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Reproductive morphology of the genus *Parafossarulus* Annandale, 1924 (Caenogastropoda: Rissooidea: Bithyniidae) with comments on its taxonomy and distribution

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A short review on the species diversity and distribution of the genus *Parafossarulus* Annandale in Annandale et Prashad, 1924 is presented. The reproductive male and female systems of two species from northern Vietnam and southern Russian Far East are studied using histological methods. Inner structure of the pallial oviduct of the *Parafossarulus* is examined for the first time. Revealed unique characters of the *Parafossarulus* oviduct morphology are discussed in comparison with those of *Bithynia* Leach in Abele, 1918.

Key words: *Parafossarulus*, *Bithynia*, reproductive morphology, gonoduct, oviduct, histology.

Репродуктивная морфология рода *Parafossarulus* Annandale, 1924 (Caenogastropoda: Rissooidea: Bithyniidae) с комментариями по его таксономии и распространению

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Представлен краткий обзор видового разнообразия и распространения моллюсков рода *Parafossarulus* Annandale in Annandale et Prashad, 1924. Изучена репродуктивная система самцов и самок двух видов с северного Вьетнама и Дальнего Востока России с использованием гистологических методик. Впервые изучена внутренняя структура паллиального овидукта *Parafossarulus*. Обнаруженные уникальные особенности репродуктивной морфологии *Parafossarulus* обсуждаются в сравнении с таковыми у представителей рода *Bithynia* Leach in Abele, 1918.

Ключевые слова: *Parafossarulus*, *Bithynia*, репродуктивная морфология, гонодукт, овидукт, гистология.

Freshwater snails of the genus *Parafossarulus* Annandale in Annandale et Prashad, 1924 are well known as the most common snail hosts of *Clonorchis sinensis* Looss, 1907, the third most prevalent worm parasite in the world [Acha, Szyfres, 2001;

Mas-Coma, Bargues, 1997; etc.]. The worm causes clonorchiasis in humans, a widely distributed disease in East Asia, ranging from the southern Russian Far East to Vietnam and Taiwan [Abbot, 1948; Mas-Coma, Bargues, 1997; etc.]. The prevalence of this disease explains the importance of investigating species of this genus, especially their reproductive biology.

The genus *Parafossarulus* was established by Annandale first as a subgenus for South Asian bithyniids having spiral ribs [Annandale, Prashad, 1924]. The type species of the genus *Parafossarulus*: *Paludina* (*Bithynia*) *striatula* Benson, 1842 was described from Zhoushan (=Chusan) Island in the Yangtze River mouth [Benson, 1842]. Later two other closely related taxa were described: *Bithynia manchourica* Gerstfeldt, 1860 from the Amur River [Bourguignat, 1860] and *Bithynia striatula* var. *japonica* Pilsbry, 1901 from Honshu [Pisbry, 1901]. Abbott [1948] proposed that *B. striatula* of Japan and China should be incorporated into the species *Parafossarulus manchouricus* (Gerstfeldt in Bourguignat, 1860), which is widely distributed, not only in the Amur River basin but also throughout China, Japan, Taiwan and probably Indochina. This point of view is still accepted by some parasitologists [Mas-Coma, Bargues, 1997; Acha, Szyfres, 2001; etc.]. Some others identified *Parafossarulus* species from China, Taiwan and Vietnam as *P. striatulus* [Dang et al., 1980; etc.]. Nevertheless, the malacological literature includes 13 species of *Parafossarulus*: *P. striatulus* (Benson, 1842), *P. manchouricus* (Gerstfeldt in Bourguignat, 1860), *P. eximius* (Frauenfeld, 1864), *P. subangulatus* (Martens, 1877), *P. chaperi* (Morlet, 1886), *P. sinensis* (Neumayr, 1887), *P. japonicus* (Pilsbry, 1901), *P. woodi* Walker, 1927; *P. zeni* (Ping et Yen, 1932), *P. anomalospiralis* Liu Y., Li et Liu T., 1985, *P. sungariensis* Moskvicheva in Starobogatov et Zatravkin, 1987, *P. spiridonovi* Zatravkin et Starobogatov in Zatravkin, Dovgalev et Starobogatov, 1989, *P. globosus* Liu, Zhang et Wang in Liu et al., 1994. These species occupy East Asia from the southern Russian Far East [Bourguignat, 1960; Starobogatov et al., 2004; etc.] in the north to northern Vietnam [Morlet, 1886; Grove, 1900; Dang et al., 1980; Richter, 2012; Prozorova et al., 2016] in the south, including Taiwan [Abbot, 1948; The Taiwan Malacofauna Database, 2013] and Japan [Pilsbry, 1901, 1902; Higo, Goto, 1993]. Records of the genus in Malay Peninsula [Laidlaw, 1940] are not supported by later field surveys and are probably misidentification of *Digoniostoma* Annandale, 1920. Species *Hydrobioides nana* Annandale, 1918, described from the Lake Inle in Myanmar [Annandale, 1918], was later erroneously regarded as *Parafossarulus nana* [Rao, 1928; Starobogatov, 1970], endemic to the lower Salween River drainage [Starobogatov, 1970, p. 206]. Data on distribution of the *Parafossarulus* in the Mekong River basin in Vietnam and Cambodia [Dang et al., 1980; Dang, Ho, 2007] are rather doubtful as well.

The Amur River drainage is inhabited by *P. manchouricus* and *P. spiridonovi*, and the Sungari River by *P. sungariensis* [Zatravkin et al., 1989; Starobogatov et al., 2004]. Records of *P. manchouricus* in South Korea [Min et al., 2004; Kim, 1989; etc.] are probably misidentifications. The taxonomy of the Korean *Parafossarulus*

obviously needs revision. Species *P. japonicus*, described from Japan [Pilsbry, 1901], occurs in Honshu, Shikoku [Kuroda, 1963], Kyushu and Korea [Higo, Goto, 1993], at least, in the extreme south of the Korean Peninsula. In contrast with the southern area of the peninsula, its northern regions are probably inhabited by other continental *Parafossarulus* species.

In China, Abbot [1948] recorded *P. sinensis* from the Yangtze River drainage and *P. eximius* from more northern and eastern regions. He regarded *P. striatulus* and *P. zeni* as junior synonyms of *P. manchouricus*. According to Starobogatov [1970], the Hwang-Ho (Huang He) River drainage is inhabited by *P. striatulus*, *P. eximius*, and *P. longicornis* (Benson, 1942); the latter species belongs to another bithyniid genus, *Alocinma* Annandale et Prashad, 1919. Species *P. zeni* is endemic to the Hwang-Ho River drainage; the more southern Chinese waterbodies are inhabited by *P. sinensis*, *P. subangulatus* and *P. woodi*, described from the Yangtze River drainage [Walker, 1927]. Two species, *P. subangulatus* and *P. woodi* were not cited in malacological monographs of China [Liu Y.Y. et al., 1979, 1993], or in recent papers on the Chinese freshwater fauna [e.g., Pan et al., 2011]. After the publication of Starobogatov's [1970] monograph, two new *Parafossarulus* species were described in China: *P. globosus* from the Yangtze [Liu et al., 1994] and *P. anomalospiralis* from the Laohe River basin [Liu et al., 1985]. The latter species probably occurs also in the Korean Peninsula.

For Taiwan, *P. annandalei* [The Taiwan Malacofauna Database, 2013], as well as two other *Parafossarulus* species, *P. japonicus* and *P. striatulus* (as *P. striatus*), were recorded [Higo, Goto, 1993]. Two latter species are probably misindefication of *P. annandalei*.

Species of the genus *Parafossarulus* from northern Vietnam are more often identified as *P. striatulus* [Dang et al., 1980; Dang, Ho, 2007; etc.]. Some parasitologists agreed with Abbott [1948], who proposed that the *Bithynia striatula* should be incorporated into the species *Parafossarulus manchouricus* distributed from Amur to Indochina. We support opinion that Vietnamese specimens belong to the species *P. chaperi* described by Morlet [1886] from the Tonkin Bay region. The species is probably endemic for the lower Red River basin and adjacent area [Grove, 1900; Richter, 2012; Prozorova et al., 2016]. Local data on its more wide distribution in Vietnam, including Mekong River delta [Dang, Ho, 2007] are rather doubtful.

The taxonomy of the genus is obviously in need of revision at the species level. Similar shell shape and corrosion of upper whorls make difficult to discriminate these species based only on morphology. To clearly define status of nominal *Parafossarulus* species, genetic data are necessary.

The status of the species listed above should be re-assessed. Synonymy of some of the older taxa is possible. The new data on the internal morphology presented below may be used in a taxonomical revision of the *Parafossarulus*.

Materials and methods

The structure of reproductive system of species belonging to the genus *Parafossarulus* was described earlier based on the specimens from Japan [Itagaki, 1965], South Korea [Kim, 2005] and the southern Russian Far East [Rasshepkina, Prozorova, 2011]. Recent study is undertaken because of contradictions in previous studies. The main problem to solve is structure of pallial oviduct in the *Parafossarulus* representatives. It is of interest whether the oviduct comprise both seminal receptacle and bursa copulatrix like that in the *Bithynia* Leach in Abele, 1918 species [Lilly, 1953; Beriozkina, 2011]. To study in detail the structure of reproductive system in the genus *Parafossarulus*, the histology of male and female gonoduct of two species the extreme northern and southern areas of the geographical range was examined. Specimens of *Parafossarulus chaperi* and *P. manchouricus* were collected by V. Besprozvannykh (IBSS FEB RAS) in rice paddies in Nam Dinh Province (northern Vietnam) and in the Bolshaya Ussurka River (Amur River tributary) drainage in the southern Russian Far East.

Specimens were fixed with 75% ethanol, removed from the shell, and dissected to extract reproductive organs from the posterior portion of the foot. Tissues for histological investigations were embedded in paraffin using the standard procedure [Roskin, 1951] and sectioned (7–8 μm) using the HM 340E rotary microtome (Microm, Thermo Scientific, UK) and were stained with hematoxylin and eosin. Histological sections were photographed with the light microscope Axioscop 40 (Carl Zeiss, Germany) with the camera AxioCam HRc using the Axiovision 4.6 software.

Results of the study are presented below in comparison with other bithyniids. Different parts of reproductive systems and their organs are designated mainly in accordance with Lilly [1953] and Beriozkina [2011].

Results and discussion

Common characters of the female and male reproductive systems of four different *Parafossarulus* species have been studied earlier [Itagaki, 1965; Kim, 2005; Rasshepkina, Prozorova, 2011]. Oviduct of the *Parafossarulus* consists of gonadial, renal, and pallial parts [Itagaki, 1965; Rasshepkina, Prozorova, 2011] similar to oviduct of *Bithynia* [Lilly, 1953; Beriozkina, 2011]. In the *Bithynia*, oviduct comprises seminal receptacle, bursa copulatrix, uterus and pallial glands [Lilly, 1953; Beriozkina, 2011]. There are contradictions in published data on the pallial oviduct structure of the *Parafossarulus* [Itagaki, 1965; Kim, 2005; Beriozkina, 2011; Rasshepkina, Prozorova, 2011]. Itagaki [1965] depicted seminal receptacles, but did not find the bursa copulatrix in Japanese species of the *Parafossarulus*. The same structure mistakably identified as bursa copulatrix was depicted in the Korean [Kim, 2005] and

Russian *Parafossarulus* species [Rasshepkina, Prozorova, 2011]. To facilitate study of the structure of pallial part of the oviduct in the genus *Parafossarulus*, female reproductive system of *P. manchouricus* was examined in details iteratively. Below we present more correct data on pallial oviduct structure of the species.

The pallial oviduct of *P. manchouricus* comprises a wide glandular tube with an oriented ventrally seminal receptacle in its proximal one-third portion as in studied species of *Bithynia* and *Parafossarulus* [Lilly, 1953; Itagaki, 1965; Starobogatov, 1970; Beriozkina, 2011]. Glandular tissue is developed only from the one side of the pallial oviduct of *Parafossarulus*; another side and proximal portion of the pallial oviduct are formed mainly by connective tissue (Fig. 1A). There are at least two pallial glands, the proximal albumen (Fig. 1A–D) and the distal capsule (Fig. 1D). The albumen gland extending to the proximal top of the pallial oviduct produces egg capsule matrix similar that in *Bithynia* [Lilly, 1953; Beriozkina, 2011].

Significant differences were found in the inner structure of the pallial oviduct of representatives of *Parafossarulus* and *Bithynia* characterized by bursa copulatrix isolated from lumen of the pallial oviduct functioning as the uterus [Lilly, 1953;

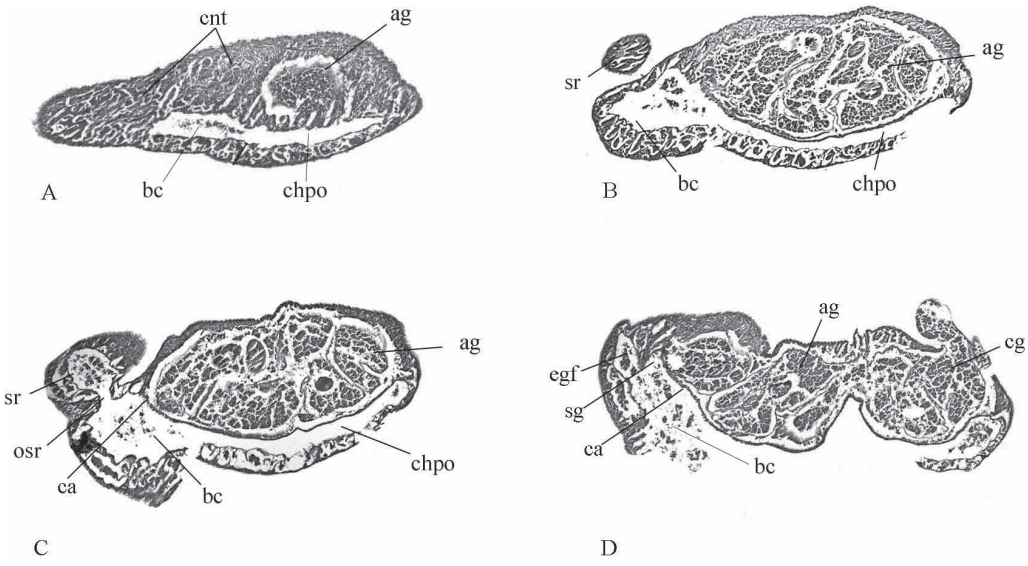

Fig. 1. Transverse histological sections of *Parafossarulus manchouricus* female through proximal one-third of pallial oviduct: **A** – section through the beginning of albumen gland surrounded by connective tissue; **B** – section through the pallial oviduct including upper part of seminal receptacle; **C** – section through pallial oviduct on the level of opening of seminal receptacle; **D** – section through pallial oviduct distal to opening of seminal receptacle. Abbreviations: *acg* – accessory gland of the penis, *ag* – albumen gland, *bc* – bursa copulatrix, *ca* – ciliated area, *cg* – capsule gland, *chpo* – slit-like channel of pallial oviduct (uterus), *cnt* – connective tissue, *c* – ctenidium, *dg* – digestive gland, *egf* – egg guide fold, *osr* – opening of seminal receptacle, *pd* – prostate diverticula, *sg* – sperm gutter, *sr* – seminal receptacle, *sv* – seminal vesicles, *t* – testis, *vd* – vas deferens.

Beriozkina, 2011]. On the contrary, in *Parafossarulus*, lumen of the pallial oviduct is divided longitudinally forming two chambers, more or less dorsal and ventral, communicating along its whole length via a wide slit. Dorsal half of the lumen in its proximal part comprises slit-like chamber of the pallial oviduct as a part of uterus (Fig. 1). More wide ventral chamber is characterized by ciliated area on inner wall and longitudinal sperm gutter leading to a seminal receptacle (Fig. 1C, D). Ventral chamber of pallial oviduct contains spermatozoa inside and functions as a bursa copulatrix. Thus, in *Parafossarulus*, dorsal portion of the pallial oviduct functioning as a uterus is closely connected with its ventral part functioning as a bursa copulatrix.

The seminal receptacle of *P. manchouricus* adjoining the oviduct closely in its proximal one-third portion has thick walls with deep inner plicae (Fig. 1B, C). The interior wall of the pallial channel under the opening of seminal receptacle comprises two folds (Fig. 1D). The deepest one is probably an egg guide fold connected with renal oviduct where fertilization takes place; the other fold covered by a ciliated epithelium is regarded as a sperm gutter (Fig. 1D).

The male reproductive system of *P. chaperi* as in other studied *Parafossarulus* and *Bithynia* species, is composed of the testis, seminal vesicles, prostate gland, vas deferens, and penis with accessory gland and flagellum [Lilly, 1953; Itagaki, 1965; Starobogatov, 1970; Beriozkina, 2011; Rasshepkina, Prozorova, 2011]. Below we present more detailed data on male gonoduct structure of *P. chaperi* from Vietnam.

The multibranched testis of the species examined spreads over the digestive gland (Fig. 2A). Cells of the digestive gland have eosinophillic cytoplasm with secreted granules (Fig. 2A, B). Well developed, coiled seminal vesicles, running from the testis to the prostate gland, are embedded in the digestive gland (Fig. 2A, B). In transverse histological sections, numerous seminal vesicles filled by spermatozoa with haploid nuclei inside are quite visible [Rasshepkina, Prozorova, 2011]. The thicker portion of the seminal vesicles of *P. chaperi* (Fig. 2) is nearly 0.50–0.55 mm in diameter similar to that of species from Korea [Kim, 2005].

The pallial part of the male reproductive system of *Parafossarulus* includes the prostate gland located on the right side of the rectum and the vas deferens (Fig. 1C). The prostate of Vietnamese *P. chaperi* is composed of diverticula arranged in a flat belt with one side widely fringed (Fig. 2C) like that in other studied *Parafossarulus* and *Bithynia* species [Lilly, 1953; Itagaki, 1965; Starobogatov, 1970; Beriozkina, 2011; Rasshepkina, Prozorova, 2011]. However these data contradict to results presented for Korean «*P. striatulus*» [Kim, 2005] which may be explained by the misidentification of the studied Bithyniidae specimens from South Korea.

The distal part of the male gonoduct is composed of penis with flagellum and tubular accessory gland similar to that of studied *Parafossarulus* and *Bithynia* species (Fig. 2D). The gland is formed by a coiled thin-walled tube (Fig. 2D) merging with a flagellum at the proximal end of the penis.

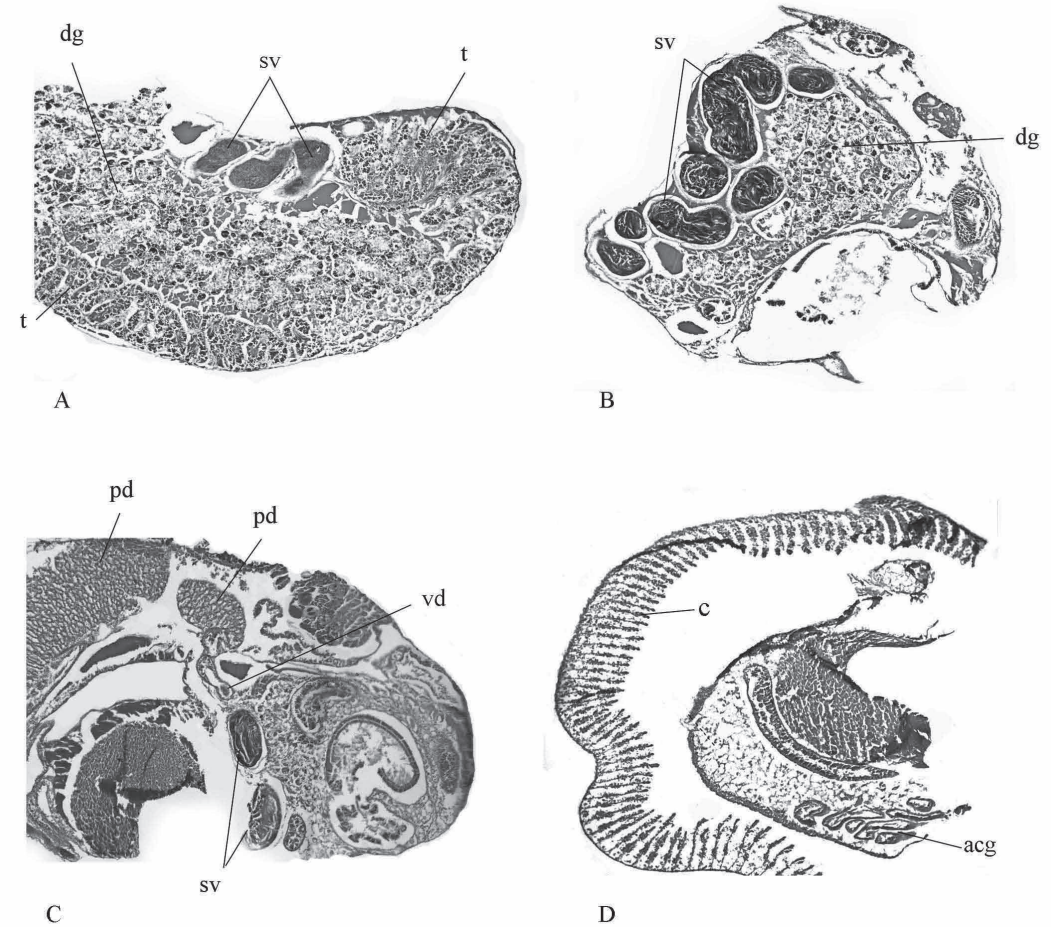

Fig. 2. Transverse histological sections of the male *Parafossarulus chaperi* through different parts of gonoduct: **A** – section through gonadial part, showing testis and digestive gland; **B** – section through renal part, showing proximal portion of renal digestive gland and seminal vesicles; **C** – section through pallial part of gonoduct, showing structure of prostate; **D** – section through pallial part of gonoduct, showing accessory gland of the penis. For abbreviations, see Fig. 1.

Conclusion

The female reproductive system of the *Parafossarulus* is composed of an ovary, renal and glandular pallial oviduct with seminal receptacle like that in *Bithynia* species [Lilly, 1953; Beriozkina, 2011]. There are significant differences in the inner structure of the pallial oviduct of *Parafossarulus* and *Bithynia* characterized by bursa copulatrix isolated from lumen of the pallial oviduct functioning as the uterus. In *Parafossarulus*, lumen of the pallial oviduct is longitudinally divided for two chapters. Dorsal chapter

functioning as the uterus is closely connected with the ventral that functioning as the bursa copulatrix. This kind of inner structure of the pallial oviduct could be interpretated as plesiomorphic in comparison with that of *Bithynia*.

The male reproductive system of *Parafossarulus* is composed of the testis, seminal vesicles, prostate gland, vas deferens, and penis with accessory gland and flagellum similar to the male gonoduct of *Bithynia*.

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