FOLIA PARASITOLOGICA 46: 123-131, 1999

Morphology and taxonomy of *Salvelinema* species (Nematoda: Cystidicolidae), swimbladder parasites of Pacific area salmonids

(Dedicated to the memory of the late Dr. Leo Margolis, a distinguished Canadian fish parasitologist)

František Moravec [1,2]and **Kazuya Nagasawa**[2]

[1]Institute of Parasitology, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic;

[2]National Research Institute of Far Seas Fisheries, Fisheries Agency of Japan, 5-7-1 Orido, Shimizu, Shizuoka 424-8633, Japan

Key words: *Salvelinema*, swimbladder nematodes, *Oncorhynchus*, *Salvelinus*, Japan, Canada

Abstract. The morphology of two *Salvelinema* Trofimenko, 1962 species, *S. salmonicola* (Ishii, 1916) and *S. walkeri* (Ekbaum, 1935), swimbladder nematodes of salmonids, was studied in detail, including scanning electron microscopy (SEM), on the basis of newly collected materials from *Oncorhynchus masou, O. mykiss* and *Salvelinus malma* from Japan and from *Oncorhynchus clarki*, *O. kisutch* and *O. nerka* from North America (Vancouver Island, B.C., Canada and Gulf of Alaska). Both nematode species proved to be morphologically very similar, differing substantially in the numbers and arrangements of egg filaments. Deirids were described for the first time for *Salvelinema*. *Salvelinema iwana* (Fujita, 1928), *S. amemasu* (Fujita, 1939), *S. kosugii* (Fujita, 1939), *S. oncorhynchi* (Fujita, 1939) and *S. salvelini* (Fujita, 1939) (= *S. ishii* (Fujita, 1941)) were synonymised with *S. salmonicola*. *Comephoronema* Layman, 1933 is re-erected as a valid genus related to *Salvelinema*.

At present, the genus *Salvelinema* Trofimenko, 1962 (syn. *Pseudometabronema* Bogdanova, 1963) includes six species reported from salmonids from East Asia and two species from the Pacific coast of North America; of them, one species occurs both in Asia and America. All Asian species, except for *Salvelinema salmonicola* (Ishii, 1916), were inadequately described by Fujita (1928, 1939) from Japan, being later designated by Margolis (1968) as possibly identical with *S. salmonicola*. However, the latter author did not carry out their synonymisation and all of them were reported as valid species in the list of parasites of salmonids in Japan by Nagasawa et al. (1987).

According to Margolis (1967), who revised swimbladder cystidicolid nematodes from Pacific salmon (*Oncorhynchus* spp.), there are two well established species of *Salvelinema*, *S. salmonicola* and *S. walkeri* (Ekbaum, 1935); whereas the former is a parasite of various salmonid species (*Oncorhynchus*, *Salvelinus*) in eastern Asia (Japan, Russian Far East) and on the western coast of North America (northern British Columbia, Alaska), the latter is known only from *Oncorhynchus kisutch* from the western coast of North America (southern British Columbia, northern California) (Margolis 1967, Margolis and Arthur 1979, Bauer 1987). Both species are closely related and the only reliable distinguishing feature is the number and arrangement of egg filaments. New collections of both these nematode species from salmonids in Japan and North America made it possible to study in detail and compare their morphology, including the complicated structure of cephalic ends, for the first time studied by SEM. The results obtained are presented herein.

MATERIALS AND METHODS

The following *Salvelinema* specimens were studied:

***Salvelinema salmonicola*:** 34 males and 37 females from the swimbladder of *Oncorhynchus mykiss* (Walbaum) from Tsugaru-Juniko Lakes in Aomori Prefecture, northern Honshu, Japan, collected on 24 and 25 May 1991, and numerous, mostly immature specimens collected from the same host species and the same locality on 13 January 1994 by A. Ohtaka; 2 males and 1 female from the swimbladder of *Oncorhynchus masou* (Brevoort) from Japan (locality not given) from the collection of the Pacific Biological Station in Nanaimo, B. C., Canada; and 2 males and 2 females from the swimbladder of *Salvelinus malma* (Walbaum) from Japan (exact locality unknown) from the collection of the Pacific Biological Station in Nanaimo, B.C., Canada.

***Salvelinema walkeri*:** Numerous specimens from the swimbladder of *Oncorhynchus kisutch* (Walbaum) from the Gulf of Alaska (52°06'N; 144°56'W), eastern North Pacific Ocean, collected on 19 December 1992 by the junior author (K. N.); numerous, largely young specimens collected by the senior author (F. M.) from salmonids from two localities on Vancouver Island, B.C., Canada: from *O. kisutch* smolts (22 specimens; body length 9-13 cm) (prevalence 77%, intensity 1-26 (mean 5)) from Henderson Lake (24 April 1979) and from *O. kisutch* smolts (5 specimens; 6-13 cm) (prevalence 80%, intensity 3-425 (134) and *Oncorhynchus clarki* (Richardson) (2 specimens; 13 and 16 cm) (prevalence 100%, intensity 1 and 2 nematodes) from the De Mamiel Creek (7 May 1979).

Address for correspondence: F. Moravec, Institute of Parasitology, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic. Phone: ++420 38 7775432; Fax: ++420 38 47743; E-mail: moravec@paru.cas.cz

Salvelinema sp. (probably *S. salmonicola*): Numerous, mostly young specimens (no gravid females present) collected by the senior author (F. M.) from the swimbladder of *Oncorhynchus nerka* (Walbaum) smolts (8 specimens; 7-10 cm) (prevalence 50%, intensity 1-9 (5) from Henderson Lake, Vancouver Island, B.C., Canada (24 April 1979).

Nematodes were fixed and preserved in 70% ethanol and cleared with glycerine for optical microscopy examination. Drawings were made with the aid of a NIKON microscope drawing attachment. For examination in SEM, the specimens were postfixed in 1% OsO_4, dehydrated through an ethanol and acetone series and then critical point dried. The specimens were coated with gold and examined with a JSM-6300 scanning electron microscope at an accelerating voltage of 15 kV. All measurements are given in micrometres unless otherwise stated. Voucher specimens have been deposited in the Institute of Parasitology, ASCR, in České Budějovice (Cat. Nos. N-64 and N-697) and in the National Science Museum in Tokyo (Cat. Nos. NSMT-As-2846 and NSMT-As-2847).

RESULTS

Salvelinema salmonicola (Ishii, 1916) Figs. 1, 2

Syn.: *Ancyracanthus salmonicola* Ishii, 1916; *Cystidicola iwana* Fujita, 1928; *Metabronema amemasu* Fujita, 1939; *M. kosugii* Fujita, 1939; *M. oncorhynchi* Fujita, 1939; *M. salvelini* Fujita, 1939; *Cystidicola chitosensis* Fujita, 1940; *Metabronema ishii* Fujita, 1941; *Salvelinema cristata* Trofimenko, 1962; *Pseudometabronema sachaliense* Bogdanova, 1963.

Description: Medium sized, whitish nematodes with smooth cuticle. Body somewhat narrowed to anterior end; cephalic end rounded in lateral view. Oral opening large, almost circular, surrounded by four small submedian cephalic papillae and pair of lateral amphids. Lateral pseudolabia well developed, relatively broad. Cuticle surrounding mouth thickened dorsally and ventrally to form two semicircular bands extending from one pseudolabium to other. Vestibule (stoma) divided into anterior, well developed prostom and posterior, narrower cylindrical part of vestibule. Prostom broad, cup-shaped in lateral view, but actually being constricted centrally into two main chambers, dorsal and ventral, and its posterior portion laterally twisted. Muscular oesophagus short, cylindrical, glandular oesophagus relatively narrow, approximately 3-4 times longer than muscular one. Nerve ring encircling muscular oesophagus near its middle. Excretory pore near junction of both parts of oesophagus. Deirids very small, anterior to nerve ring. Tail of both sexes conical, long.

Male (10 specimens from *O. mykiss*; some measurements of specimens from *S. malma* (2) and *O. masou* (2) given in round and square brackets, respectively): Length of body 15,660-18,990 (10,550-13,020) [6,560-11,160], maximum width 288-474 (195-233). Length of whole vestibule including prostom 116-144 (74-110); prostom 36-44 (23-35) long, 60-72 (35 to 46) wide in lateral view. Muscular oesophagus 444-487 (276-382) long and 44-52 wide; glandular oesophagus 1,440-1,820 (930-1,023) long, 70-104 in maximum width; length ratio 1 : 3.0-3.8 (1 : 2.7-3.4). Deirids, nerve ring and excretory pore 278-320 (219-246), 365-426 (244-276) and 609-705 (276), respectively, from anterior extremity. Caudal alae and ventral precloacal cuticular ridges well developed. Preanal papillae: 19-21 (19) pairs of subventral papillae present, being mostly arranged in couples, but some pairs of papillae may be simple; members of each couple formed by a narrower and longer more lateral papilla and a broader and shorter papilla shifted more ventrally. Postanal papillae: 6 (6) pairs of single papillae present, papillae of last pair being very small; occasionally, 7 papillae on right side and 6 papillae on left side present (Fig. 1F). Left spicule slender, 960-1,050 (989) [728-1,242] long; its shaft measuring 180-228, representing 17-22% of spicule length; proximal end of spicule somewhat broader, distal tip sharply pointed. Right spicule short, boat-shaped, 128-160 (112-127) [110-124] long; its proximal end blunt, distal end rounded, with narrow membranous cover. Length ratio of spicules 1 : 6.6-7.1 (1:7.8) [1 : 6.6-10.0]. Tail 224-264 (179-253) long.

Female (10 specimens from *O. mykiss*; some measurements of specimens from *S. malma* (1) and *O. masou* (1) given in round and square brackets, respectively): Length of body of gravid specimens 20,830-27,910 (12,648) [13,280], maximum width 577-824 (279) [115]. Length of whole vestibule including prostom 120-160 [115]; prostom 48-60 [39] long, 92-100 [58] wide in lateral view. Muscular oesophagus 539-566 [322] long, 44-61 wide; glandular oesophagus 1,700-2,130 [2,500] long, 87-113 in maximum width; length ratio 1 : 3.1-4.0 [1:7.8]. Deirids, nerve ring and excretory pore 344-348, 409-522 [294] and 679-722, respectively, from anterior extremity. Tail slender, 409-487 [353] long, with distal tip separated by cuticular constriction to form a knob-like appendage 6-8 long. Vulva near middle of body, 11,310-14,730 (5,022) [5,630] from anterior extremity, 48-54% (40%) [42%] of body length. Vagina muscular, narrow, about 1,000 long, directed anteriorly from vulva. Uterus amphidelphic, ovaries situated in anterior and posterior parts of body. Mature eggs oval, thick-walled, larvated, size 42-50 × 18-20 (48-51 × 21) [48 × 21]; each pole of egg with small polar plug and two thread-like filaments up to about 140 (230) in length; exceptionally, three filaments may be present on one egg pole.

H o s t s : *Oncorhynchus masou* (Brevoort) (type host), *O. mykiss* (Walbaum) and *Salvelinus malma* (Walbaum); nongravid specimens of the present material from *Oncorhynchus nerka* (Walbaum) probably also belonged to this species. Previously reported also from *Oncorhynchus keta* (Walbaum), (?) *O. kisutch* (Walbaum), *O. tshawytscha* (Walbaum), *Salvelinus leucomaenis* (Pallas), *S. pluvius* (Hilgendorf) (all Salmonidae), and *Hypomesus olidus* (Pallas) (Osmeridae) (both Salmoniformes) (Margolis 1968, Margolis and Arthur 1979, Bauer 1987, Nagasawa et al. 1987).

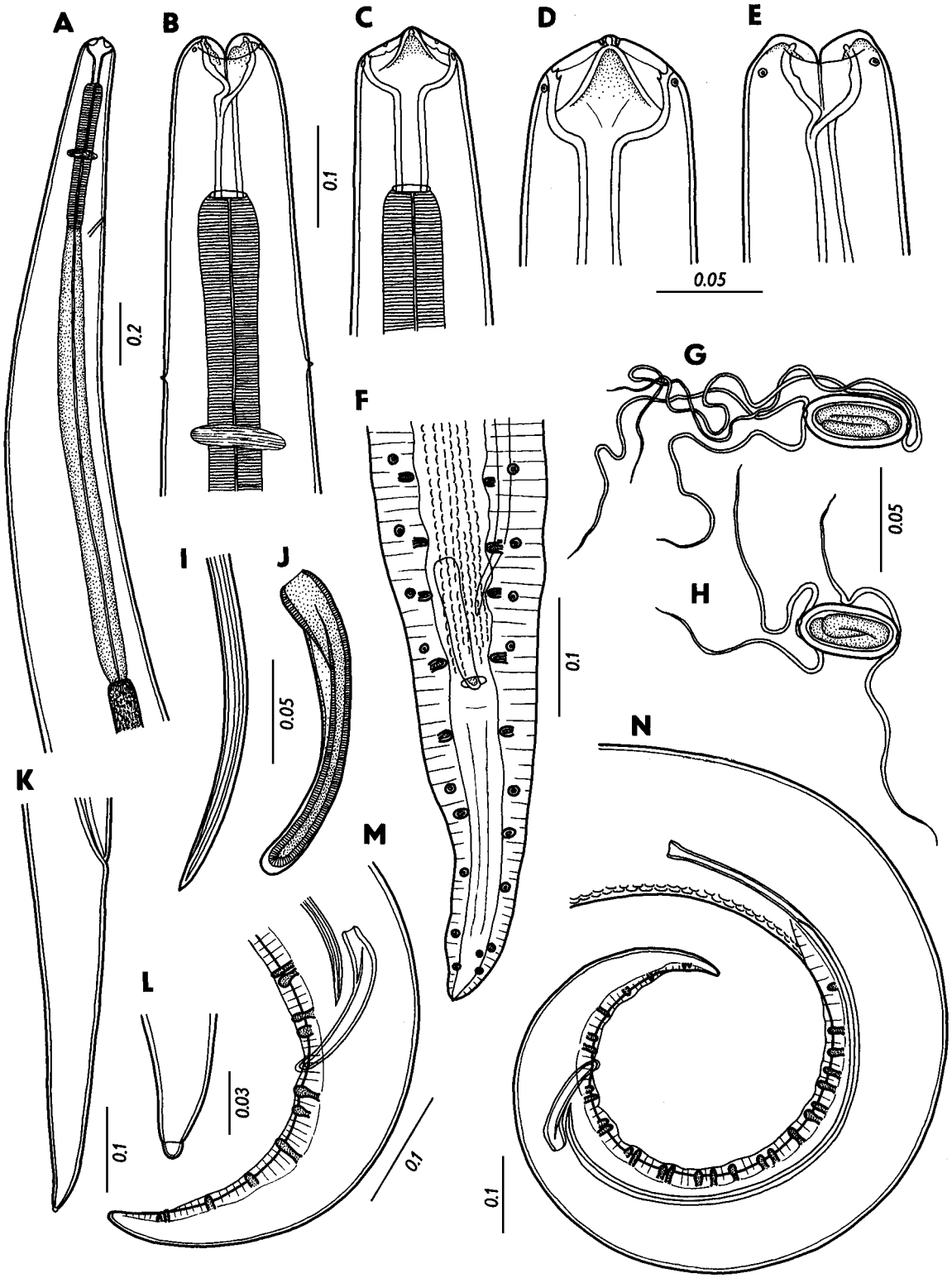

Fig. 1. *Salvelinema salmonicola* (Ishii, 1916) from *Onchorhynchus mykiss* from Japan. **A** – anterior end of gravid female, lateral view; **B**, **C** – cephalic end of female, dorsoventral and lateral views; **D**, **E** – cephalic end of male, lateral and dorsoventral views; **F** – tail of male, ventral view; **G**, **H** – mature egg; **I** – distal end of large spicule; **J** – small spicule; **K** – tail of gravid female; **L** – distal tip of female tail; **M** – tail of male, lateral view; **N** – posterior end of male. Scale bars in mm.

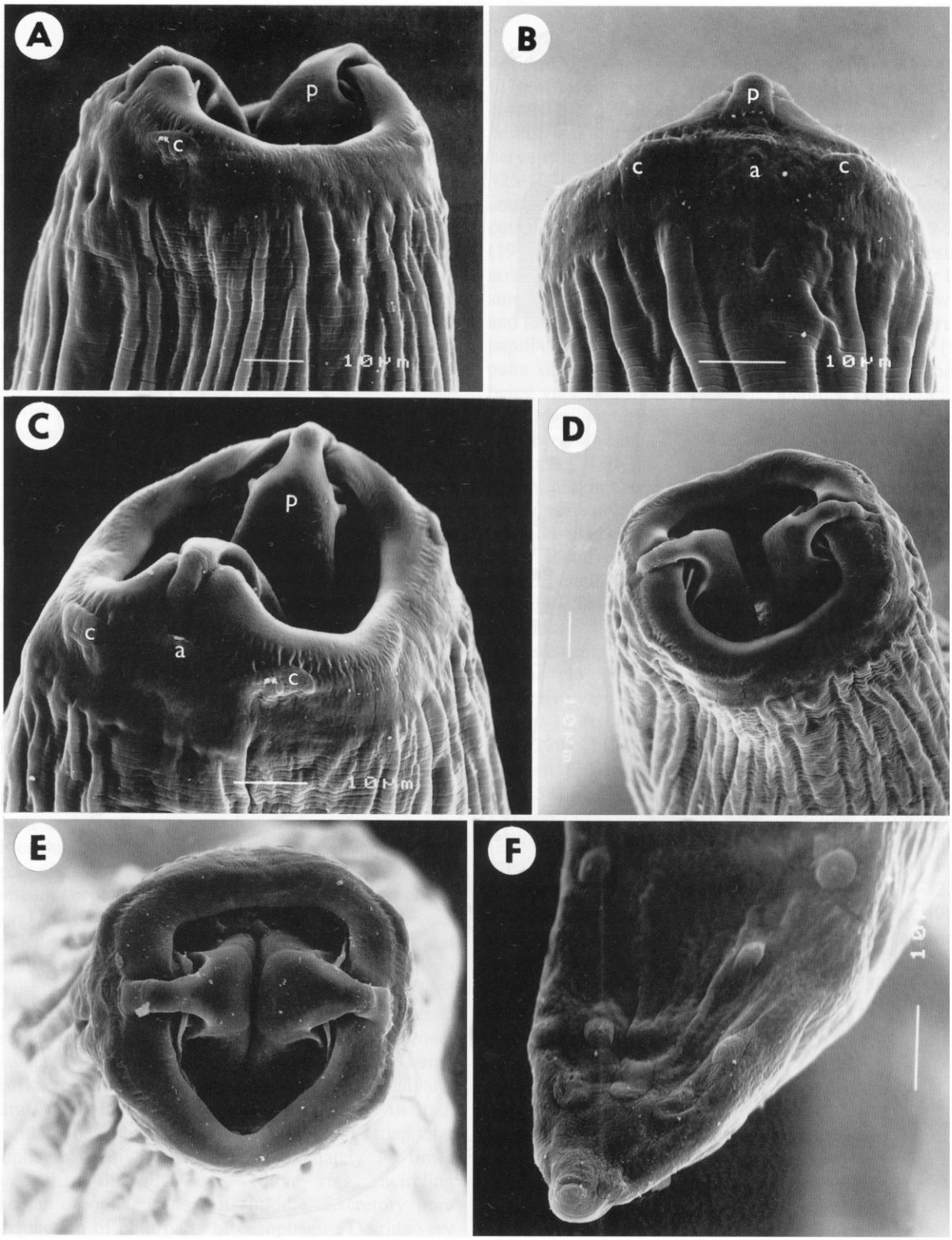

Fig. 2. *Salvelinema salmonicola* (Ishii, 1916), SEM micrographs. **A** – cephalic end, dorsoventral view; **B** – same, lateral view; **C** – same, sublateral view; **D** – same, subdorsoventral view; **E** – same, sublateral view; **F** – end of male tail, ventral view. Abbreviations: a – amphid; c – cephalic papilla; p – pseudolabium.

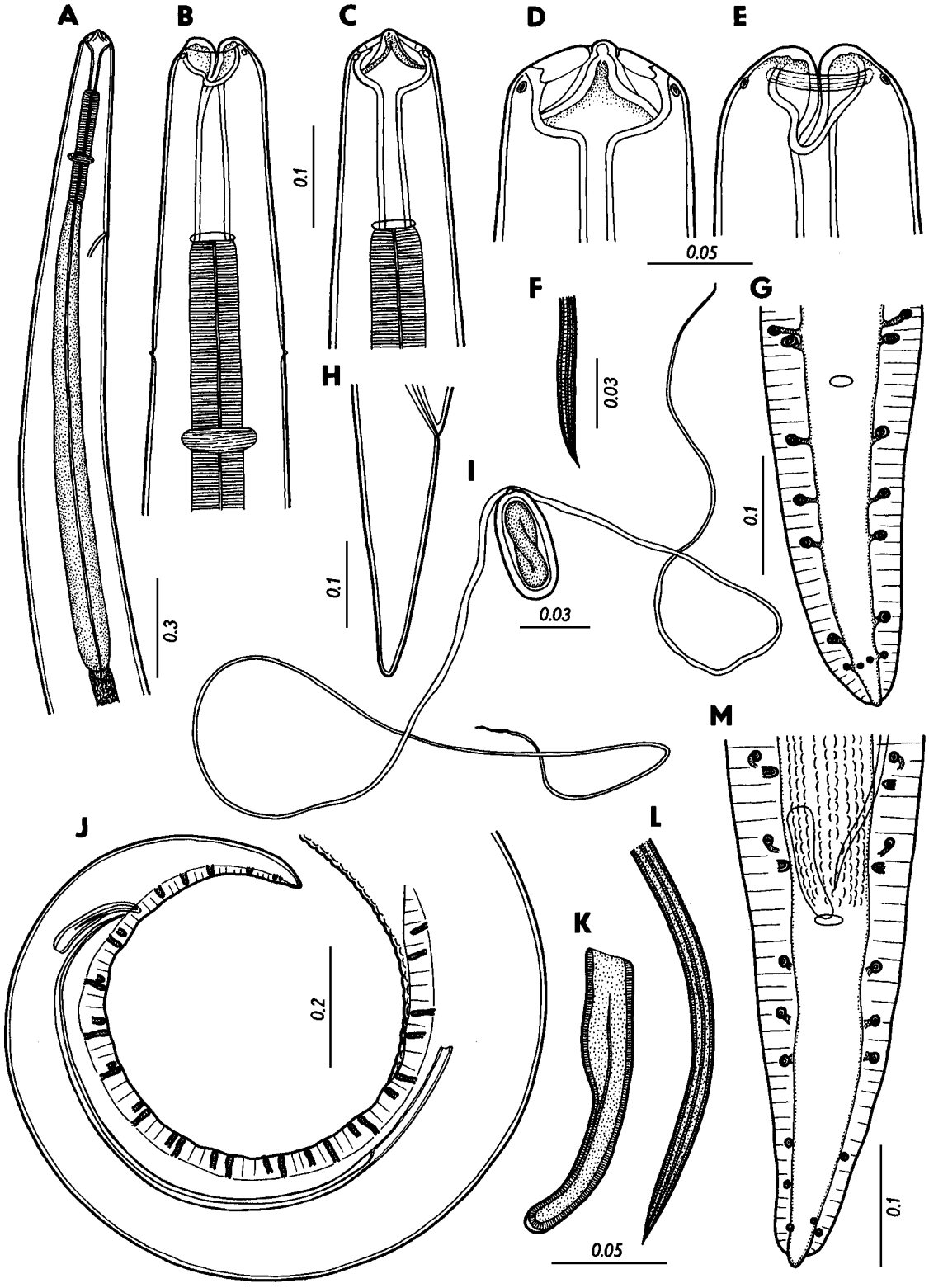

Fig. 3. *Salvelinema walkeri* (Ekbaum, 1935) from *Onchorhynchus kisutch* from Gulf of Alaska. **A** – anterior end of male, lateral view; **B**, **C** – cephalic end of male, dorsoventral and lateral views; **D**, **E** – cephalic end, lateral and dorsoventral views (enlarged); **F** – distal tip of large spicule protruding out of body; **G** – tail of male, ventral view; **H** – tail of gravid female; **I** – mature egg; **J** – posterior end of male; **K** – small spicule; **L** – distal end of large spicule; **M** – tail of male, ventral view. Scale bars in mm.

Site of infection: Swimbladder

Localities: Tsugaru-Juniko Lakes, Aomori Prefecture, northern Honshu, Japan (*O. mykiss*) (24-25 May 1991, 13 January 1994) and Japan (localities unknown) (*O. masou*, *S. malma*); probably also Henderson Lake, Vancouver Island, B. C., Canada (nongravid specimens - apparently *S. salmonicola*) (24 April 1979). Otherwise previously reported from Japan (Hokkaido, Honshu, Etorofu Island, Shikotan Island), Russian Far East (Kamchatka, Sakhalin, Kurile Islands) and western coast of North America (northern British Columbia, Alaska) (Margolis 1967, Margolis and Arthur 1979, Bauer 1987, Nagasawa et al. 1987).

Intermediate hosts: In Japan *Gammarus* sp. and *Paramoera japonica* (Tattersall) (both Amphipoda) (Koshida 1905, 1910, Moravec and Nagasawa 1986).

Salvelinema walkeri (Ekbaum, 1935) Figs. 3, 4

Syn.: *Cystidicola walkeri* Ekbaum, 1935.

Description (based on specimens from *O. kisutch*): Medium sized, whitish nematodes with smooth cuticle. Body somewhat narrowed towards anterior end; cephalic end rounded in lateral view. Oral opening large, almost circular, surrounded by four small submedian cephalic papillae and pair of lateral amphids. Lateral pseudolabia well developed, relatively broad. Cuticle surrounding mouth thickened dorsally and ventrally to form two semicircular bands extending from one pseudolabium to other. Vestibule (stoma) divided into anterior, well developed prostom and posterior, narrower cylindrical part of vestibule. Prostom broad, cup-shaped in lateral view, but actually being constricted centrally into two main chambers, dorsal and ventral, and its posterior portion laterally twisted. Muscular oesophagus short, cylindrical, glandular oesophagus relatively narrow, approximately 3-4 times longer than muscular one. Nerve ring encircling muscular oesophagus near its middle. Excretory pore near junction of both parts of oesophagus. Deirids very small, hardly visible, short distance anterior to nerve ring level. Tail of both sexes conical.

Male (10 specimens): Length of body 16,890-20,190, maximum width 371-412. Length of whole vestibule including prostom 180-208; prostom 28-48 long, 72-76 wide in lateral view. Muscular oesophagus 383-539 long, 44-61 wide; glandular oesophagus 1,510-1,870 long, 87-174 in maximum width; length ratio 1 : 3.1-4.1. Deirids, nerve ring and excretory pore 310-362, 383-461 and 635-679, respectively, from anterior extremity. Caudal alae and ventral precloacal cuticular ridges well developed. Preanal papillae: 18-26 pairs of subventral papillae present, being arranged in couples; members of each couple formed by a narrower and longer more lateral papilla and a broader and shorter papilla shifted more ventrally. Postanal papillae: 6 pairs of single papillae present, those of last pair being very small and shifted more ventrally; next to last pair may be highly asymmetrical (Fig. 2M). Left spicule slender, 1,140-1,170 long; shaft measuring 224-232, representing 19 to 20% of spicule length; proximal end of spicule somewhat broader, distal tip sharply pointed. Right spicule short, boat-shaped, 152-192 long; proximal end blunt, distal end rounded, with narrow membranous cover. Length ratio of spicules 1 : 5.9-7.1. Tail 310-362 long.

Female (10 gravid specimens): Length of body 18,150-29,030, maximum width 453-597. Length of whole vestibule including prostom 136-220; prostom 48-56 long and 72-88 wide in lateral view. Muscular oesophagus 365-531 long, 52-61 wide; glandular oesophagus 1,470-1,840 long, 87-104 in maximum width; length ratio of both parts of oesophagus 1 : 3.2-4.0. Deirids, nerve ring and excretory pore 246-400, 296-487 and 661-809, respectively, from anterior extremity. Tail conical, 357-409 long, with rounded tip. Vulva situated in anterior half of body, 8,490-8,760 from anterior extremity (at 30-40% of body length). Vagina muscular, narrow, about 870 long, directed posteriorly from vulva. Uterus amphidelphic. Mature eggs oval, thick-walled, larvated, size 42-54 × 20-24; one pole of egg provided with small polar plug and two long, thread-like filaments about 360 long; opposite egg pole smooth.

Hosts: *Oncorhynchus kisutch* (Walbaum) (type host) and *O. clarki* (Richardson) (Salmonidae, Salmoniformes).

Site of infection: Swimbladder.

Localities: Gulf of Alaska (52°06'N; 144°56'W), eastern North Pacific Ocean (*O. kisutch*; 19 December 1992); Henderson Lake (*O. kisutch*; 24 April 1979) and De Mamiel Creek (*O. kisutch* and *O. clarki*; 7 May 1979), Vancouver Island, B.C., Canada. Otherwise previously reported from the western coast of southern British Columbia, Canada, and northern California, USA (Margolis 1967, Margolis and Arthur 1979, McDonald and Margolis 1995).

Intermediate hosts: In Canada *Ramellogammarus vancouverensis* Bousfield (Amphipoda) (Margolis and Moravec 1982).

DISCUSSION

A detailed study of *Salvelinema* specimens of the present material showed that two species, *S. salmonicola* and *S. walkeri*, were included. Their morphology proved to be very similar and, although some additional small differences were found between them, the only feature by which these species can be reliably distinguished seems to be the number and arrangement of polar filaments on mature eggs. Whereas the eggs of *S. walkeri* possess two filaments on only one pole, those of *S. salmonicola* are provided regularly with two filaments on either pole or, sometimes, even three filaments were found on one pole of some eggs. Interspecific differences were found in the direction of the vagina, but the importance of this feature needs further verification.

Although it was not difficult to assign specimens of the present material from *O. kisutch*, *O. masou*, *O. mykiss* and *S. malma* to the respective *Salvelinema*

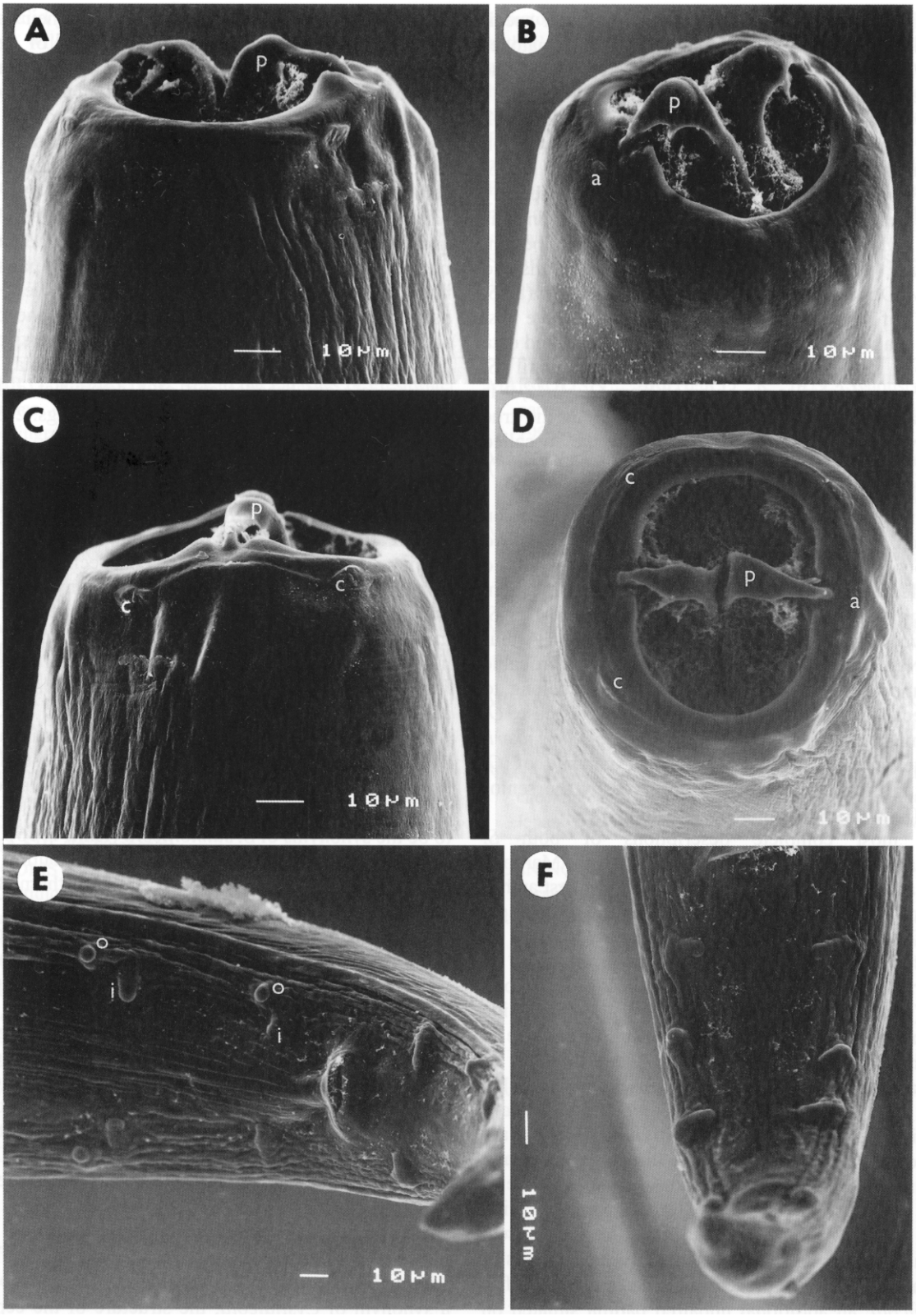

Fig. 4. *Salvelinema walkeri* (Ekbaum, 1935), SEM micrographs. **A** – cephalic end, dorsoventral view; **B** – same, subapical view; **C** – same, lateral view; **D** – same, apical view; **E** – region of cloaca, ventral view; **F** – male tail, ventral view. Abbreviations: a – amphid; c – cephalic papilla; i – inner preanal papilla; o – outer preanal papilla; p – pseudolabium.

species, because these samples included gravid specimens with mature eggs, the identification of nematodes from *O. clarki* and *O. nerka* was more problematic due to the lack of gravid females.

However, the specimens from *O. clarki* (1 male and 2 young females) from the De Mamiel Creek on Vancouver Island in Canada were identified as *S. walkeri*, because their vagina was directed posteriorly and because *S. salmonicola* does not occur in this locality, whereas *S. walkeri* occurs in large numbers in *O. kisutch* (personal communication of L. Margolis and T. E. McDonald); also the species identification (as *S. walkeri*) of larvae from the amphipod intermediate host in this locality has been based on these unpublished data (Margolis and Moravec 1982). However, until *S. walkeri* gravid females are obtained from *O. clarki*, it is not clear whether this host species serves as the true definitive host for this nematode or only the so called paradefinitive host in the conception of Odening (1976), in which the parasite cannot reproduce.

The nematode sample from *O. nerka* from Henderson Lake on Vancouver Island in Canada contained numerous males, young females and larvae, but no gravid females were obtained for species identification. Although *O. nerka* has been reported as the host of *S. salmonicola* in Canada and Japan (Margolis and Arthur 1979, Nagasawa et al. 1987) and it is highly probable that nematodes of the present material also belong to this species, it cannot be excluded that, in this case, *O. nerka* might act as a paradefinitive host of *S. walkeri*; the latter species is a very abundant parasite of *O. kisutch* in the same locality as observed by the senior author (F. M.) (see Materials and methods).

The most complete descriptions of both *S. salmonicola* and *S. walkeri* were provided by Margolis (1967) and Margolis and Kabata (1967). The first author mentions that *S. salmonicola* males have, on average, three fewer couples of preanal papillae than in *S. walkeri*, although some overlap occurs in the range of numbers of these papillae in the two species; he reports 12-24 (commonly 16-20) preanal papillae on each side in *S. salmonicola* and 20-30 (mostly 20-26) papillae in *S. walkeri*. This almost corresponds to the findings of these papillae in nematodes of the present material (19-21 and 18-26 papillae in *S. salmonicola* and *S. walkeri*, respectively). Postanal papillae in both species are reported by Margolis (1967) to be formed by five pairs of distinct subventral papillae and, in some specimens, by an additional sixth pair of small papillae, lying medial to the fifth subventral pair. In the present material, in all males of both species always six pairs of postanal papillae were present; in some specimens of *S. salmonicola*, an additional unpaired papilla situated on the left side between the papillae of the last two pairs was observed (Fig. 1F). Thus there is considerable variability in the numbers and arrangements of male caudal papillae in both of these species which cannot be used for their distinction. It is also possible to confirm the statement of Margolis (1967) that there is not a sharp dividing line between these two species in their various measurement characteristics. The presence of deirids, found in both *S. salmonicola* and *S. walkeri*, has not previously been reported for any *Salvelinema* species.

The SEM study of the cephalic end of both *Salvelinema* species showed no substantial interspecific differences in the structure of cephalic details. As compared to the illustrations of the cephalic ends of *S. salmonicola* and *S. walkeri* given by Margolis (1967) and Margolis and Kabata (1967), the pseudolabia of both species have markedly narrow distal parts and much broader proximal parts in an apical view, each pseudolabium being provided with a pair (one dorsal and one ventral) of small spike-like outgrowths situated approximately at its middle. The pseudolabia of *S. salmonicola* are broader and of a somewhat different shape as compared to those of *S. walkeri* (Figs. 2 C, E, 4 B, D).

Margolis (1968), reviewing the Japanese *Salvelinema* species, considered *S. iwana* (Fujita, 1928), *S. amemasu* (Fujita, 1939), *S. kosugii* (Fujita, 1939), *S. oncorhynchi* (Fujita, 1939) and *S. salvelini* (Fujita, 1939) (= *S. ishii* (Fujita, 1941)) as possibly conspecific with *S. salmonicola*, but he did not formally synonymised them with the latter species. All these species were inadequately described and their type specimens were not found. Since the hosts of these species (*Salvelinus leucomaenis*, *S. pluvius* and *Oncorhynchus masou*) are all reported as hosts of *S. salmonicola* in Japan (Nagasawa et al. 1987) nor can they be distinguished from *S. salmonicola*, and the second established *Salvelinema* species, *S. walkeri*, has not been recorded from Japan, we consider all the above mentioned species to be the synonyms of *S. salmonicola* (Ishii, 1916).

According to Margolis (1967), the distribution of *S. salmonicola* in North Americas is from northern British Columbia to the Alaska Peninsula, whereas that of *S. walkeri* is from southern British Columbia to northern California. However, the present data show that *S. walkeri* is also distributed northward up to the Gulf of Alaska by the host's ocean migration.

In our opinion, *Salvelinema* is a well established genus, distinctly separated from the closely related genus *Cystidicola* Fischer, 1798 mainly by the presence of well developed pseudolabia inserted on the base of the prostom forming an almost complete partition. However, it seems to be very similar to *Comephoronema* Layman, 1933, at present represented by two species, *C. werestschagini* Layman, 1933 (type species) and *C. oschmarini* Trofimenko, 1974, both intestinal parasites of Palaearctic freshwater fishes. Although Chabaud (1975) considered *Comephoronema* a synonym of *Cystidicola*, the structure of the cephalic end of *C. oschmarini* described by Trofimenko (1974) shows that it is more similar to *Salvelinema* than to *Cystidicola*. Unfortunately, the cephalic end of the type species of *Comephoronema*, *C. werestschagini*, has been inadequately described. Nevertheless, for the time

being, we consider it necessary to take *Comephoronema* for a valid genus. It cannot be excluded that subsequent studies will show the identity of *Comephoronema* and *Salvelinema*; in this case the latter would become a junior synonym of the former.

Acknowledgements. We thank A. Ohtaka and his students, Faculty of Education, Hirosaki University, Japan for providing nematode specimens from *O. mykiss* from Tsugaru-Juniko Lakes, northern Honshu, and the late L. Margolis, Pacific Biological Station, Nanaimo, B.C., Canada for lending us the Japanese specimens of *Salvelinema* from the collection of his institute and for enabling a new collection of *Salvelinema* nematodes from fishes on Vancouver Island during the senior author's (F. M.) short stay in Canada in 1979; T. E. McDonald and N.P. Boyce, Pacific Biological Station in Nanaimo, helped with collecting in the field. We also thank the staff of the Laboratory of Electron Microscopy of the Institute of Parasitology, ASCR, České Budějovice, for their technical assistance and I. Husáková from the Laboratory of Helminth Biology of the same Institute for helping prepare the illustrations. Part of the work was done during F. Moravec's stay at the National Research Institute of Far Seas Fisheries, Shimizu, which was supported by the Japan Science and Technology Corporation.

REFERENCES

BAUER O. N. (Ed.) 1987: Key to the Parasites of Freshwater Fishes of the Fauna of the USSR. Part 3. Nauka, Leningrad, 583 pp. (In Russian.)

CHABAUD A. G. 1975: Keys to genera of the order Spirurida, Part 2. Spiruroidea, Habronematoidea and Acuarioidea. CIH Keys to the Nematode Parasites of Vertebrates 3. Commonwealth Agricult. Bureaux, Farnham Royal, Bucks, 58 pp.

FUJITA T. 1928: Further studies on nematodes from fishes of Lake Biwa. Dobutsugaku Zasshi 40: 303-314. (In Japanese, Engl. Summary.)

FUJITA T. 1939: On the Nematoda-parasites of the Pacific salmon. J. Fac. Agric. Hokkaido Imp. Univ. 42: 239-265 + Plts. X-XIV.

KOSHIDA T. 1905: On a species of Nematoda parasitic in salmonid fishes. Hokkaido Suisan Zasshi 5: 7-9. (In Japanese.)

KOSHIDA T. 1910: Survey of parasitic nematodes in fish farms. Third Annu. Rep. Hokkaido Fish. Exp. Stn., pp. 516-519. (In Japanese.)

MARGOLIS L. 1967: The swimbladder nematodes (Cystidicolinae) of Pacific salmons (genus *Oncorhynchus*). Can. J. Zool. 45: 1183-1199.

MARGOLIS L. 1968: Review of the Japanese species of *Cystidicola*, *Metabronema* and *Rhabdochona* (Nematoda) from salmonoid fishes. Res. Bull. Meguro Parasitol. Mus., No. 2, 23-44.

MARGOLIS L., ARTHUR J. R. 1979: Synopsis of the parasites of fishes of Canada. Bull. Fish. Res. Board Can. 199: vi + 269 pp.

MARGOLIS L., KABATA Z. 1967: The structure of the buccal region of *Salvelinema* Trofimenko, 1962 (Nematoda: Cystidicolinae). Can. J. Zool. 45: 1067-1072.

MARGOLIS L., MORAVEC F. 1982: *Ramellogammarus vancouverensis* Bousfield (Amphipoda) as an intermediate host for salmonid parasites in British Columbia. Can. J. Zool. 60: 1100-1104.

McDONALD T. E., MARGOLIS L. 1995: Synopsis of the parasites of fishes of Canada: Supplement (1978-1993). Can. Spec. Publ. Fish. Aquat. Sci. 122: 265 pp.

MORAVEC F., NAGASAWA K. 1986: New records of amphipods as intermediate hosts for salmonid nematode parasites in Japan. Folia Parasitol. 33: 45-49.

NAGASAWA K., URAWA S., AWAKURA T. 1987: A checklist and bibliography of parasites of salmonids of Japan. Sci. Rep. Hokkaido Salmon Hatchery, No. 41, 1-75.

ODENING K. 1976: Conception and terminology of hosts in parasitology. Adv. Parasitol. 14: 1-93.

TROFIMENKO V. YA. 1974: New data on nematodes of the genera *Cottocomephoronema* and *Comephoronema*, parasites of burbot. Tr. GELAN 24: 199-207. (In Russian.)

Received 25 February 1998

Accepted 1 October 1998