

Parasitic flatworms infecting thorny skate, *Amblyraja radiata*: infection by the monogeneans *Acanthocotyle verrilli* and *Rajonchocotyle emarginata* in Svalbard

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1 **Parasitic flatworms infecting thorny skate, *Amblyraja radiata*:**
2 **infection by the monogeneans *Acanthocotyle verrilli* and**
3 ***Rajonchocotyle emarginata* in Svalbard**

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5 Raquel Hermans¹, Maarten P. M. Vanhove^{1,2}, Oleg Ditrich³, Tomáš Tymi³, Milan Gelnar², Tom
6 Artois¹, Nikol Kmentová^{*1,2}

7
8 ¹ Hasselt University, Centre for Environmental Sciences, Research Group Zoology: Biodiversity
9 & Toxicology, Agoralaan Gebouw D, B-3590 Diepenbeek, Belgium

10 ² Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, 611
11 37 Brno, Czech Republic

12 ³ Centre for Polar Ecology, Faculty of Science, University of South Bohemia in České
13 Budějovice, Branišovská 31, 370 05 České Budějovice, Czech Republic

14 *Corresponding author. Laboratory of Parasitology, Department of Botany and Zoology,
15 Masaryk University, Kamenice 5, 625 00 Brno, Czech Republic. E-mail address:
16 kmentovan@mail.muni.cz

17 **Abstract**

18 Parasite diversity above the Arctic circle remains understudied even for commercially valuable
19 host taxa. Thorny skate, *Amblyraja radiata*, is a common bycatch species with a growing
20 commercial value. Its natural range covers both sides of the North Atlantic including the Arctic
21 zone. Svalbard is a Norwegian archipelago located on the northwest corner of the Barents
22 Shelf which sustains a spectacular species diversity. So far, several monogenean species have
23 been reported infecting thorny skate across the Atlantic Ocean. In the present study, we
24 intend to fill in the knowledge gap on monogenean parasites infecting thorny skate in the
25 northern part of its range and thus indirectly assess the connectivity between the thorny skate
26 populations off the Svalbard coast and from previously studied locations. 46 monogenean
27 individuals were recovered from 11 specimens of thorny skate. Following morphological and
28 molecular assessment, two species of monogeneans, *Acanthocotyle verrilli* and
29 *Rajonchocotyle emarginata*, were identified. The results serve as the northernmost record for
30 both parasite genera and the first record of monogenean species off Svalbard. Detailed
31 morphometric evaluation revealed a relatively high level of morphological variation in *A.*
32 *verrilli* compared to its congeners. Phylogenetic reconstruction placed *A. verrilli* in a well-
33 supported clade with *A. imo*. Our study also suggests high diagnostic significance of sclerotised
34 structures in the identification of *Rajonchocotyle*. Even though the occurrence of two directly
35 transmitted parasite species supports the previously suggested long-distance migration of *A.*
36 *radiata*, future studies employing highly variable genetic markers are needed to assess the
37 ongoing and historical migration patterns.

38

39 **Highlights**

- 40 • First record of monogenean species in Svalbard
- 41 • Northernmost record for representatives of Acanthocotylidae and Hexabothriidae
- 42 • Transatlantic occurrence of parasites supports connectivity of thorny skate
43 populations

44 **Keywords:** Rajidae, Acanthocotylidae, Hexabothriidae, first monogenean in Svalbard

45 **1. Introduction**

46 Thorny skate (Chondrichthyes, Rajidae) is a common bycatch species with growing commercial
47 value. It prefers shallow coastal waters with muddy or sandy substrate [1] and temperatures
48 from -1.4°C to 16°C [2]. Increased fishing effort during the last decades severely impacted the

49 overall biomass of this skate species characterized by low fecundity, slow growth rate, and
50 late maturity [3,4]. Its known geographic distribution ranges from South Carolina in the
51 Western part of the Atlantic Ocean to Greenland and the North Sea in the East and Svalbard
52 in the Arctic zone [5–11].

53

54 Svalbard is an archipelago in the Arctic Ocean located on the northwest corner of the Barents
55 Shelf. The Arctic Ocean is the smallest of all oceans with a mean depth of 1361 m and a total
56 area of approximately 10 million km² [12,13]. It consists of four abyssal plains surrounded by
57 continental shelves comprising c. 50% of the total area [13]. The northern and western
58 margins of the Barents Shelf end in the continental slope down to the Polar Ocean Basin and
59 the oceanic Norwegian Greenland Sea, respectively [14]. The wide range of habitats on
60 continental shelves sustains a spectacular biodiversity in this marine ecosystem [15] and
61 harbours species of Atlantic and Pacific affinities due to ancient connections. However,
62 continental shelves were an important migration barrier especially to shallow-water
63 organisms [16] between the Arctic and adjacent oceans [17] during the last Pleistocene
64 glacial/interglacial cycles. Overall, the inventory of biodiversity on Svalbard is far from
65 complete because of the focus of most studies on its west coast in view of the better
66 accessibility of this region. Similar to terrestrial habitats, the inventory of marine biodiversity
67 off Svalbard's coast has been limited and biased by sampling techniques (e.g., pelagic trawls)
68 or towards certain taxonomic groups such as Crustacea and Mollusca [18,19].

69

70 In general, parasite biodiversity in the Arctic is mostly understudied and many species remain
71 unknown including fish parasites [20–23]. Data about parasite fauna of *Amblyraja radiata*
72 from the North Atlantic and Arctic regions of its distribution are missing. Scientific exploration
73 of the marine parasite fauna in this part of the world has been mainly concentrated on Franz
74 Josef Land and heteroxenous parasite taxa [22]. Recently, Murzina et al. [24] reported on the
75 parasite fauna of *Leptoclinus maculatus* (Perciformes, Stichaeidae) (Fries 1838), being the first
76 record of parasitic flatworms (Trematoda) at the Svalbard coast. Globally, there are almost
77 1500 parasite species described from 900 elasmobranch species to date [25]. Helminth
78 infections of the thorny skate were reported worldwide (see Table 1). So far, representatives
79 of two monogenean families and three species have been reported. Monogenea is a group of
80 parasitic flatworms (Neodermata, Platyhelminthes) with worldwide occurrence and a mostly

81 ectoparasitic life-style. They are primarily parasites of fish characterised by a direct life-cycle
82 and predominantly narrow host-specificity [26,27]. The basic division is between members of
83 blood feeding Polyopisthocotylea and epithelial feeding Monopisthocotylea, representatives
84 of both of which have been reported to infect the thorny skate [28,29]. The northernmost
85 distribution of a parasitic flatworm infecting *A. radiata* was *Acanthocotyle verilli* Gotto, 1899
86 recorded off Tromsø, Norway [30], see Table 1). Hence, flatworm infections on *A. radiata* have
87 never been recorded above the Arctic Circle.

88

89 In the present study, we intend to fill in this gap of knowledge in the distribution of
90 monogenean parasites infecting thorny skate, *A. radiata*, at the northern part of its known
91 range, in Spitsbergen, Svalbard.

92

93 **2. Material and Methods**

94

95 2.1. Host collection

96 In total, eleven specimens of *A. radiata* were examined for the presence of monogenean
97 individuals during a field expedition in Spitsbergen, Svalbard, July 2016 organised by the
98 Centre for Polar Ecology (University of South Bohemia, Czech Republic). Host specimens were
99 caught in the Adventfjorden near Hotellneset, Spitsbergen, Svalbard (78°15'18"N, 15°30'58"E)
100 using benthic gill nets at a depth of 30–40 m and immediately transported to the laboratory
101 in seawater containers. Prior to dissection and subsequent examination, skates were
102 euthanised by overdosing with tricaine methane sulphonate (Sigma-Aldrich, Darmstadt,
103 Germany).

104

105 2.2. Parasite collection and morphological examination

106 The fins, gills and nasal cavity were examined for the presence of monogeneans. Monogenean
107 individuals were transferred with a needle and mounted on slides using a solution of glycerine
108 ammonium picrate (GAP). Selected specimens were kept in 99% ethanol and subsequently
109 stained using acetocarmine combined with Gomori trichrome, cleared with clove oil and
110 mounted in Canada balsam. Two species were found in this study, *Acanthocotyle verilli* and
111 *Rajonchocotyle emarginata*. Infection parameters per parasite species namely prevalence
112 (percentage of infected hosts), infection intensity (mean number of monogenean individuals

113 per infected host) and abundance (mean number of monogenean individuals per examined
114 host) were calculated following Ergens and Lom [31]. In total, 13 and 21 morphological
115 characters including hard and soft parts following Kearn et al. [32] and Bullard and Dippenaar
116 (2003), respectively, were measured and photographed using a Leica DM 2500 LED
117 microscope (Leica Microsystems, Wetzlar, Germany) and the software LasX v3.6.0. Voucher
118 specimens are deposited in the collection of the Research Group Zoology: Biodiversity and
119 Toxicology at Hasselt University in Diepenbeek, Belgium (HU) under the following accession
120 numbers: xx-xx. Type specimens from the Helminthological Collection of the South Australian
121 Museum, South Australia, Australia (AHC) and the National Museum of Natural History of the
122 Smithsonian Institution, Washington, USA (USNM), were examined for comparative purposes:
123 *Acanthocotyle atacamensis* Ñacari, Sepulveda, Escribano & Oliva, 2019 – 1 paratype (1 slide)
124 USNM 1480281; *A. gurgesiella* Ñacari, Sepulveda, Escribano & Oliva, 2018 – 1 paratype (1
125 slide) USNM 1422089; *A. imo* Ñacari, Sepulveda, Escribano & Oliva, 2019 – 1 paratype (1 slide)
126 USNM 1480278; *A. lobianchi* Monticelli, 1888 - 2 vouchers (2 slides) AHC 36231, 36232; *A.*
127 *pacifica* Bonham & Guberlet, 1938 – 2 paratypes (2 slides) USNM 1321942; *A. pugetensis*
128 Bonham & Guberlet, 1938 – 2 paratypes (2 slides) USNM 1321940; *A. verrilli* – 1 paratype (1
129 slide) USNM 135051; *A. urolophi* Kearn, Whittington, Chisholm & Evans-Gowing, 2016 - 4
130 paratypes (4 slides) AHC 36222, 36223, 36224, 36225; *Branchotenthes octohamatus* Glennon,
131 Chisholm & Whittington, 2005 – 2 paratypes (2 slides) AHC28769, 28770; *B. robinoverstreeti*
132 Bullard & Dippenaar, 2003 – 1 holotype (1 slide) USNM 1387687; *Callorhynchocotyle*
133 *callorhynchi* (Manter, 1955) – 2 paratype (2 slides) AHC29747; *C. amato*i Boeger, Kritsky &
134 Pereira, 1989 – 1 paratype (2 slides) AHC29749; *Erpocotyle antarctica* (Hughes, 1928) – 2
135 paratypes (2 slides) AHC29725; *E. somniosi* – 4 paratype (4 slides) USNM 1349221;
136 *Heteronchocotyle gymnurae* Neifar, Euzet & Ben Hassine, 2001 – 1 paratype (1 slide) USNM
137 1385030; *Paraheteronchocotyle amazonensis* Mayes, Brooks & Thorson, 1981 – 2 paratypes
138 (2 slides) USNM 1372658; *Rajonchocotyle emarginata* Olsson, 1876 – 1 paratype (1 slide)
139 USNM 1337399; *R. laevis* Price, 1942 – 1 syntype (1 slide) USNM1337422; *R. wehri* Price, 1942
140 – 4 paratypes (4 slides) USNM 1337421; *Squalonchocotyle borealis* (Van Beneden, 1853)
141 Cerfontaine, 1899 – 4 paratypes (4 slides) USNM 1349221; *S. callorhynchi* – 1 paratype, 1
142 holotype (2 slides) USNM 1338129; *S. impristi* – 1 holotype (1 slide) USNM 1338749. Selected
143 specimens of both collected species were drawn using a drawing tube and afterwards edited
144 using the software GIMP v2.10.20. Interspecific morphological differences and the level of

145 intraspecific phenotypic variability were evaluated using measurements relative to the total
146 length of the parasite's body because of the correlation between morphological variables and
147 the total length [34]. Morphometric parameters were subsequently analysed by principal
148 component analysis (PCA) in the R software package stats [35] and visualised using ggplot2
149 [36]. Only specimens mounted on slides with GAP were part of the analyses to avoid effects
150 of the staining method on the results [37]. The following variables were used in PCA: (1) the
151 ratios body width/total length (TL), (2) body length/TL, (3) pharynx length/TL, (4) pharynx
152 width/TL, (5) diameter of the pseudohaptor/TL, (6) number of sclerite rows/TL, (7) testes
153 maximum width/TL, (8) germarium length/TL and (9) germarium width/TL. Raw
154 measurements are provided as Supplementary material (see Table S1&S2).

155

156 2.3. Scanning electron microscopy (SEM)

157 Following host examination, live monogenean individuals were fixed with hot 4% neutral
158 buffered formaldehyde solution and transported to the Parasitology Laboratory of the Centre
159 for Polar Ecology in České Budějovice, Czech Republic. Subsequently, samples were washed in
160 0.1 M phosphate buffer solution (three times for 15 minutes), post-fixed in 2% osmium
161 tetroxide solution (for 60 minutes), washed again and dehydrated with an ascending acetone
162 series (30%, 50%, 70%, 80%, 90%, 95%, 100%), each step for 15 minutes. Following
163 dehydration, monogenean specimens were dried in liquid CO₂ using a critical point method,
164 placed on metal targets using double-stick tape, gold coated in a BAL-TEC SCD 050 sputter
165 coater (Bal-Tec, Los Angeles, USA) and observed using a SEM JEOL JSM-7401F scanning
166 electron microscope (JEOL, Tokio, Japan) at the Laboratory of Electron Microscopy, Institute
167 of Parasitology, Biology Centre CAS in České Budějovice.

168

169 2.4. Molecular data generation

170 The posterior part of the body or complete specimens were used for genomic DNA isolation.
171 The total genomic DNA was extracted using the Qiagen Blood and Tissue Isolation Kit (Qiagen,
172 Hilden, Germany) following the manufacturer's instructions. A portion of the large ribosomal
173 subunit (28S rRNA) gene was amplified using the primer combination C1 (5'-
174 ACCCGCTGAATTTAAGCAT-3') and D2 (5'-TGGTCCGTGTTTCAAGAC-3') [38]. Each PCR reaction
175 contained 1.5 unit of *Taq* Polymerase (ThermoFisher Scientific, Waltham, USA), 1X buffer
176 containing 0.1 mg/ml bovine serum albumin, 1.5 mM MgCl₂, 200 mM dNTPs, 0.5 mM of each

177 primer and 50 ng of genomic DNA in a total reaction volume of 30 μ l under the following
178 conditions: initial denaturation at 95 °C for 2 min followed by 39 cycles of 94 °C for 20 s,
179 annealing at 58 °C for 30 s, extension at 72 °C for 1 min and 30 s, and a final extension step at
180 72 °C for 10 min. PCR products were purified using ExoSAP-IT (ThermoFisher Scientific,
181 Waltham, USA) under the following conditions: 15 min at 37 °C and 15 min at 80 °C. Targeted
182 DNA fragments were sequenced using the same primers as in the amplification reactions
183 together with a Big Dye Chemistry Cycle Sequencing Kit v3.1 (ThermoFisher Scientific,
184 Waltham, USA). Following clean up using the BigDye XTerminator Purification Kit
185 (ThermoFisher Scientific, Waltham, USA), fragments were visualised on an ABI 3130 capillary
186 sequencer (ThermoFisher Scientific, Waltham, USA). Electropherograms were visually
187 inspected and assembled in MEGA7 [39]. The obtained sequences were deposited in NCBI
188 GenBank under the accession numbers MW260310-12.

189

190 2.5. Phylogeny

191 Phylogenetic placement of collected monogenean species was inferred based on 28S rDNA at
192 family level. Sequences generated during this study were aligned using MUSCLE [40] under
193 default distance measures as implemented in MEGA v7 [39], together with 28S rRNA gene
194 sequences of other *Acanthocotyle* spp. Selected representatives of related monogenean
195 families (Bothitrematidae, Anoplodiscidae and Udonellidae) were used as outgroup [41].
196 Genetic distances among the species of *Acanthocotyle* were calculated as the pairwise
197 difference (uncorrected p-distance) in MEGA v7 [39]. Poorly aligned and overly divergent
198 regions were trimmed using Gblocks v0.91b [42] under the less strict flanking position option
199 and allowing gap positions within the blocks. The final alignment consisted of 825 bp. The
200 most appropriate evolutionary model, the HKY + Γ model [43], was selected based on the
201 Bayesian information criterion in jModelTest v2 [44]. Phylogenetic relationships were inferred
202 under Bayesian inference (BI in MrBayes v3.2.0 [45]) based on two independent runs (20⁵
203 generations, sampled every 1,000th generation and with a burn-in of 10%). Parameter
204 convergence and run stationarity were assessed in Tracer v1.6 [46]. Moreover, a maximum
205 likelihood (ML) search was performed in RAxML v8.2.12 with tree search conducted using
206 RAxML's standard tree search algorithm and bootstrap support calculated using the option
207 with an automated number of replicates to obtain stable support values under the frequency

208 stopping criterion [47]. Phylogenetic trees were edited in FigTree v1.4.2
209 (<http://tree.bio.ed.ac.uk/software/figtree>).

210 **3. Results**

211 In total, 37 and 9 monogenean individuals were found on fins and gills, respectively.
212 Based on a detailed morphological examination, two species of monogeneans were identified.

213
214 To comply with the regulations set out in article 8.5 of the amended 2012 version of the
215 International Code of Zoological Nomenclature [48], details of *Acanthocotyle verrilli* and
216 *Rajonchocotyle ermaginata* have been submitted to ZooBank based on their respective
217 original descriptions. For each taxon, the Life Science Identifier (LSID) is reported in the
218 taxonomic summary.

219

220 **3.1. *Acanthocotyle verrilli* Goto, 1899**

221 Monogenea van Beneden, 1858

222 **Family** Acanthocotylidae Monticelli, 1903

223 **Genus** *Acanthocotyle* Monticelli, 1888

224 **Type-host:** *Amblyraja radiata* (Donovan, 1808) (Chondrichthyes, Rajidae)

225 **Other hosts:** *Bathyraja spinicauda* (Jensen, 1914) (Chondrichthyes, Arhynchobatidae);

226 *Leucoraja erinacea* (Mitchill, 1825) (Chondrichthyes, Rajidae)

227 **Site on host:** Fins.

228 **Prevalence:** 72,7% (8 out of 11 infected)

229 **Intensity of infection:** 4,6 (1-12)

230 **Abundance:** 3,4 (0-12).

231 **Type-locality:** Cape Cod, USA

232 **Other localities:** Adventfjorden, Spitsbergen; Chaleur Bay, Canada; Coast of Maine, USA; off
233 Bergen, Norway; off Newfoundland, Canada; North-eastern Norwegian Sea

234 **ZooBank registration:** The LSID for *Acanthocotyle verrilli* is
235 urn:lsid:zoobank.org:act:FF7F506B-FB65-446C-9F91-255C45BF2E86.

236

237 **3.1.1. Remarks**

238 In total, 13 morphological characters including soft body parts and sclerotised structures were
239 measured (see Table 2, Figs. 1&2). Body elongate, circular pseudohaptor with radial rows of

240 sclerites (26 – 34) covered by tegument (Fig. 2G). Pseudohaptor with 28 – 34 rows of sclerites,
241 each row consists of 4 – 10 sclerites. Marginal valve of pseudohaptor with distinct fringe. The
242 central part of the pseudohaptor, between the radial rows of sclerites, shows a depression
243 indicating this part to be responsible for the attachment to the body (Fig 2E). True haptor with
244 16 marginal hooks located subterminally at the posterior margin of pseudohaptor (Fig. 2E).
245 Hooks in the true haptor organised into one central pair and 14 hooks in a peripheral row,
246 the latter pointing centrally (Fig. 2G) with shafts free of tegument (Fig. 2H). Pharynx globular.
247 Three anterior adhesive lobes on each side of head with sense organs located at the side of
248 each internal lobe (Fig. 2B). Accessory glands at the level of pharynx. Excretory bladders on
249 each side, anterior to vitellarium field. Eyes absent. Testes (26 – 47) mainly rounded usually
250 arranged in several (2 – 3) rows. Seminal vesicle unlobed, anterior part communicates with
251 male genital opening via curved ejaculatory duct immediately posterior to pharynx. Male
252 accessory gland reservoirs 2, adjacent to ejaculatory duct. Common opening at the level of
253 intestinal bifurcation. Penis sclerite absent. Germarium immediately anterior to testes. Small
254 uterine receptaculum seminis adjacent to germarium. Vagina absent. Germinal appendix not
255 observed. Uterine pore opening on right side of the body, at the level of posterior part of
256 pharynx. Eggs attached externally by an abopercular appendage (Fig. 2C). The egg operculum
257 shows a pointed end (Fig. 2D). Vitelline follicles not discrete with lobed and overlapping
258 margins, extending from level of germarium to near the posterior end of body proper.

259 3.1.2. Differential diagnosis

260 Based on the recent revision of Acanthocotylidae published by Kearns et al. [32] combined with
261 new species descriptions of Ñacari et al. [49,50], there are 12 species of *Acanthocotyle*
262 currently considered valid: *Acanthocotyle atacamensis*; *Acanthocotyle elegans* Monticelli,
263 1890; *Acanthocotyle greeni* Macdonald & Llewellyn, 1980; *Acanthocotyle gurgesiella*;
264 *Acanthocotyle imo*; *Acanthocotyle lobianchi*; *Acanthocotyle pacifica*; *Acanthocotyle*
265 *patagonica* Kuznetsova, 1971; *Acanthocotyle pugetensis*; *Acanthocotyle urolophi*;
266 *Acanthocotyle verrilli*; *Acanthocotyle williamsi* Price, 1938. *Acanthocotyle verrilli* most closely
267 resembles *A. atacamensis*, *A. gurgesiella*, *A. imo* and *A. urolophi*. All these species have more
268 than 20 testes, a haptor armed with 21-39 radial rows of sclerites, and a dextral opening of
269 the uterine pore. *Acanthocotyle urolophi* is distinguished from the other species by the form
270 of the vitelline follicles. Unlike in *A. atacamensis*, *A. gurgesiella*, *A. imo* and *A. verrilli*, the
271 vitelline follicles of *A. urolophi* are discrete and easy to count. The number of testes ranges

272 from 26 to 47 (mode 36) in *A. verrilli*, 40 to 58 (mode 50) in *A. atacamensis*, 28 to 43 (mode
273 30) in *A. gurgesiella*, 32 to 47 (mode 41) in *A. imo* and 40 to 70 (mode 55) in *A. urolophi*. Testes
274 of *A. verrilli* are organised in numerous rows compared to two rows in the case of *A. imo* and
275 *A. gurgesiella*. Unlike in *A. atacamensis*, *A. imo* and *A. gurgesiella*, testes of *A. verrilli* have
276 overlapping margins. The number of radial rows of sclerites range from 28 to 34 (mode 32) in
277 *A. verrilli*, 28 (no variation) in *A. atacamensis*, 36 to 40 (mode 40) in *A. gurgesiella*, 30 to 35
278 (mode 32) in *A. imo* and 32 to 37 (mode 35) in *A. urolophi*. In specimens of *A. verrilli* possessing
279 28 radial rows of sclerites in the pseudohaptor, there are only 4–5 sclerites in the first row
280 (counting from the position of the true haptor) compared to 6 in *A. atacamensis*. The
281 difference between *A. verrilli* and *A. imo* is then visible in a smooth marginal valve of the
282 pseudohaptor in *A. imo* compared to a distinct fringe in *A. verrilli*. *Acanthocotyle verrilli* can
283 be distinguished from *A. gurgesiella* by the absence of an armed male genital aperture.

284

285 3.1.3. Interspecific differentiation based on multivariate statistics

286 Principal component analysis combining metric and meristic data (see Material & Methods)
287 was performed to examine and visualise differences between three morphologically similar
288 species of *Acanthocotyle* for which raw data are available (Fig. 3A-C). Figure 3A shows the
289 comparison of all three species. The first PC explained 64.5% and the second 12.3% of the
290 variation in the dataset. In the resulting biplot, specimens of *A. verrilli* collected in this study
291 are clearly distinguished from the other two species along the first axis and display more
292 intraspecific variability. Figure 3B presents a PC biplot of *A. verrilli* and *A. imo* and shows clear
293 differentiation along the first axis (PC1 explained 54.5% and PC2 17.3% of the variation in the
294 dataset). Figure 3C presents a PCA biplot of *A. verrilli* and *A. atacamensis* and shows clear
295 differentiation along the first axis (PC1 explained 67.1% and PC2 12.6% of the variation in the
296 dataset). The diameter of the pseudohaptor and the total body length display the highest
297 contribution to the separation in all datasets of all parameters.

298

299 3.1.4. Phylogenetic reconstruction

300 In total, three identical sequences of the 28S rDNA region from *A. verrilli* were generated in
301 this study (Genbank accession numbers xx-xx). Phylogenetic reconstruction placed *A. verrilli*
302 in a well-supported clade with *Acanthocotyle imo* (Fig. 4). Genetic interspecific differences

303 between the species of *Acanthocotyle* with available 28S rDNA region sequences are
304 presented in Table 3.

305 **3.2. *Rajonchocotyle emarginata*** (Olsson, 1876)

306 Monogenea van Beneden, 1858

307 **Family** Hexabothriidae Price, 1942

308 **Genus** *Rajonchocotyle* Cerfontaine, 1899

309 **Type-host:** *Amblyraja radiata* (Donovan, 1808) (Chondrichthyes, Rajidae)

310 **Other hosts:** *Bathyraja brachyurops* (Fowler, 1910); *Bathyraja magellanica* (Philippi, 1902)
311 (Chondrichthyes, Arhynchobatidae); *Leucoraja naevus* (Müller & Henle, 1841); *Raja brachyura*
312 Lafont, 1871; *Raja clavata* Linnaeus, 1758; *Raja microocellata* Montagu, 1818; *Raja montagui*
313 Fowler, 1910; *Raja undulata* Lacepède, 1802 (Chondrichthyes, Rajidae) and *Psammobatis*
314 *scobina* (Philippi, 1857) (Chondrichthyes, Arhynchobatidae)

315 **Site on host:** Gills.

316 **Prevalence:** 27,3% (3 out of 11 specimens infected)

317 **Intensity of infection:** 3 (1-6)

318 **Abundance:** 0,8 (0-6).

319 **Type-locality:** Bohuslän Coast, Sweden

320 **Other localities:** Adventfjorden, Spitsbergen; Cardigan Bay, Wales; Chaleur Bay, Canada;
321 Galway Bay, Ireland; Marine Bahusiae, Scandinavia; Mediterranean Sea, Italy; off Plymouth,
322 UK; off Roscoff, France; Northwest coast of Spain; Patagonian Shelf; off Tromsø, Norway

323 **ZooBank registration:** The LSID for *Rajonchocotyle emarginata* is
324 urn:lsid:zoobank.org:act:865F76DA-FADB-49F1-9B43-24F4AAC88256.

325

326 3.2.1 Remarks

327 In total, 21 morphological characters including soft body parts as well as sclerotised structures
328 were measured (see Table 4, Figs. 5&6). Body elongate with tegument covered by numerous
329 transverse ridges organised in radial rows (Fig. 6A). Haptor symmetrical with six suckers,
330 armed with three pairs of C-shaped haptor sucker sclerites of similar shape and size (Fig. 5)
331 and with a sharp hook (Fig. 6F). Peduncles of suckers of similar size. Each of the suckers
332 contains a large sclerite ending in a hook pointing to the deep lumen (Fig. 6B&F). Sclerites
333 form a bulge structure visible at the terminal region of each sucker (Fig. 6G). The sucker margin
334 surmounted by a rim supporting the sclerite (Fig. 6F&H). Marginal haptor appendix with a

335 pair of terminal suckers with three valves (Fig. 6D) and of V-shaped hamuli possessing a
336 sharply pointed and curved tip (Fig. 6E) situated near the distal end of appendix. Mouth
337 subterminal, situated on the ventral side of the body and formed by the oral sucker (Fig. 6C).
338 Pharynx spherical, reaching the posterior end of oral sucker. Intestinal tract bifurcation at the
339 level of pharynx. Testes occupy area in the central part of the body, irregular in size and shape,
340 number of testes not ascertainable. Other parts of male reproductive system not
341 distinguishable. Slightly lobed ovary (paratype USNM 1337399) and Y-shaped structure of
342 vaginal ducts. Vitellaria extending from the level of intestinal bifurcation (paratype USNM
343 1337399) to the posterior end of the body into the haptor. Eggs fusiform with two incipient
344 polar filaments (Fig. 5), located at level of anterior part of vitellarium.

345 3.2.2 Differential diagnosis

346 Up to now, there have been 17 genera of hexabothriid monogeneans described:
347 *Branchotenthes* Bullard et Dippenaar, 2003; *Callorhynchocotyle* Suriano & Incorvaia, 1982;
348 *Dasyonchocotyle* Hargis, 1955; *Epicotyle* Euzet & Maillard, 1974; *Erpocotyle* Van Beneden &
349 Hesse, 1863; *Heteronchocotyle* Brooks, 1934; *Hexabothrium* von Nordmann, 1840;
350 *Hypanocotyle* Chero, Cruces, Sáez, Camargo, Santos & Luque, 2018; *Mobulicola* Patella &
351 Bullard, 2013; *Neonchocotyle* Ktari & Maillard, 1972; *Paraheteronchocotyle* Mayes, Brooks &
352 Thorson, 1981; *Pristonchocotyle* Watson & Thorson, 1976; *Protocotyle* Euzet & Maillard, 1974;
353 *Pseudohexabothrium* Brinkmann, 1952; *Rajonchocotyle* Cerfontaine, 1899;
354 *Rhinobatonchocotyle* Doran, 1953 and *Squalonchocotyle* Cerfontaine, 1899. Species of
355 *Rajonchocotyle* can be distinguished by the presence of a symmetrical haptor in comparison
356 to *Callorhynchocotyle*, *Epicotyle*, *Heteronchocotyle*, *Neonchocotyle*, *Paraheteronchocotyle*,
357 *Pristonchocotyle*, *Pseudohexabothrium* and *Rhinobatonchocotyle*. Species of *Rajonchocotyle*
358 also differ from those within *Dasyonchocotyle* and *Hexabothrium* by having an unarmed male
359 copulatory organ. Unlike representatives of *Branchotenthes*, *Erpocotyle*, *Hypanocotyle*,
360 *Mobulicola* and *Squalonchocotyle* where the vagina is differentiated into muscular and
361 glandular portions and possesses parallel vaginal ducts, species of *Rajonchocotyle* have an
362 undifferentiated vagina and Y-shaped vaginal ducts. Species of *Rajonchocotyle* closely
363 resemble representatives of *Protocotyle* but they differ by having undifferentiated vaginal
364 ducts that are Y-shaped while the vaginal ducts of *Protocotyle* are also undifferentiated but
365 parallel [51]. According to Boeger & Kritsky (1989), four species of *Rajonchocotyle* are

366 currently considered valid: *Rajonchocotyle batis* Cerfontaine, 1899, *R. emarginata* (Olsson,
367 1876), *Rajonchocotyle laevis* Price, 1942 and *Rajonchocotyle wehri* Price, 1942.

368 *Rajonchocotyle emarginata* can be distinguished from its congeners by the total and
369 proportional size of the haptoral sclerites. Unlike in *R. emarginata*, the size of sclerites of *R.*
370 *batis* and *R. laevis* is not equal. While the anterior pair of *R. batis* is bigger than the posterior
371 pair, sometimes even twice of the size, the posterior pair of *R. laevis* is just a bit smaller
372 compared to the anterior pair. The difference between *R. emarginata* and *R. batis* is also
373 visible in the shape of the anchor roots. The different pairs of haptoral sclerites of *R. wehri*
374 and *R. emarginata* are all of equal size but the overall size of sclerites of *R. emarginata* is
375 smaller than in *R. wehri* (median sclerites of 404–561 μm compared to 924–956 μm in *R.*
376 *wehri*). *Rajonchocotyle emarginata* can also be distinguished from all its other congeners by
377 having eggs with 2 long filaments (total egg length 353–446 μm) in comparison to the lack of
378 polar filaments in *R. batis*, a small knob at each pole in *R. laevis* and two very short, fusiform
379 egg filaments in *R. wehri* (total egg length 285–300 μm) [52–54].

380

381 4. Discussion

382 Invertebrate diversity is understudied in polar regions, with available information biased
383 towards a few taxa [18,19]. In general, knowledge about the parasite fauna in cold areas
384 remains poor, and zoonotic parasitosis received most attention so far [21]. Despite an
385 intensified effort, reflected by the numerous parasitological surveys conducted recently [55–
386 58], fish flatworms are rarely studied in the Svalbard archipelago. Rokicka (2009) does not
387 mention a single monogenean infection for over 94 examined fish specimens belonging to 4
388 species [59]. Our study is the first record of monogenean species off Spitsbergen Island and
389 the Svalbard archipelago.

390

391 4.1. Species richness and geographic distribution of *Acanthocotyle* and *Rajonchocotyle*

392 In total, 12 currently valid species of Acanthocotylidae have been reported out of 15 species
393 accounting for 5.6% of the species diversity of Rajiformes. Two teleost fish species,
394 *Reinhardtius hippoglossoides* (Walbaum, 1792) and *Sebastes alutus* (Gilbert, 1890), were also
395 recorded as hosts for *Acanthocotyle williamsi* [60,61]. The recorded infection of *Acanthocotyle*
396 sp. on *Narcine maculata* (Torpediniformes) is rather considered to result from transfer during
397 fish capture [62]. With an estimation of over 800 species, the number of potential

398 elasmobranch and holocephalan hosts of species of *Acanthocotylidae* is high. From less than
399 10% of them [63,64], only 59 species of *Hexabothriidae* have been described [51]. Considering
400 the overall high species richness and rather strict host-specificity of monogeneans, the known
401 diversity of both examined monogenean groups infecting cartilaginous fishes can be assumed
402 to be proportionally minimal.

403 The overall worldwide occurrence of *Acanthocotyle* spp. seems to follow the geographical
404 distribution of their skate hosts as summarised in Nacari et al. [49]. Host-specificity ranges
405 from one (9 species of *Acanthocotyle*) to five host species in *A. lobianchi*. However, the known
406 distribution of *A. lobianchi* is currently mostly restricted to Plymouth, UK [65] with one record
407 from Naples, Italy [66]. A similar host (four rajid species) and geographical range was reported
408 for *A. pacifica* [67–69]. The distribution of *A. verrilli* overlaps with the cross-Atlantic
409 occurrence of *A. radiata*. This monogenean species was further reported from two other rajid
410 species so far (see Table 5). However, reported differences in host-specificity and distribution
411 patterns of *Acanthocotyle* spp. are suggested to result from biased sampling toward a few
412 host species.

413 Unlike in *Acanthocotyle*, species of *Rajonchocotyle* seem to be less host specific as several
414 representatives were recorded from different rajid hosts with a maximum number of 10 in
415 the case of *R. emarginata*. This difference in host-specificity possibly can be driven by the site
416 of infection (skin in *Acanthocotyle* spp. versus gills in *Rajonchocotyle* spp.) or mode of
417 reproduction (eggs being attached to the parasite body by stalks in *Acanthocotyle* spp. [70,71]
418 and floating eggs and free-swimming larvae in *Rajonchocotyle* spp. [72,73]. However,
419 discovery of cryptic species that are more host specific than the species they were originally
420 assigned to, has already changed views on parasite species richness and host-specificity [74].
421 Given the lack of genetic data on species of *Rajonchocotyle* and hexabothriids in general, and
422 their close interspecific morphological similarity, the presence of cryptic species cannot be
423 excluded. Further research is needed to verify the level of host-specificity and overall
424 distribution patterns of both monogenean families as large parts of the host distribution
425 remains devoid of parasitological investigation.

426

427 4.2. Morphological and genetic diversity

428 The specimens of *A. verrilli* analysed in this study did not differ in most morphological
429 characteristics from earlier reports but some differences were observed. Goto (1899) and

430 Sproston (1946) counted 30 or 32 radials rows of sclerites in the haptor while in our specimens
431 the rows ranged from 28 to 34 (32 most frequently, in 14 of the 34 specimens). Thus,
432 intraspecific variation in the number of radial rows of sclerites was reported in *A. verrilli*, as in
433 other congeners [32,49,50]. Interestingly, a relationship between age and the number of
434 radial rows of polyopisthocotylean monogenean species was suggested [75]. However, such
435 pattern does not emerge for our data (see Supplementary Table S1). Moreover, because the
436 number of rows in the pseudohaptor and the number of rows of testes can overlap, the
437 difference between *A. verrilli* and *A. atacamensis* was revised. We propose the number of
438 sclerites in the first row (counting from the position of the true haptor) as an additional
439 diagnostic character. This study confirms that the morphology and size of sclerotised
440 structures are of a high diagnostic significance in *Acanthocotyle*. Close morphological
441 similarities of *A. verrilli* with *A. imo* and *A. atacamensis* are reflected in the genetic distance
442 matrix (Table 3). Interestingly, the two species of *Acanthocotyle* collected from
443 representatives of *Amblyraja* formed a clade in the phylogenetic reconstruction (Fig. 6).
444 However, molecular data on the remaining *Acanthocotyle* spp. as well as haplotypes of *A.*
445 *verrilli* from other rajid genera are needed to shed light on the evolutionary history of this
446 parasite-host system.

447 As pointed out in previous studies, boundaries between hexabothriid monogenean species
448 are mostly defined by variable characters, as they are unstable across different fixation and
449 staining methods [51,76]. Vaughan and Christison (2012), using multivariate statistics,
450 combined measurements of the hamulus and sucker sclerites to distinguish species of
451 *Callorhynchocotyle*. Our study confirmed that the morphology of the hamulus and the size of
452 sucker sclerites is of a high diagnostic significance. As a result, the combination of the
453 proportional size of sclerotised structures and egg filaments is proposed for species
454 identification of *Rajonchotyle* spp. Moreover, multiple staining methods should be used for
455 correct assignment of hexabothriid monogeneans in general and species of *Rajonchocotyle* in
456 particular.

457

458 4.3. Parasites of *A. radiata* as a tag for host population structure

459 To date, 28 helminth parasite species were reported from *A. radiata* worldwide. Even though
460 our study was restricted to monogeneans, ongoing investigations suggest the presence of at
461 least 9 endoparasitic helminth species infecting *A. radiata* in Svalbard (unpublished).

462 *Acanthocotyle verrilli* was further reported from *A. radiata* by Sproston, 1946 off Bergen,
463 Norway, North-eastern Norwegian Sea (Rokicki and Berland, 2009), on the opposite side of
464 the Atlantic Ocean off Newfoundland and Chaleur Bay in Canada [29,78] and the northern East
465 coast of the USA [79]. Unlike in *A. verrilli*, the known occurrence of *R. emarginata* on *A. radiata*
466 also spans the southern hemisphere, on the Patagonian Shelf [80]. Moreover, *R. batis* and two
467 monogenean species from Monocotylidae were reported parasitizing on *A. radiata* in previous
468 studies (see Table 1).

469 Although our results match with the previous records of monogeneans collected from *A.*
470 *radiata*, the new locality off Svalbard represents the highest known latitude in the northern
471 hemisphere those two monogenean genera have ever been recorded from (see Tables 5&6).
472 As monogeneans display a direct life cycle and short-lived larval stage [73,81], their
473 distribution is primarily affected by the distribution and migration patterns of their host. Given
474 the previous reports of both monogenean species from *A. radiata* on both sides of Atlantic
475 Ocean, historical and ongoing overseas connectivity of skate species at the Svalbard coast is
476 proposed as suggested in Chevolut et al. [82]. Differences in life history traits such as total
477 length and density between the populations of thorny skate were observed [5,83,84]. In
478 contrast to the previously recorded high level of fidelity and relatively small home range
479 (mostly fewer than 100 km [85–88]), long-term connectivity between thorny skate
480 populations from the eastern and western part of the Atlantic facilitated by historical
481 population expansion was recently documented [82]. These recently suggested large
482 migratory capacities of thorny skates concur with the occasional records at depths down to
483 1000 m [89] with continental shelves considered as important migration barrier [16].
484 However, there are low levels of migration between the North Sea population and other
485 European areas [82]. Given their expected higher mutation rate and reproduction coefficient
486 compared to their hosts, parasitic flatworms including monogeneans were proposed as tags
487 for historical and ongoing host migration [90–92]. However, both reported species of
488 monogeneans infecting thorny skate are not strictly host specific (see Table 5&6). Other skate
489 species can therefore contribute to the worldwide occurrence of *R. emarginata* and the
490 occurrence throughout the northern hemisphere of *A. verrilli*. In general, monogeneans tend
491 to be less host specific in pelagic and deepwater areas in comparison to littoral habitats due
492 to the lower host availability connected also with fish population size [93–96]. On the other
493 hand, an influence of light intensity on the larval hatching of *R. emarginata* as a result of

494 adaptation to the behavioural differences between the hosts was proposed [72]. Such an
495 adaptation might therefore have resulted in depth-dependent host specificity of this parasite
496 species. Keeping in mind the rather plastic nature of currently used morphological characters
497 in both examined monogenean families, phenotypic evaluation of any differentiation would
498 need to be employed over a large number of specimens per population.

499 More variable genetic markers would need to be applied in order to investigate the historical
500 connectivity of the parasite populations in Svalbard and other areas and evaluate the level of
501 geographically/host species driven differentiation.

502

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515

516 **Figure captions**

517 Fig. 1: *Acanthocotyle verrilli* ex *Amblyraja radiata*. A) Ventral view of the whole body. B)
518 Reproductive system. Abbreviations: aa, anterior adhesive lobes; ag, accessory glands; bl,
519 excretory bladders; ed, ejaculatory duct; ge, germarium; gr, male accessory gland reservoir;
520 h, haptor; in, intestine; ph, pharynx; sr, seminal receptacle; sv, bipartite seminal vesicle; te,
521 testes; th, true haptor; up, uterine atrium; ut, uterus; vd, vas deferens; vt, vitelline duct; vi,
522 vitelline.

523 Fig. 2: SEM observations of *Acanthocotyle verrilli*. A) Ventral view of the whole body, B) View
524 of the anterior part of the body with adhesive lobes on each side, visible sense organ and
525 pharynx opening. C) Uterus opening with an externally attached egg. D) Detailed apical view

526 of an egg with abopercular appendage. E) Posterior part of the body formed by haptor and
527 convex pseudohaptor, pseudohaptor with marginal valve. F) Detailed view of
528 pseudophaptoral sclerites organised in rows. G) Detailed view of haptor located at the
529 posterior margin of pseudohaptor armed with 14 peripheral and 2 central marginal hooks. H)
530 aa – adhesive lobes, eg – egg operculum, h – haptor, m – marginal valve, mh – marginal hook,
531 po – pharynx opening, mhs – marginal hooks sclerite, ps – pseudohaptor, so – sense organ.

532 Fig. 3: Biplots showing the interspecific differences of *Acanthocotyle* spp. based on
533 proportional morphometric measurements standardized by the total body length. Only the
534 first two axes are shown. A) Principal component analysis (PCA) of *A. verrilli* (this study), *A.*
535 *atacamensis* [49] and *A. imo* [49]. B) PCA of *A. verrilli* (this study) and *A. atacamensis* [49]. C)
536 PCA of *A. verrilli* (this study) and *A. imo* [49].

537 Fig. 4: Bayesian inference phylogram based on available 28S rDNA sequences of
538 Acanthocotylidae with specification of the host species. Representatives of three other
539 families of Gyrodactylidea were used as outgroup. Bootstrap percentages for maximum
540 likelihood (before slashes) and posterior probabilities for Bayesian inference (behind slashes)
541 are shown. The scale bar indicates the expected number of substitutions per site.

542 Fig. 5: *Rajonchocotyle emarginata* ex *Amblyraja radiata*. A) Ventral view of the whole body.
543 B) Anterior haptoral sucker sclerites. C) Middle haptoral sucker sclerites. D) Posterior haptoral
544 sucker sclerites. E) Hamuli. F) Egg. Abbreviations: ap, appendix; eg, egg; h, haptor; ha, hamuli;
545 it, intestine; os, oral sucker; ph, pharynx; sc, sclerite; su, sucker; te, testes; vd, vaginal duct; vi,
546 vitellarium.

547 Fig. 6: SEM observations of *Rajonchocotyle emarginata*. A) Ventral view of the whole body, B)
548 Haptoral structures formed by six suckers each armed with a sclerite, and appendix, C) View
549 of the anterior part of the body with the oral sucker, D) Lateral view of the posterior part of
550 the appendix with two terminal suckers. E) Bottom-up view on the posterior part of the
551 appendix with two terminal suckers. F) Haptoral sucker rounded by the rim with a sclerite
552 bulge ending in a hook. G) Side view of haptoral suckers with peduncle structure on the left
553 side. H) Detailed view of the sucker rim and hook. ap – appendix, as – appendicular sucker, h
554 – hook, hp – haptor, rm – sucker rim, sb – sucker bulge, sp – sucker peduncle os – oral sucker.

555 **Supplementary material**

556 Table S1: Raw morphometric data for *Acanthocotyle verrilli* ex *Amblyraja radiata*.
557 Measurement are given in micrometers.

558 Table S2: Raw morphometric data for *Rajonchocotyle emarginata* ex *Amblyraja radiata*.

559 Measurement are given in micrometers.

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918 **Table 1:** List of helminth species reported from *Amblyraja radiata* with taxonomic
 919 designation and locality of the report.

920

Class	Species	Family	Locality	Reference
Cestoda	<i>Anthobothrium cornucopia</i> Van Beneden, 1850	Tetraphylidea	off Newfoundland, Canada	[78]
	<i>Calyptrobothrium riggii</i> Monticelli, 1893	Phyllobothriidae	off Kattegat, Denmark Barent Sea	[97] Review in [23]
	<i>Echeneibothrium canadensis</i> Keeling & Burt, 1996	Echeneibothriidae	Bay of Fundy, Canada Northwestern Atlantic Ocean	[98] [99]
			Chaleur Bay, Canada	[29]

	<i>Echeneibothrium dubium</i> Van Beneden, 1858		Barent Sea	Review in [23]
	<i>Echeneibothrium variabile</i> Van Beneden, 1850		Barent Sea	Review in [23]
	<i>Echinobothrium raji</i> Heller, 1949	Echinobothriidae	Atlantic Coast of North America	[100]
	<i>Grillotia (Grillotia) erinaceus</i> (Van Beneden, 1858)	Lacistorhynchidae	Barent Sea	Review in [23]
	<i>Grillotia (Grillotia) brayi</i> Beveridge & Campbell, 2007		Kolkugrunn, Iceland Chaleur Bay, Canada	[101] [29]
	<i>Grillotia</i> sp. Guiart, 1927		North-eastern Norwegian Sea	[102]
	<i>Phormobothrium affine</i> (Olsson, 1867)	Phyllobothriidae	Northwestern Atlantic Ocean	[99]
	<i>Phyllobothrium dagnalium</i> Southwell, 1927		Chaleur Bay, Canada	[29]
	<i>Phyllobothrium</i> sp. Van Beneden, 1850		Northwestern Atlantic Ocean	[103]
	<i>Phyllobothrium thridax</i> Van Beneden, 1849		off Newfoundland, Canada	[78]
	<i>Pseudanthobothrium hanseni</i> Baer, 1956	Echeneibothriidae	Barent Sea	Review in [23]
	<i>Scyphophyllidium giganteum</i> (Van Beneden, 1858)		North-eastern Norwegian Sea	[102]
	<i>Trilocularia acanthiaevulgaris</i> Olsson, 1867	Phyllobothriidae	Chaleur Bay, Canada	[29,78]
	<i>Tritaphros retzii</i> Lönnberg, 1889		Barent Sea	Review in [23]
Trematoda	Aporocotylidae <i>gen. sp.</i>	Aporocotylidae	off Newfoundland, Canada	[78]
	<i>Gonocerca phycidis</i> Manter, 1925	Gonocercidae	Barent Sea	Review in [23]
	<i>Hemiurus levinseni</i> Odhner, 1905	Hemiuridae	North Sea south of Fair Isle, UK	[104]
	<i>Otodistomum cestoides</i> (Van Beneden, 1870)	Azygiidae	Barent Sea	[23]
			Chaleur Bay, Canada	[29]
			off Newfoundland, Canada	[78]

			North-eastern	[102]
			Norwegian Sea	
			Barent Sea	Review in
				[23]
Monogenea	<i>Acanthocotyle verrillii</i> Goto, 1899	Acanthocotylidae	Cape Cod, USA	[105]
			off Bergen, Norway	[106]
			Chaleur Bay, Canada	[29]
			off Newfoundland,	[78]*
			Canada	
			North-eastern	[102]*
			Norwegian Sea	
			Barent Sea	Review in
				[23]
			Adventfjorden,	This study
			Spitsbergen	
	<i>Dictyocotyle coeliaca</i> Nybelin, 1941		off Trondheim,	[107]
			Norway	
			North Sea, UK	[104,108,109]
			North-western Atlantic	[110]
			Ocean, Canadian coast	
	<i>Rajonchocotyle batis</i> Cerfontaine, 1899	Hexabothriidae	North-eastern	[102]
			Norwegian Sea	
	<i>Rajonchocotyle emarginata</i> (Olsson, 1876)		Chaleur Bay, Canada	[29]
			Barent Sea	Review in
				[23]
			Patagonian Shelf	[111]
			off Tromsø, Norway	[112]
			Adventfjorden estuary,	This study
			Spitsbergen	
Acanthocephala	<i>Echinorhynchus gadi</i> Zoega in Müller, 1776	Echinorhynchidae	North-eastern	[102]
			Norwegian Sea	
Nematoda	<i>Anisakis</i> sp. Dujardin, 1845	Anisakidae	off Newfoundland,	[78]
			Canada	
	<i>Anisakis simplex</i> (Rudolphi, 1809)		Barent Sea	[23]
	<i>Contracaecum</i>		North-eastern	[102]
	<i>plagiostomorum</i> (Linstow, 1905)		Norwegian Sea	
	<i>Contracaecum</i> sp. Railliet & Henry, 1912		West coast of Norway	[113]
			Barent Sea	Review in
				[23]

<i>Hysterothylacium aduncum</i> (Rudolphi, 1802)	Raphidascarididae	off Newfoundland, Canada	[78]
<i>Phocasaris</i> sp. Höst, 1932	Anisakidae	North-eastern Norwegian Sea	[102]
<i>Porrocaecum</i> sp. Railliet & Henry, 1912	Ascarididae	off Newfoundland, Canada	[78]
<i>Pseudanisakis tricupola</i> Gibson, 1973	Acanthocheilidae	Bay of Fundy, Canada Barent Sea	[98] Review in [23]

921

922 **Table 2:** Meristic and morphometric data for *Acanthocotyle verrilli* ex *Amblyraja radiata* from
923 Adventfjorden, Spitsbergen. Measurements are given in micrometers.

Acanthocotyle verrilli (n=30)

Total body length	1069–5855 (3541) ^a
Body proper length	715–4688 (2757) ^b
Body width at the level of ovary	330–925 (632) ^b
Pharynx	
Length	124–340 (233) ^b
Width	77–413 (252) ^b
Pseudohaptor	
Number radial rows of sclerites	28–34 (mode=32) ^b
Length	354–1167 (767) ^b
Width	312–1112 (765) ^b
Testes	
Testicular field length	393–2583 (1522) ^c
Number	18–47 (mode=34) ^d
Maximum width	80–267 (173) ^c
Germarium	
Length	60–419 (215) ^c
Width	98–347 (203) ^c

924 Notes: ^a(n=28); ^b(n=29); ^c(n=26); ^d(n=22)

925 **Table 3:** Uncorrected pairwise genetic distances (%) between *Acanthocotyle* spp. based on
926 844bp of 28S rDNA gene portion. GenBank accession numbers are given in brackets.
927

	<i>A. verrilli</i>	<i>A. atacamensis</i>	<i>A. gurgesiella</i>	<i>A. imo</i>
<i>A. verrilli</i> (MW260310)				
<i>A. atacamensis</i> (MH511079)	0.75			
<i>A. gurgesiella</i> (KY379329)	2.01	2.26		
<i>A. imo</i> (MH511085)	0.25	0.50	1.76	
<i>A. urolophi</i> (FJ971962)	3.01	3.01	3.27	2.76

928

929 **Table 4:** Meristic and morphometric data for *Rajonchocotyle emarginata* ex *Amblyraja radiata*
 930 from Adventfjorden, Spitsbergen. Measurements are given in micrometers.

<i>Rajonchocotyle emarginata</i> (n=5)	
Total body length	8497–10556 (9449) ^a
Body proper length	6465–7943 (7093) ^b
Body width at level of ovary	1604–2601 (2073) ^b
Anterior sucker	
Length	101–530 (280) ^a
Width	120–858 (506) ^a
Pharynx	
Length	113–116 (115) ^c
Width	121–121 (121) ^c
Haptor	
Length	1547–2642 (2199) ^a
Width	2113–3337 (2556) ^a
Haptoral sclerites	
Anterior sclerite length	417–495 (455) ^a
Median sclerite length	402–503 (447) ^a
Posterior sclerite length	316–523 (420) ^a
Appendix	
Length	1913–4078 (3247) ^a
Width	605–939 (749) ^a
Hamulus	
Outer root length	42–51 (46) ^c
Inner root length	37–43 (40) ^c
Testes	
Testicular field length	1822–4075 (3088) ^a
Number	10–36 (mode=24) ^a
Egg	
Proper length	248–303 (280) ^a
Number of filaments	2 ^d
Length of filament	105–143 (123) ^c

931 Notes: ^a(n=4); ^b(n=5); ^c(n=2); ^d(n=3)

932 **Table 5:** List of *Acanthocotyle* spp. with host species designation and locality of the report.

Parasite species	Host species	Family	Locality	Reference
<i>Acanthocotyle atacamensis</i> Ñacari, Sepúlveda, Escribano & Oliva, 2019	<i>Bathyraja peruana</i> McEachran & Miyake, 1984	Arhynchobatidae	off Tocopilla, Chile	[49]
<i>Acanthocotyle elegans</i> Monticelli, 1890	<i>Raja clavata</i> Linnaeus, 1758	Rajidae	off Plymouth, UK	[65]
<i>Acanthocotyle greeni</i> Macdonald & Llewellyn, 1980	<i>Raja clavata</i>	Rajidae	off Naples, Italy off Plymouth, UK	[66] ¹ [70]
<i>Acanthocotyle gurgesiella</i> Ñacari, Sepúlveda, Escribano & Oliva, 2017	<i>Gurgesiella furvescens</i> de Buen, 1959	Gurgesiellidae	off Valparaiso, Chile	[50]
<i>Acanthocotyle imo</i> Ñacari, Sepúlveda, Escribano & Oliva, 2019	<i>Amblyraja frerichsi</i> Krefft, 1968	Rajidae	off Tocopilla, Chile	[49]
<i>Acanthocotyle lobianchi</i> Monticelli, 1888	<i>Bathyraja brachyurops</i> (Fowler, 1910) ^a	Arhynchobatidae	off Plymouth, UK	[65]
	<i>Leucoraja naevus</i> (Müller & Henle, 1841) ^b	Rajidae		
	<i>Raja clavata</i>	Rajidae	off Naples, Italy off Plymouth, UK	[66] [65]
	<i>Raja microocellata</i> Montagu, 1818	Rajidae		
	<i>Raja montagui</i> Fowler, 1910	Rajidae		
<i>Acanthocotyle pacifica</i> Bonham & Guberlet, 1938	<i>Beringraja binoculata</i> (Girard, 1855) ^c	Rajidae	Puget Sound, USA	[67]
			Friday Harbour, USA	[69]
	<i>Raja rhina</i> Jordan & Gilbert, 1881	Rajidae	Puget Sound, USA Friday Harbour, USA	[68] ² [69]
<i>Acanthocotyle patagonica</i> Kuznetsova, 1975	<i>Bathyraja brachyurops</i> ^a	Arhynchobatidae	Patagonian Shelf	[80]
<i>Acanthocotyle pugetensis</i> Bonham & Guberlet, 1938	<i>Beringraja binoculata</i> ^c	Rajidae	Friday Harbour, USA off San Francisco, USA	[69] [114]
<i>Acanthocotyle urolophi</i> Kearn, Whittington,	<i>Urolophus cruciatus</i> (Lacepède, 1804)	Urolophidae	off Tasmania, Australia	[32]

Chisholm & Evans-Gowing,				
2016				
<i>Acanthocotyle verrilli</i> Goto,	<i>Amblyraja radiata</i> (Donovan, 1808) ^d	Rajidae	Cape Cod, USA	[105]
1899				
	<i>Amblyraja radiata</i> ^d		off Bergen, Norway	[106]
	<i>Amblyraja radiata</i> ^e		Chaleur Bay, Canada	[29]
	<i>Amblyraja radiata</i> ^d		off Newfoundland, Canada	[78] ²
	<i>Amblyraja radiata</i> ^d		Continental slope between Norway and Spitsbergen	[77] ²
	<i>Amblyraja radiata</i>		Barent Sea Adventfjorden estuary, Spitsbergen	Review in [23] ² This study
	<i>Bathyraja spinicauda</i> (Jensen, 1914)	Arhynchobatidae	Continental slope between Norway and Spitsbergen	[77] ²
	<i>Leucoraja erinacea</i> (Mitchill, 1825) ^f	Rajidae	Cape Cod, USA Coast of Maine, USA	[105] [79]
<i>Acanthocotyle williamsi</i> Price, 1938	Unidentified skate	-	Bering Sea, Aleutian Island (Salt Island)	[115]
<i>Acanthocotyle</i> sp.	<i>Bathyraja brachyurops</i> ^a	Rajidae	Northwest coast of Spain	[116]
	<i>Narcine maculata</i> (Shaw, 1804) ^g	Narcinidae	off Plymouth, UK	[62]
	<i>Raja clavata</i>	Rajidae	off Plymouth, UK Belgian Coast	[106]
	<i>Raja microocellata</i>	Rajidae	Northwest coast of Spain	[116]
	<i>Sympterygia bonapartii</i> Müller & Henle 1841	Arhynchobatidae	off Puerto Deseado, Argentina	[117]

933 ^a reported as *Raja brachyurops* Fowler, 1910
934 ^b reported as *Raja naevus* Müller & Henle, 1841
935 ^c reported as *Raja binocularata* Müller & Henle, 1841
936 ^d reported as *Raja radiata* Donovan, 1808
937 ^e reported as *Raja scabrata* Garman, 1913
938 ^f reported as *Raja erinacea* Mitchill, 1825
939 ^g reported as *Raja maculate* Shaw, 1804
940 ¹ reported as *Acanthocotyle oligoterus* Monticelli, 1899

941 ² reported as *Pseudoacanthocotyle*

Table 6: List of *Rajonchocotyle* spp. with host species designation and locality of the report.

Parasite species	Host species	Family	Locality	Reference
<i>Rajonchocotyle batis</i> Cerfontaine, 1899	<i>Amblyraja hyperborea</i> (Collett, 1879) ^a	Rajidae	Continental slope between Norway and Spitsbergen	[77]
	<i>Amblyraja radiata</i> (Donovan, 1808) ^b	Rajidae	Continental slope between Norway and Spitsbergen	
	<i>Beringraja binocularata</i> (Girard, 1855) ^c	Rajidae	Friday Harbor, Salish Sea, USA	[69]
	<i>Bathyraja spinicauda</i> (Jensen, 1914)	Arhynchobatidae	Continental slope between Norway and Spitsbergen	[77]
	<i>Dipturus batis</i> (Linnaeus, 1758) ^d	Rajidae	off Skagerrak, Denmark	[54]
			off Liège, Belgium	[52]
			off Ostend, Belgium	
			Porcupine Bank, Ireland	[118]
			off Plymouth, UK	[65]
		<i>Raja clavata</i> Linnaeus, 1758	Rajidae	off Roscoff, France
<i>Rajonchocotyle emarginata</i> (Olsson, 1876)	<i>Amblyraja radiata</i> ^e	Rajidae	Chaleur Bay, Canada	[29]
	<i>Amblyraja radiata</i> ^b		Patagonian Shelf	[111]
	<i>Amblyraja radiata</i>		off Tromsø, Norway	[30]
			Barent Sea	Review in [23]
			Adventfjorden estuary, Spitsbergen	This study
	<i>Bathyraja brachyrops</i> (Fowler, 1910) ^f	Arhynchobatidae	Patagonian Shelf	[111]
	<i>Bathyraja magellanica</i> (Philippi, 1902) ^g			
	<i>Leucoraja naevus</i> (Müller & Henle, 1841) ^h	Rajidae	off Plymouth, UK	[65]
	<i>Psammobatis scobina</i> (Philippi, 1857) ⁱ	Arhynchobatidae	Patagonian Shelf	[111]
	<i>Raja brachyura</i> Lafont, 1871	Rajidae	off Plymouth, UK Northwest coast of Spain	[65] [116]

	<i>Raja clavata</i>	Rajidae	off Plymouth, UK Mari Bahusiae, Scandinavia Mediterranean Sea, Italy Cardigan Bay, Wales off Roscoff, France Patagonian Shelf Galway Bay, Ireland	[119] [65] [120] [121,122]
	<i>Raja microocellata</i> Montagu, 1818	Rajidae	off Plymouth, UK Northwest coast of Spain	[65] [116]
	<i>Raja montagui</i> Fowler, 1910	Rajidae	off Plymouth, UK	[65]
	<i>Raja</i> sp.	Rajidae	Northwest coast of Spain	[116]
	<i>Raja undulata</i> Lacepède, 1802	Rajidae	Northwest coast of Spain	
<i>Rajonchocotyle laevis</i> Price, 1942	<i>Dipturus laevis</i> (Mitchill, 1818) ^j	Rajidae	Woods Hole, USA	[53]
<i>Rajonchocotyle wehri</i> Price, 1942	<i>Raja asterias</i> (Delaroche, 1809) ^k	Rajidae	Friday Harbor, USA	[53]

^a reported as *Raja hyperborea* Collett, 1879

^b reported as *Raja radiata* Donovan, 1808

^c reported as *Raja binoculata* Girard, 1855

^d reported as *Raja batis* Linnaeus, 1758

^e reported as *Raja scabrata* Garman, 1913

^f reported as *Raja brachyurops* Fowler, 1910

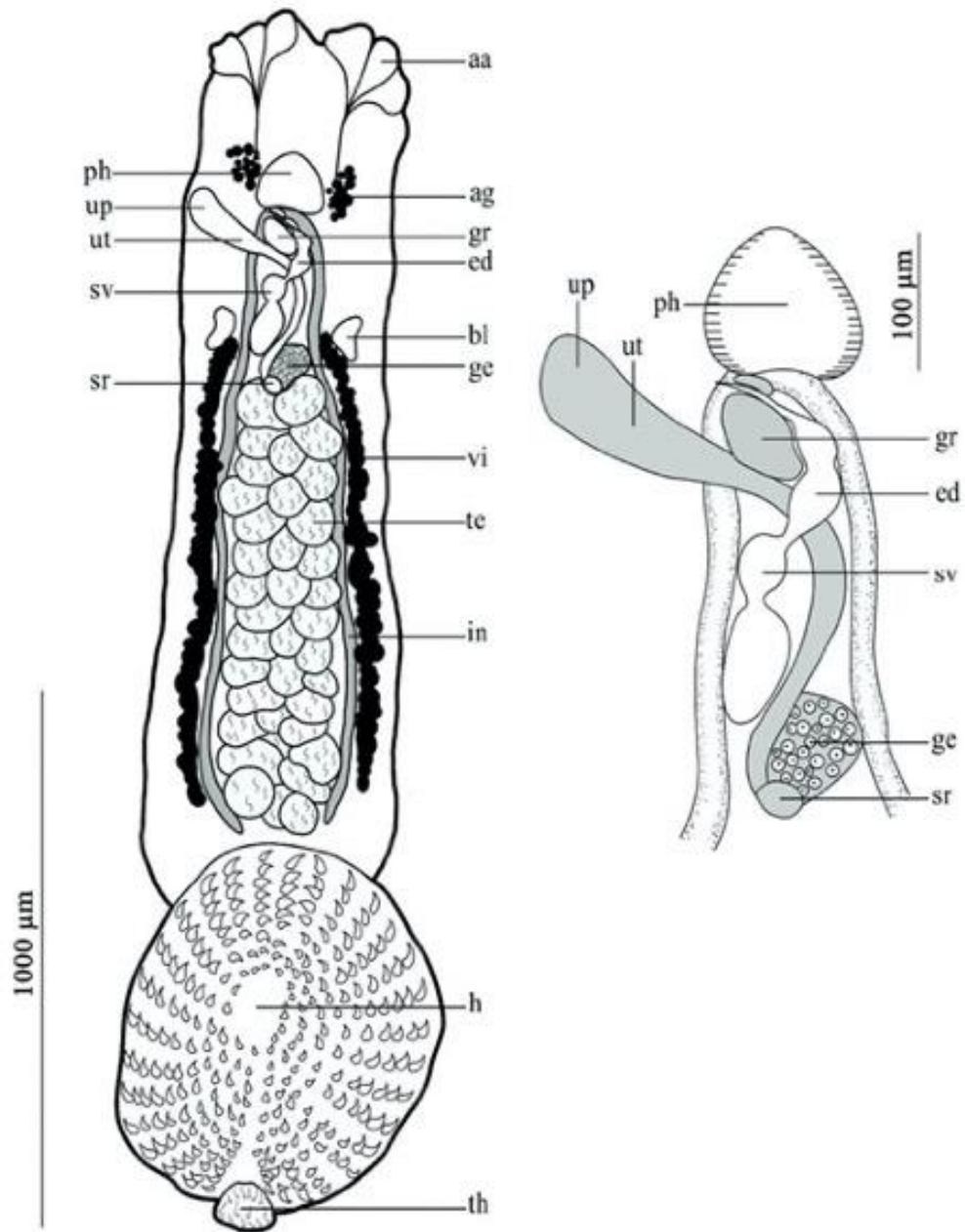
^g reported as *Raja magellanica* Philippi, 1902

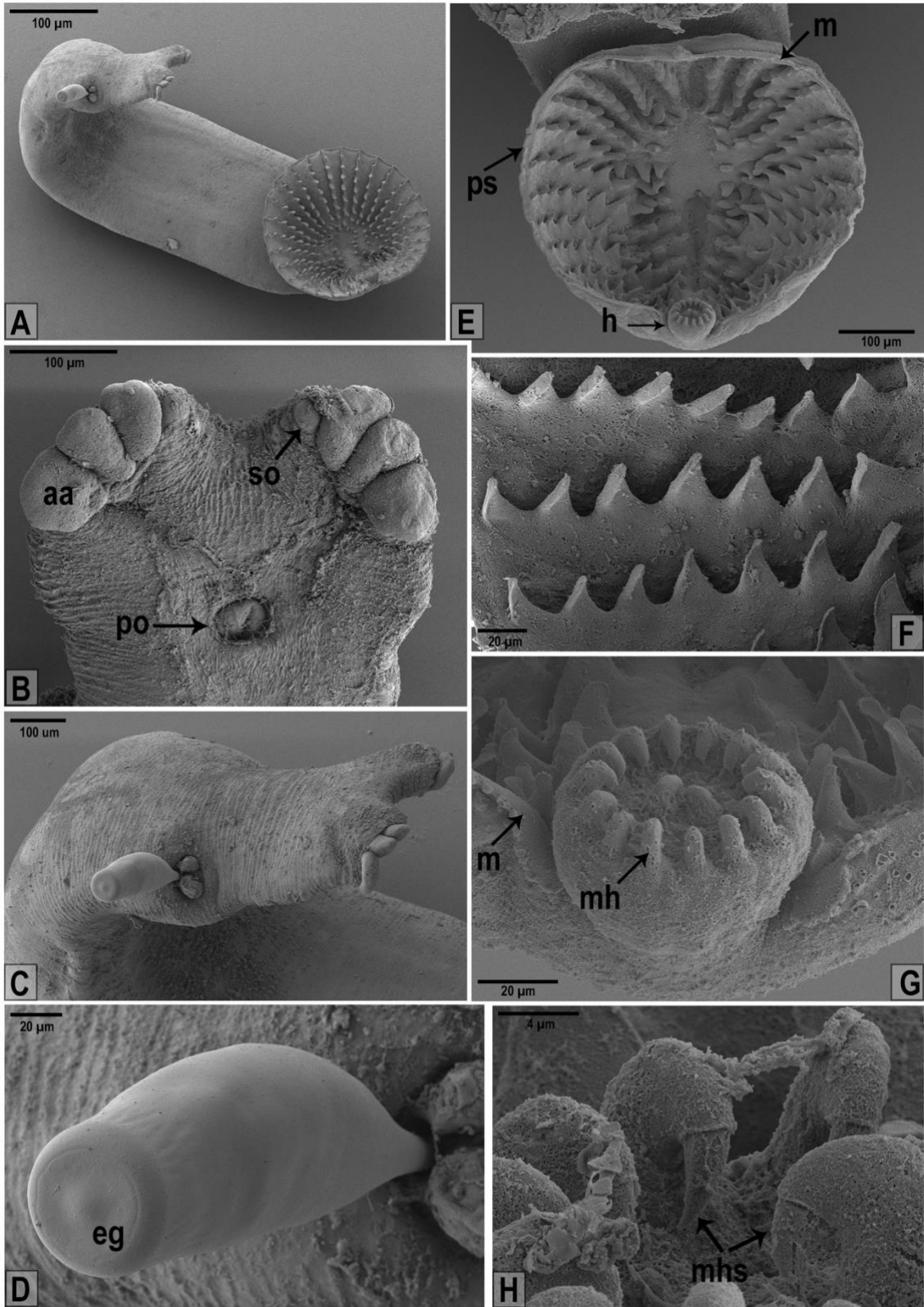
^h reported as *Raja naevus* Müller & Henle

ⁱ reported as *Raja scobina* Philippi, 1857

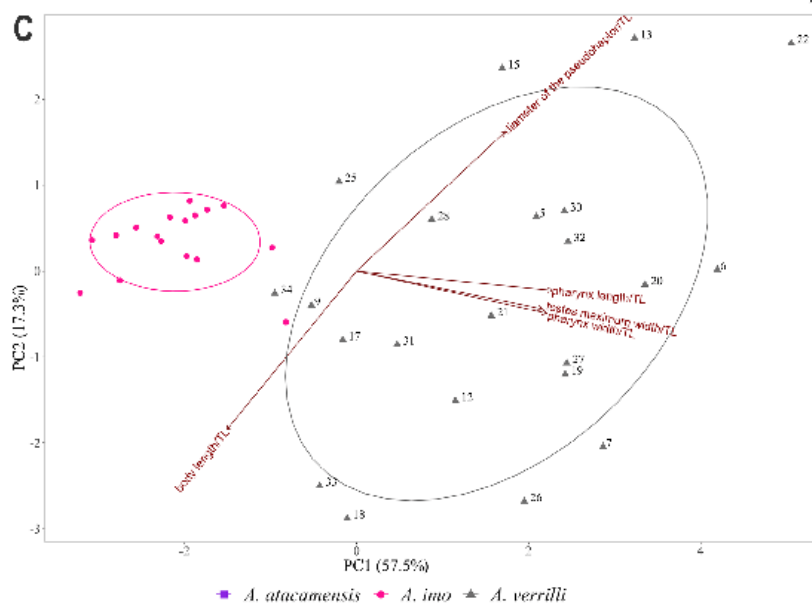
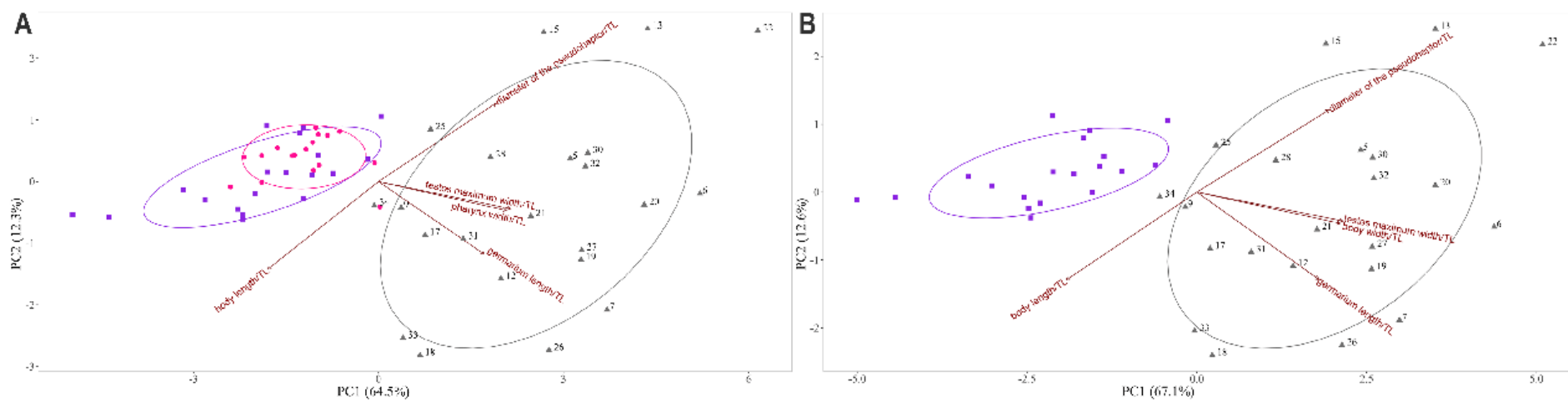
^j reported as *Raja laevis* Mitchill, 1818

^k reported as *Raja stellata* Delaroche, 1809

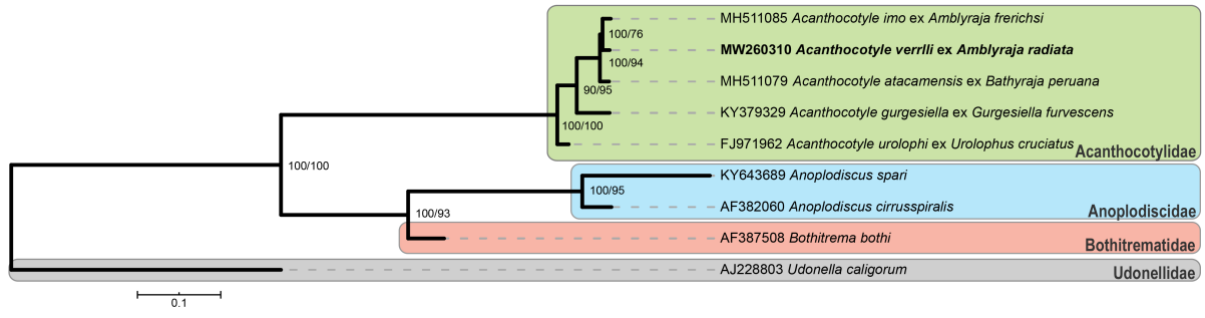




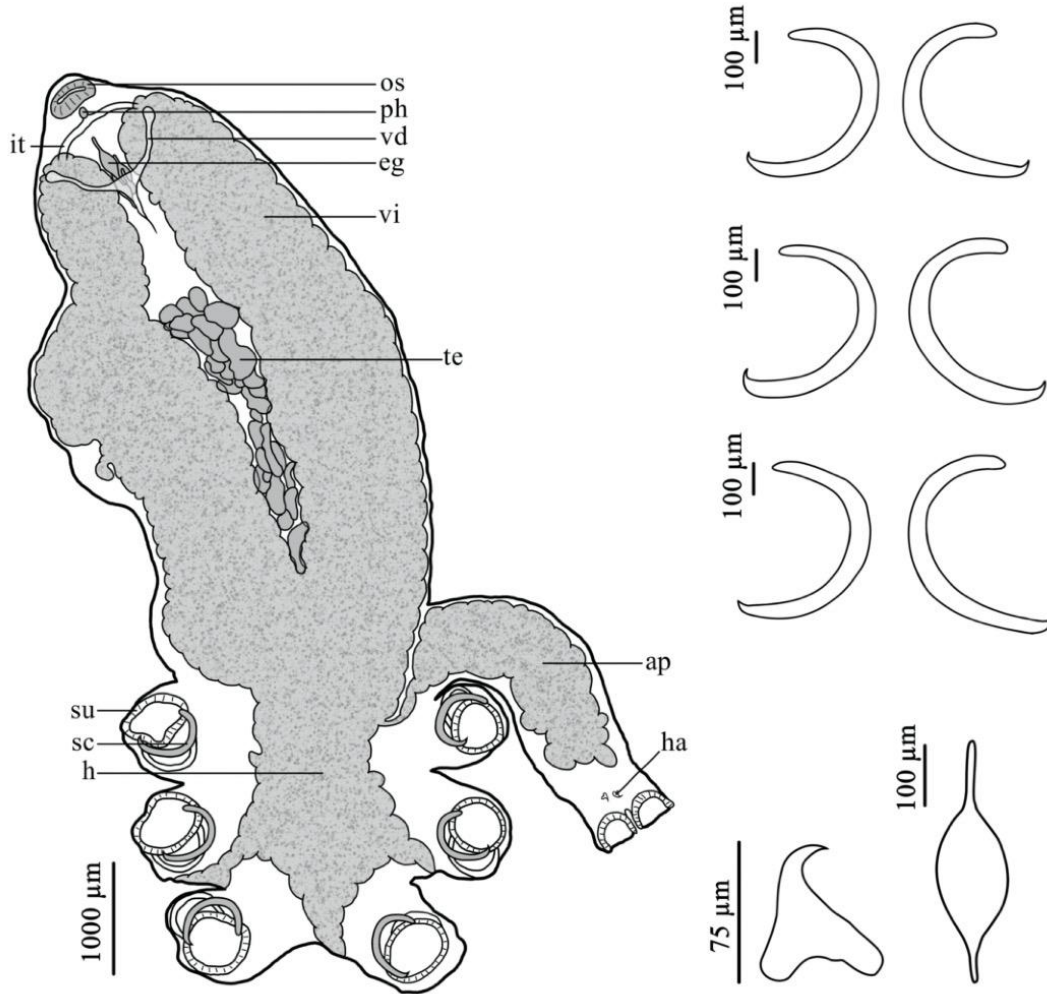
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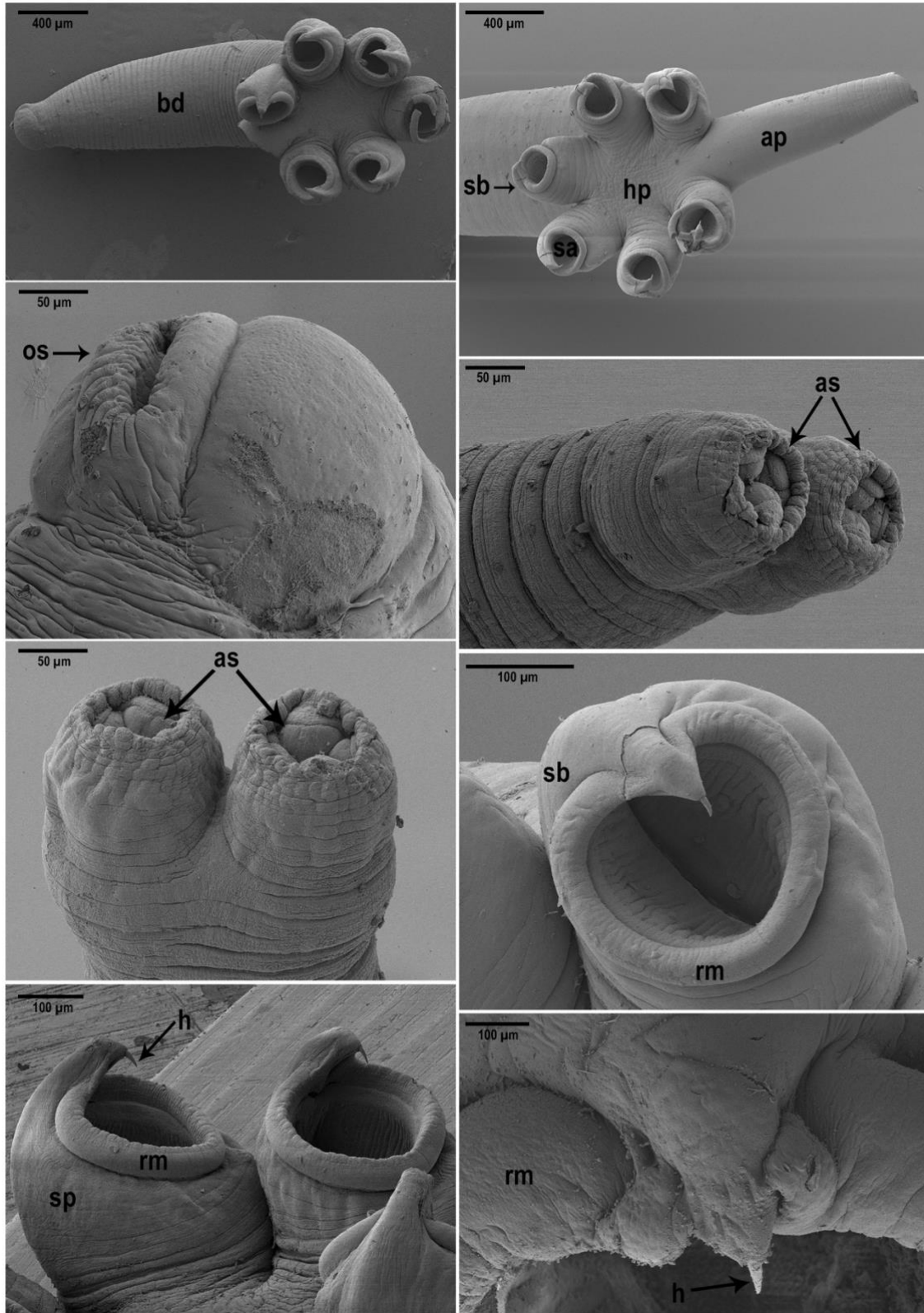
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