GUIDE TO NOTOCOTYLIDAE (DIGENEA) PARASITIZING COASTAL GASTROPODS OF THE WHITE AND BARENTS SEAS

© 2022 A. Gonchar[a, b, *], K. V. Galaktionov[b, a]

[a]St Petersburg University, Universitetskaya emb., 7/9, St Petersburg, 199034 Russia
[b]Zoological Institute of the Russian Academy of Sciences,
Universitetskaya emb., 1, St Petersburg, 199034 Russia
*e-mail: anya.gonchar@gmail.com

Recent studies on the digenean fauna at the White and Barents Seas have shown that there are more species than previously thought. These data are emerging in a series of publications, and we suggest to summarize them in a form that is convenient for practical use. Here we provide a guide that covers the 11 species from the family Notocotylidae that we have recorded in the intertidal gastropods *Ecrobia ventrosa*, *Peringia ulvae*, *Littorina* spp. and *Onoba aculeus*. We recap brief descriptions of rediae and cercariae, documented host and geographic range, though for several species the information is incomplete. We also refer to the DNA barcodes from GenBank, including the new ones. For the better usability, we include hints on the mollusc identification and explain how to deal with the parasites (field and lab procedures).

Gastropods at the White and Barents Seas serve as the first intermediate hosts for a variety of digeneans. Many of these parasites have been subject to at least some research, but the actual set of species within each family of Digenea in this region is still unclear. Recent integrative taxonomy studies have revealed diversity that had been hidden before, for example, in Brachycladiidae (Kremnev et al., 2020), Fellodistomidae (Krupenko et al., 2020), Himasthlidae (Galaktionov et al., 2021), Derogenidae (Krupenko et al., 2022), Renicolidae (Galaktionov et al., 2022), and a few other families. These data are emerging in a number of publications that are not so easy to follow. At the same time, the correct species identification of the digeneans' intramolluscan stages is a key to any type of research

on this material. That is why we take up a task to summarize the available data and compile a series of guides. This paper deals with the representatives of the family Notocotylidae.

Notocotylidae (Pronocephaloidea) are digeneans with a two-host life cycle. Their maritae (sexual adults) infect birds and, to a lesser extent, mammals. The eggs get into the environment, but there is no free-swimming miracidium. The first intermediate host, a gastropod, gets infected after accidental ingestion of eggs. In the gastropod host, rediae develop and reproduce, and eventually cercariae get formed. Cercariae of most notocotylids have a tail and leave the mollusc. There is no second intermediate host, and the definitive host gets infected by consuming metacercariae that had encysted on some object in the water.

Until recently, life cycles of two species of notocotylids were known at the White and Barents Seas. For *Parapronocephalum symmetricum* Belopolskaja, 1952 the life cycle was part of the original species description; for *Paramonostomum alveatum* (Mehlis in Creplin, 1846) Lühe, 1909 the intermediate host was discovered later (Kulachkova, 1954). However, more species were actually recorded (Chubrik, 1966; Podlipaev, 1979), at least in *Littorina* spp. and *Onoba aculeus* (A. Gould, 1841). Employing the molecular genetic data, we have preliminary estimated that at least 11 species of Notocotylidae occur in *Littorina* spp., *Peringia ulvae* (Pennant, 1777), *Ecrobia ventrosa* (Montagu, 1803) and *O. aculeus* at the White and Barents Seas.

This guide includes the overview of the mollusc identification, sampling and research procedures; and the information on all the notocotylid species that we found.

MATERIALS AND METHODS

The guide was compiled from the results of our own research conducted in 2002–2022, both published and unpublished. We collected most of our samples at the White Sea (various locations in the vicinity of Keret Archipelago, Chupa Inlet, Kandalaksha Bay); Barents Sea (Western and Eastern Murman, Pechora Sea); and in Iceland. We screened at least 20 thousands of molluscs (*E. ventrosa*, *P. ulvae*, *Littorina* spp. and *O. aculeus*) for infection with the Notocotylidae. We also acknowledge relevant earlier research on the Notocotylidae at the White and Barents Seas, as well as in the North Atlantic, commenting on its validation.

We open the guide with some tips on the correct identification of the gastropod intermediate host species. Next, we provide the description of the typical procedures to collect and identify notocotylid intramolluscan stages (according to our research experience). It is followed by the summary of identification characters that allow distinction of the Notocotylidae from other digeneans that are common in the same region and the same snail hosts. Then, the guide is structured by the gastropod intermediate host taxa. Taxonomy follows the WoRMS (WoRMS editorial board, 2022).

Some species of Notocotylidae are properly named and characterized, while other are just temporarily denoted, with most details lacking. We call these "Notocotylidae gen. sp." followed by a number that happened to be in use in our laboratory, "WS" standing for their origin from the White Sea and a letter addressing the cercaria morphotype (see below); for example, Notocotylidae gen. sp. 2 WSM (White Sea Monostomi). We include information on size and structure of cercariae and rediae, occurrence, and the definitive hosts. Size in micrometers is given as range with mean

in parenthesis (if more than five measurements were made), or simply as mean (less than five measurements); length and width are separated with "×" sign.

We refer to the GenBank IDs of the reference sequences, both previously published and the new ones.

The photographs were taken at different times between 2002 and 2022, using a variety of compound microscopes and cameras. The appropriate image modifications, drawings and figure layout were made in Corel Photo-Paint 24.0.0.301 and CorelDRAW 24.0.0.301.

<div align="center">RESULTS AND DISCUSSION</div>

Highlights on gastropod identification

Before further work with any parasite, its host must be correctly identified. We emphasize this for Notocotylidae and their molluscan hosts, because their specificity is not yet clear. Still, this guide is structured by molluscan taxa, and we start with a brief comment on their specific differentiation. All of the molluscs we are dealing with are now classified in Caenogastropoda, Littorinimorpha.

Hydrobiidae

Two members of Hydrobiidae (Truncatelloidea) are found at the White Sea: *E. ventrosa* and *P. ulvae*; these mudsnails are also widely known under their old generic name, *Hydrobia* W. Hartmann, 1821. No distinction between the two species had been made in this region until their co-existence was highlighted (Gorbushin, 1992). So, in earlier records of digeneans from "*Hydrobia* spp.", information on the host species is not quite accurate: it could have been either *E. ventrosa* or *P. ulvae*, or a mixture of two.

Hydrobiidae belong to an abundant superfamily Truncatelloidea where many representatives are morphologically and ecologically uniform (Falniowski, 2018). Its systematics has recently been revised, so we call for attention when addressing the old data on digeneans from "hydrobiids" – some of the species are now in different genera and families (Wilke et al., 2001). For example, *Hydrobia salsa* (Pilsbry, 1905) from North America is now classified as *Spurwinkia salsa* (Cochliopidae) (Davis et al., 1982).

At the White Sea, *E. ventrosa* and *P. ulvae* occur in sympatric populations and inhabit mudflats, often in the estuaries. However, they differ ecologically (Gorbushin, 1995) and in their response to harsh environmental conditions (Berger, Gorbushin, 2001). Morphological distinction is as obvious as it is ambiguous (Gorbushin, 1992). The size range of the two species overlaps, though *P. ulvae* are generally larger. The shell morphology is not a reliable character, especially in infected snails and when the surface is eroded. Most of the times, however, the periostracum differs in two species. In *P. ulvae* it is strong and coloured in copper to dark brown. In *E. ventrosa* it is thin and transparent, often faded, resulting in the pale bluish appearance of the shell. The oval aperture always has a narrowed tip in *P. ulvae* and just sometimes in young *E. ventrosa*. The umbilicus is slitlike and covered by the fold of the inner lip almost completely (*P. ulvae*) or just in half (*E. ventrosa*). The distinct external character that allows to distinguish species is the dark spots of pigment near the tip of the tentacles of *P. ulvae* (absent in *E. ventrosa*). The penis shape is a good

discriminating character: it is "small and pointed" in *E. ventrosa* and "big and stout" in *P. ulvae* (Muus, 1963, p. 135). Although this is not directly relevant for practical species discrimination, an important difference is that *P. ulvae* has a free-swimming larva, while *E. ventrosa* has direct development (Gorbushin, 1992).

Distribution of *E. ventrosa* is validated in the Mediterranean, as well as in northern Europe: Iceland, North and Baltic Seas (Vandendorpe et al., 2019). *P. ulvae* has a slightly different range: it is absent from Iceland, and may spread further north along the European coast (Wilke, Davis, 2000). At the Barents Sea both species probably have patchy distribution: they are not found in the Pechora Sea and around Dalniye Zelentsy (Eastern Murman), but present in the south-western Barents Sea in Varangerfjord and in Sommarøy (personal observations).

Rissoidae

O. aculeus is a member of Rissooidea, Rissoidae. It is distributed on both sides of the northern Atlantic, and apparently is the only species of this genus in the White Sea (Matveeva, 1974; Golikov, 1987; Loskutova, Granovitch, 2006). *Onoba aculeus* inhabits the intertidal and the upper subtidal (Matveeva, 1974; Golikov, 1987). At the Barents Sea, three other species of *Onoba* occur, but they can be differentiated from *O. aculeus* morphologically (Nekhaev et al., 2014).

Littorinidae

The common periwinkle *Littorina littorea* (Linnaeus, 1758) is not considered here because in our samples these snails were never infected with Notocotylidae.

Other periwinkles in the European north Atlantic are two groups of cryptic species from the subgenus *Neritrema* (Littorinoidea, Littorinidae): "saxatilis" (*L. saxatilis* (Olivi, 1792), *L. arcana* Hannaford-Ellis, 1978, *L. compressa* Jeffreys, 1865) and "obtusata" (*L. obtusata* (Linnaeus, 1758), *L. fabalis* (W. Turton, 1825)). Conchiological characters are used to distinguish between these two groups. The shell is more conical in the "saxatilis" and more spherical in the "obtusata" group; in the "obtusata" group, the periostracum bears fine longitudinal striation; the sutures are deeper in "saxatilis" group (Reid, 1996; Granovitch et al., 2004). Species identification within each group is possible only based on the reproductive anatomy. *Littorina saxatilis* are special in being ovoviviparous.

Both at the White and Barents Seas, *L. obtusata* and *L. fabalis* co-occur. Discrimination between them is unambiguous following dissection (Reid, 1996; Granovitch et al., 2004; Maltseva et al., 2021b). Males of *L. fabalis* bear few (below six) penial glands arranged in one row, and a long thin filament. In *L. obtusata* they have small glands arranged in several rows, and a short filament. In *L. obtusata* females, the *bursa copulatrix* is almost as long as the jelly gland, and in *L. fabalis* it is less than ½ of the jelly gland length.

At the Barents Sea, all three species of the "saxatilis" group co-occur. Their identification also requires dissection, but may remain inconclusive (Reid, 1996; Granovitch et al., 2004; Maltseva et al., 2021b). Females differ in the relative size of the glands in the reproductive system; also, *bursa copulatrix* is broad and long in *L. arcana* and short and

slim in *L. compressa.* Males differ in penis morphology: two or more rows of relatively small penial glands and triangular filament (*L. arcana*); one row of large penial glands (not more than six) and an indistinct filament (*L. compressa*); one row with more than six (up to 45) small penial glands and a triangular filament (*L. saxatilis*). At the White Sea, only *L. saxatilis* has been recorded.

There is some ecological niche differentiation between the *Neritrema* species (Reid, 1996; Granovitch et al., 2013; Maltseva et al., 2021a). *Littorina arcana* are more frequent in the upper intertidal, *L. compressa* – in the lower intertidal, and *L. fabalis* – in the upper subtidal. *Littorina saxatilis* and *L. obtusata* can be found from the lower to the upper zones. *Littorina obtusata* and *L. fabalis* inhabit the macrophytes, with the first species preferring *Fucus vesiculosus* Linnaeus, 1753 and *Ascophyllum nodosum* (Linnaeus) Le Jolis, 1863, and the second species – *F. serratus* Linnaeus, 1753. Species of the "saxatilis" group prefer to live on stones and gravel.

Hybrids occur within both "obtusata" and "saxatilis" groups (Mikhailova et al., 2009; Costa et al., 2020). Identification problems also arise when the snails are immature or castrated following digenean infection. Genotyping is possible for the "obtusata" group (Reid et al., 2012; Costa et al., 2020), but DNA barcoding is problematic for members of the "saxatilis" group.

Summing up the story of distinction between the *Neritrema* species, the best practice for collecting notocotylids from these snails is along with the host species identification based on the anatomy features. If this has not been done, we recommend stating explicitly that the hosts were identified only as "obtusata" or "saxatilis" group members, and the actual species is unknown. This should be, however, taken more liberally for sampling in areas where only *L. saxatilis* and/or *L. obtusata* are known to occur. If in future it is confirmed that for species within each group ("saxatilis" and "obtusata") the spectrum of notocotylid parasites is the same, the laborious task to distinguish periwinkles will be fine to cease.

Field and laboratory procedures for identification of intramolluscan Notocotylidae

Snails that serve as the first intermediate hosts of Notocotylidae at the White and Barents Seas inhabit the intertidal. They are usually sampled at low tide, by hand (periwinkles) or by sieving sediment through a sieve with 1-mm^2 mesh size (mud snails and *O. aculeus*). Smaller snails usually have dramatically lower prevalence of infection and are not sampled, unless there is a specific goal to estimate this prevalence. In the lab the snails are kept in natural or artificial sea water at 4–12°C, depending on the available equipment. While the fridges with 4°C temperature are more common, higher temperature is more favourable for activity of snails and development of cercariae, and subsequently for their shedding (see below).

One method to detect infected snails is to induce cercariae shedding. To do so, snails are placed individually in the wells of a 24-welled cell culture plate (for mudsnails and *O. aculeus*), or similar larger vessels (for periwinkles), containing sea water. Cercariae usually leave the snails after exposure to bright artificial light or, more effectively, sunlight. The

favourable period to try this procedure is usually between 10 am and 2 pm. It is important to observe wells with the snails regularly because cercariae of Notocotylidae often form cysts soon after release. The rough plan is look through the water in the wells under the stereomicroscope after 30 min of illumination, and then 2–4 times more at 15 min intervals.

Another method is to dissect snails. This allows to detect early infection, when no cercariae are yet ready for shedding; also it is a way to observe the rediae. Additionally, the specific identification of snails may require dissection (see above).

The best way to observe diagnostic features of cercariae is to prepare temporary mounts and study them under the compound microscope. Any sharp movements may trigger cercariae encystment, so pipetting should be smooth and coverslip should be placed slowly. In a thick layer of water, cercariae can swim and no details of the structure are visible. When excess water is removed, cercariae start to contract and stretch their body; this way they can crawl. Such a medium coverslip pressure is best for identifying cercariae, with special emphasis to their morphotype (see below; Fig. 1F–1H). When water is deficient, cercariae stop moving and get over-flattened. The ideal moment to take photographs is before this moment, when cercarial activity is already low.

For measurements, the standard procedure is to kill the cercariae by heating over the flame of a spirit lamp in a drop of water on a glass slide; to make a temporary mount with a medium coverslip pressure; and to use an ocular micrometer or an image produced by the camera. Using photographs for measurements is also possible (e.g. in ImageJ; Schneider et al., 2012).

To verify identification with DNA sequencing, usually one redia or even one cercaria is enough to extract DNA with any protocol. In this guide, we offer two rDNA barcodes: ITS1 (800–100 b.p.) and D2 domain of the 28S rDNA (590 b.p.). The primers for their amplification are BD1 (GTCGTAACAAGGTTTCCGTA) and 4S (TCTAGATGCGTTC-GAARTGTCGATG) for the ITS1 (Luton et al., 1992); and C2'B (GAAAAGTACTTT-GRARAGAGA, Bayssade-Dufour et al., 2000) and D2 (TCCGTGTTTCAAGACGGG, Vân Le et al., 1993) for the D2. Amplification protocols are in our published articles on Notocotylidae (e.g. Gonchar, Galaktionov, 2021). The D2 domain of the 28S rDNA amplifies very robustly, but it may lack variations to distinguish some of the close species (one such example is mentioned below). ITS1 also amplifies well and is distinct in all the species we discovered, but it contains a varying number of repeats, and this should be accounted for during alignment. Neither of the two fragments is powerful enough for phylogenetic reconstructions.

The new sequences generated in this study and submitted to GenBank are OP942346–OP942361.

Recognition of Notocotylidae in the molluscs

Identification of the intramolluscan stages of Notocotylidae to the family level is simple and reliable. Stereomicroscope is usually sufficient. In a dissected mollusc, one clear feature is the presence of rediae, they often take up much space in the snail's haemocoel

(Fig. 1A). The rediae have prominent pharynx and caecum (as opposed to the daughter sporocysts in some other digeneans), germinal mass in the posterior region and some developing cercariae (Fig. 1B). Rediae of different species are similar and mostly differ in size and the number of embryos. Cercariae have body length of about 250–450 μm and a set of typical characters: two lateral and one median (usually less prominent) eyespots; oral sucker but no ventral sucker; dorsal adhesive pockets at the posterolateral edges of the body (Fig. 1C). The cercariae are pigmented and have excretory ducts filled with refractive granules. Notocotylid cercariae encyst in the external environment (Fig. 1D–1E); this also happens in the lab dishes where no natural substrates are available. Observations on the behaviour of notocotylid cercariae are summarized by Krupenko and Gonchar (2017).

Immature cercariae are often seen inside and outside of the rediae within a mollusc (Fig. 1A). They may lack median eyespot and have pigment unevenly distributed, but otherwise have typical appearance of notocotylid cercariae.
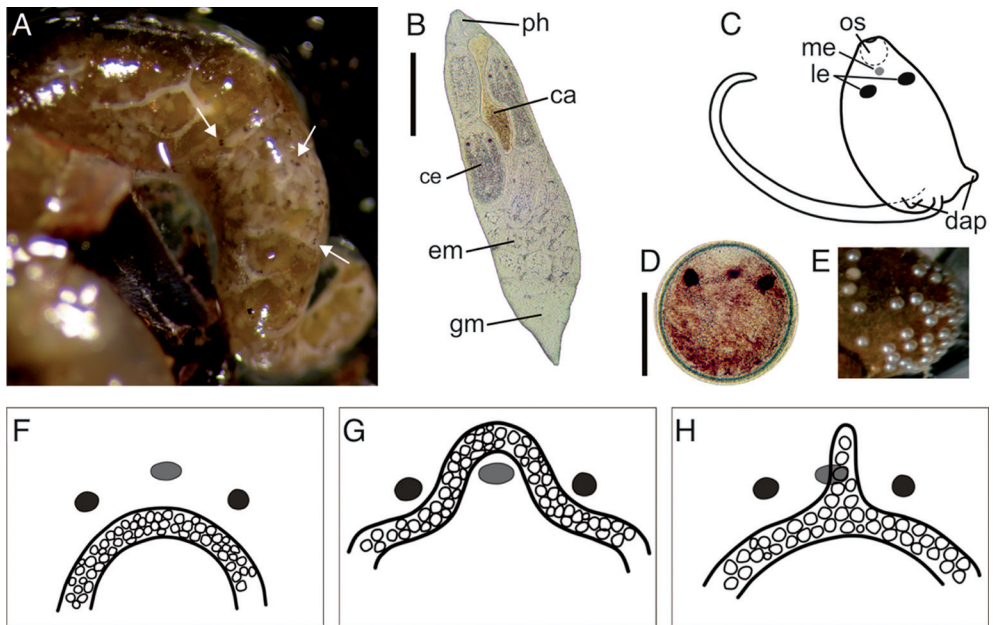

Figure 1. Helpful features to identity infection of a mollusc by Notocotylidae and distinguish between the species. A – hepatopancreas of a periwinkle infected with *Tristriata anatis*, showing multiple rediae and cercariae, the arrows are pointing at their eyespots. B – appearance of a notocotylid redia (exemplified by *Paramonostomum alveatum*); ph – pharynx, ca – caecum, ce – developing cercariae, em – embryos, gm – germinal mass; scale bar 100 μm. C – general structure of a notocotylid cercaria, modified from Krupenko, Gonchar, 2017; os – oral sucker, me – median eyespot, le – lateral eyespot, dap – dorsal adhesive pocket. D – microphotograph of a metacercarial cyst (*Paramonostomum alveatum*) with eyespots and excretory granules still visible; scale bar 100 μm. E – cysts on the surface of the molluscan shell. F–H – schemes of the anterior part of the main collecting ducts of the excretory system in notocotylid cercariae that correspond to three cercarial morphotypes: Monostomi (F), Imbricata (G) and Yenchingensis (H), modified from Rotschild, 1938.

The minority of notocotylid cercariae lack eyespots, have a knob-like tail and encyst inside the molluscan first intermediate host. In our study region, these belong to a single species *P. symmetricum* (see below).

A couple of other digeneans occur in the similar set of coastal snails and have rediae as an intramolluscan developmental stage, but they can be readily distinguished from Notocotylidae. Cercariae of *Cryptocotyle* spp. (Opisthorchiidae) also lack ventral sucker and have eyespots (two), but they have fin folds on the tail and peculiar intermittent swimming; they also are smaller (body length below 200 μm) (Stunkard, 1930). Cercariae of *Himasthla* spp. (Himasthlidae, Echinostomatoidea) are about as large as notocotylid cercariae, but they have a collar with spines and a ventral sucker, and no eyes (Galaktionov et al., 2021).

Within Notocotylidae, cercariae are classified into three groups, or morphotypes, depending on the appearance of the main collecting ducts (MCD) of their excretory system (Rothschild, 1938). The MCD in notocotylid cercariae merge at the front, forming a circle. In the Monostomi group, the anterior part of the MCD is behind the median eyespot (Fig. 1F). In the Imbricata group, the anterior part of the MCD forms a loop at/in front of the median eyespot (Fig. 1G). In the Yenchingensis group, the anterior part of the MCD forms a diverticulum reaching the median eyespot or further forward (Fig. 1H). Some variations to the Monostomi morphotype are possible, in particular – one, two or three shorter inconspicuous diverticula (not to be confused with Yenchingensis).

Summary of Notocotylidae species from different hosts[1]
Hydrobiidae
Notocotylus atlanticus Stunkard, 1966 (Fig. 2A)

(From Gonchar et al., 2019) Living rediae vary in size: mature rediae are 770–1570 × 290–370 (1185 × 330); young rediae are 270–600 × 114–257 (418 × 176). Cercariae are of Yenchingensis morphotype. Heat-killed cercariae are 257–371 (300) × 114–229 (153); the tail is 243–400 (305) × 29–43 (34); the oral sucker is 29–47 (35). Excretory granules are located 4–7 in rows across the main excretory ducts, their size is 0.88–1.84 (1.32). Cystogenous glands cells contain uniform rod-shaped secrete. The cysts are 170–200 (186) in diameter.

The species was originally described in North America, with *S. salsa* as the first intermediate hosts (Stunkard, 1966). We found *E. ventrosa* infected with this parasite at the White Sea and in Iceland. There has yet been no ultimate genetic validation of the conspecificity of the European and American material. Indirect genetic evidence suggests that *N. atlanticus* is also found in Japan (Gonchar, Galaktionov, 2022).

The type host is *Somateria mollissima* (Linnaeus, 1758). We found the maritae of *N. atlanticus* in *Anas platyrhynchos* Linnaeus, 1758, *Mareca penelope* (Linnaeus, 1758) and *A. acuta* Linnaeus, 1758. Maritae are difficult to distinguish from several other species: *N. intestinalis* Tubangui, 1932, *N. magniovatus* Yamaguti, 1934, *N. imbricatus* (Looss, 1893) Szidat, 1935, *N. attenuatus* (Rudolphi, 1809) Kossack, 1911.

Molecular references MH818008 (28S rDNA) and MH818012 (ITS1).

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[1] The actual range of molluscan hosts for each species of Notocotylids may be wider; this possibility has to be tested in all future studies.
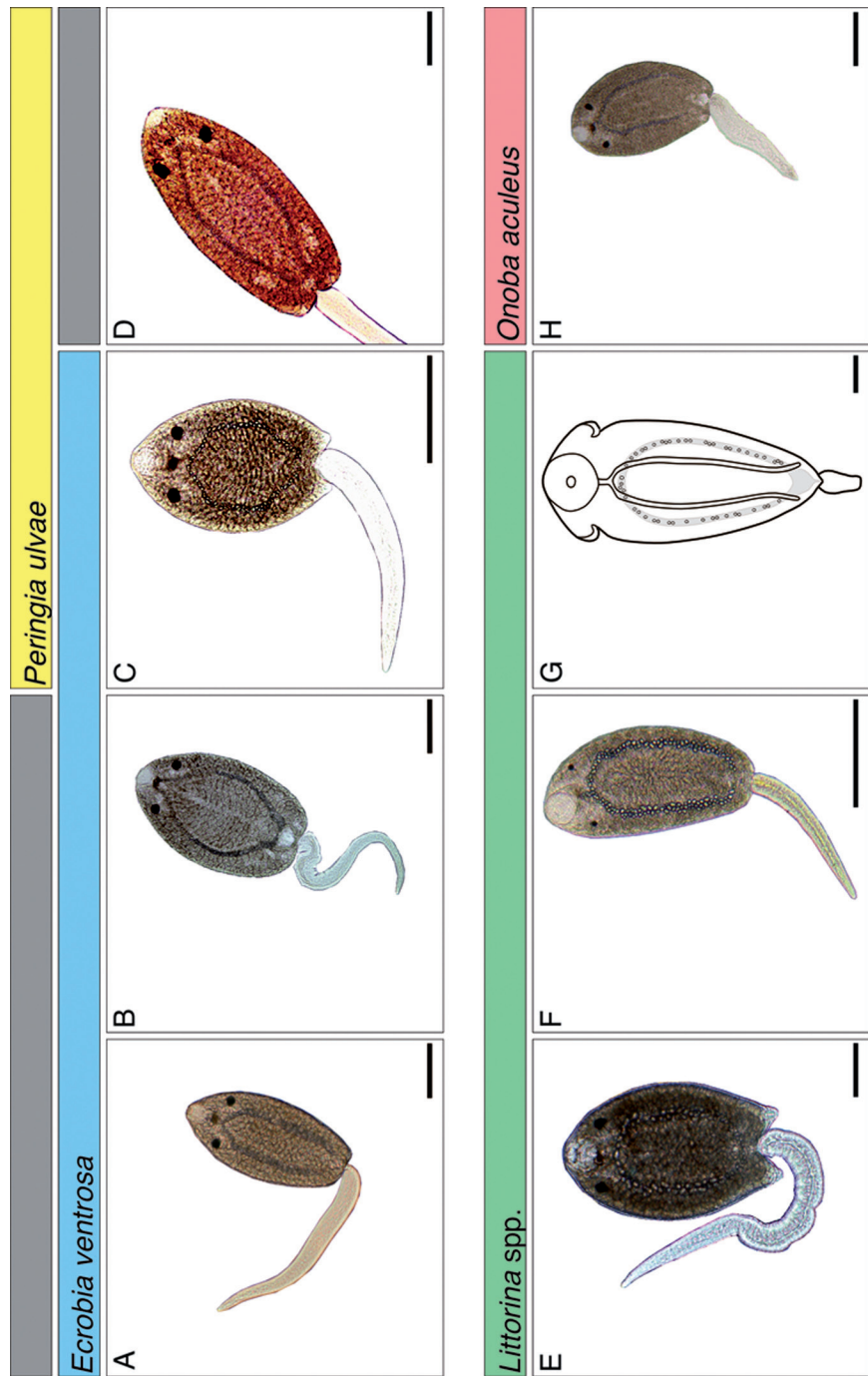
Figure 2. Appearance of cercariae in eight species of Notocotylidae from the White and Barents Seas. (Images for three more species are not available). The species of molluscan host species are provided above the cercariae images. All scale bars are 100 μm. A – *Notocotylus atlanticus*, B – *Paramonostomum anatis*, C – *Paramonostomum alveatum*, D – *Notocotylidae gen. sp. 3 WSI*, E – *Tristriata anatis*, F – Notocotylidae gen. sp. 6 WSY, G – *Parapronocephalum symmetricum* (modified from James, 1969), H – *Catatropis onobae*.

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Paramonostomum anatis Garkavi, 1965 (Fig. 2B)

Mother rediae reach up to 150–450 × 45–90, and daughter rediae measuring 540 × 180 and more start producing cercariae (Garkavi, 1968). We found that cercariae belong to the Imbricata morphotype; their body is 270 × 151, the tail is 300 × 30, the oral sucker is 32 (our unpublished data). Cercariae are equally willing to encyst on both vegetate substrate and the shell of the mollusc which they have left (Fig. 1E) (Gonchar, Galaktionov, 2016). We found this species only in *E. ventrosa*, at the White Sea and in Iceland.

The species was originally described at the coast of the Sea of Azov; its life cycle was also elucidated there, with *E. ventrosa* as the first intermediate hosts (Garkavi, 1968). There were no further records of its intramolluscan stages, but *Cercaria* Notocotylidae sp. no. 12 Deblock, 1980 from *Peringia ulvae* have similar appearance, particularly the morphotype.

Definitive hosts are *A. platyrhynchos* (type host, also our unpublished data) and probably other *Anas* spp. (Filimonova, 1985).

Molecular references OP942354 (28S rDNA) and OP942347 (ITS1).

Paramonostomum alveatum (Mehlis in Creplin, 1846) Lühe, 1909 (Fig. 2C)

Rediae (measured from the photograph) are 1120 × 283 and contain about four developing cercariae (Fig. 1B). The cercarial body is 240 × 135, the tail is 300 × 30, the oral sucker is 32 (our unpublished data). Cercarial morphotype is Monostomi, but some variations occur: one, two or three short extensions in the anterior part of the main collecting ducts. Cercariae tend to encyst on the vegetate substrate (Gonchar, Galaktionov, 2016).

We found *P. alveatum* in both *E. ventrosa* and *Peringia ulvae* at the Keret Archipelago, the White Sea; and in *E. ventrosa* in Iceland.

Earlier records of the geographic and host range are not clear: it is impossible to confidently interpret them because we might deal with a group of morphologically similar species. At the White Sea, the intermediate hosts of *P. alveatum* were identified as *Peringia ulvae* (Kulachkova, 1954; Zelikman, 1966; Chubrik, 1966). In North America, this species is supposedly hosted by *S. salsa* (Stunkard, 1967). *Cercaria* Notocotylidae sp. no. 11 Deblock, 1980 from *E. ventrosa* in the Mediterranean may represent this species, too (Deblock, 1980).

Definitive hosts are *Somateria mollissima* (our data) and many other species of anatids (Filimonova, 1985); type host is unclear.

Molecular references OP942355 (28S rDNA) and OP942346 (ITS1). Sequence of the D2 domain of the 28S rDNA does not ensure reliable distinction from the species Notocotylidae gen. sp. 2 WSM (see below).

Notocotylidae gen. sp. 3 WSI (Fig. 2D)

We found cercariae of Imbricata morphotype measuring 350–409 × 168–220 (body), 380–415 × 38–50 (tail); 31–35 × 33–37 (oral sucker) uniquely in *Peringia ulvae* (our unpublished data). We matched them by molecular genetic data to (1) maritae from *A. platyrhynchos* that comply with the diagnosis of *P. anatis*; and (2) a GenBank sequence for the marita from a wader *Tringa erythropus* Pallas, 1764 (Charadriiformes) from Kherson

Region, Ukraine (Tkach et al., 2001) that is also named *P. anatis*. However, there is genetic divergence between the *P. anatis* from *E. ventrosa* (described above) and this species.

The morphological distinction between Notocotylidae gen. sp. 3 WSI and *P. anatis* is scarce, but it appears that the former might have larger cercariae.

Molecular references OP942358 (28S rDNA) and OP942350 (ITS1).

Notocotylidae gen. sp. 2 WSM (no image available)

According to our unpublished data, the body of cercariae is 265 × 152; their tail is 344 × 36; and the oral sucker is 36 × 35. Cercariae are of Monostomi morphotype and very similar to those of *P. alveatum*, but appear genetically distinct from them. Both *E. ventrosa* and *P. ulvae* serve as the first intermediate hosts.

We found maritae in *S. mollissima* from the White Sea that matched these cercariae genetically; this material was not sufficient for species identification or morphological description.

Molecular references OP942361 (28S rDNA) and OP942349 (ITS1). Sequence of the D2 domain of the 28S rDNA does not ensure reliable distinction from the species *P. alveatum* (see above).

Notocotylidae gen. sp. 5 WSM (no image available)

One *Peringia ulvae* mollusc from Krasnyi Island (White Sea, Kandalaksha Bay) was infected with Notocotylidae that had Monostomi cercariae, but were genetically distinct from *P. alveatum*. As for now, this species is delineated only based on molecular data; no matching maritae have been found. Notocotylidae gen. sp. 5 WS appears as a sister species to *P. alveatum*.

Cercariae of Monostomi morphotype from *P. ulvae* were described in the life cycle of *Catatropis lagunae* Bayssade-Dufour et al., 1996 in France. This is the only prior record that may potentially refer to the same species.

Molecular references OP942360 (28S rDNA) and OP942352 (ITS1).

Notocotylidae gen. sp. 4 WSY (no image available)

In March 2018 and 2019 we collected two *P. ulvae* molluscs shedding notocotylid cercariae with Yenchingensis morphotype in the Sukhaya Salma inlet at the White Sea. The definitive host is unknown. The putative species is suspected based on molecular data. It appears as a sister species to *Catatropis onobae* Gonchar, Galaktionov, 2021.

Molecular references OP942359 (28S rDNA) and OP942353 (ITS1).

***Littorina* spp.**

Tristriata anatis Belopolskaja, 1953 (Fig. 2E)

(From Gonchar, Galaktionov, 2017) There may be up to a thousand rediae in one mollusc (Fig. 1A), they differ in size depending on their age, roughly from 300 to 1800 in length. Cercariae are of Monostomi morphotype, their body size is 315–510 (425) × 165–270 (230), the tail is 315–488 (408) × 37–83 (62), and the oral sucker is 45–60 (55). The secrete of the cystogenous glands in rod-shaped.

We found *T. anatis* in three species of *Littorina*: *L. saxatilis*, *L. obtusata* and (in the Sea of Okhotsk) *Littorina sitkana* Philippi, 1846.

The species is found across a large geographic range: in the North Pacific (Sea of Okhotsk) and North Atlantic (Barents Sea, Celtic Sea, Iceland) (Gonchar, Galaktionov, 2020).

Definitive hosts are *S. mollissima*, *Somateria spectabilis* (Linnaeus, 1758), *Histrionicus histrionicus* (Linnaeus, 1758) and *A. platyrhynchos*.

Molecular references KX833042 (28S rDNA) and KX833023 (ITS1).

Notocotylidae gen. sp. 6 WSY (Fig. 2F)

We found notocotylid cercariae with Yenchingensis morphotype in *L. saxatilis* in Kem-ludy Archipelago (White Sea, Kandalaksha Bay, Chupa Inlet) and in Roscoff (the English Channel). Few photographs are available, and when measured from a photo, the cercarial body is 194 × 99, the tail is 146 × 18, and the oral sucker is 29. The corresponding maritae and the definitive host are unknown. We consider this an independent species based on the molecular genetic data.

Yenchingensis cercariae from *L. obtusata* and *L. littorea* in Roscoff were called *Cercaria lebouri* (Stunkard, 1932). Later accounts of supposedly the same cercariae were from *L. littorea* (e.g. Werding, 1969) and *L. saxatilis* (e.g. James, 1969). The experimental infection study revealed that *Cercaria lebouri* from *L. littorea* correspond to the maritae identified as *Paramonostomum chabaudi* van Strydonck 1965 (Evans et al., 1997). This leaves a question on a specific identity of Yenchingensis cercariae from the representatives of the subgenus *Neritrema* – both *L. saxatilis* and *L. obtusata*: do they also belong to *P. chabaudi* or to some different species? And are our Yenchingensis isolates from *L. saxatilis* at the White Sea conspecific to those from the British Isles (James, 1969)?

Molecular references OP942356 (28S rDNA) and OP942351 (ITS1).

Parapronocephalum symmetricum Belopolskaja, 1952 (Fig. 2G)

(Based on the description from James, 1969). Rediae and cercariae are found in the visceral haemocoel. There is a single first (410–750 × 120–350) and six to ten second (600–900 × 290–580) generation rediae, their pharynx is 50–70 in diameter. The body of the fully-developed cercariae is 710–720 × 280–300, their oral sucker is 140–145, the tail is stumpy and measures just 100. They have a collar that is 300–305 wide. Cercariae migrate towards the stomach and encyst there in the haemocoel lining. The cysts are oval, 380–400 × 250–280.

We found *L. obtusata* infected with *P. symmetricum* in Kem-ludy Archipelago, Chupa Inlet, White Sea; and also detected it in the Eastern Murman. The species was originally described from *L. saxatilis* in the Seven Islands Archipelago, Barents Sea (Belopolskaja, 1952). It was later recorded, also in *L. saxatilis*, on the British Isles (Celtic Sea – Bristol Channel (James, 1969) and Isles of Scilly (Newell, 1986); the North Channel – St Mary's Portavogie harbour (Matthews et al., 1985) and Belfast Lough (Irwin et al., 1989)). Accounts in Iceland are from both *L. saxatilis* and *L. obtusata* (Skírnisson, Galaktionov, 2002).

In a study covering the extended region in the north of Europe, *P. symmetricum* was found in both *L. saxatilis* and *L. obtusata* in the west (Trøms, Finnmark and Western Murman), only in *L. saxatilis* on the Eastern Murman coast and only in *L. obtusata* in the White Sea (Galaktionov, Bustnes, 1996).

Type hosts are *Calidris maritima* (Brünnich, 1764). Adult worms also bear a collar and resemble the metacercariae from the periwinkles, but reach larger size.

Molecular references OP942357 (28S rDNA) and OP942348 (ITS1).

Onoba aculeus

<u>*Catatropis onobae* Gonchar, Galaktionov, 2021</u> (Fig. 2H)

(From Gonchar, Galaktionov, 2021) The rediae measure 218–800 (492) × 106–234 (174), the pharynx is 31–49 (43) × 31–44 (37). In ethanol-fixed cercariae, body size is 243–361 (300) × 118–180 (145); tail is 322–588 (463) × 33–48 (41); oral sucker is 27–40 × 30–43. In living cercariae, body size is 248–379 (297) × 163–215 (181). The morphotype is Yenchingensis, MCD contain excretory granules 1.45–2.28 (1.86, $n = 38$) in diameter; 1–2 granules are in a row across main excretory ducts. Secretory granules in cystogenous glands uniform.

O. aculeus infected with *C. onobae* occur in Kem-ludy Archipelago, Chupa Bay, White Sea; Dalniye Zelentsy, Barents Sea; and Grótta, Grindavik (Iceland). In the same regions, notocotylids (probably also belonging to *C. onobae*) had been registered in *O. aculeus* before the species was described (Chubrik, 1966; Gorbushin, Levakin, 1999; Galaktionov, Skírnisson, 2000; Skírnisson, Galaktionov, 2002).

Definitive (and type) hosts are common eiders *S. mollissima*, maritae are morphologically indistinguishable from those of at least several other species: *C. verrucosa* (Frölich, 1789) Odhner, 1905, *Pseudocatatropis joyeuxi* Kanev and Vasiliev, 1986, and *P. dvoryadkini* Izrailskaia, Besprozvannykh, Tatonova et al., 2019.

Molecular references MN963021 (28S rDNA) and MN962974 (ITS1).

CONCLUSIONS

We have shown that the diversity of Notocotylidae infecting intertidal gastropods at the White and Barents Seas was highly underestimated. The current total of eleven species may also not be the final number, but probably is close to reality, considering the sampling effort. The non-genetic discriminating features for these species are limited, but future research may discover more of these. Particularly intriguing is the specificity of Notocotylidae to their intermediate host. Now there seem to be examples of both strict (one species of gastropods) and relaxed (members of several families within one superfamily) specificity. This issue also requires further studies. Moreover, the definitive hosts and maritae are yet well-defined for just five species out of 11.

Overall, if similar trends are found in other regions, the family Notocotylidae will likely grow following integrative taxonomy research. This will also lead to better understanding their evolution, and contribute to the development of evolutionary concepts for the whole Digenea.

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ВИДОВОЙ СОСТАВ NOTOCOTYLIDAE (DIGENEA) В ЛИТОРАЛЬНЫХ ГАСТРОПОДАХ НА БЕЛОМ И БАРЕНЦЕВОМ МОРЯХ

А. Г. Гончар, К. В. Галактионов

Ключевые слова: нотокотилиды, трематоды, церкарии, редии, промежуточные хозяева, ДНК-баркоды

РЕЗЮМЕ

Как показали недавние исследования, фауна трематод в брюхоногих моллюсках на Белом и Баренцевом морях характеризуется бо́льшим видовым богатством, чем предполагалось ранее. Эти данные, опубликованные в сериях статей, мы предлагаем обобщить в форме, удобной для практического использования. В данной работе мы объединили сведения об 11 видах из сем. Notocotylidae, которых мы обнаружили в литоральных моллюсках *Ecrobia ventrosa*, *Peringia ulvae*, *Littorina* spp. и *Onoba aculeus*. Мы приводим размеры и краткие описания редий и церкарий, известный спектр хозяев и географическое распространение, хотя для некоторых видов информация пока неполная. Мы также ссылаемся на последовательности ДНК из базы данных GenBank, которые могут послужить для идентификации видов – включая несколько новых последовательностей. Для удобства использования мы предваряем список видов нотокотилид советами по идентификации моллюсков-хозяев и проведению основных полевых и лабораторных процедур.