meeting of the Society of Natural Scientists of Kanzan University, No. 245.

Cited in Raikova, 1961b.

LIPIN, A.N. 1909. Uber den Bau des Susswasserpolypen Polypodium hydriforme Uss. Vorlaufenden Mitteilungen, Zool. Anz. 34: 11-12.

LIPIN, A.N. 1910. To the biology of Polypodium hydriforme Uss. Khazani Tr. Obshch. Estest. 42-(5): 5-23. [In Russian]

LIPIN, A.N. 1911a. On the life cycle of Polypodium hydriforme Uss. Khazani Prot. Obshch. Estest. 42 Beilage (1-6). [In Russian]

LIPIN, A.N. 1911b. Uber ein neues Entwicklungsstadium von Polypodium hydriforme Uss. Zool. Anz. 37: 97-99.

Stages in the development of Polypodium are reported that have hitherto not been reported. Two specimens of these youngest stages were recov-

ered from two infected eggs of one sterlet. The two infected eggs were larger than normal ones. The parasites appeared as irregular masses with one specimen slightly longer than the other. The cells of the ectoderm and endoderm are described. The endodermal cells appear similar to those found in the later stages and no tentacles were formed as yet.

LIPIN, A. N. 1911c. Die Morphologie und Biologie von Polypodium hydriforme Uss. Zool. Jahrb. Abt. Anat. 31: 317-426.

The life cycle is described. The parasitic stage is the coiled stolon within the eggs of the Volga sturgeon, with the germ layers everted so that the endodermis is in contact with the yolk which surrounds the stolon within the egg. The stolon develops buds along its length and the buds become immature polyps and develop tentacles. During spawning, the basal portion of the stolon splits and the entire structure everts so that the germ layers assume their normal position with the ectodermis facing the outside. During this eversion, a mass of yolk gets trapped within the basal part of each polyp which supplies the polyp with nutrition in the free living stage. Each polyp has twelve tentacles, made up of two types, with which it moves around on the river bottom. The tentacles increase in number to twenty-four, after which the polyp divides to give rise to two individuals with twelve tentacles each, and further to give forms with six tentacles. These polyps with six tentacles eventually form polyps with twelve tentacles. Several months after the sturgeon eggs are laid, only polyps with twelve or twenty-four tentacles are seen.

LIPIN, A. N. 1915. The sexually mature form,the phylogeny, and the systematic position of Polypodium hydriforme Ussov 1885. Tr. Obshch. Estest. Khazan. Univ. 47(4): 1-145. [In Russian]

LIPIN, A. N. 1922. On the problem of the number and the position of gonads in Polypodium hydriforme Uss.]. Russ. Hydrobiol. Zeitschr. 1: 41-43, 91-96. [In Russian]

The ovaries of the twelve tentacled polyp of Polypodium hydriforme were originally reported (in 1915, same author) as being eight in number, arranged in four groups of two. Material examined from the sterlet eggs showed that there were actually two gonads with two ovaries in each, giving a total of four ovaries per polyp.

LIPIN, A. N. 1926. Geschlechtliche Form, Phylogenie und systematische Stellung von. Polypodium hydriforme Uss. Zool. Jahrb. Jena Abt. Anat. 47: 541-635.

Free living forms of the coelenterate parasite of sturgeons, Polypodium hydriforme are described with detailed considerations of the different organ systems. These are polyp stages with twelve to twenty-four tentacles. Polyps with immature gonads are described. The gonads are closed saccular structures which contain the ovaries, indicating that the polyp is modified to also function as a medusa. These ovaries are connected to the base of the sac by an oviduct. Detailed comparisons are made between Polypodium and Paraphyllina and Nausithoe. The phylogenetic position of Polypodium within the coelenterates is discussed. It was argued that Polypodium is a reduced form of the Coronatae among the Scyphomedusae.

LYUBARSKAYA, O. D. and I. I. LAVRENT'EVA. 1985. Parasite fauna of the sterlet (Acipenser ruthenus) in the middle Volga River and Kuibyshev Water Reservoir, Russian-SFSR, USSR. Parazitologiya (Leningr.) 19: 320-323. [In Russian]

Twelve species of parasites including Polypodium hydriforme were recovered from an examination of 89 sterlet ranging from 1 to 12 years old, from the Volga branch of the Kyubishev water reservoir. This was over the period 1981-1982, twenty years after the reservoir was constructed.

MAIER, E. M. 1974. Coelentorata, p. 40-41, illustr. In F.D. Mordukhai-Boltovskogo, (ed.) Atlas of the Aral Sea invertebrates. Pishchevaya Promyshlennost, Moscow, 1974, 271 p. [In Russian]

MARKOV, G. S., V. Z. TRUSOV and A. V. RESHETNIKOVA. 1964. (Title unavailable). Vch. Zap. Volgogradsk. Ped. Inst. 16: 111.

Cited in Andreev and Markov (1971), referring to the occurrence of Polypodium in sturgeon during certain times of the year, and rarely during other times.

MOKHAYER, B. 1981. Parasites des poissons du bassin de Sefid-Roude. J. Vet. Fac. Univ. Tehran, 36: 59-75.

The parasites of Acipenser gueldenstaedti from the Sefid-Roude Basin of the Caspian Sea drainage system are listed. Polypodium hydriforme was found in the eggs.

NECHAT, H. A. and B. MOKHAYER. 1974. Parasites de l'appareil genital des esturgeons. Rev. Med. Vet. 125: 355-360.

One hundred and seventyone sturgeons belonging to three species, and caught from seven fishing stations on the Iranian side of the Caspian Sea,

were examined for parasites. The eggs of Acipenser stellatus from the Sefidroude stream was found infected with Polypodium hydriforme. The percentage of parasitized eggs were low. The infected eggs, 5.5 - 7.7 mm in diameter, were two to three times the size of the normal eggs. The parasite within the eggs measured 1.605 X 0.100-0.370 mm. The low intensity of infection, compared to that in Acipenser ruthenus (reported by Raikova, 1958), is explained by the fact that infection can take place only during the time that this sturgeon moves through the rivers during spring and autumn. Hence parasitism by Polypodium is accidental and takes place in those individuals that depart late in spring and arrive early during the fall. The pathological effect of this parasite is manifested in the destruction of infected eggs.

OWSJANNIKOW, PH. 1872. Uber ein neuen Parasiten in den Eiern des Sterlet. Melanges biologiques Tires du Bulletin de L'Academie Imperiale des Sciences de St.-Petersbourg Tom. 8 (1871-1872-). Presented October 1871.

Unusual pale coloured eggs amongst darker normal ones were found in the ripe egg masses in sterlets. One of these abnormal eggs was placed in water and after a few hours a colony of small worm like creatures emerged, each forming a group of four. Each individual was a heart shaped pyramidal structure with six hollow retractible tentacles, of which two were different in structure. These lived for a few days in pure water, but for over two weeks in water full of microorganisms. Sometimes the digestive cavity appeared full and at other times empty. One individual was seen capturing a Cyclops. Individuals were seldom seen living very long in the paired form, and more rare as individuals. This organism is considered an exclusive fresh-water form.

PETRUSHEVSKI, K. G. and S. S. SHULMAN. 1958. Parazitarme zabolevania rib v promislovih vodoemah SSSR. In Osnovnie problemi parasitologhii ryb. Izd. Akademiya Nauk SSSR. Leningrad. [In Russian]

RAIKOVA, E. V. 1958a. The life cycle of Polypodium hydriforme Ussov (Coelenterata). Zool. Zh. 37: 345-358.In Russian]

Eggs of 78% of Acipenser ruthenus females, of stages III, IV and V of maturity, were infected with Polypodium in the lower stream of the Kama river. The parasites life cycle is correlated with the developmental cycle of the hosts ovaries. Infection of the eggs takes place in June-July, at stage III of ovarian maturity. The parasite has inversely arranged embryonic layers, and in the eggs of stage IV, the larva becomes a stolon with buds. In the spring, prior to spawning the stolons evaginate, exposing their ectoderm to the outside and this phenomenon may be brought about artificially by pituitary injection. During spawning, stolons emerge from released infected eggs and divide into single polyps which reproduce by means of longitudinal division. Polyps cultured for 130 days had male and female gonad development after 6-7 weeks. Unisexual individuals were found more often than hermaphroditic ones. The infection with Polypodium is not transmitted to succeeding generations of oocytes; after spawning and following development to stage III, the sturgeon eggs are free from Polypodium. As the period of oocyte maturation from the IIIrd. stage to maturity lasts less than a year, the life cycle presumably takes no more than a year to complete. (From the summary following the Russian original)

RAIKOVA, E. V. 1958b. A histochemical investigation of the parasitic larva of Polypodium hydriforme Ussov (Coelenterata). Dokl. Acad. Nauk SSSR. 121: 549-552. [In Russian] (English version in Doklady Akademii Nauk SSSR, Biological Sciences Section, 121: 604-608].

Early stages of Polypodium hydriforme were found in sturgeon in stage III of maturity. The material was fixed in a variety of fixatives, embedded in paraffin and sectioned at 5, 7 and 10 um thickness. The outer and inner layers of the parasite body is made of epithelial cells 9 um X 5 um, separated by a layer of interstitial cells. Cells of the outer layer are ciliated. DNA content was found to be the same in cells of these three layers, while cystoplasmic RNA is particularly abundant in the interstitial cells. Distal granules of the inner cell layer of the embryo contained acid mucopolysaccharides while the parasitic stolon has such granules in the outer layer, indicating that this layer is the ectoderm. The capsule of parasite origin, is formed of a homogeneous substance containing large, often complex shaped nuclei, and may be involved in the hypothesized extracellular yolk digestion.

RAIKOVA, E. V. 1959a. Polypodium hydriforme. In Parasites of freshwater fish and the biological basis for their control. Bulletin No. 49 of State Sci. Research Institute of Lake and River Fisheries. (Translation No. TT61-31056. U.S. Department of Commerce)

RAIKOVA, E. V. 1959b. On the infection of the Volga sterlet with Polypodium hydriforme Ussov (Coelenterata). Izv. Gos. Nauchno-issled. Inst. Ozern. Rechn. Rybn. Khoz. 47: 207-208. [In Russian]

One hundred and thirty three Volga sturgeon (Acipenser gueldenstaedti) were examined; 53 summer samples (shortly before spawning migration) and

80 winter samples (in the stage III of ovarian development). Only 10 individuals were infected, all of them from the winter sample. Parasitic stage of Polypodium was found in stage III of egg maturity. During the anadromous migration of the sterlet, and after the sterlet ova have already reached stage IV of maturity, the parasitic stolons possess buds. In August, near Saratow, stolons with reversed germ layers, buds, but no tentacles, were recovered from sterlet ova in Stage IV of development. The tentacles are formed in September and the stolon overwinters in this state within stage IV sterlet eggs. In May of the next year, just before spawning, the germ layers attain their normal positions, and finally the Polypodium leaves the sterlet along with healthy eggs, when the eggs are laid. The developmental cycle of Polypodium closely follows the maturation cycle of the sterlet ova. It is supposed that the infection of eggs with Polypodium depends upon the stage of maturity of the eggs with which the sterlet enters the streams, and Polypodium can infect only the immature ova of the winter sterlet. It is probable that Polypodium lives only in freshwater and cannot enter marine environments. (From the German summary following the Russian original)

RAIKOVA, E.V. 1960b. Morphological and cytochemical investigation of parasitic stage of the life cycle of Polypodium hydriforme Ussov (Coelenterata). Tsitologiya 2: 235-251. [In Russian]

Histological sections (5-10 um thick) were prepared from "roe-corn" of 35 sturgeon females infected with Polypodium hydriforme. The differentiation of the larval tissues is described. The larval capsule is formed by the migration of the endodermal cells and the confluence of the cytoplasm and nuclei of these cells. The nuclei become polyploid and phagocytosis of yolk granules by the capsule is observed. With an increase in size of the stolon, the capsule becomes thinner and eventually disappears during evagination of the stolon. Larval endodermal cells are initially identical and each have a rhizoplast and one flagellum. The beginning of endodermal differentiation occurs with the formation of the tentacle anlagen. As the capsule fragments, the endodermal cells in contact with the yolk become tall and narrow, with elongated nuclei at their bases. These cells begin phagocytosis of yolk. The distal ends of the cells accumulate neutral mucopolysaccharides or mucoprotein. Structures comparable with ergastoplasm rings appear in some endodermal cells. Muscle cells differentiate before tentacle formation and are rich in glycogen but poor in RNA. The mesoglea of the tentacles contains proteins, polysaccharides and glycogen and the ectodermal cells contain prominent vacuoles, with basally situated nuclei. The cytoplasm contains glycogen and spheroid granules of acid mucopolysaccharides and proteins at the distal ends. Thread cells develop in clumps at the site of the tentacle anlagen, with large or small capsules without protein or glycogen, but containing cndocils. Cnidoblasts with large capsules predominate in the anlage of the supporting tentacles, while those with small capsules are found in the feeler tentacles. Cnidoblasts contain RNA and glycogen. The cnidial anlage elongates, forming an anlage of a proteinaceous thread cell filament, and acid mucopolysaccharides appear in it during maturation. Glycogen content decreases in all but the stolon tentacle cells, during evagination.

RAIKOVA, E. V. 1961a. The development of male gonads and spermatogenesis in Polypodium hydriforme. Tsitologiya 3: 528-544. [In Russian]

Male gonads can develop in individuals that already may or may not have female gonads. Such observations made by culturing free-living polyps in microaquaria, also showed that individuals in which female gonads develop, resorb these structures after fulfilling their function and become male polyps. Normally four, but occasionally eight, male gonads form by invaginations of the endoderm into the gastral cavity at the aboral end. Cells of the endodermal folds are identical to one another at first, but subsequently they differentiate into spermatogonia which fill the cavity of the male gonads. During the diakinesis and metaphase I stages of the spermatogonia, there are 23 bivalents. At this stage, the gonads produce small cells, possibly feeder cells, that adhere to the developing primary spermatocytes, and are later absorbed by the secondary spermatocytes. The first division forms a spermatocyte and a small reduction body that subsequently dies. The second division does not end in cytokinesis and hence yields one spermatid with two unequal nuclei. The binucleate spermatids, with special ectodermal coverings, are released by the polyp into the external environment. (From Biological Abstracts)

RAIKOVA, E. V. 1961b. Cytological peculiarities of free-living stages of development of Polypodium hydriforme Ussov (Coelenterata). Tsitologiya 3: 400-412. [In Russian]

Polyps were collected from infected roe of sterlets and cultured in a microaquaria. Histological sections (5-7 um thick) of the polps were prepared at regular intervals during the free-living period, and variously stained. Cells of the endoderm and ectoderm are described. Ectodermal cells are made up of epithelial, nettle and interstitial cells and are the same as those of the parasitic stolon. The acid mucopolysaccharide layer at the distal ends of the ectodermal cells are in contact with the environment and dissolve to form a protective mucous membrane around the polyp. Interstitial cells are

more basophilic than the epithelial ectodermal cells. Cells of the muscle layer are formed from the interstitial cells of the ectoderm. The cnidia represents a hollow tube that is everted when ejected. Endodermal cells are made of flagellated columnar epithelium. At the beginning of the free-living stage, the endodermal cells are packed with yolk granules. Differentiation of endodermal cells begins at the time polyps develop oral openings and feeding begins. The endoderm is divided into three regions based on cell type; a pharyngeal region with albumin glands and gland cells containing polysaccharides, a region containing "pockets"- special folds at the junction of the manubrium and tentacles, and cells at the bottom of the gastral pit containing vacuoles with food inclusions. Digestion in polyps is intracellular and extracellular in the gastral cavity. Nerve cells are present in the tentacles, adjacent to the muscle cells.

RAIKOVA, E. V. 1963a. Morphological andcytochemical changes in The oocytes of the sterlet and the sturgeon induced by Polypodium hydriforme Ussov (Coelenterata). Dokl. Akad. Nauk SSSR 152: 985-988. [In Russian]

Polypodium was found in stages II-III of oocyte development in sturgeon and a comparison is given between uninfected and infected oocytes. In the infected ovum, the nucleus was misshapen and infected oocytes become enlarged. At this stage, there is more glycogen and yolk in the infected oocyte than in corresponding parts of healthy oocytes, whereas in stage IV of oocyte maturity, healthy ova have more glycogen than infected ones. The peripherally situated stolon of the parasite surrounds the yolk, which does not differentiate. Polarity is thus not achieved. The nucleus is deformed and the chromosomes are scarcely ever seen. Starting at the stolon stage, the oocyte nucleoli become enlarged, and vacuolized, and remain hypertrophied till the spawning stage. RNA in the nuclei of infected oocytes is more firmly bound to protein. At stage IV, the fat is distributed evenly in the yolk, now at the centre. At stage V, the yolk is drawn out to form the gastral pouch of Polypodium and the nucleus is destroyed.

RAIKOVA, E. V. 1963b. A cytomorphological study of female gonads of the coelenterate Polypodium hydriforme (Coelenterata). Tsitologiya 5: 391-403. [In Russian]

Two to four sexual complexes, each made up of two ovaries and two oviducts, constitutes the female reproductive system of Polypodium hydriforme. The oviducts open into the gastral cavity. These structures are purely of endodermal origin. Hermaphroditism in polyps is transient, since female gonads degenerate immediately after formation of male gonads which continue to develop. The endodermal cells of the membrane covering the female sexual complex remain unchanged and identical to the endodermal cells of the gastral cavity. The cells of the oviduct can be distinguished into two types; the thin generating cells forming the oogonia and the nutritive iron cells. The iron cells of the ovary contain secretory granules of protein and acid mucopolysaccharide and have a vacuolated cytoplasm with large polyploid nuclei. The oogonia in the ovarian cavity multiply by mitosis and accumulate the secretory granules from the iron cells by absorption. The oogonia pass from the ovary, via the oviduct, to the gastral cavity. The fate of these oogonia remain unknown. In two cases, male sex cells have been found in the female gonads. (From Biological Abstracts)

RAIKOVA, E. V. 1964a. Unicellular parasitic stages in the life cycle of Polypodium hydriforme Ussov (Coelenterata). Zool. Zh. 43: 409-411. [In Russian]

Oocytes of Acipenser ruthenus measuring 100 um were found infected with early stages in the development of Polypodium. These were binucleate single cells with one large polyploid nucleus and one small nucleus. The large nucleus develops a deep invagination that engulfs the small nucleus. The large nucleus and a part of the cytoplasm forms a capsule around the remaining cytoplasm containing the small nucleus. The latter gives rise to the blastomeres. These binucleate early stages resemble the spermatids within the male gonads of the free living polyp stage. (From Biological Abstracts)

RAIKOVA, E. V. 1964b. Early parasitic stages of the developmental cycle of Polypodium hydriforme Ussov (Coelenterata). Dokl. Akad. Nauk SSSR 154: 742-743. [In Russian]

Sterlet ovaries in the II-III stage of maturation were sectioned and three fish were found infected. The earliest parasitic stage of Polypodium was found in oocytes measuring 0.33 mm in diameter and lacking yolk. The parasite consisted of a cluster of 22-23 cells lying in a cavity surrounded by a cellular envelope undergoing syncytial merging of cells - the capsule. The capsule measured 45-50 um. In another case, the morula like compact mass of cells measured 50 X 30 um and the capsule 110 um in diameter. In the third infected fish (stage II - III of gonad maturation), the parasite body was made up of a large number of cells, covered by a well developed capsule. The early capsule formation is considered a long standing adaptation to parasitism.

RAIKOVA, E. V. 1965. A cytomorphometric study of the DNA content in the cell nuclei of Polypodium hydriforme Ussov (Coelenterata) at various

stages of its life cycle. Zh. Obshch. Biol. 26: 546-552. [In Russian]

Diploid ectodermal and endodermal cells, studied by Feulgen cytophotometry, contained identical amounts of DNA. The small nuclei of both the binuclear spermatid (in male gonads) and the binuclear parasitic cell in sturgeon oocytes, contain half the DNA of somatic cell nuclei. Early embryogenesis in Polypodium is initiated without fertilisation since cleaving blastomeres are haploid, but the diploid condition is regained later during development. The large nucleus of the spermatid, on the other hand is 4n - 6n, while that of the parasitic binuclear cell is 400n. Polyploid nuclei (8n - 32n) are also present in nurse cells of Polypodium ovaries. Gonads of the polyp stage of Polypodium release sex cells which are polyploid and these are therefore thought to correspond to oogonia. (From Biological Abstracts).

RAIKOVA, E. V. 1973. Life cycle and systematic position of Polypodium hydriforme Ussov (Coelenterata), a cnidarian parasite of the eggs of Acipenseridae, p.165-173. In T. Tokoika and S. Nishimura (ed.) The Proceedings of the Second International Symposium on Cnidaria, Shirahama and Kushimoto, October 16-19, 1972. Seto Marine Biological Laboratory, 1973; 165-173.

A review of the life cycle of this parasite is presented. The earliest investigated stage of the parasite, found in sterlet (Acipenser ruthenus) oocytes, is a one cell stage 20-30 um in diameter, with two unequal sized nuclei, a small haploid one and large polyploid one (up to 400n). As the oocyte grows, the small nucleus with some differentiating cytoplasm surrounding it enters the deep cavity formed by the large nucleus, and later gives rise to the cleaving blastomeres of the embryo. The main mass of the binucleated cell along with the large nucleus material forms a peculiar capsule around the parasite and carries out feeding functions. Cleavage of the polyploid nucleus into polymorphic nuclei leads to the formation of a compact morula. At vitellogenesis, the infected oocyte already has a two-layered planula like larva with inverted embryonic layers: the flagellated entoderm outside and the ectoderm inside, surrounded by the capsule. In August the planula grows into the stolon stage and in winter the capsule degenerates. In spring, just before sturgeon spawning, the embryonic membranes of the stolons assume the normal position by everting. After spawning, the free living stolons separate into buds, and form mature unisexual polyps with development of first female and then male gonads, in addition to development of hermaphroditic individuals. The female sexual complex (1-8/polyp) is entirely entodermal in formation, including two sexual glands opening via gonoducts to the gastral cavity. The male gonads (4/polyp) have no gonoducts, and are also entodermally produced. After meiosis, cells have two unequal nuclei, the small nuclei being haploid while the larger one reaching 4n by polyploidization. Such gonads fall out of polyps intact and cases are known where polyps actively attach such units to juvenile sturgeon. The fate of these female and male gonads is unknown as is the method of infection. Based on the unusual life cycle and morphological features, Polypodium may deserve a separate class status within the Cnidaria.

RAIKOVA, E. V. 1978. Electron microscopical investigation of the nematocyst development in the parasitic stolon of Polypodium hydriforme Ussov (Coelenterata). Tsitologiya 20: 384-386. [In Russian]

Primordia of large and small nematocysts appear in the cystoplasm of the developing cnidoblasts as membrane-bound vacuoles containing granular material which later forms the nematocyst wall and a dense matrix. The outer surface of the wall of the developing nematocyst has a microtubule lining. As the nematocyst primordium elongates, an extracapsular tube, coated with a dense wall and lined with microtubules, develops in the cnidoblast cytoplasm and contains alternating dark and light portions of the matrix. The nematocyst enlarges and develops a corrugated hollow internal filament. The maturing nematocyst rounds up, its wall differentiates into two layers and its internal filament forms short barbs on it.(From the English summary following the Russian original)

RAIKOVA, E. V. 1980a. Morphology, ultrastructure and development of the parasitic larva and its surrounding trophamnion of Polypodium hydriforme Ussov (Coelenterata). Cell Tissue Res. 206: 487-500.

Polypodium has a planuliform parasitic stage, with inverted germ layers, developing inside the oocytes of acipenserid fishes. The trophamnion is a compact layer of cytoplasm, 6-10 um thick, and characterized by microvilli on the inside, numerous prominent Golgi bodies, ingested yolk platelets and lysosome like vesicles. Digestion and protection are likely functions of the trophamnion. Nutrition uptake appears to be by phagocytosis of yolk by the trophamnion. Products of digestion are exocytosed into the parasite containing cavity to be absorbed by the endodermal cells. The trophamnion is now considered to be a giant hollow cell rather than a symplast as was previously thought (Raikova 1960b). Endodermal cells on the exterior of the larva are flagellated, with basal vacuoles and a subapical nucleus. The cytoplasm is rich in ribosomes, polyribosomes, and contains many microtubules. Ectodermal cells are not ciliated, (unlike in other coelenterates), but like endodermal cells are vacuolated and contain large

nuclei with well developed nucleoli. The characteristic apical layer of acid mucopolysaccharides, absent in some larvae, apparently form during the planuliform stage. The cells of both layers occasionally interdigitate, and the lateral surfaces of endodermal cells have microtubules. The mesoglea, 0.5-1.5 um thick, has many 10 nm thick fibrils.

RAIKOVA, E. V. 1980b. Trophical adaptations of Polypodium hydriforme Ussov on the larval stage, p.92-95. In D.V. Naumov and S.D. Stepanyants (ed.) The theoretical and practical importance of the coelenterates. Akademiya Nauk SSSR, Leningrad. [In Russian]

RAIKOVA, E. V. 1982. Ultrastructure of the trophamnion of Polypodium hydriforme Ussov (Coelenterata) at the final stages of its functioning. Parazitologiya 16: 30-34. [In Russian]

The trophic envelope covering the parasitophorous vacuole was examined in autumn and summer oocytes of the sterlet and sturgeon. This trophamnion shows maximum trophic activity during intensive oocyte vitellogenesis in August and September. The ultrastructure of the fully functional trophamnion with associated structures such as abundant trophic inclusions and anastomosing microvilli, is described. This is compared to the degenerating trophamnion with its component structures such as the pycnotic nucleus and degenerating cytoplasmic membrane.

RAIKOVA, E. V. 1984. Ultrastructure of the stolons of Polypodium hydriforme Ussov (Coelenterata) parasitic in oocytes of acipenserid fishes. Monit. Zool. Ital. 18: 1-24.

The stolon of the parasitic coelenterate Polypodium hydriforme in the eggs of the sterlet and sturgeon, is surrounded by a giant hollow cell called the trophamnion that lines the parasitophorous vacuole. This functions as the feeding organ for the parasite. The trophamnion shows greatest trophic activity during August and September when it has many food inclusions and microvilli in the shape of a sieve. The trophamnion degenerates in May by fragmentation, pycnotisation of its nucleus and cytoplasmic degeneration. Following this, the endodermal cells which make up the outer layer due to inversion of the germ layers almost throughout stolon development, begin phagocytosing and become packed with yolk. Endodermal cells also differentiate into cells of the tentacle axis, feeding cells, and gland cells. Feeding cells have microvilli-like pseudopodia, and contain vesicles, and occasionally granular endoplasmic reticulum. The ectodermal cells differentiate into cnidocytes and epidermal cells. Golgi complexes within ectodermal cells produce numerous acid mucopolysaccharide granules which accumulate at their apical ends. Underlying the ectoderm are myocytes forming the muscle layer. Myofibrils lie adjacent to microtubules and consist of both thick and thin protofilaments. Muscle cells contain a considerable amount of glycogen with intercalated disc type intercellular contact. Nerve cells were not found. Prominent among the differences with other coelenterates is the absence of muscle fibres in the endodermal cells, and the presence of muscle cells in the form of myocytes instead of the typical epithelio-muscular or digestive-muscular cells.

RAIKOVA, E. V. 1985. Cytological paradoxes in the life cycle of Polypodium hydriforme - an intracellular coelenterate parasite of oocytes of the acipenserid fishes. Tsitologiya 27: 391-401. [In Russian]

The embryonic development of the parasitic phase of the life cycle of Polypodium hydriforme is considered. Development of the parasite embryo takes place parthenogenetically (without fertilisation) and develops from aberrant binucleate gametes formed by meiosis within the gonads of free-living stages. This type of gametogenesis is considered to be oogenesis [earlier considered as spermatogenesis (Raikova 1961)]. The gonads of free living animals, which were earlier thought to be female, produce no mature sex cells and seem to be abortive rudimentary organs. Adaptations to parasitism include a long-lasting block of cytokinesis of the second meiotic division and the utilisation of the polar body of this division as a phorocyte, and later, as a trophamnion. Polypodium differs from other coelenterates in possessing highly polyploid feeding cells at the parasitic (trophamnion; 500 cells) and free living (trophocytes in rudimentary female gonads; 8-32 cells) phases of the life cycle.

RAIKOVA, E. V. 1986. Polypodium hydriforme (Coelenterata) from the eggs of sturgeons from the Ural River. Parazitologiya 20: 364-372. [In Russian]

Histological preparations were made of healthy and Polypodium infected oocytes of acipenserids caught in the Ural River. Acipenser nudiventris and Huso huso were found infected with this parasite. The parasitic stages of Polypodium in the oocytes of these species as well as those of Acipenser stellatus are described for the first time. The development of this parasite precisely follows the stages of oogenesis within the host. Stolons with inverted germ layers are found in immature females while stolons with normally positioned germ layers are present in maturing hosts. A binucleate cell as an early stage of infection has been found in a young generation of oocytes in Acipenser nudiventris. Similar coordination of the parasite life-cycle with the stages of oocyte development, similar reactions of infected oocytes to the presence of the para-

site, and similar sizes of cnidocysts of Polypodium occurring in oocytes of the three acipenserid species suggest that they are the same as the species found in the Volga.

RAIKOVA, E. V. 1987. Peculiarities of the embryonic development of Polypodium hydriforme Ussov (Coelenterata), a parasite of acipenseric oocytes. Gegenbaurs morphol. Jahrb. 133: 99-121.

One hundred and seven specimens of the unicellular stage and sixty-four specimens of the multicellular stage of Polypodium were recovered from the eggs of fourteen sterlet (Acipenser ruthenus). The parasitic stages were investigated by light microscopy, cytophotometry, and autoradiography following incubation with ^{3}H-uridine. The unicellular stage transforms to the bicellular and multicellular stage in the following pattern characterized by; a binucleate cell with unequally sized nuclei, development of a two celled complex with the larger cell surrounding the smaller cell, formation of a cavity inside the larger cell-nucleus and migration of the small cell into it. The large trophic cell surrounding the smaller generative cell gives rise to a hypertrophied but unicellular envelope around the parasite embryo- the trophamnion. The multicellular stage starts with the segmentation of the generative cell into blastomeres. This results in a morula within the trophamnion cavity. The inversion of germ layers is apparently formed during gastrulation. Bastomeres are haploid and diploidy is restored during segmentation. As the trophamnion grows its cytoplasm accumulates mucoprotein inclusions and the nucleus becomes highly polyploid. The blastomere nuclei and the trophamnion nuclei actively synthesize RNA. Although the embryonic development of Polypodium lasts several years and is the slowest among coelenterates, it has features typical of the class Hydrozoa.

RAIKOVA, E. V. 1988. Embryonic stages of development of Polypodium hydriforme (Coelenterata) in oocytes of Acipenser ruthenus. Parazitologiya 22: 201-209. [In Russian]

In sterlet (Acipenser ruthenus) oocytes, 107 specimens of unicellular stages and 64 specimens of cleavage stages of Polypodium were studied by light microscopy. The developmental stages of the parasite correspond to the oocyte maturation in the hosts. The embryonic development of Polypodium lasts several years and is probably the slowest developing and has the smallest eggs among the coelenterates. The eggs develop without fertilisation within a nutritive cell called the trophamnion, which separates at the II meiotic division of the oocyte. Cleavage is total and the morula stage is long-lasting. Gastrulation occurs by morular delamination and the inversion of the germ layers is likely to take place at this time. The blastomeres and trophamnion have large nucleoli and actively synthesize RNA.

RAIKOVA, E. V., V. C. SUPPES, and G. L. HOFFMAN. 1979. The parasitic coelenterate Polypodium hydriforme Ussov, from the eggs of the American acipenseriform Polyodon spathula. J. Parasitol. 65: 804-810.

Histological investigations of parasitic stolon and free living polyps of Polypodium sp. obtained from Polyodon spathula eggs showed essentially the same features as those described from Polypodium hydriforme in the Volga sterlet (Acipenser ruthenus). Parasitic stolons investigated were inside oocytes of stages IV and V. The acid mucopolysaccharide granules in the meshes of the reticulated apical cytoplasm of entodermal cells, common in Volga Polypodium, were not observed in the North American material. This has been attributed to the fixatives used in the study. The study indicates with a high degree of probability that the two Polypodium populations are one species.

RASIN, K. 1930. Nalez parasitu Polypodium hydriforme Ussov a Cystoopsis acipenseri Wagn. v nasi sterledi Reparat ze 168. Schuze Csl. biolog. spoleen v. Brne dne 44, 11 prosince 1929. Biolog. Listy. 10.

REICHENBACH-KLINKE, H. H. and E. ELKAM. 1965. Infectious diseases, p. 66-67 In The principal diseases of lower vertebrates. Academic Press, London and New York.

SALIAIEVA, E. V. 1957. Studies on Polypodium hydriforme - a parasite of acipenserid eggs, its biology and epizootological importance. Sovesch po bolezniam ryb, 22-27 goda. Izd. Akad. Nauk. SSSR. (Moscow-Leningrad) [In Russian]

SKLYAROVA, T. V. and E. V. RAIKOVA. 1967. Free living stages of the parasite of Sterlet eggs (Polypodium hydriforme Ussov, Coelenterata) in the Upper Don. Parazitologiya 1: 200-206. [In Russian]

Free living polyps of Polypodium hydriforme were found in July, 1961 and July, 1962 in the Upper Don. Morphological and histological characteristics of the polyps are described and their similarity with the polyps cultured in aquaria is shown. Tne presence of this parasite in plankton samples indicates that they are not purely benthic and may be distributed downstream through drifting.

SMOL'YANOV, I. I. and E. V. RAIKOVA. 1961. The

occurrence of sexually mature Polypodium hydriforme Ussov (Coelenterata) on sturgeon juveniles. Dokl. Akad. Nauk SSSR 141: 1271-1274. [In Russian]

Free-living stages of Polypodium hydriforme were collected in the course of examining sturgeon larve from the Sarotovsk and Turbensk spawning beds. Some of the polyps were found to have produced a hemispherical formation and all were closely applied to the body of the prelarval fish. These structures corresponded to large mature male gonads, four per polyp situated at the aboral end. Gonads are sealed within an ectodermal operculum containing cnidoblast glutinants, indicating that they function as spermatophores. The behaviour of the mature polyps is described under aquarium conditions. Polyps adhere strongly to the fish by their tentacles and deposit the gonads in various positions; on the yolk sac, on the muscular portion of the trunk, and on the fin folds and tail ends. (From the original English version)

SUPPES, V. C. and F. P. MEYER. 1975. Polypodium sp. (Coelenterata) infection of paddlefish (Polyodon spathula) eggs. J. Parasitol. 61: 772-774.

Polypodium, detected and identified from the eggs of paddlefish Polyodon spathula in 1971. Eighty-eight percent of the female fish were parasitized, and percentage of paddlefish eggs infected ranged from 0.04-0.37 per fish. Abnormal eggs were pale and measured 3.6 mm while normal eggs measured 2.5 mm. Preserved parasite stolons had 44-60 buds. Parasite polyps were maintained for a maximum of 35 days, but no feeding was observed.

SVIRSKY, V. G. 1984. Polypodium hydriforme (Coelenterata) of the sturgeon fishes from the Amur River. Parazitologiya 18: 362-367. [In Russian]

The rate of Polypodium infections in Acipenser baeri schrenki (Amur sturgeons) was 23.3% ("intensiveness" of infection being 15; 1237 stolons from eggs of a female) and 42.8% in the kaluga, Huso dauricus ("intensiveness" of infection being 83; 4356 parasites from eggs of a female). The coefficient of elimination is $E = N/IP \times 10^3$, where N is the number of eggs with Polypodium stolons and IP is individual fecundity. This exponent for sturgeon is within an interval of 0.5 - 6.5, with an average of 2.2. Polypodium as a factor of elimination accounts for 1130 sturgeons (11 t) and 900 kaluga (45 t), per year.

USSOV, M. M. 1885. Polypodium hydriforme. Novaya forma presnovodnykh tselenterat. Trudy Obshchestva Estestvoispytatelei pri Imperatorskhom' Khazanskhom' Universitete, Khazany 14(6): 1-24. [In Russian]

USSOV, M. M. 1887. Eine neue Form von Susswasser-Coelenteraten. Morph. Jahrb. 1886: 137-153.

The species of coelenterate parasite of sterlet eggs reported by Owsjannikoff (1871) and Grimm (1873), was named Polypodium hydriforme. Larger fish (50-70 cm) are more often infected than smaller fish (20-25 cm). The youngest stage in the life cycle of Polypodium was a hollow cylindrical blind tubular structure, 15-17 mm long and 1 1/2 - 2 mm thick, bearing primary buds. The development of the stolon after release from the eggs is described upto the tentacled, fully formed, individual polyp. The ectoderm, endoderm, and mesoderm and their components are described. Other anatomical features described include tentacles, oral opening, gastral cavity, cnidoblasts, and a mathematical scheme is developed for the organisation of successive generations of Polypodium. Polyps feed on microorganisms (Infusoria and rotifers) by preying on them with their tentacles.

WESENBERG-LUND, C. 1937. Ferskvandsfaunaen Biologisk Belyst Invertebrata I. p.29-59 (Coelenterata) Copenhagen.

Pages 58-59 of this book on the biology of freshwater invertebrates contains an account on Polypodium hydriforme. This coelenterate is considered unusual considering its partially parasitic life cycle. Its relationship with other cnidarians is considered unclear as is its complete life cycle. The morphology of the free living polyp is described.

WESENBERG-LUND, C. 1939. Biologie de Susswassertiere-Wirbellose Tiere 1939, p. i-xi, 1-817, pls. 1-24, text figs. Wien (Coelenterata, p. 25-57).

Pages 55-57 of this book on the biology of freshwater invertebrates describes the biology of Polypodium hydriforme with diagrams. This is the German version of the previous reference and essentially contains the same account.