

Research Article

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Redescription of *Proteocephalus fallax* La Rue, 1911 (Cestoda) and a list of proteocephalid tapeworms of whitefish (*Coregonus* spp.)

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Abstract: Tapeworms of the genus *Proteocephalus* Weinland, 1858 (Cestoda: Proteocephalidae) are common and widespread intestinal parasites of whitefish (*Coregonus* spp., Salmonidae: Coregoninae). Previous taxonomic studies, based solely on morphology and inconsistently fixed specimens, concluded that all salmoniform fish, including whitefish, are parasitised by a single euryxenous and highly polymorphic species, *Proteocephalus longicollis* (Zeder, 1800). However, recent molecular phylogenetic analyses have revealed the existence of several species specific to individual genera or even species of salmoniform fish. In this study, *Proteocephalus fallax* La Rue, 1911 is redescribed based on newly collected and genetically characterised specimens from several *Coregonus* species in Switzerland, the type locality of the species, and in Norway. This cestode was previously synonymised with *P. exiguus* La Rue, 1911, a parasite of whitefish in North America, but the two species are not closely related. *Proteocephalus fallax* differs from *P. exiguus* in its larger body size, wider proglottids, shorter cirrus sac and broader scolex. In addition, the other *Proteocephalus* species described in whitefish are briefly discussed, with comments on their validity, host range and distribution.

Keywords: Eucestoda, Proteocephalidae, Salmonidae, morphology, taxonomy, distribution, Europe

Freshwater whitefish belong to the subfamily Coregoninae, which includes freshwater and anadromous whitefish species as well as ciscoes. This subfamily is one of three within the salmon family Salmonidae, whose members are mainly distributed in the cooler waters of the northern hemisphere. Many species or ecotypes of whitefish, especially those from the Great Lakes and perialpine lakes of Europe, are either extinct or threatened with extinction (Kottelat 1997, Kottelat and Freyhof 2007, Vonlanthen et al. 2012). Of the 12 freshwater fish that are considered extinct in Europe, six belong to the genus *Coregonus* (Closs et al. 2016). All *Coregonus* species are also protected under Appendix III of the Bern Convention.

Whitefish harbour numerous parasites, including tapeworms of the genus *Proteocephalus* Weinland, 1858 (Cestoda: Proteocephalidae), which are among the most common intestinal parasites of whitefish (Hoffman 1999, Gibson et al. 2005). Seven species of the *Proteocephalus* species-aggregate (see de Chambrier et al. 2004) were described in whitefish, but all of them were later synonymised with *Proteocephalus longicollis* (Zeder, 1800), as they do not exhibit distinct morphological features and share a uniform morphological appearance (Scholz and Hanzelová 1994, 1998, Han-

zelová et al. 1995, Hanzelová and Scholz 1999, Scholz et al. 2007). Moravec (2004) subsequently reported *P. longicollis* in the following whitefish species in Europe: *Coregonus autumnalis* (Pallas), *C. fera* Jurine, *C. gutturosus* (Gmelin), *C. lavaretus* (Linnaeus), *C. macrophthalmus* Nüsslin, *C. nasus* (Pallas), *C. peled* (Gmelin), *C. wartmanni* (Bloch), *C. widegreni* Malmgren, and *Stenodus leucichthys* (Güldenstädt).

However, Brabec et al. (2023) have demonstrated, using cytochrome c oxidase subunit I (*cox1*) sequence data, that different salmonids in Europe and North America harboured different and unrelated *Proteocephalus* species. Their phylogenetic analyses also showed that *Proteocephalus* populations in European whitefish (*Coregonus* spp.) formed a clearly defined monophyletic species-level lineage, despite the wide geographical dispersion of the collected specimens (Switzerland and northern Norway).

Brabec et al. (2023) also provided data that allowed for the resurrection of two *Proteocephalus* species, *P. exiguus* La Rue, 1911 from the North American coregonids, and *P. fallax* La Rue, 1911 from the European whitefish. In addition, a population genetic analysis based on reduced-representation genomic data of *P. fallax* populations from sympatric *Coregonus* spp. within and across lakes confirmed that

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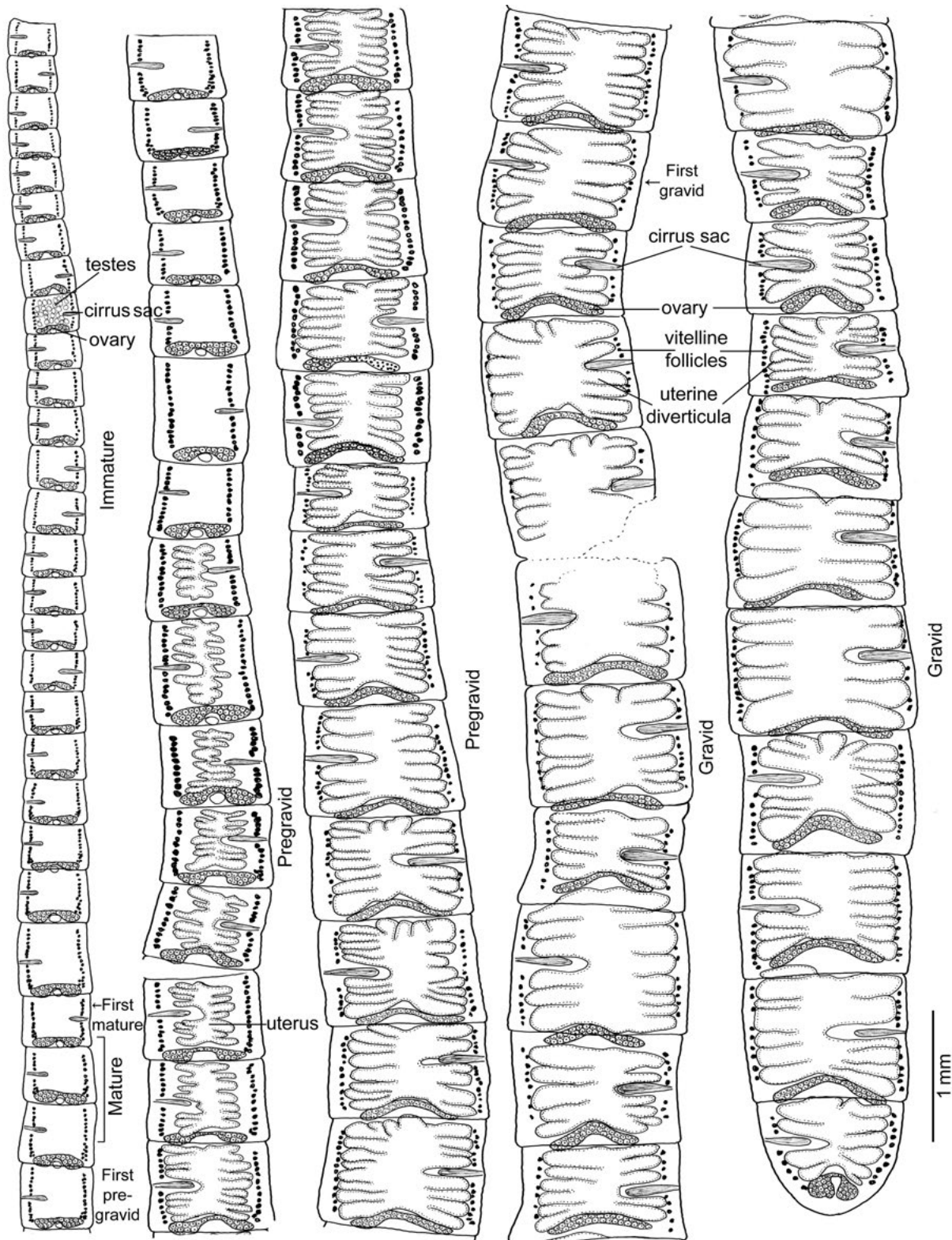


Fig. 1. *Proteocephalus fallax* La Rue, 1911 from *Coregonus heglingus* Schinz, Lake Walen, Switzerland – strobila. Immature proglottids – without spermatozoa in vas deferens; mature proglottids – with spermatozoa in vas deferens; pregravid proglottids – with unripe eggs devoid of embryonic hooks; gravid proglottids – with fully formed eggs, i.e., with oncospheres bearing three pairs of embryonic hooks.

the tapeworm is allopatrically differentiated between lakes, and to some extent different between sympatric hosts within lakes, but represents a single species (Brabec et al. 2024).

In the present work, *P. fallax* is redescribed on the basis of uniformly fixed and genetically characterised spec-

imens from several whitefish species in Switzerland and Norway. In addition, *Proteocephalus* tapeworms described from whitefish in the Palearctic and Nearctic are briefly discussed, with comments on their taxonomic status, host range and distribution.

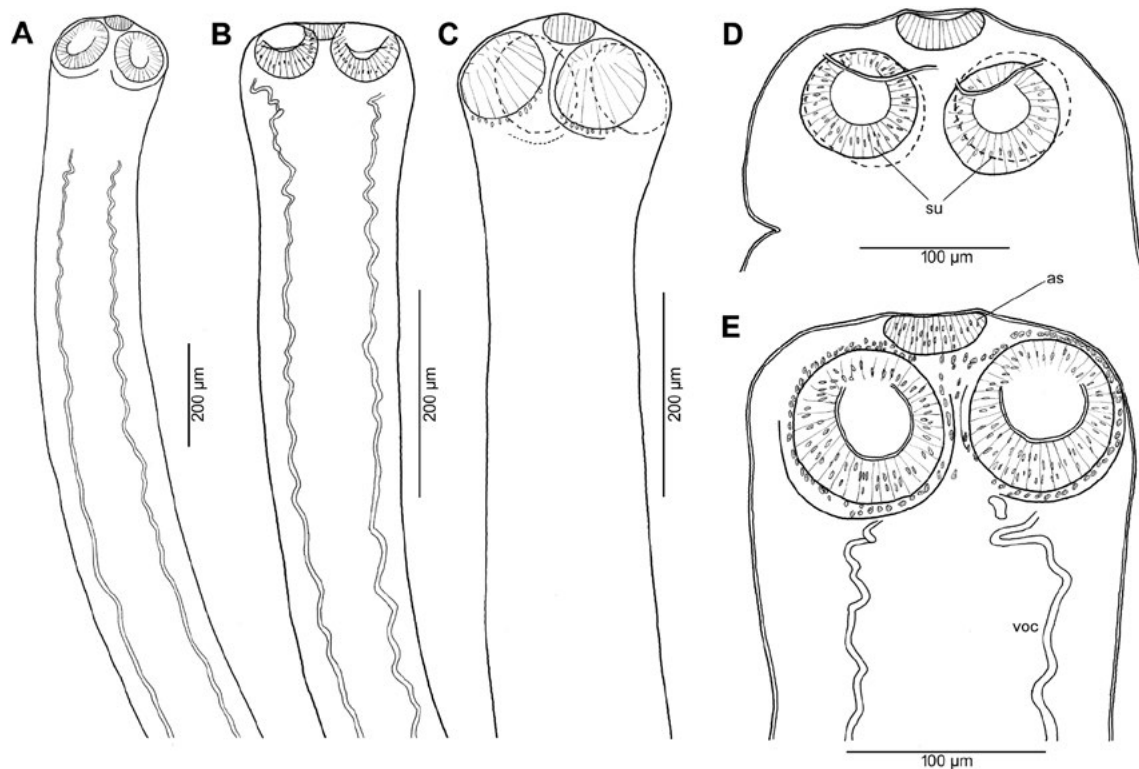


Fig. 2. *Proteocephalus fallax* La Rue, 1911 from *Coregonus heglingus* Schinz, Lake Walen, Switzerland (A, C); *C. lavaretus* (Linnaeus), Lake Suohpatjávri, Norway (B, E); *C. confusus* Fatio, Lake Biel, Switzerland (D). A–C – anterior end; D, E – scolex.

MATERIALS AND METHODS

The following specimens were examined as part of the present study and are deposited in the Natural History Museum, Geneva, Switzerland (MHNG-PLAT) and the Helminthological collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic (IPCAS): numerous heat-killed specimens from *Coregonus confusus* Fatio, Lake Biel (Lac Bienné), collected in July 2017; from *C. profundus* Selz, Dönz, Vonlanthen et Seehausen, Lake Thun, January 2018; from *C. heglingus* Schinz, Lake Walen, November 2017 and January 2018; from *C. muelleri* Selz et Seehausen, Lake Lucerne, August 2017, all specimens from Switzerland, collected by Brabec et al. (2024); from arctic *C. lavaretus* (littoral ecomorph), Lake Langfjordvatn, September 2017 and Lake Suohpatjávri, September 2017, all specimens from Norway, collected by Brabec et al. (2024) (MHNG-PLAT-130093–130102, 130104–130125, 130127, 130128; IPCAS C-999/1, C-999/2). In addition, the data of Scholz and Hanzelová (1994), who studied the types of *Proteocephalus fallax* (National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA – USNM 1348661) and *Proteocephalus exiguus* (USNM 1348659, 1348660), were considered.

RESULTS

Proteocephalus fallax La Rue, 1911 Figs. 1–4; Table 1

Type host: *Coregonus fera* Jurine (Salmonidae: Coregoninae; currently considered extinct – Froese and Pauly 2024).

Additional hosts (confirmed by molecular data): *Coregonus alpinus* Fatio, *C. confusus*, *C. heglingus*, *C. lavaretus* (littoral ecomorph), *C. steinmanni* Selz, Dönz, Vonlanthen et Seehausen, and those in Brabec et al. (2024).

Type locality: Lake Luzern, Switzerland.

Distribution and records (confirmed molecularly): Europe – Norway, Switzerland (La Rue 1911, 1914, Brabec et al. 2023, 2024).

Type material: Syntypes (fragments of two specimens) from *Coregonus fera*, found by Fritz Zschokke in Lake Lucerne, Switzerland in 1882–1883 and designated by him as “*Taenia ocellata*” Rudolphi, 1802 (USNM 1348661; see Scholz and Hanzelová 1994).

Representative DNA sequences: OP972513–OP971515 (*lsrDNA*), OP972569, OP972571 (*cox1*). Gene assemblies derived from double digest restriction-site associated DNA (ddRAD) data are available from Zenodo (10.5281/zenodo.7404234) (see Brabec et al. 2023, 2024).

Redescription (strobilar data taken from seven specimens from *Coregonus heglingus*, *C. muelleri* and *C. profundus* in Switzerland and *C. lavaretus* in Norway – Table 1; measurements of scoleces were taken from 8 and 15 specimens from Switzerland and Norway, respectively; measurements of syntype taken by Scholz and Hanzelová 1994 in brackets; all measurements are in micrometres unless otherwise stated).

Proteocephalidae, Proteocephalinae, *Proteocephalus*-aggregate. Total body length up to 121 mm, maximum width up to 1.4 mm [1.2 mm]. Strobila acraspedote, anapolytic, slightly, continuously widening towards posterior end (Fig. 1), consisting of numerous immature proglottids (up to appearance of spermatozoa in vas deferens; > 24 in specimen illustrated in Fig. 1), very few mature (up to appearance of eggs in uterus; only three proglottids in Fig. 1), many pregravid (up to appearance

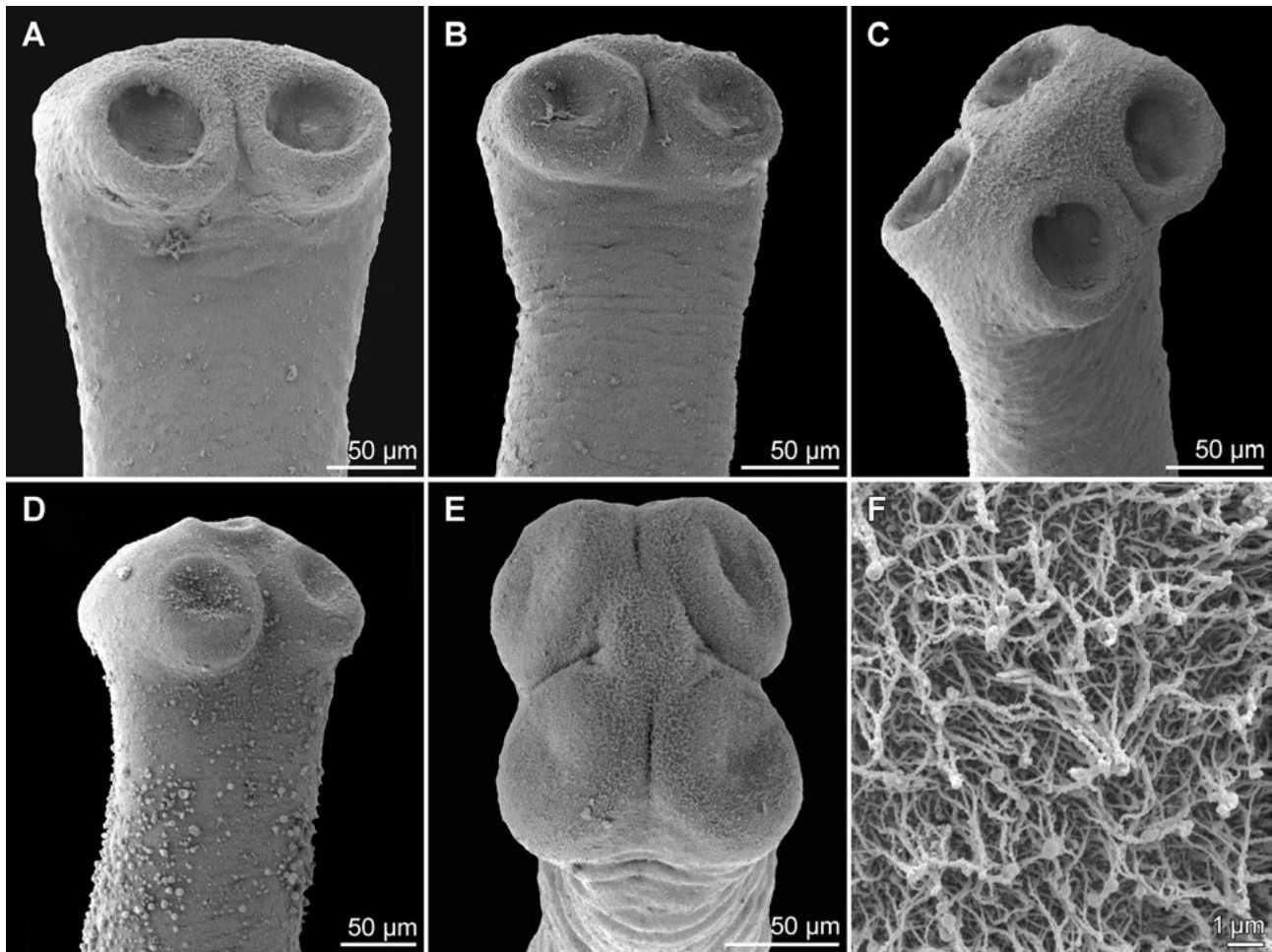


Fig. 3. Scanning electron micrographs of scoleces of *Proteocephalus fallax* La Rue, 1911 (Cestoda: Proteocephalidae) from *Coregonus heglingus* Schinz, Lake Walen, Switzerland (A–C), *C. profundus* Selz, Dönz, Vonlanthen et Seehausen, Lake Thun, Switzerland (D) and *C. lavaretus* (Linnaeus), Lake Langfjordvatn, Norway (E, F). A, B, D – frontal view; C – subapical view; E – apical view; F – filiform microtriches on the apex of the scolex. Note that the rudimentary apical sucker, which lacks a functional cavity, is not always clearly visible under the scanning electron microscope (as in Fig. 3C,E).

of hooks in oncospheres; 30 proglottids in Fig. 1), and numerous gravid (with eggs containing oncospheres with three pairs of embryonic hooks; 21 proglottids in Fig. 1). Immature proglottids wider than long to slightly wider than long (Fig. 1), mature proglottids wider than long to longer than wide, 330–710 × 410–760 (length: width ratio 1: 0.69–1.17), pregravid proglottids variable in shape, from wider than long to longer than wide, 475–980 × 320–850 (length: width ratio 1: 0.55–1.45), gravid proglottids quadrate to longer than wide, 660–1,550 × 490–1,370 (length: width ratio 1: 0.84–1.74) (Fig. 1).

Anterior part of body without proglottids narrow, with round to almost blunt scolex slightly wider than neck region (proliferative zone) 115–275 [93] wide (n = 21) (Figs. 2, 3). Scolex 165–260 [173] wide (n = 21), with four spherical suckers directed anterolaterally (Figs. 2, 3). Suckers 60–110 [63–71] in diameter (n = 45), relatively large compared to width of scolex (Fig. 4B–D), representing 30–50% of scolex width (n = 35). Apical sucker present, rudimentary (without functional cavity; not always clearly visible under the scanning electron microscope), 20–31 long (thick) (n = 16) and 36–64 [40] wide (n = 17); apical

sucker width representing 51–80% of diameter of lateral suckers (n = 25). Numerous cells with granular content surrounding suckers and in apical part of scolex (Fig. 2E). Whole surface of scolex covered with dense filiform microtriches (filitriches) (Fig. 3F).

Inner longitudinal musculature well developed. Two pairs of almost straight osmoregulatory canals present. Ventral canals thin-walled, 10–20 in diameter, without lateral canals (Fig. 4B,C,E), sinuous in neck region and scolex (Fig. 2A,B,E); dorsal canals thick-walled, much narrower than ventral canals, 3–5 in diameter (Fig. 4A).

Testes medullary, ovoid to subspherical, 40–80 × 35–75 [39–67 in diameter], in two irregular, incomplete layers (Fig. 4A), 38–71 [32–39] in number (means in individual specimens 46–60; n = 31). Testes densely packed, forming single field between anterior margin of proglottid, ovary and vitelline follicles, only slightly overlapping osmoregulatory canals laterally (Fig. 4A); testes missing only in middle of proglottid with loops of vas deferens (Fig. 4A).

Vas deferens strongly coiled, with loops occupying large median field, with numerous loops overlapping proximal half of cirrus sac on ventral side (Fig. 4E). Cirrus sac elon-

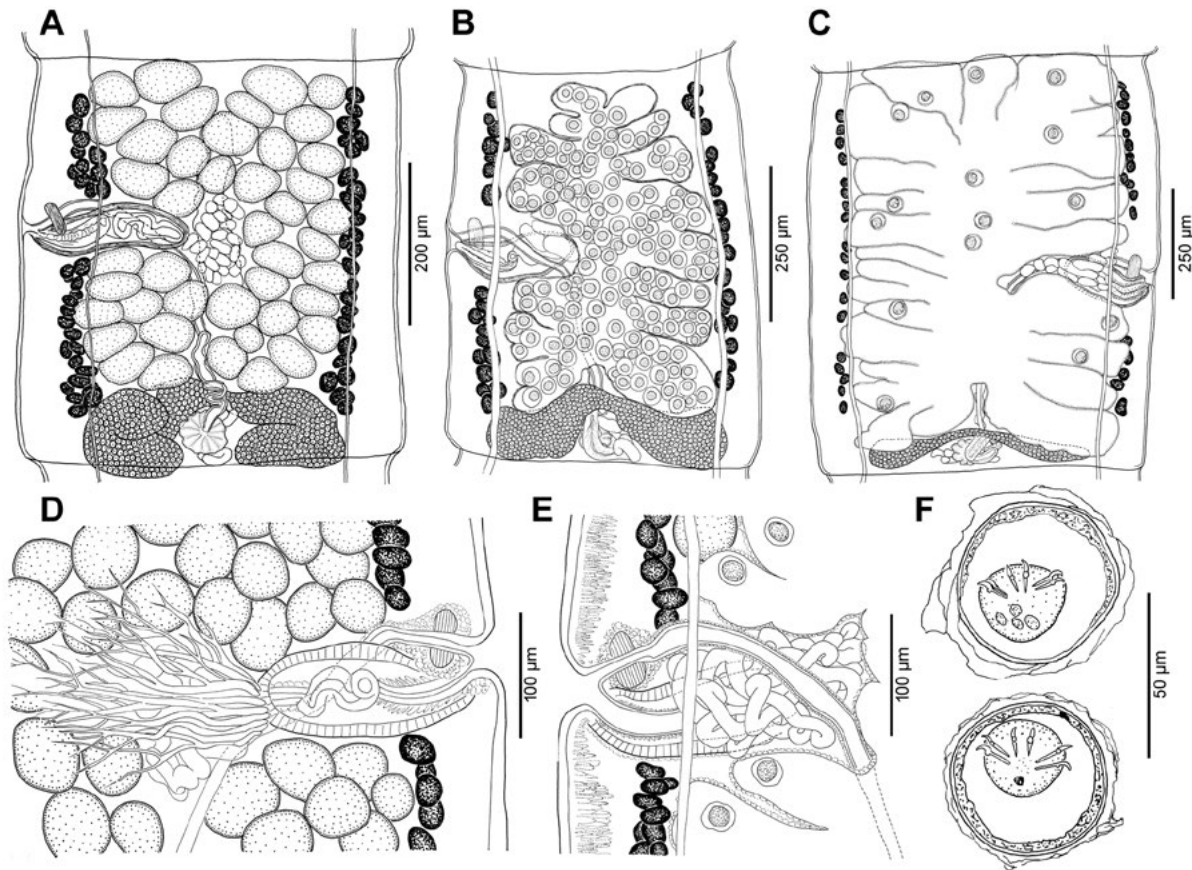


Fig. 4. *Proteocephalus fallax* La Rue, 1911 from *Coregonus lavaretus* (Linnaeus), Lake Suohpatjávri, Norway (A, C–E); and *C. muelleri* Selz et Seehausen, Lake Lucerne, Switzerland (B). **A** – mature proglottid, dorsally; **B** – pregravid proglottid, ventrally; **C** – gravid proglottid, ventrally; **D, E** – terminal genitalia, dorsally and ventrally; **F** – eggs. Note numerous muscle fibres attached to the proximal end of the cirrus sac in D.

gated, thick-walled (Fig. 4D), 120–240 [189–366] long \times 43–95 [61–96] wide, cirrus sac length: width ratio 1.90–3.43; length of cirrus sac represents 26–42% [32–52%] ($x = 28$ –37% in individual specimens; $n = 41$) of proglottid width. Proximal end of cirrus sac attached to numerous muscle fibres (retractors; Fig. 4D). Internal sperm duct coiled, occupies proximal half of cirrus sac (Fig. 4A,D). Cirrus short, muscular, representing about 1/2 of length of cirrus sac (Fig. 4D). Common genital atrium narrow, deep (Fig. 4D,E), alternating irregularly, slightly pre-equatorial to slightly postequatorial, at 43–58% ($x = 46$ –58%; $n = 39$) of length of proglottid from its anterior margin (Fig. 4A–C).

Ovary compact, medullary, bilobed, with narrow isthmus and lateral wings only slightly surpassing osmoregulatory canals laterally (Fig. 4A,B). Length of ovary, i.e. width of ovarian lobes, representing 14–27% of proglottid length ($x = 17$ –21%; $n = 57$); total width of ovary (horizontal) representing 64–79% of proglottid width ($x = 68$ –76%; $n = 57$). Mehlis' gland subspherical to spherical, 40–80 wide; width of Mehlis' gland representing 9–19% of proglottid width ($x = 10$ –14; $n = 46$). Relative ovarian size (see de Chambrier et al. 2012), 7.7–11.6% ($n = 8$).

Vaginal canal slightly sinuous proximally, with elongate ovoid seminal receptacle situated anterodorsal to ovarian isthmus, crossing proximal part of cirrus sac ventrally. Terminal (distal) part of vaginal canal (pars copulatrix vagi-

nae) always anterior to cirrus sac (Fig. 4A–E), with large, ring-like vaginal sphincter, 36–70 [27–65] in diameter, surrounded by chromophilic cells (Fig. 4D,E).

Vitelline follicles medullary, forming two narrow lateral bands of relatively large follicles between anterior margin of proglottids and anterior margin of ovary (Fig. 4A,B), absent at level of cirrus sac and vagina on ventral side (Fig. 4E). Length of bands represents 73–87% ($x = 78$ –84%; $n = 41$) and 69–89% ($x = 76$ –86; $n = 41$) of length of proglottid on poral and aporal side, respectively.

Uterus medullary, with type 2 development (see de Chambrier et al. 2004). Uterine stem lined with chromophilic cells appearing in last immature proglottids; in mature proglottids, uterine lumen gradually extends from base to apex into each digitate diverticula lined with chromophilic cells as in pregravid and gravid proglottids. Uterus with 5–12 [5–9] and 6–12 [5–9] lateral diverticula on poral and aporal sides, respectively (Fig. 4B,C); width of uterus represents up to 98% of proglottid width.

Eggs (measured in distilled water) spherical, hyaline outer envelope not observed in whole mounts; embryophore bilayered, with external layer 41–50 in diameter ($n = 11$) and internal envelope variable in size; oncosphere spherical to ovoid, 18–27 in diameter ($n = 11$) (Fig. 4F).

Comments. *Proteocephalus fallax* was described by La Rue (1911) and characterised in more detail three years lat-

Table 1. Measurements of *Proteocephalus fallax* La Rue, 1911 from whitefish (*Coregonus* spp.) in Europe. Minimum and maximum values are in bold.

Host code	LUZ 50c	THU 60a	WAL 24b	SUO 101c	LAN 087a-c	
Collection No.	USNM 1348661	MHNG -PLAT-0159523	MHNG -PLAT-0159525	MHNG -PLAT-0159524	MHNG- -PLAT-0130100	IPCAS C-999/1
Country	Switzerland	Switzerland	Switzerland	Switzerland	Norway	Norway
Note	Lake Lucerne (type locality)	Lake Lucerne (type locality)	Lake Thun	Lake Walen	Lake Suohpatjärvi	Lake Langfjordvatn
	measurements of syntypes	hot fixative	hot fixative	hot fixative	hot fixative	hot fixative
Total length (mm)	25	12	45	51	96	79– 121
Maximum width (mm)	1.2	0.5	0.7	0.7	1.1	1.0– 1.4
Mature proglottids – length	120–410	420	510–610	330 –365	355–465	475– 710
Mature proglottids – width	180–460	465	465–545	410 –435	515–540	550– 760
Length : width ratio	0.67–0.93	0.81–0.94	1.02– 1.17	0.78–0.88	0.69 –0.89	0.71–0.95
Pregravid proglottids – length	N/A	620	560–740	515–555	510–555	475–980
Pregravid proglottids – width	N/A	560	560–600	430–479	320 –580	510– 850
Length: width ratio	N/A	1.08–1.30	0.99–1.12	1.09–1.28	0.55 –1.07	0.77– 1.45
Gravid proglottids – length	490–1,340	N/A	765–795	660 –1,000	720–1,140	920– 1,550
Gravid proglottids – width	430–1,240	N/A	640–655	490 –635	635–855	760– 1370
Length : width ratio	0.96–2.14	N/A	1.16–1.22	1.30– 1.74	1.11–1.48	0.84 –1.22
Scolex width*	173	200**	N/A	200–222	165 –233	212– 260
Sucker diameter	63–71	60 –70	N/A	73–100	67–90	70– 110
Sucker diameter/scolex width ratio (%)	36–41%	30 –35%	N/A	36–45%	33– 50 %	33–41%
Apical organ – diameter	40	48	N/A	64	36 –51	37–47
Apical organ – length (thickness)	N/A	21	N/A	28– 31	20 –26	25–26
Apical sucker/sucker diameter (%)	N/A	69 – 80 %	N/A	64–73%	51 –64%	59–67%
Width of neck	93	N/A	N/A	130–180	115 – 275	160–200
Testis number (mean; n)	32–39	38 –56 (x = 46 , n = 8)	55– 71 (x = 60 , n = 8)	49–62 (x = 56, n = 5)	40–58 (x = 50, n = 10)	47–71 (x = 57, n = 12)
Testis length	39–67	55–70	50–75	40 – 80	42–66	50–75
Testis width	N/A	54–67	45–70	35 – 75	39–64	40–75
Cirrus sac length	189–366	130–185	170–210	120 –165	140–165	175– 240
Cirrus sac width	61–96	60–80	60–85	50–65	43 –64	50– 95
Length : width ratio (%)	2.60–4.20	1.90 –2.46	2.36–3.18	2.25–2.80	2.44 – 3.43	2.32–3.0
Cirrus sac – relative length	32–52%	32–38% (x = 35%, n = 11)	34 – 42 % (x = 37 %, n = 11)	29–38% (x = 34%, n = 9)	26 –31% (x = 28 %, n = 10)	29–37% (x = 32%, n = 12)
Genital pore – position	N/A	43 –49 (x = 46 %, n = 9)	45–55% (x = 49%, n = 10)	46–56% (x = 52%, n = 10)	51– 58 % (x = 54 %, n = 10)	43–53% (49%, n = 12)
Ovary – relative length ⁶	N/A	15–22% (x = 18%, n = 11)	20–24% (x = 21 %, n = 20)	15– 27 % (x = 20%, n = 12)	14 –26% (x = 20%, n = 14)	15–22% (x = 17 %, n = 16)
Ovary – relative width ⁴	N/A	69–76% (x = 73%, n = 12)	74 – 79 % (x = 76 %, n = 10)	70–77% (x = 74%, n = 10)	64 –72% (x = 68 %, n = 10)	71–78% (x = 75%, n = 11)
Ovary – surface ratio ⁵	N/A	N/A	9.9– 11.6 %	10.2–10.9%	8.0–9.6%	7.7 –8.6%
Mehlis' gland – width	N/A	55–67	55–75	45–60	40 –60	55– 80
Mehlis' gland – relative size ⁷	N/A	13–16% (x = 14 %, n = 10)	9–14% (x = 12%, n = 8)	10–14% (x = 12%, n = 10)	10 – 19 % (x = 13%, n = 7)	9–12% (x = 10 %, n = 11)
Vagina – position to cirrus-sac	anterior	anterior	anterior	anterior	anterior	anterior
Vaginal sphincter diameter	27–65	36 –40	45–55	40–55	43–52	45– 70
Poral vitelline follicles – relative length ⁹	N/A	77–83% (x = 80%, n = 9)	74–81% (x = 78 %, n = 11)	73 –82% (x = 78%, n = 11)	78–84% (x = 81%, n = 10)	80– 87 % (x = 84 %, n = 11)
Aporal vitelline follicles – relative length ⁸	N/A	69 –84% (x = 76 %, n = 9)	72–81% (x = 76%, n = 11)	76–86% (x = 81%, n = 11)	79–88% (x = 83%, n = 10)	82– 89 % (x = 86 %, n = 11)
Uterine diverticula on poral side	5–9	5 –7	8–10	8–9	8–10	8– 12
Uterine diverticula on aporal side	5–9	6 –8	8–9	8–11	9–10	8– 12
Embryophore diameter	31–41 (internal envelope)	N/A	N/A	N/A	41 –43***	42– 50
Oncosphere diameter	23–31	N/A	N/A	N/A	18 –21***	24– 27

*Measurements of scoleces were taken from 8 and 15 specimens from Switzerland and Norway, respectively; ** scolex of specimen from *C. confusus*, Lake Biel

*** Measurements were taken on whole-mounted slides

er (La Rue 1914), based on two specimens found in *Coregonus fera* from Lake Lucerne in Switzerland. Scholz and Hanzelová (1994), after examining type and voucher specimens, synonymised *P. fallax* with *P. exiguus*, as both species parasitise whitefish (*Coregonus* spp.) and do not differ morphologically. Later, the two species were synonymised with *P. longicollis* by Scholz and Hanzelová (1998) on the basis of the polymorphism of proteocephalid tapeworms of salmoniform fish (Hanzelová and Scholz 1999).

However, the most recent molecular phylogenetic study by Brabec et al. (2023) showed the existence of several *Proteocephalus* species in salmonids. These authors also demonstrated that the *Proteocephalus* specimens from

North American lake whitefish (= *P. exiguus*) are not closely related to the tapeworms of European whitefish, so that *P. fallax* is restricted to Europe. Therefore, *P. exiguus* and *P. fallax* have been resurrected and the latter taxon is redescribed here on the basis of consistently fixed and genetically characterised specimens from several *Coregonus* species in northern Norway and Switzerland.

La Rue (1914) distinguished *P. fallax* and *P. exiguus* on the basis of some metric characters. However, these often overlapped or did not correspond to the actual measurements of the individual species. Consequently, Scholz and Hanzelová (1994) synonymised the two species based on a study of their type specimens (syntypes), which were not

properly fixed (they were deformed and fragmented – see figs. 1 and 2 in Scholz and Hanzelová 1994). Molecular phylogenies show that *P. fallax* and *P. exiguus*, although morphologically similar, do not form sister lineages.

The present study, based on uniformly fixed specimens of *P. fallax*, revealed some minor, but consistent differences between the two otherwise quite similar species. *Proteocephalus fallax* has a larger and broader strobila (total length up to 12 cm and maximum width up to 1.4 mm compared to < 4 cm and 0.8 mm in *P. exiguus*, respectively), consisting of more proglottids which are usually slightly wider than long (Fig. 1), compared to the mostly elongate (longer than wide) proglottids of *P. exiguus* (see fig. 2 in Scholz and Hanzelová 1994). *Proteocephalus fallax* has also a wider scolex (165–260 µm compared to 112–160 µm in *P. exiguus*) and relatively shorter cirrus sac (1/4–2/5 of the proglottid width in *P. fallax*) compared to *P. exiguus* (length of the cirrus sac represents about 1/2 of proglottid width).

Proteocephalus fallax is closely related to *Proteocephalus percae* (Müller, 1780), a specific parasite of the European perch *Perca fluviatilis* Linnaeus in the Palearctic region (Brabec et al. 2023). The two species share a long cirrus sac and a well-developed, large vaginal sphincter (Fig. 4D,E; Scholz and Hanzelová 1998). However, *P. percae* differs from *P. fallax* by a more robust strobila consisting of broader proglottids. The anterior end of *P. percae* tapers continuously to the scolex, which is narrower than the neck region, whereas the scolex of *P. fallax* is clearly demarcated from the narrower neck region (Figs. 1–3; Scholz and Hanzelová 1998).

Molecularly characterised specimens of *P. fallax* are currently only available from Switzerland and Norway, but future research may confirm the presence of *P. fallax* in other European countries where whitefish occur.

DISCUSSION

Proteocephalus fallax is one of the earliest described cestode parasites of whitefish (La Rue 1911) and a common parasite of these fish in Switzerland and Norway (Brabec et al. 2024). However, its exact distribution range is not precisely known, as there are no molecular data on tapeworms of *Coregonus* spp. in other European countries and the eastern part of the Palearctic region, including Russia (Karelia, Kola Peninsula), where Freze and Kazakov (1969) described *Proteocephalus albulae* Freze et Kazakov, 1969 from the vendace *Coregonus albula* (Linnaeus).

The following text lists all taxa of the *Proteocephalus* species-aggregate of de Chambrier et al. (2004) described from whitefish (Coregoninae) and provides comments on their taxonomic status, hosts and distribution. The species are listed in chronological order. *Proteocephalus* species originally described from other salmonid genera such as *Oncorhynchus* Suckley, *Prosopium* Jorran, *Salmo* Linnaeus, *Salvelinus* Richardson and *Thymallus* Linck are not included. They were treated in detail by Scholz and Hanzelová (1998) and Hanzelová and Scholz (1999), who examined all available type specimens of these species.

Proteocephalus exiguus La Rue, 1911 – valid species

This cestode was briefly described by La Rue (1911) from several whitefish (*Coregonus* spp.) in Lake Michigan, Michigan, USA, with the blackfin cisco *Coregonus nigripinnis* (Milner) serving as the type host. La Rue (1914) provided a more detailed morphological characterisation of this tapeworm, which was frequently reported from North American whitefish, particularly lake whitefish *Coregonus clupeaformis* (Mitchill) and cisco *Coregonus artedi* Lesueur (Hoffman 1999).

Scholz and Hanzelová (1994) redescribed *Proteocephalus exiguus* on the basis of the type specimens, but Scholz and Hanzelová (1998) synonymised this species with *Proteocephalus longicollis* on the basis of morphological similarity. However, Brabec et al. (2023) resurrected the former species, which is a common parasite of whitefish in North America, while *P. longicollis* is a parasite of brown trout *Salmo trutta* Linnaeus in Europe. Reports of *P. exiguus* from Europe and Asia (see Freze 1965 for a list of suspected definitive hosts) were most likely misidentifications.

Proteocephalus fallax La Rue, 1911 – valid species

This species was resurrected by Brabec et al. (2023) and is redescribed in this paper (see above). It is a common parasite of *Coregonus* spp. in Switzerland and Norway; records in other European countries need to be confirmed by molecular data.

Proteocephalus laruei Faust, 1919 – taxonomic status uncertain

This species was described by Faust (1919) in the mountain whitefish *Prosopium williamsoni* (Girard) in Montana (USA) and then recorded in whitefish (*Coregonus* spp.), round whitefish *Prosopium cylindraceum* (Pennant) and sheefish *Stenodus leucichthys* in Canada and the United States (Freze 1965, Margolis and Arthur 1979, Hoffman 1999). *Proteocephalus laruei* has also been reported by Bangham and Adams (1954) in Canada from the sockeye salmon *Oncorhynchus nerka* (Walbaum) and from cutthroat trout *Oncorhynchus clarkii* (Richardson) in Wyoming, USA.

Proteocephalus laruei was synonymised by Hanzelová and Scholz (1999), who examined the holotype, but the species may be valid as it is the only *Proteocephalus* species described from *Prosopium*. Molecular data are needed to distinguish this taxon, which has also been commonly reported from whitefish (*Coregonus* spp.) in Canada (Margolis and Arthur 1979, McDonald and Margolis 1995), from *P. exiguus*, a common parasite of whitefish in North America (Hoffman 1999).

Proteocephalus coregoni Wardle, 1932 – taxonomic status uncertain

Proteocephalus coregoni was described by Wardle (1932) from *Coregonus* sp., probably *C. clupeaformis*, at an unspecified location in the Hudson Bay watershed. It was later reported from *C. artedi* and *C. clupeaformis* in Manitoba and Ontario (McDonald and Margolis 1995). The description of *Proteocephalus coregoni* by Wardle (1932) closely resembles that of *P. luciopercae* Wardle, 1932,

which was described by the same author from walleye and sauger (*Sander* spp.) in Canada. Therefore, it cannot be ruled out that the tapeworms found by Wardle (1932) actually belong to *P. luciopercae*. As the type material of this species does not exist, Hanzelová and Scholz (1999) did not include *P. coregoni* in their taxonomic revision and de Chambrier et al. (2017) listed this species as valid.

***Proteocephalus wickliffi* Hunter et Bangham, 1933 – taxonomic status uncertain**

Hunter and Bangham (1933) described this species from a single complete specimen and nine incomplete strobilae from *Leucichthys artedi* (= *Coregonus artedi*) in Lake Erie, Pennsylvania. Meyer (1954) later reported this species from *C. clupeaformis* in Maine. *Proteocephalus wickliffi*, as described by Hunter and Bangham (1933), resembles *P. stizostethi* Hunter et Bangham, 1933 (= *P. luciopercae*), a parasite of walleye and sauger (*Sander* spp.) (see Scholz et al. 2019 for a redescription of this species).

Hanzelová and Scholz (1999) synonymised *P. wickliffi* with *P. longicollis*, but the low number of testes (31–51) reported for *P. wickliffi* by Hunter and Bangham (1933) suggests that the species may be conspecific with *P. exiguus*, which is common in the same fish hosts and has been reported from the same watershed (Great Lakes).

***Proteocephalus pollanicola* Gresson, 1952 – taxonomic status uncertain**

This species was described by Gresson (1952) and Gresson and Corbett (1954) from the Irish pollan *Coregonus pollan* Thompson in Lough Neagh, Northern Ireland. Since then, the species has not been recorded anywhere (Chubb et al. 1987). Based on morphological, biometric and DNA data (random amplified polymorphic DNA method – RAPD), Scholz et al. (1998) found no significant differences between *P. pollanicola* and *P. exiguus*. Therefore, *P. pollanicola* was considered a synonym of *P. exiguus* by these authors. Based on more recent data from Brabec et al. (2023), this synonymy may be incorrect as *P. exiguus* only occurs only in North America, but it is possible that *P. pollanicola* is a junior synonym of *P. fallax*, a parasite of whitefish in Europe.

***Proteocephalus albulae* Freze et Kazakov, 1969 – taxonomic status uncertain**

Proteocephalus albulae was described by Freze and Kazakov (1969) from the vendace *Coregonus albula* on

the Kola Peninsula and in Karelia, Russia. Due to negligible morphological and biometric differences, Scholz et al. (1998) synonymised this species with *P. exiguus*, assuming that all *Proteocephalus* tapeworms in whitefish in the Holarctic are conspecific. Molecular data are required to confirm this synonymy based solely on morphology.

In summary, the taxonomy of this group of fish tapeworms requires a fundamental revision, as previous attempts to clarify species composition based on morphology alone have been unsuccessful in capturing the complex diversity of this group. The present study based on hologenophores collected and molecularly analysed by Brabec et al. (2023, 2024) shows that standardised fixation of specimens with preparation of hologenophores is a cornerstone for species delimitation in *Proteocephalus* as well as in other parasitic flatworms. The identification of *Proteocephalus* specimens infecting different salmonid genera in Europe and the assessment of the status of *P. albulae*, *P. coregoni*, *P. laruei*, *P. pollanicola* and *P. wickliffi* require the application of a similar approach to clarify the host range of *Proteocephalus* species and their appropriate delimitation.

Acknowledgements. This research was funded by Biodiversa+, the European Biodiversity Partnership, in the context of the IM-PACT project under the 2022–2023 BiodivMon joint call. It was co-funded by the European Commission (GA No. 101052342) and the following funding organisations: Swiss National Science Foundation (SNSF) grant 216810 to Isabel Blasco-Costa and Joëlle Salomon Cavin, and by the Technology Agency of the Czech Republic grant SS73020005 to Tomáš Scholz, and by the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences (BC) (RVO: 60077344). The collection of the tapeworms studied in this work was funded by the SNSF grant 169211 to I.B.-C. and Jean Mariaux. We would like to thank Eloïse Rochat, Mia Delacombaz, Pierre Rizzolo and Janik Pralong from the Natural History Museum of Geneva (MHNG) for their help with the fish dissections and Jean Mariaux (MHNG) for informal discussions and comments. Blanka Škoríková (BC) prepared plates with illustrations and SEM micrographs. Two anonymous reviewers provided helpful suggestions.

Author contribution. Jan Brabec, Rune Knudsen and Isabel Blasco-Costa collected and fixed all tapeworms for the subsequent study. Tomáš Scholz and Alain de Chambrier performed the morphological analysis. Tomáš Scholz wrote the original draft of the manuscript. All authors read and corrected the manuscript. Isabel Blasco-Costa and Tomáš Scholz received financial support.

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Received 25 June 2024

Accepted 30 September 2024

Published online 22 October 2024

Cite this article as: Scholz T., de Chambrier A., Brabec J., Knudsen R., Blasco-Costa I. 2024: Redescription of *Proteocephalus fallax* La Rue, 1911 (Cestoda) and a list of proteocephalid tapeworms of whitefish (*Coregonus* spp.). *Folia Parasitol.* 71: 019.