Proceedings of the Zoological Institute RAS
Vol. 324, No. 2, 2020, pp. 242–251
10.31610/trudyzin/2020.324.2.242

УДК 594.151

Larval and juvenile development of the Iceland cockle *Ciliatocardium ciliatum* (Fabricius, 1780) (Bivalvia: Cardiidae)

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ABSTRACT

The paper considers the development of *Ciliatocardium ciliatum* from the stage of straight hinge to juvenile. In the White Sea the spawning of *C. ciliatum* begins at the end of June, larvae at different stages of development occur in plankton until the end of September. The earliest of the larvae found had shell lengths of 123–130 μm. The paper first examined the anatomy and structure of the larval shell of *C. ciliatum*. During the development, the main stages of organogenesis were described and special attention was paid to the formation of the digestive and muscular systems. The digestive system begins to function when the larva reaches a size of 170–180 μm. The digestive gland has a two-blade shape and is shifted to the right side. The foot is formed at a size of 230 μm, the gill rudiments appear when the larva reaches 270 μm. The development of the larval shell and larval hinge of the mollusc is considered in detail. The development of the larval shell of *C. ciliatum* is similar to the development of other family members. Throughout all the larval stages, the shell has a rounded shape with a low umbos, and the prodissoconch II has a clearly visible concentric structure. The *C. ciliatum* larval hinge is characterized by weak differentiation and the absence of pronounced cardinal teeth typical for other Cardiidae. However, the lateral structures of the castle – ridges and flanges – are well developed. The ligament begins to form at a size of 240–250 μm and occupies a lateral position. The settlement of the cockle takes place in September in the subtidal zone. After the metamorphosis, a large radial sculpture is formed on the dissoconch and a number of small spikes are formed at the rib of the posterior shoulder.

Key words: Bivalvia larvae, *Ciliatocardium*, development of molluscs, veliger

Личиночное и ювенильное развитие *Ciliatocardium ciliatum* (Fabricius, 1780) (Bivalvia: Cardiidae)

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РЕЗЮМЕ

В работе рассматривается развитие *Ciliatocardium ciliatum* от стадии прямого замка до ювенильной особи. В Белом море размножение *C. ciliatum* начинается в конце июня, личинки на разных стадиях развития встречаются в планктоне до конца сентября. Самые ранние из найденных личинок имели длину раковины 123–130 мкм. В работе впервые рассмотрена анатомия и особенности строения личиночной раковины *C. ciliatum*. На протяжении развития описаны основные этапы органогенеза, отдельное внимание уделяется формированию пищеварительной и мышечной систем. Пищеварительная система начинает функционировать при размере личинки 170–180 мкм. Пищеварительная железа имеет двулопастную форму и смещена на правую сторону. Нога формируется при размере 230 мкм, зачатки жабр появляются при достижении личинкой 270 мкм. Подробно рассмотрено развитие личиночной

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раковины и личиночного замка моллюска. Развитие личиночной раковины *C. ciliatum* сходно с развитием других представителей семейства. На протяжении всех личиночных стадий раковина имеет округлую форму с низкой макушкой, продиссоконх II несет хорошо заметную концентрическую исчерченность. Личиночный замок *C. ciliatum* отличается слабой дифференциацией и отсутствием выраженных кардинальных зубов, характерных для других Cardiidae. Однако отмечается хорошее развитие латеральных структур замка – гребней и фланцев. Лигамент начинает формироваться при размере 240–250 мкм и занимает латеральное положение. Оседание кардиума происходит в сентябре в сублиторальной зоне. После метаморфоза на диссоконхе образуется крупная радиальная скульптура, в задней части раковины формируется ряд небольших шипов.

Ключевые слова: личинки Bivalvia, *Ciliatocardium*, развитие моллюсков, велигер

INTRODUCTION

The Iceland cockle *Ciliatocardium ciliatum* (Fabricius, 1780) is one of the most common species in the cold and temperate waters of the northern hemisphere (Kafanov 2001). This species is circumpolar, occurs in the Arctic seas of Europe, Asia and North America (Clench and Smith 1944; Filatova 1948; Ockelmann 1958; Fedyakov 1986; Kafanov 2001). *Ciliatocardium ciliatum* settles on muddy and muddy-sandy substrates at depths from 0 to 700 meters; it is a common food object for walruses, whales and bentophagous fish (Filatova 1948; Kafanov 2001).

Despite the widespread and frequent occurrence of *C. ciliatum*, very little is known about its life cycle and development. Some information on reproduction periods, specific features of gametogenesis and early stages of development can be found in the literature (Thorson 1936; Ockelmann 1958; Kaufman 1977; Günther and Fedyakov 2000). However, the larval development of this species is still unknown.

The purpose of this study is to review the early ontogeny of the Iceland cockle *Ciliatocardium ciliatum* from the D-shape stage to juvenile mollusc.

MATERIAL AND METHODS

The studies were performed at the White Sea Biological station Kartesh of the Zoological Institute RAS (Kandalaksha Bay, White Sea) (66°20.230′N; 33°38.972′E) in 2008–2018. Material was collected in the Chupa Inlet near the biological station.

Larvae of *C. ciliatum* at different developmental stages were obtained from plankton, using a Juday net with a 100-µm mesh. Settled juveniles and adult animals were collected from depths of 5–10 meters by SCUBA divers or dredging.

To determine the time of spawning, the maturity of the gonads of adult animals was estimated. The estimation was carried out under a microscope on dissected gonads. The collected larvae and juveniles were reared in the laboratory until preparation. Animals, 1–2 individuals per 1 ml of water, were maintained in plastic containers with constant aeration at temperature and salinity corresponding to those in the sea (11–12.5 °C, 24 ppt).

Images of live larvae were made using a Biomed-6 microscope and a Canon PowerShot A560 camera. The method of multiple overlaying of images was used to study organogenesis of the larvae (Baker 2001; Flyachinskaya and Lezin 2008).

The study of larval hinge and the structure of the shell were carried out on cleaned valves (Flyachinskaya and Lezin 2008). Images of the larval shells and larval hinges were taken by the microscope and the Canon PowerShot A560 camera.

RESULTS

Spawning of *Ciliatocardium ciliatum* in the White Sea occurs in June–July. The larvae occur in plankton during the summer-autumn season from June to September.

The smallest larvae we encountered had shell lengths of 123–130 µm. The shape of the shell is typical for the D-stage, the anterior end is slightly longer (Fig. 1A). The shell at this stage is represented mainly by prodissoconch I. The provincular edge of the larval shell is straight, without any expressed structures. The larva is actively floating due to the presence of velum covered with a large number of locomotor cilia. In the center of the velum there is an apical tuft at the base of which there is an apical disc (Fig. 3A). Retraction of the velum is achieved

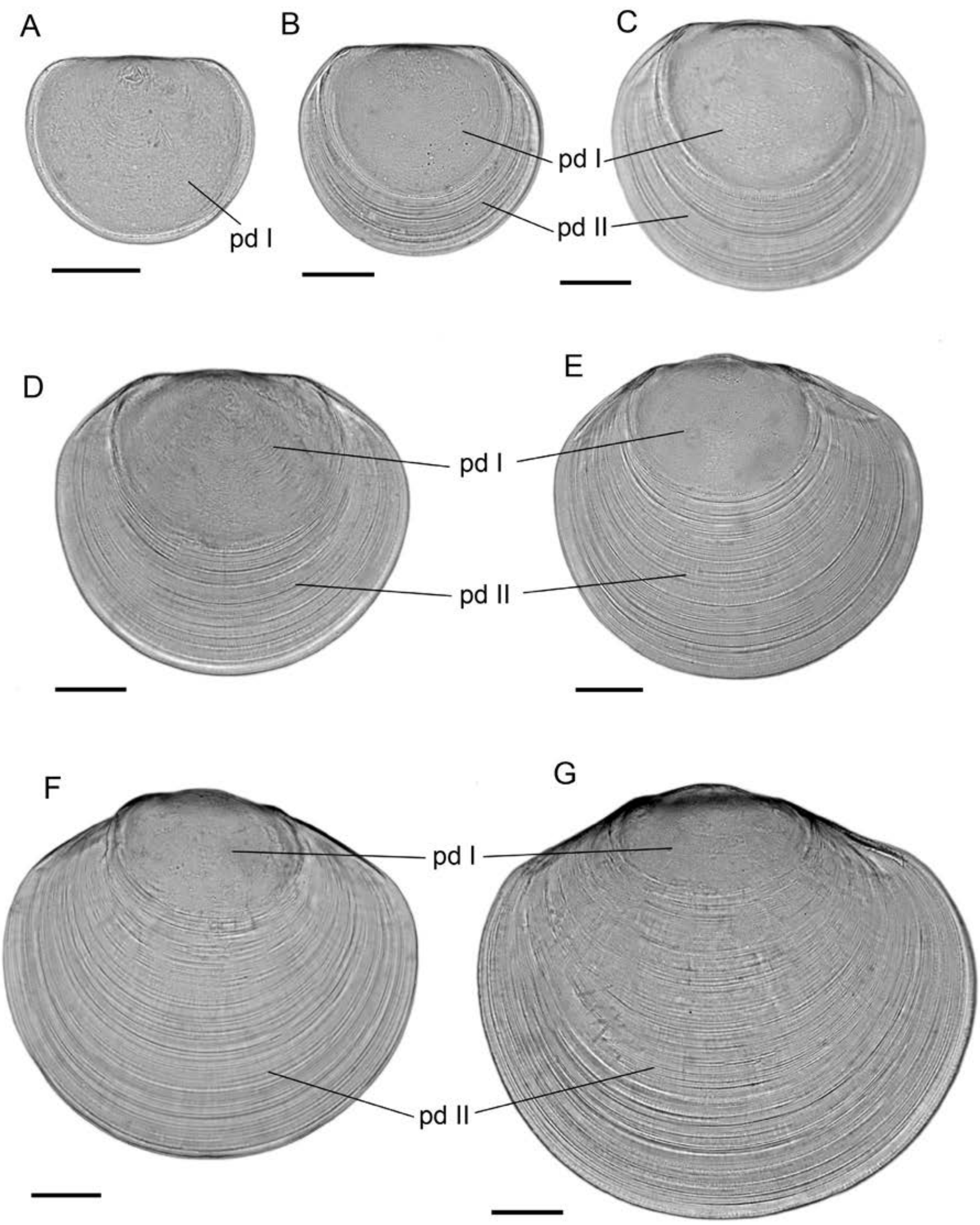

Fig. 1. Larval shell of *Ciliatocardium ciliatum* at different stages of development (right valves). A – 130 µm; B – 170 µm; C – 220 µm; D – 250 µm; E – 275 µm; F – 300 µm; G – 350 µm. Abbreviations: pd I – prodissoconch I; pd II – prodissoconch II. Scale bars = 50 µm.

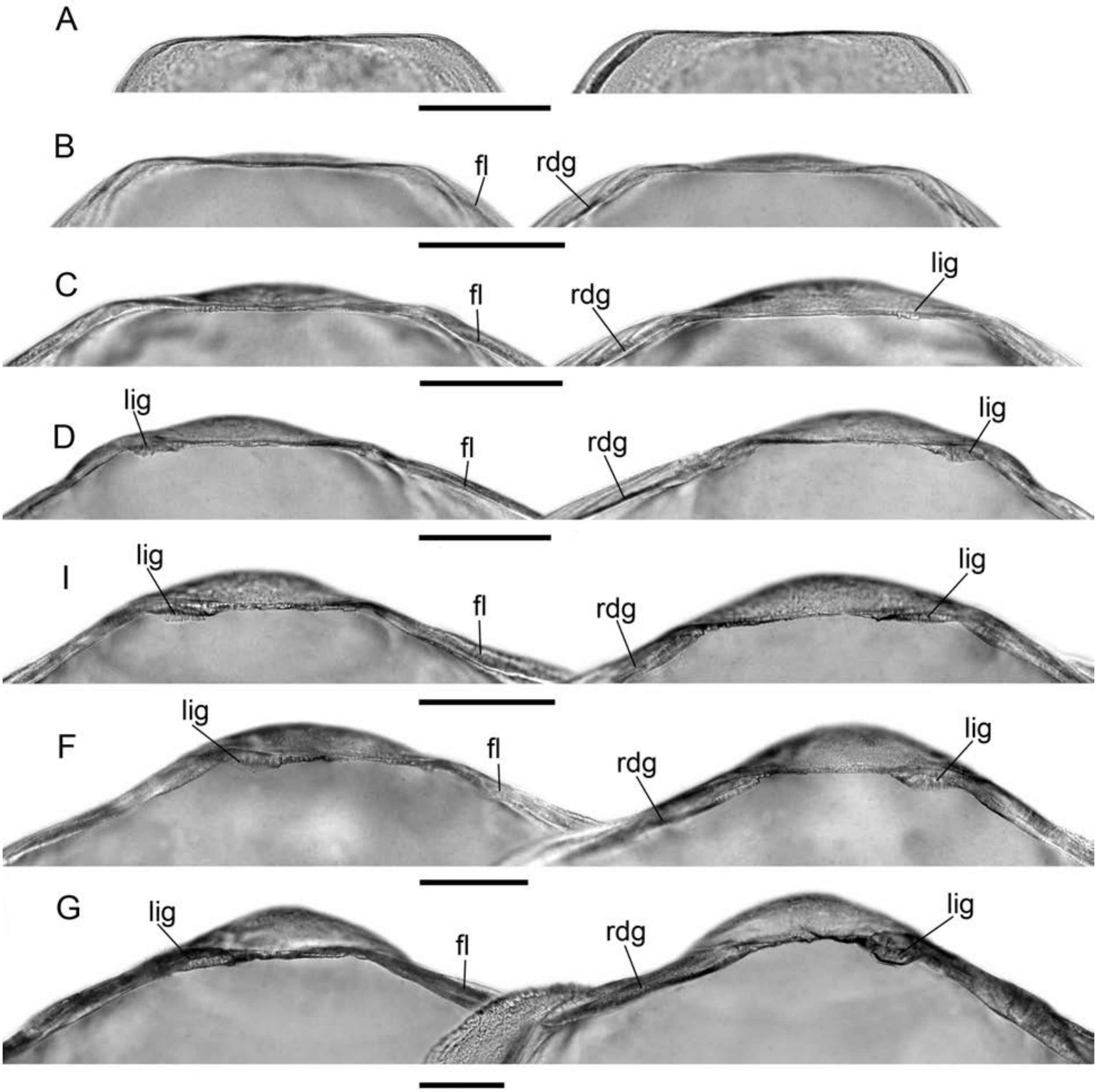

Fig. 2. Larval hinge of *Ciliatocardium ciliatum* at different stages of development. The left valve is on the left. A – 165 µm; B – 215 µm; C – 245 µm; D – 300 µm; E – 350 µm; F – 380 µm; G – 540 µm. *Abbreviations*: fl – flanges; lig – ligament; rdg – ridges. Scale bars = 50 µm.

by the anterior and posterior retractor muscles (Fig. 3A; vrm). When the velum is retracted, the apical disc is adjacent to the esophagus. The movement of the valves is controlled by a well-developed anterior adductor muscle (Fig. 3A; aam).

The digestive tract consists of the mouth, esophagus, stomach, digestive gland and posterior intestine (Fig. 3A). The anus is not yet formed and is blindly closed. Thus the digestive system is not yet functional and is in the formation stage. The larval tissues are filled with numerous fat inclusions.

With a shell size of 135–150 µm, prodissoconch II begin to form. Prodissoconch II has a distinctive concentric sculpture. At a size of 170–180 µm, the larval shell acquires a more rounded shape with a straight hinge edge and straight shoulders clearly outlined as well (Fig. 1B). The provincular edge of the shell is thin, without any pronounced structures (Fig. 2A).

At this stage, the larva forms an anus and the animal begins to actively feed on phytoplankton. All components of the digestive tract (mouth, esophagus, stomach, style sac, digestive gland consisting of two lobes (one on either side of the stomach), intestine, and anus emptying into the mantle cavity) were present at this stage (Fig. 3B). Compared to the previous stage, the intestine is much longer, a loop of intestine appears (Fig. 3B; li). The digestive gland acquires a yellow-orange color, which remains unchanged until metamorphosis. The esophagus is covered with cilia that create a water current when the larvae are feeding. The beating of the cilia is clearly visible in live larvae. During development the number of velar retractors increases, a pair of central retractors of the velum appears. A pair of posterior body retractors appears, attached to the back of the body, which move the body of the larva inside the shell (Fig. 3C; pbr).

On reaching a length of 210–220 μm, the shell of *C. ciliatum* assumes a rounded shape with a slightly pointed anterior edge, the umbos of the shell begin to form (Fig. 1C). The umbo is still poorly defined, shoulders are straight and have an almost equal length. The provincular edge is thin, with a barely noticeable exhaustion on the left valve (Fig. 2B). A system of lateral flanges and ridges begins to form in the areas of the shell adjacent to the hinge edge (Fig. 2B; fl, rdg).

The digestive system is becoming more complex at this stage (Fig. 3C). The intestine becomes longer and the digestive gland changes its shape. The right lobe of the digestive gland becomes noticeably larger than the left one. The intestine leaves the stomach in the area of the digestive gland on the left side and makes one loop, then the loops go to the right side of the larva (Fig. 3C). The muscle system of the larva's velum develops and additional muscle retractors appear. Later the muscular system becomes much more complex and cannot be observed without using special methods. The foot becomes first apparent in 230-μm long larvae as a small ciliated rudiment in the posterior-ventral region between the mouth and anus. Around the same time, the formation of the statocyst and the posterior adductor begins (Fig. 4A; stc, pam).

Upon reaching a length of 240–250 μm, the shape of the larva becomes more elongated (Fig. 1D). The provincular edge thickens and small cloves (bumps) appear (Fig. 2C). In the posterior part of the larval hinge, a ligament begins to form. The umbo is slightly pronounced, the shoulders of the shell are straight. When the larva reaches 275 μm, the umbo is separated and the shoulders become sloping (Fig. 1E).

Gill rudiments are first visible in larvae about 270 μm in length. Each gill plate begins to develop three primary gill filaments (Fig. 4B; gr). The posterior adductor muscle is clearly differentiated and gill plates are developing on the mantle at either side of the prepodium (Fig. 4B).

The larval shell of *C. ciliatum* at 300 μm has a generally rounded shape (Fig. 1F). The umbo is clearly separated and the shoulders are inclined. The anterior shoulder is slightly longer than the posterior one. The hinge has small cloves (more pronounced on the left valve), the ligament is well developed and takes a lateral position (Fig. 2D). The foot is fully functional and larvae are often observed crawling on the substrate or swimming with the foot extended.

Before settlement, with a shell size of 350–360 μm, the shoulders become shorter and have an approximately equal length (Fig. 1G). The ligament is well developed, the hinge of both valves has small cloves (Fig. 2E). The gills are covered with cilia and begin to function. The resorption of the velum and its associated systems begins, and the larvae of *C. ciliatum* proceed to metamorphosis (Fig. 4C).

The settlement in the studied region occurs in August–September. Molluscs settle on the ground in the subtidal zone. After settling, the shape of the shell becomes round, with inclined shoulders and a slightly anterior front end; a distinct radial sculpture characteristic of the adult animals begins to form on the dissoconch (Fig. 5A; dc). A number of small spikes are formed at the rib of the posterior shoulder (Fig. 5B; sp). The structure of the hinge of postmetamorphic molluscs in the early juvenile stages remains similar to that of the larvae (Fig. 2F–G).

DISCUSSION

Spawning of Iceland cockle occurs in different parts of the distribution range in late July–early August (Thorson 1936), in some regions (Greenland) spawning occurs in April–May (Petersen 1978). In the White and Barents Seas, reproduction

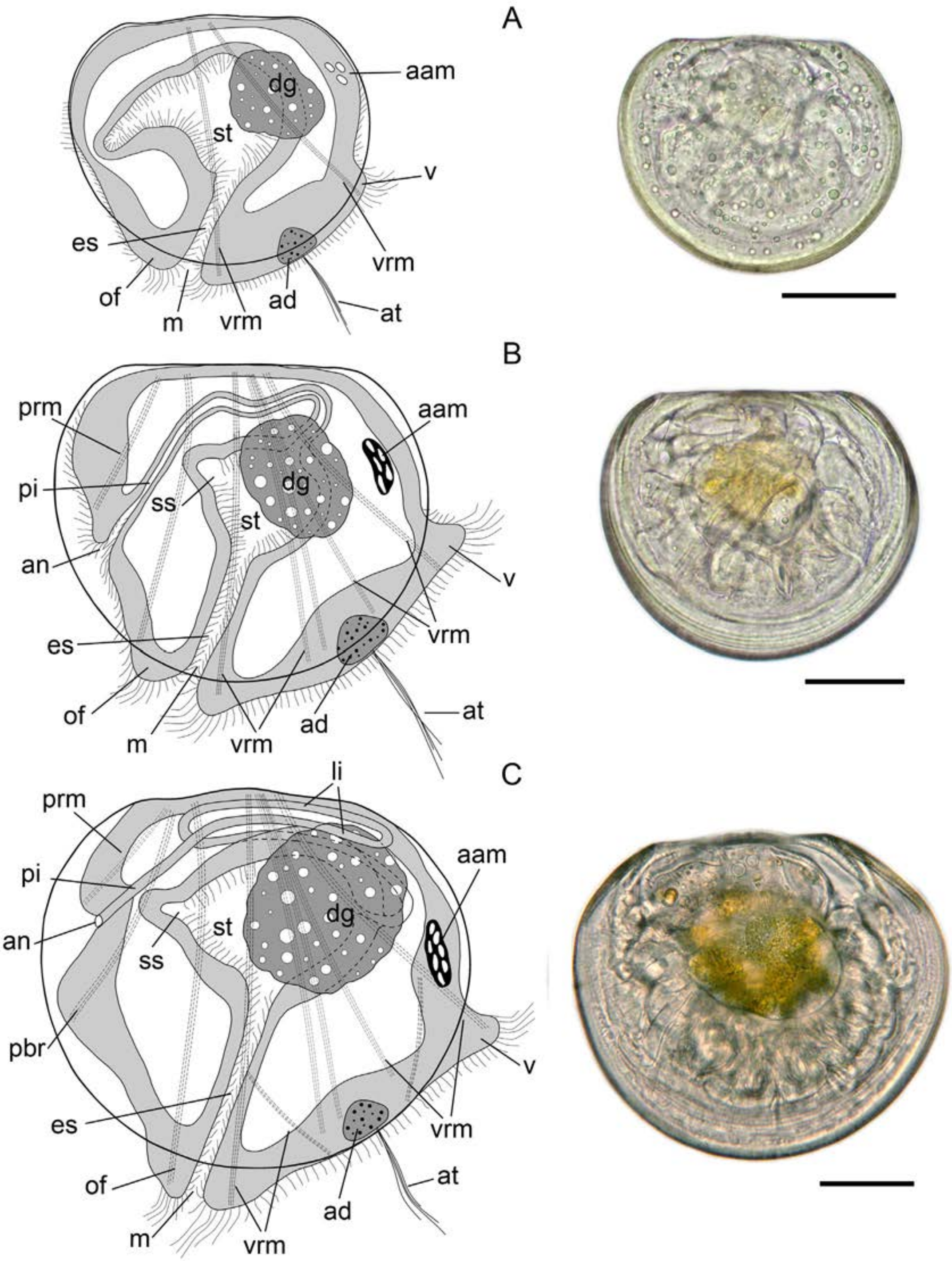

Fig. 3. Anatomy of *Ciliatocardium ciliatum* larvae at different stages of development. Left: anatomical diagram, right: live individual. A – 125 µm; B – 160 µm; C – 200 µm. Abbreviations: aam – anterior adductor muscle; ad – apical disc; an – anus; at – apical tuft; dg – digestive gland; es – esophagus; li – loop of intestine; m – mouth; of – oral flap; panm – post-anal muscles; pbr – posterior body retractor; pi – posterior intestine; prm – post-anal retractor muscles; ss – style sac; st – stomach; v – velum; vrm – velar retractor muscles. Scale bars = 50 µm.

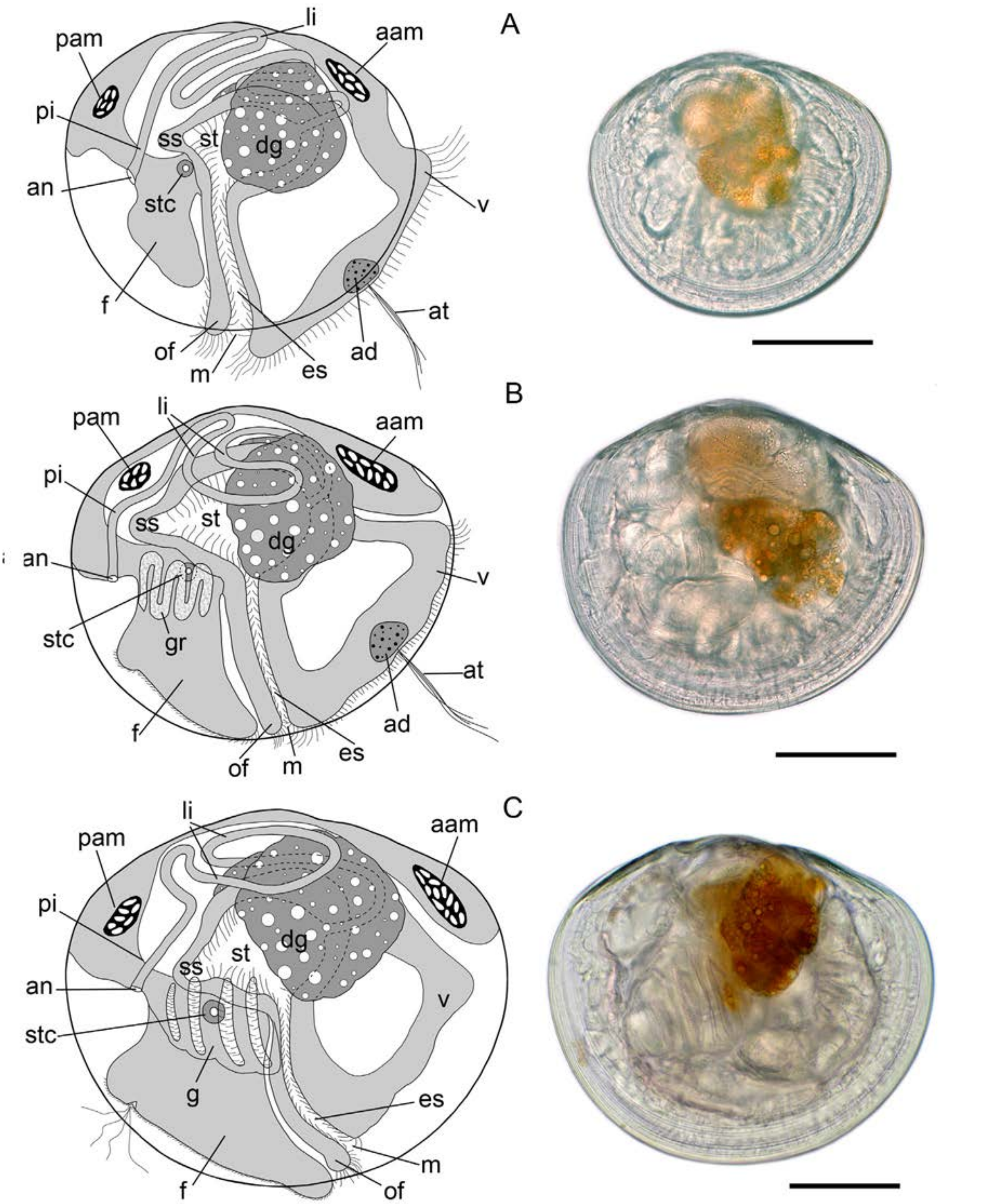

Fig. 4. Anatomy of *Ciliatocardium ciliatum* larvae at different stages of development. Left: anatomical diagram, right: live individual. A – 250 μm; B – 300 μm; C – 350 μm. Abbreviations: aam – anterior adductor muscle; ad – apical disc; an – anus; at – apical tuft; dg – digestive gland; es – esophagus; f – foot; g – gills; gr – gill rudiments; li – loop of intestine; m – mouth; of – oral flap; pam – posterior adductor muscle; pi – posterior intestine; ss – style sac; st – stomach; stc – statocyst; v – velum. Scale bars = 50 μm.

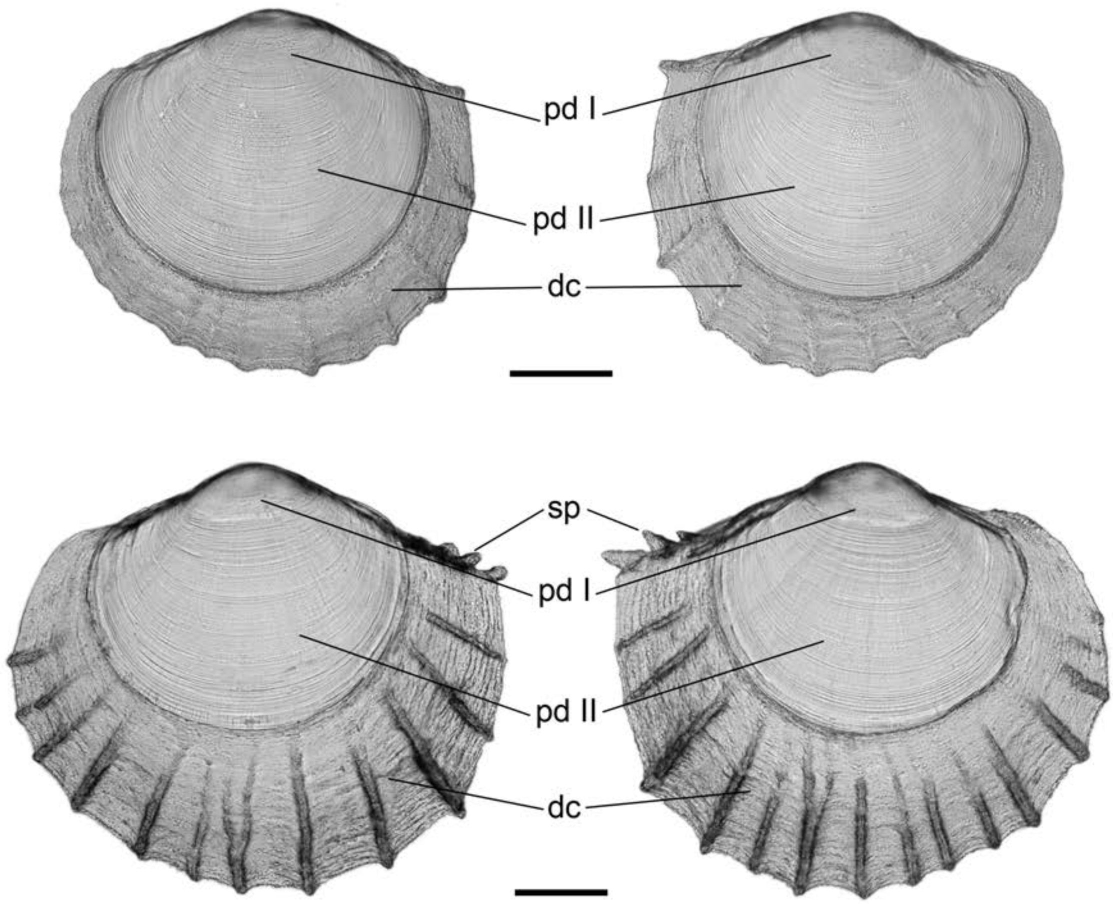

Fig. 5. Juvenile shell of *Ciliatocardium ciliatum* (right valves). A – 435 μm; B – 550 μm. Abbreviations: dc – dissoconch; pd I – prodissoconch I; pd II – prodissoconch II; sp – spikes. Scale bars = 100 μm.

and development take place from July to September (Kaufman 1977; Günther and Fedyakov 2000). According to our data, spawning occurs in late June–July, and larvae occur in plankton until September, which is generally consistent with the data obtained earlier for this region.

Thorson (1936) notes that the fertilized *C. ciliatum* egg is 120 μm in diameter. From this fact he concluded that the development of this species is lecithrophic, pelagic stage is very short or entirely absent. Later, Ockelmann (1958) refuted Thorson's conclusions. On the basis of the analysis of egg size and prodissoconch I it is concluded that the development of *C. ciliatum* is planktonic with a rather long pelagic stage. Studies by Kaufman (1977) have shown that in the White Sea, the *Ciliatocardium* egg size is 90 μm. The smallest planktonic larvae we found had a shell length of 123 μm, which agrees well with Kaufman's data.

Organogenesis of the Clinocardiinae larvae has not been studied at present. Among close species, the development of the *Cerastoderma edule* (Linnaeus, 1758) was examined in detail (Creek 1960). In general, the development of *Ciliatocardium ciliatum* is similar to the development of *C. edule* described by Creek (1960).

In this paper we consider the stage of late trochophore – early veliger that was not previously described for the Cardiidae. At this stage, the digestive system is already formed, but not yet functioning. Larvae probably get nutritious substances from numerous fat droplets stored in the egg and left after cleavage. Also at this stage, the rudiments of the muscular system are already appearing.

At the early veliger stage, the composition of the digestive system is very similar to that described for *Cerastoderma edule* (Creek 1960). It is still a U-shaped structure but the limbs of the U have become separated by the growth of the epithelium between the mouth and anus. Further development of the digestive system of *Ciliatocardium ciliatum* is also similar to that of *C. edule*, but shows significant asymmetry: the right lobe of the digestive gland acquires a noticeably larger size than the left. The intestine leaves the stomach in the area of the digestive gland on the left side, and makes one loop, then the loops go to the right side of the larva.

The general plan of the muscle system composition at the early stages of the *Ciliatocardium ciliatum* larval development is similar to that in *Cerastoderma edule* (Creek 1960). It consists of several pairs of velum retractors and a rear retractor. The difference is that *Ciliatocardium ciliatum* develops a pair of postanal muscles.

According to Creek (1960), the gills and statocyst in *Cerastoderma edule* begin to develop during metamorphosis. In *C. ciliatum*, the statocyst appears during the transition from the veliger to the pediveliger stage approximately at the same time as the posterior adductor is formed and the foot begins to form. This is the middle of the plankton life period of the larva. Gill rudiments also appear long before metamorphosis, at a larval size of 300 μm. The gills begin to function at a size of 350 μm, shortly before metamorphosis.

The development of the *Ciliatocardium ciliatum* larval shell is typical of the family Cardiidae. The round shape of the shell and the concentric striation of the prodissoconch observed in *C. ciliatum* is typical for many species of the family (Jørgensen 1946). Despite the early separation of the umbos of the *Ciliatocardium ciliatum* larval shell, the umbos remain small in size. Rees (1950), when describing the Cardiidae larval shells, distinguishes two morphotypes that differ in umbo's height (Rees 1950). *Ciliatocardium ciliatum*, thus, can be attributed to the group with low umbos. The structure of the Cardiidae larval hinge is quite variable (Rees 1950). Some authors describe the larval hinges of taxon representatives as indistinct, with poor differentiation of teeth (Odhner 1914; Jørgensen 1946). Other researchers have noted the weak differentiation of the larval hinge in the early stages of development, but at the stages of veliger and pediveliger describe two well-defined cardinal teeth (Zakhvatkina 1959; Le Pennec 1980; Le Pennec and Yankson 1985). Good development of lateral structures – flanges and ridges – is also noted (Zakhvatkina 1959; Kasyanov et al. 1998). The data we obtained indicate a weak differentiation of the *Ciliatocardium ciliatum* hinge and a lack of clearly defined teeth throughout the larval and early juvenile development. This hinge structure is consistent with the data of Rees (1950), who notes the dependence of the Cardiidae hinge structure on the morphology of umbo and a weak differentiation of the hinge structures in species with a low umbo. At the same time, it should be noted that *Ciliatocardium ciliatum* has a well-developed lateral structures and has clearly defined ridges and flanges. The time of ligament formation and its posterior position in *C. ciliatum* are similar to those in most members of the family (Zakhvatkina 1959; Kasyanov et al. 1998).

The development of *C. ciliatum* shells after metamorphosis is typical for the members of the family. Early formation of a shell's radial sculpture observed in the Iceland cockle, is a characteristic of many Cardiidae (Odhner 1914; Lebour 1938; Sullivan 1948; Zakhvatkina 1959). The formation of spikes or needles in the posterior part of the shell is typical for a number of species with an advanced sculpture of the definitive shell (Lebour 1938).

CONCLUSION

The development of *Ciliatocardium ciliatum* in general is typical for *Cardiidae*. Development of the main systems of organs with small differences is similar to development of other species of the family. The main stages of formation of the *C. ciliatum* shell are also typical for cardiids. However, the structure of the larval and juvenile hinge is very weak. The lack of individual hinge teeth, which is observed in our case, is unusual for cardiids and was noted only for some species of the family.

ACKNOWLEDGEMENTS

We wish to express our gratitude to Dr. A.A. Sukhotin (Zoological Institute RAS) for his help in preparing the manuscript. This work was carried out as part of the State Task (state registration number no. AAAA-A19-119022690122-5).

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Submitted March 15, 2020; accepted May 19, 2020.