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MORPHOLOGICAL TRAITS OF THE RADULA IN VIVIPARIDAE (MOLLUSCA, CAENOGASTROPODA) AS A MASTER KEY TO DISCRIMINATION OF CLOSELY RELATED SPECIES

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Morphological Traits of the Radula in Viviparidae (Mollusca, Caenogastropoda) as a Master Key to Discrimination of Closely Related Species. **Anistratenko V. V., Ryabceva Yu. S., Degtyarenko E. V.** — The radula morphology and variability in four European species of the family Viviparidae *viz. Viviparus viviparus* (Linnaeus, 1758), *V. sphaeridius* (Bourguignat, 1880), *V. ater* (Cristofori et Jan, 1832) and *Contectiana listeri* (Forbes et Hanley, 1853) were examined using scanning electron microscopy (SEM). Statistical methods reveal a certain value of rachidian tooth dimensional parameters as an efficient tool for taxonomy and discrimination of closely related species of the family.

Key words: morphology, radula, taxonomy, Viviparidae, *Viviparus*, *Contectiana*, Europe.

Морфологические особенности радулы Viviparidae (Mollusca, Caenogastropoda) как эффективный инструмент для разграничения близких видов. Анистратенко В. В., Рябцева Ю. С., Дегтяренко Е. В. — С использованием сканирующей электронной микроскопии (СЭМ) изучены морфологические особенности и изменчивость радулы у четырех европейских видов семейства Viviparidae: *Viviparus viviparus* (Linnaeus, 1758), *V. sphaeridius* (Bourguignat, 1880), *V. ater* (Cristofori et Jan, 1832), а также *Contectiana listeri* (Forbes et Hanley, 1853). Статистическими методами показана возможность использования некоторых размерных характеристик рахидального зуба для эффективной диагностики близких видов Viviparidae и систематики семейства.

Ключевые слова: морфология, радула, таксономия, Viviparidae, *Viviparus*, *Contectiana*, Европа.

Introduction

Representatives of the family Viviparidae are one of the most ancient inhabitants of continental freshwaters among the Gastropoda — they may be rooted in fossil record as early as up to the Carboniferous age.

A process of gradual transition of marine ancestors of Viviparidae into habitation in fresh-waters and adaptation to present life pattern in the nutrition habit (by filtering food with their gill) resulted in considerable reorganization in the radular apparatus morphology though the general mode of their feeding remained the same (Golikov, Starobogatov, 1989). The transformation of ancestral (trochoid-like) type of radula into that of recent viviparids is expressed mainly in reduction of teeth number in transverse row (1), redistribution of marginal teeth function (2), modifications of their shape (3), etc. (see Starobogatov, 1990).

In spite of long-aged study of the group Viviparidae the estimation of the taxonomic value of principal characters within the family is still not widely agreed upon. It concerns mainly the conchology since the closely related species of viviparids show their remarkable similarity particularly in adult shell features. The range of their shell variability is often overlapping and the specific distinctness can be verified usually only by statistic methods (Zhadin, 1928).

A conchological hiatus between the most common viviparid snails in Europe is quite expressionless; that motivates malacologists to search for any other (non-conchological) characters that do allow their differentiation. One should try to discover the diagnostic parameters in the morphology of embryo shell (Riedel, 1993; Ryabceva, Anistratenko, 2012), caryology (Pavluchenkova, 1997), molecular genetic diversities (Sengupta et al., 2009), wall structure of the shell (Datsenko, 2008) or in regard to radula morphology (Chernogorenko, 1988; Falniowski et al., 1996; Anistratenko, Anistratenko, 2001 and others).

In the meantime the reliability of radular characters in the taxonomy of the family Viviparidae remains uncertain and have not been studied sufficiently (e. g. Cleave, Richey, 1936; Kerth, 1971; Simone, 2004).

The present study focuses on radular morphology of four European viviparid species to evaluate the range and pattern of species variability of *Viviparus viviparus* (Linnaeus, 1758), *V. sphaeridius* (Bourguignat, 1880), *V. ater* (Cristophori et Jan, 1832) and *Contectiana listeri* (Millet, 1813)[1]. Based on newly-obtained data it is aimed to estimate some dimensional parameters of radula as a tool for the taxonomy and discrimination of closely related species of the family.

Material and methods

Material for the present study was collected by the authors from 2009 to 2011 in the Middle Dnieper Basin, river South Bug, river Molochnaya, Canal Prypyat and Lake Swityaz, Volhyn region. Several lots from the fishpond in Nemeshaevo, Kyiv region (fig. 1) were provided by our colleague I. S. Mytyai.

Samples of viviparids were collected by dredging and preserved in ethanol 96 %. Shell characters of the examined specimens were studied with an optical stereomicroscope MBS-9 and documented with a "Pentax K10D"camera. To check the specific affiliation the comparatorial method elaborated by Ya. I. Starobogatov

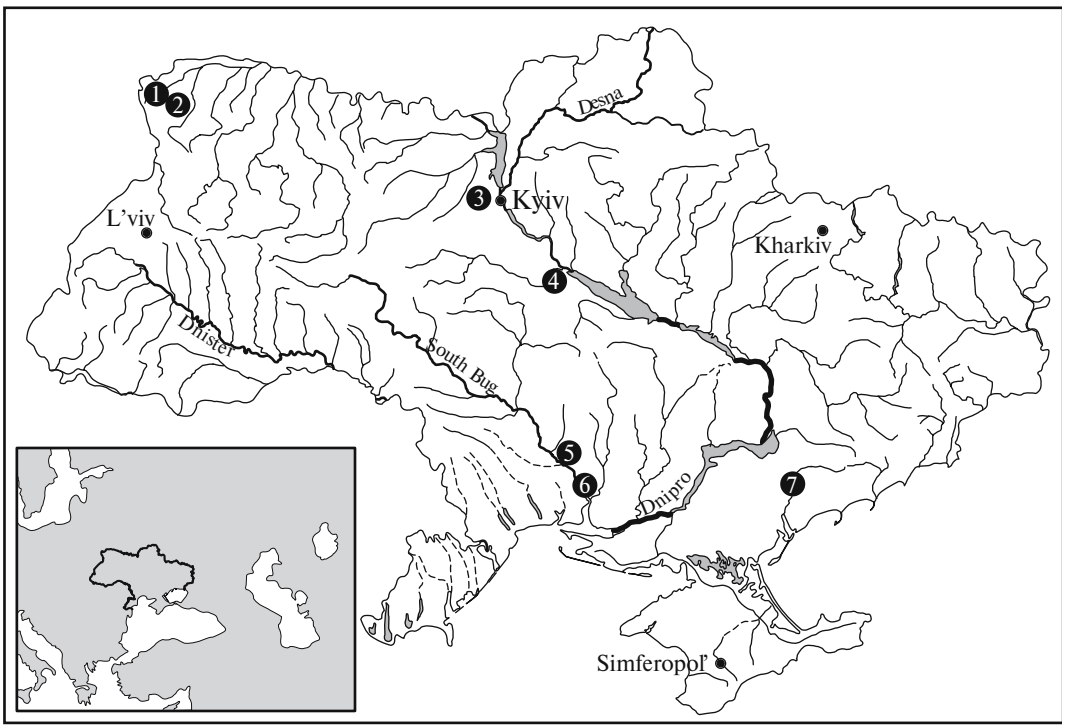

Fig. 1. Schematic map of the studied region. Circles indicate places where molluscs were gathered: 1 — Lake Swityaz, Shatsk district, Volhyn region (51°28'60" N, 23°50'33" E, 06 July 2010, coll. Yu. S. Ryabceva); 2 — Canal Prypyat near Venskoe settlement, Shatsk district, Volhyn region (51°26'48" N, 23°56'63" E, 07 July 2010, coll. Yu. S. Ryabceva); 3 — fishpond in Nemeshaevo settlement, Borodyanka district, Kyiv region (50°34'13" N, 30°05'26" E, 07 July 2010 and 24 September 2010, coll. I. S. Mytyai); 4 — Olshanka river in suburb of Moshny town, Cherkassy region (49°31'01" N, 31°45'39" E, 31 July 2010, coll. V. V. Anistratenko); 5 — Arbuzinka river (left branch of South Bug) near Trikraty village, Voznesensk district, Nikolaevskaya region (47°43'66" N, 31°23'23" E, 01 June 2009, coll. Yu. S. Ryabceva); 6 — South Bug river in Balovnoe village, Novoodessk district, Nikolaevskaya region (47°26'88" N, 31°53'32" E, 11 June 2010, 07 November 2010 and 12 April 2011, coll. Yu. S. Ryabceva); 7 — Molochnaya river near Terpen'e village, Melitopol' district, Zaporozh'e region (46°58'03" N, 35°26'29" E, 01 June 2009, coll. V. V. Anistratenko; 25 April 2011, coll. E. V. Degtyarenko).

Рис. 1. Карта-схема района исследований.

[1] The species is usually mentioned in literature as *Viviparus contectus* (e. g. Falniowski, 1996; Trüb, Ribi, 1997; Falkner et al., 2001). Meanwhile, *Contectiana contecta* (Millet, 1813) in the authors' sense does clearly distinguish from *C. listeri* by shell morphology; the former occurs in Europe quite rarely and its range is limited by the basin of the Baltic Sea, central part of Danube and Dnieper basins. The most wide-distributed in Europe species of the genus *Contectiana*, that is considered as "*Viviparus contectus*", should be named *C. listeri* (Zilch, 1955; Chernogorenko, 1988; Anistratenko, Chernogorenko, 1989; Levina, 1992 and others).

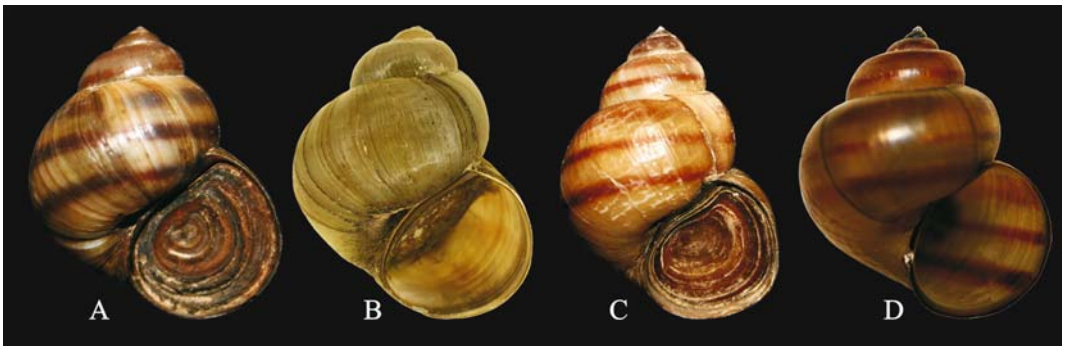

Fig. 2. Shells of Viviparidae snails studied: A — *V. viviparus* (Molochnaya river, Terpen'e village); B — *V. sphaeridius* (the same locality as A); C — *V. ater* (fishpond in Nemeshaevo settlement); D — *C. listeri* (Udai river, Korshaki village, Chernigovskaya Region).

Рис. 2. Раковина изученных моллюсков семейства Viviparidae: A — *V. viviparus* (р. Молочная, с. Терпенье); B — *V. sphaeridius* (р. Молочная, с. Терпенье); C — *V. ater* (пруд, пгт Немешаево); D — *C. listeri* (р. Удай, с. Коршаки, Черниговская обл.).

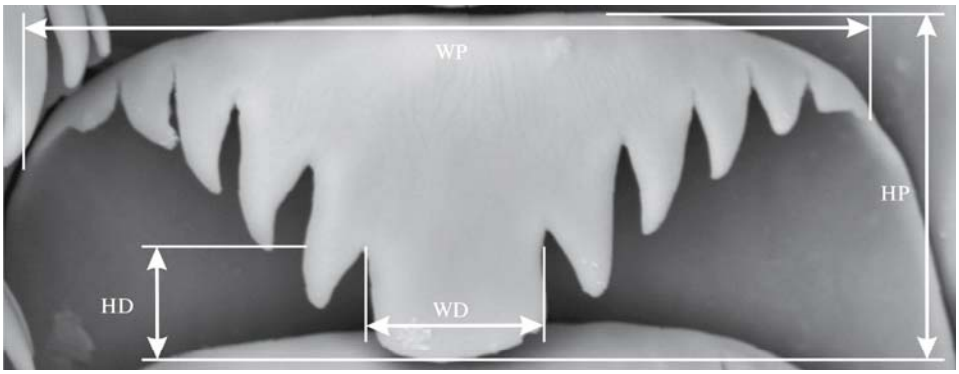

Fig. 3. Measuring of the rachidian tooth parameters. WP — width of the cutting plate; HP — height of the cutting plate; WD — width of the median denticle; HD — height of the median denticle.

Рис. 3. Промеры рахидального зуба. WP — ширина режущей пластинки; HP — высота режущей пластинки; WD — ширина срединного зубчика; HD — высота срединного зубчика.

has been used as an additional method (see Shikov, Zatravkin, 1991)[1] has been used. It allows to compare independently all of Raup's parameters of the shell tube growth (Raup, 1966).

The samples of viviparids collected in the Middle Dnieper Basin, river South Bug and river Molochnaya contained two species of the genus *Viviparus*: *V. viviparus* and *V. sphaeridius*; the only locality where the third species *V. ater* occurred is the fishpond in Nemeshaevo. The fourth species, *Contectiana listeri* has been collected from the Canal Prypyat and Lake Swityaz, Volhyn region (fig. 2).

The radula morphological features were examined with the aid of a scanning electron microscope (SEM). The SEM images were performed in the Laboratory of Physical Methods of Researches at the Institute of Geological Sciences NAS of Ukraine (Kiev). The radulae samples extracted and cleaned in KOH, rinsed in distilled water and 96 % alcohol, were mounted on stubs, sputter-coated with platinum and then documented using a digital Scanning Electron Microscope JSM-6490. Thirty radulae preparations have been studied: *V. viviparus* (8), *V. sphaeridius* (8), *V. ater* (6) and 8 radulae are of *Contectiana listeri*.

[1] The main idea of the comparatorial method is to use a "camera lucida" for the direct comparison of shells which are observed in standard orientation through stereomicroscope oculars, and directly compared with the outlines of reference specimens, usually the type specimens of other species in the same orientation. In many cases (but not always) specific distinctness of the forms can be concluded almost exclusively from the coincidence or non-coincidence of the outlines. The method is widely used by malacologists in the former USSR. Full description of the method was published in English by Shikov and Zatravkin (1991). In this paper the method is called "comparatory", but Ya. I. Starobogatov himself proposed (in additional remarks to this paper) to use the term "comparatorial" to emphasize that method is based not on just morphological comparison, but on using of "comparator" i. e. camera lucida.

Four parameters for the rachidian (central) tooth were measured (fig. 3): width of the cutting plate (WP), height of the cutting plate (HP), width of the median denticle on the rachidian tooth (WD), height of the median denticle (HD). Altogether 90 rachidian teeth were measured. A total length of radular ribbon and number of transverse rows of teeth were also estimated.

Descriptive statistics was performed using the PAST ver. 2.17 c (Hammer et al., 2001).

All the material studied is deposited in the Laboratory of Zoogeography, Schmalhausen Institute of Zoology NAS of Ukraine (Kyiv).

Results and discussion

For a long time zoologists gave much attention to the radula as a structure bearing very important characters in respect of taxonomy of many gastropods including Vivipaidae (Troschel, 1856–1863; Troschel, Thiele, 1866–1893; Cooke, 1921; Thiele, 1929; Kerth, 1971; Golikov, Starobogatov, 1975, 1989; Sitnikova, Starobogatov, 1982; Hickman, McLean, 1990; Starobogatov, 1990; Simone, 2004 and others).

Modern experts assert that morphological traits of the radula within European viviparids are of good use for delimitation of genera *Viviparus* and *Contectiana*, though the taxonomic value of these characters on the specific level is considered of little importance (e. g. Chernogorenko, 1988; Falniowski et al., 1996). At the same time the detailed study of dimensional parameters of radula neither *Viviparus* nor *Contectiana* has been carried out yet. This outstanding question instigates us to test the reliability of radular characters in the taxonomy of viviparid snails and, particularly, in the efficient discrimination of closely related species.

Mainly the dimensional parameters of rachidian tooth and its elements have been considered; the variability and features of other teeth have been analyzed in fewer details.

General remarks on the radula of studied viviparids

According to our data the radula of all the studied viviparids is approximately measures 0.5–0.6 mm wide in its distal part and 3–4 mm long. The number of transverse tooth rows ranges from 70 to 75; the rows are almost straight and bilaterally symmetrical to the rachidian tooth. No essential differences in size were discovered between the radulae of *Vivivparus* and *Contectiana*.

Radula of the family Viviparidae is of the architaenioglossate type (Sitnikova, Starobogatov, 1982), its transverse row consists of 7 teeth, radular formula is 2M — I — R — I — 2M. The cusp numbers on individual teeth within the radula of a single individual as well as between individuals of the same species of viviparid is quite variable (Krull, 1935; Bandel, 1984).

The central position is occupied by a rachidian[1] tooth; since the viviparid radula lacks both of the paracentral and the lateral teeth, the first teeth situated aside from the rachidian is the initial tooth; and behind it a pair of the marginal teeth (inner and outer) is located (fig. 4, 5).

Teeth of the adjacent longitudinal series differ in shape and usually are positioned strictly symmetrical. Each tooth consists of a more or less wide base attached to the radular membrane and bears a cutting plate on which several denticles of different shape are placed; they serve to scrape off foodstuff from the substrate or mostly to hold of the food that has been collected by gill. Viviparids practise the mode of feeding by collecting food, e. g. algal cells from the water by the gill and their transport in a mucus rod along a mantle fold to the base of the head (Rohrbach, 1937; Cook, 1949).

The rachidian tooth is medium in size, with a wide base and relatively short cutting plate (fig. 4, 5). On the cutting edge of the rachidian tooth there are usually four (occasionally up to six) lateral cusps on each side of the median denticle, which is much larg-

[1] For the radula description the nomenclature elaborated by Ya. I. Starobogatov (1990) is adopted here. A rachidian tooth is often named in literature as a "central" but this doesn't correspond to its homology.

er than the lateral cusps and more or less quadrangular in shape in all studied species except for *V. ater* in which it is triangular.

According to data obtained the radula of *V. viviparus* is about 0.50 mm wide and 3.14–3.70 mm long, bearing 68–74 rows of teeth. Similarly the representatives of *V. sphaeridius* have radula about of 0.50–0.55 mm wide and 3.90 mm long consisting of about 70 transverse rows of teeth.

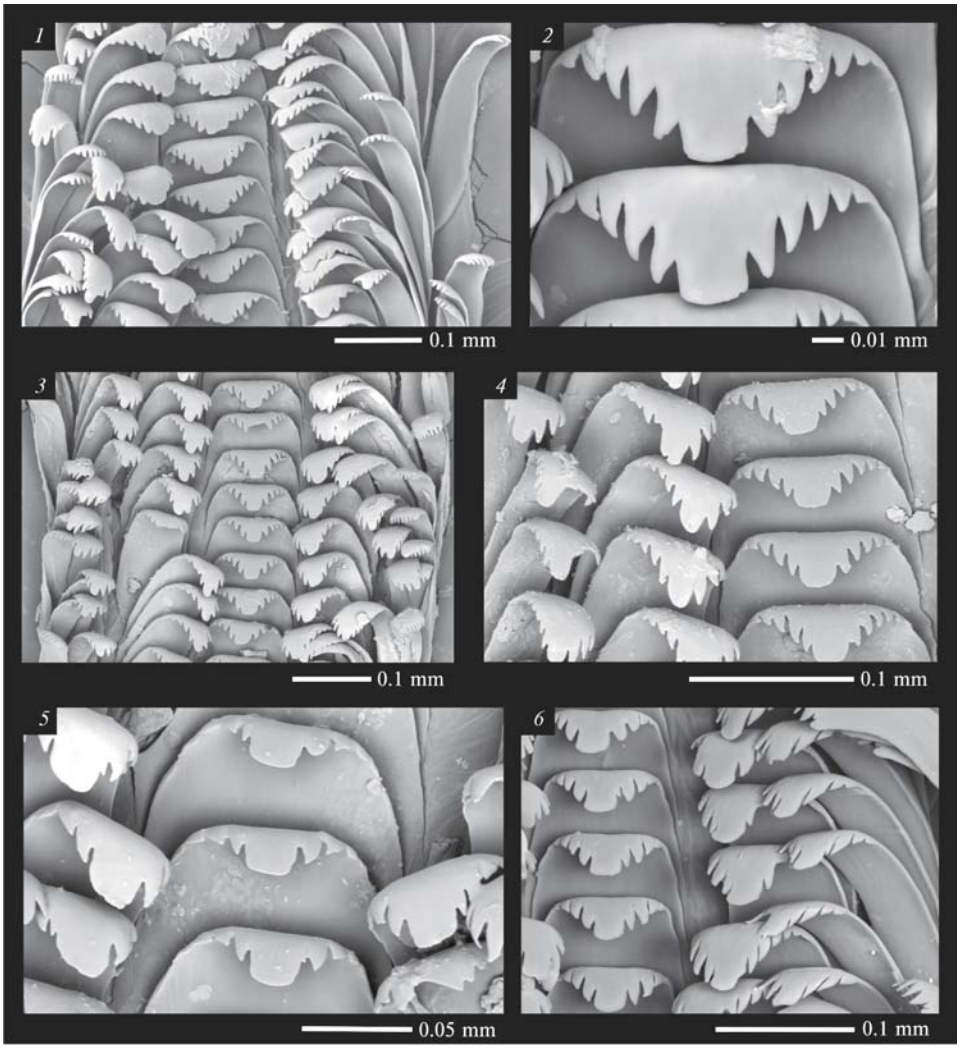

Fig. 4. Radulae of *Viviparus viviparus* (*1, 2*) and *V. sphaeridius* (*3–6*): *1* — general view of *V. viviparus* radular ribbon with teeth in natural position (Olshanka river in suburb of Moshny town); *2* — rachidian tooth of the same radula as *1*; *3* — general view of *V. sphaeridius* female radula with teeth in natural position (South Bug river in Balovnoe village); *4* — enlarged part of four transverse rows of the same radula as *3*; *5* — rachidian and initial teeth of *V. sphaeridius* male (South Bug river in Balovnoe village); *6* — enlarged half of several transverse rows of *V. sphaeridius* radula: from left to right the rachidian, initial, inner and outer marginal teeth sited (Arbuzinka river near Trikraty village).

Рис. 4. Радулы *Viviparus viviparus* (*1, 2*) и *V. sphaeridius* (*3–6*): *1* — общий вид радулы *V. viviparus* с зубами в естественном положении (р. Ольшанка на окраине г. Мошны); *2* — рахидальный зуб той же радулы, что на позиции *1*; *3* — общий вид радулы самки *V. sphaeridius* (р. Южный Буг в с. Баловное); *4* — увеличенная часть четырех поперечных рядов той же радулы, что на позиции *3*; *5* — рахидальный и инициальный зубы самца *V. sphaeridius* (р. Южный Буг в с. Баловное); *6* — увеличенная половина нескольких поперечных рядов радулы *V. sphaeridius*: слева направо расположены рахидальный, инициальный, внутренний и наружный маргинальные зубы (р. Арбузинка возле с. Трикраты).

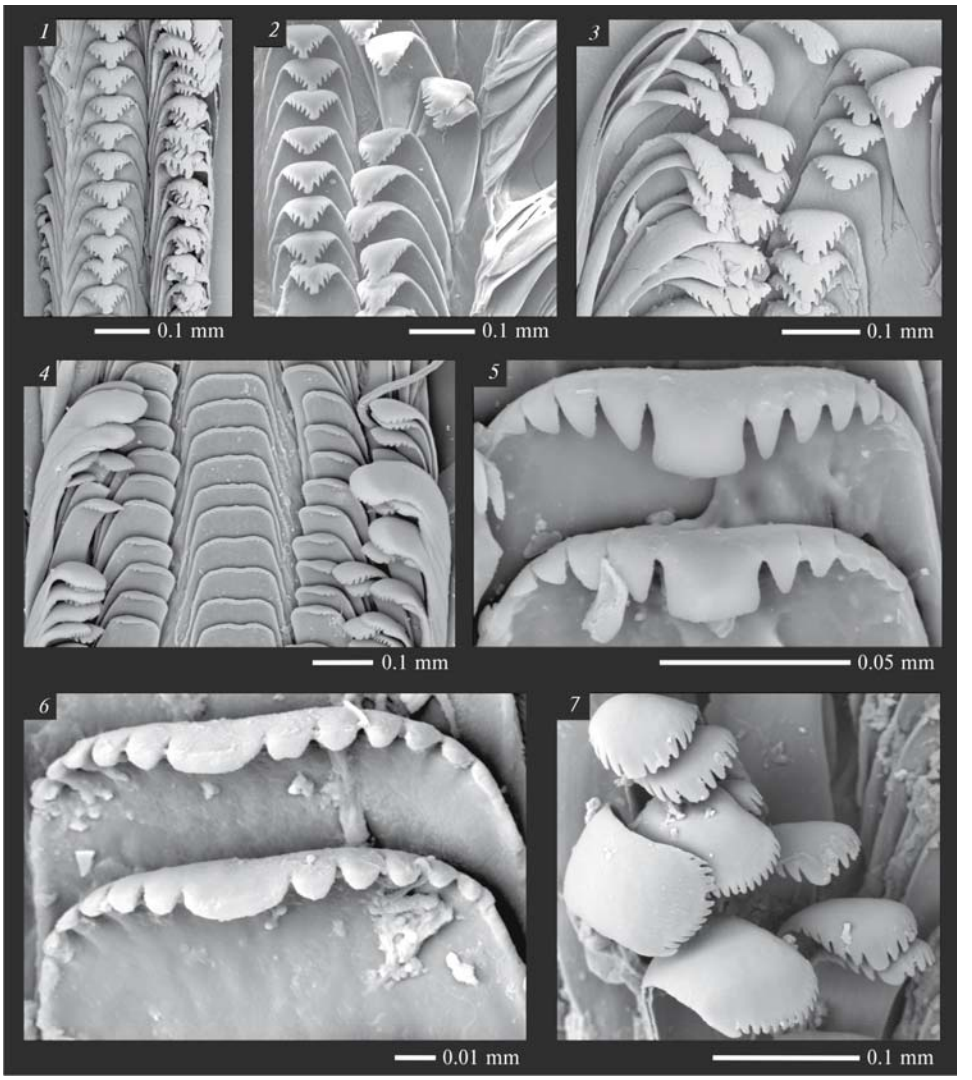

Fig. 5. Radulae of *Viviparus ater* (*1—3*) and *Contectiana listeri* (*4—7*): *1* — general view of *V. ater* radula with teeth in natural position (fishpond in Nemeshaevo settlement); *2* and *3* — enlarged half of several transverse rows of radula of two others specimens of *V. ater*. Normally a cutting edge of the rachidian tooth is of triangular shape and somewhat pointed (fishpond in Nemeshaevo settlement); *4* — general view of *C. listeri* radular ribbon with teeth in natural position (Canal Prypyat); *5* — rachidian teeth of *C. listeri* from the same locality as *4*: initially well-preserved, not-abraded cutting edge of the rachidians can be seen; *6* — rachidian teeth of the same radula as *5*: heavily-abraded cutting edge of the rachidians can be seen; *7* — enlarged inner and outer marginal teeth of the same radula as *5* and *6* are shown.

Рис. 5. Радулы *Viviparus ater* (*1—3*) и *Contectiana listeri* (*4—7*). 1 — общий вид радулы *V. ater* с зубами в естественном положении (пруд в пгт Немешаево); *2* и *3* — увеличенная половина нескольких поперечных рядов радулы двух экземпляров *V. ater*. Режущий край рахидального зуба в норме имеет треугольную форму и несколько вытянут (пруд в пгт Немешаево); *4* — общий вид радулы *C. listeri* с зубами в естественном положении (канал Припять); *5* — рахидальные зубы *C. listeri* из того же местонахождения, что на позиции *4* показан исходно хорошо сохранившийся, неистёртый режущий край рахидальных зубов; *6* — рахидальные зубы той же радулы, что на позиции *5* показан сильно изношенный режущий край рахидального зуба; *7* — внутренний и наружный маргинальные зубы той же радулы, что на позиции *5* и *6*.

The rachidian, initial and inner marginal teeth of *Viviparus* studied are with large square-shaped (*V. viviparus* and *V. sphaeridius*) or triangular (*V. ater*) median denticle. On each side of the median denticle from 4 up to 6 smaller denticles are located, their size is decreasing gradually in the direction of the rim. A second (outer) marginal tooth bears of 5—7 (occasionally up to 8) evenly elongated denticles along the cutting edge (fig. 4, 5).

The radula of *Contectiana listeri* is about 0.52–0.56 mm wide and 4.65 mm long, consisting of around 70–75 rows of teeth.

The rachidian, initial and inner marginal teeth of *Contectiana listeri* bear a rectangular median denticle. On each side of the median denticle there are 5 (rarely from 4 up to 6) smaller denticles, their size is decreasing gradually in the direction of the rim. A second (outer) marginal tooth bears of 8–10 (occasionally up to 12) evenly shorted denticles located along the cutting edge (fig. 5, *4–6*).

Normally the radula of *Contectiana* bears 5 lateral denticles on each side of the rachidian tooth (occasionally 4 or 6); sometimes partial (not reaching the base) dissection of denticles occurs. Within the radula, the number of lateral denticles in the axial row of the rachidian tooth was observed to be constant, i. e. the teeth positioned higher or lower of any rachidian tooth bore equal number of lateral denticles: whether their number was 4.5 or 6, it equalled their number in the vertical (axial) row. The same is true, as it is observed, for the denticles of *Viviparus* (compare Krull, 1935).

Comparative remarks

A comparison of radulae in different viviparid species shows their considerable similarity (fig. 4, 5). Shape, proportions and relative position of teeth in the transversal row of the radular ribbon are basically stable traits in all *Viviparus* and *Contectiana listeri* here studied. It is the configuration of the serrated surface of certain teeth that normally varies within one radula: the denticles may have more or less sharp cutting edge, be merged or have additional denticles (see below). The transversal radular row width varies according to age of the specific section of the radular ribbon: relatively old sections are comparatively wider and are composed of somewhat bigger teeth.

More or less reliable characters for differentiation of the genera *Viviparus* and *Contectiana* are provided by general shape and proportions of the rachidian tooth. It is clear that the median denticle of the rachidian tooth in *Contectiana listeri* is rectangular, while in *Viviparus* it is rather square (*V. viviparus* and *V. sphaeridius*) or shaped as a equilateral triangle (*V. ater*). The whole cutting plate of the rachidian tooth in *Contectiana listeri* has short incisions and functions rather as a scraper (scraping or grasping type feeding), while in *Viviparus* it has a notably projecting median denticle and seems to work as a food-cutter. In both cases the rachidian teeth are also widely involved in the transportation of gathered food particles. It is apparent from the feeding tracks produced by "*Viviparus contectus*" observed by Märkel (1957).

Our data suggest that interspecific differences within one genus apply only to details in structure of certain teeth, particularly of the rachidian tooth of the radula. It is connected to the number of teeth on lateral parts of cutting edge and length, width and proportions of the median (unpaired) tooth.

Absolute values of the rachidian tooth and its elements' dimensions clearly indicate the existence of stable interspecific differences in the viviparids here studied. Average height of the median denticle in *V. viviparus* and *V. ater* exceeds that in the other species here studied. The range of variability in *V. viviparus* is somewhat larger than in *V. ater* (fig. 6). The narrowest and yet the highest cutting plate of the rachidian tooth is typical in *V. ater*, which possesses the narrowest median denticle as well. Among all the viviparids studied the widest plate is in *V. sphaeridius*, which has also the widest median denticle. The cutting plate of the rachidian tooth in *Contectiana listeri* is of the medium width, the smallest height and the shortest median denticle within the group of species studied (fig. 6).

It is significant that height and width of the median denticle of the cutting edge of the rachidian tooth is directly proportional to similar measurements of the whole cutting plate of the rachidian tooth at the highest level of statistical significance ($r = 0.59$, $p < 0.01$, $n = 90$ and $r = 0.92$, $p < 0.01$, $n = 90$ respectively).

Variability of parameters studied *viz.* HP, WP, WD and HD for rachidian tooth have been analyzed using of single-factor analysis of variance (Fischer's criterion are 28.83, 7.85, 7.08 and 13.01 accordingly).

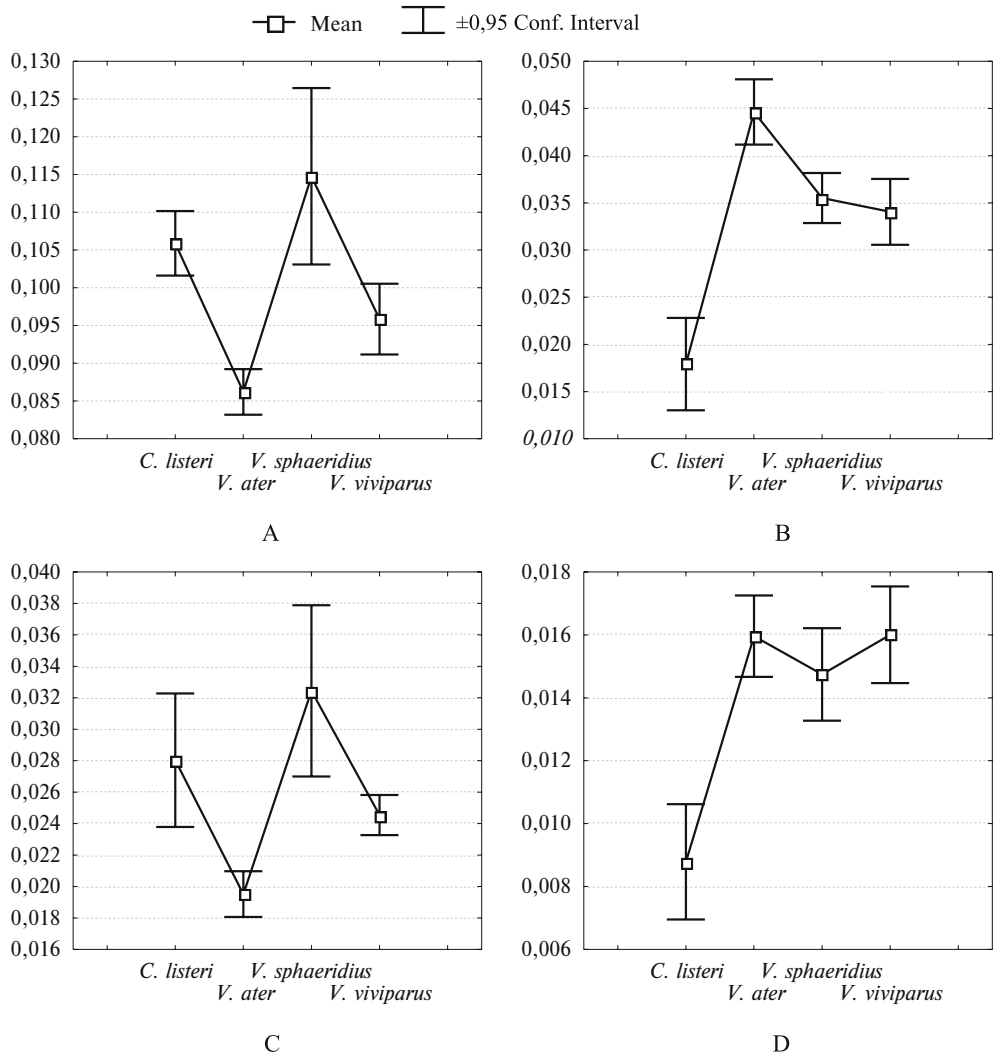

Fig. 6. Maximal, minimal and mean parameters of the rachidian tooth, in mm (confidence interval p = 0. 95): A — width of the cutting plate; B — height of the cutting plate; C — width of the median denticle; D — height of the median denticle.

Рис. 6. Максимальные, минимальные и средние значения промеров рахидального зуба, в мм (доверительный интервал при p = 0, 95): A — ширина режущей пластинки; B — высота режущей пластинки; C — ширина срединного зубчика; D — высота срединного зубчика.

Judging from the above-stated, the null hypothesis must be rejected at 1 % level of confidence. With the expectancy $p > 0.99$ it can be stated that the difference in measurements of the rachidian tooth and the median denticle is not accidental and is determined by specific affiliation.

The results of discriminate analysis (fig. 7, table 1) also show a hiatus between several species studied: 65 % of the observations are classified correctly.

The first canonical axis divides groups on the basis of median denticle measurements, *viz.* its height (68 %) and width (61 %). The second canonical axis should be interpreted as "dimensions of the rachidian tooth cutting plate" (plate width = 72 % and plate height = 36 %). *Contectiana listeri* and *V. ater* well differ from each other and from the pair *V. viviparus*-*V. sphaeridius*, which is weakly discriminated along the second canonical axis.

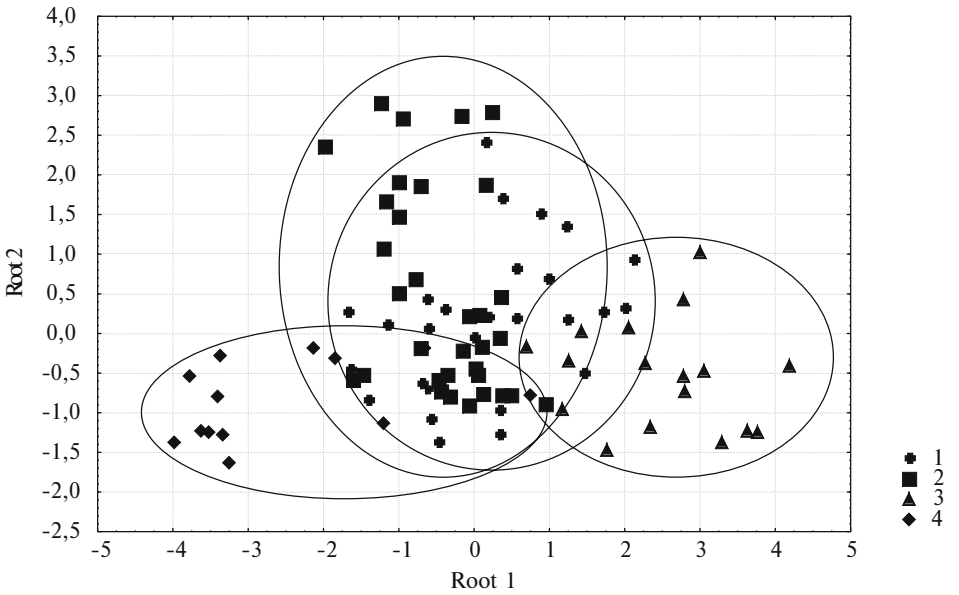

Fig. 7. Results of discriminate analysis of the rachidian tooth parameters: 1 — *Viviparus viviparus*; 2 — *V. sphaeridius*; 3 — *V. ater*; 4 — *Contectiana listeri*.

Рис. 7. Результаты дискриминантного анализа промеров рахидального зуба: 1 — *Viviparus viviparus*; 2 — *V. sphaeridius*; 3 — *V. ater*; 4 — *Contectiana listeri*.

Table 1. Results of classification

Таблица 1. Результаты классификации

Species	Predicted group membership, %				
	V. viviparus	*V. sphaeridius*	*V. ater*	*C. liseri*	Total
V. viviparus	63.0	7.4	18.5	11.1	100.0
V. sphaeridius	48.5	45.5	0.0	6.1	100.0
V. ater	17.6	0.0	82.4	0.0	100.0
C. liseri	7.7	7.7	0.0	84.6	100.0

Note. 65 % of selected original grouped cases correctly classified.

Intraspecific variability

Our observations demonstrate that the intraspecific diversity of radular teeth shape and dimensions in viviparids, especially considering all of the small details of structure, is also wide. We confine our consideration of the phenomenon to the age-related and individual variability and also to certain abnormalities as deviations from the standard.

a) An age-related variability is appearing as the abrasion of teeth in the frontal (distal) edge of the radula, while the teeth in the proximal part of radular ribbon possess an intact shape that may sharply differ from such of frontal (working) teeth. The same is concerned to all teeth of the transverse row — the rachidian, the initial, and both pairs of marginal (fig. 4, 5).

The abrasion-caused polymorphism occurs at different degree, starting from a barely visible up to almost total vanishing (reduction) of the cutting plate (fig. 5, *5, 6*). It is important that abrasion appears sharply in radulae of *Contectiana listeri*, while in all three species of the genus *Viviparus* here studied it is faintly expressed. The observed traits, presumably, refer to somewhat different diet in *Contectiana* and *Viviparus*, but this requires an additional study.

b) In order to estimate the individual teeth variability (i. e. variability within one radula) we measured the rachidian teeth of *V. viviparus* (n = 9) and *V. sphaeridius* (n = 10)

Table 2. Variability of the rachidian tooth parameters within the same radula
Таблица 2. Изменчивость размерных характеристик рахидального зуба в пределах одной радулы

Species	WP	HP	WD	HD
	CV, %			
V. sphaeridius	4.59	5.05	6.01	22.27
V. viviparus	4.71	9.21	8.79	17.00

from Molochnaya river near Terpen'e village. The values of the main parameters of the rachidian tooth within one radula vary insignificantly; all of them show a similar character of variation (table 2). The most variable trait of the rachidian tooth is the height of the median denticle — the variation coefficient (CV) is 22.3 %, while the rachidian tooth plate width exhibits the most stable dimensional parameters (CV = 4.6 %).

c) Additionally, in the studied molluscs we registered some cases of rachidian tooth abnormalities (fig. 8). A diversity of the developmental deviations is rather wide and manifold; they are: secondary splitting of the lateral denticles into two or more (*1*), their merging (*2*), changes in shape (*3*) and dimensions (*4*), finally, increasing or decreasing in the number of denticles (*5*).

Although the abnormalities are registered in viviparids from all the habitats involved, *Viviparus* from Terpen'e and from the fishpond of Nemeshaevo demonstrate the most complete set of deviations in radula; it may be related to local hydrological conditions. The patterns of these deviations are the same in both species (*V. viviparus* and *V. ater*): aberration of the teeth shape and their dimensions as well as asymmetry of tooth elements (fig. 8).

The radular dimorphism

Observations on radulae of 2 male and 3 female *V. viviparus* and *V. sphaeridius* reveal the absence of significant or at least persistent morphological differences. Solely, the male radula shows wider variability range in the number of denticles on the cutting edge of the rachidian and the second marginal teeth than the female one. The rachidian tooth in males may bear 3–5 lateral denticles at both sides of median tooth, from 5 to 8–10 denticles on the edge of the second marginal tooth; in females it counts in 5 denticles on the rachidian and 6 on the second marginal tooth respectively. Thus, apparently no sexual dimorphism of radula exists in species within the genus *Viviparus*.

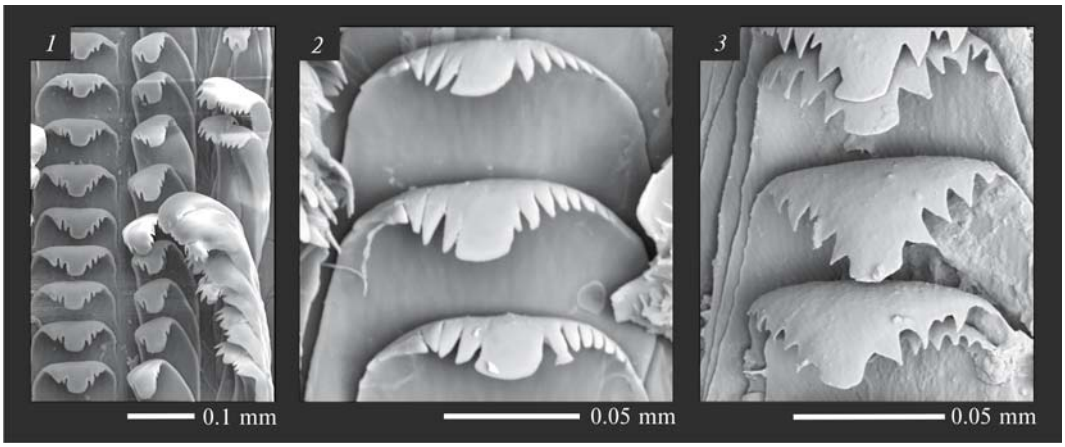

Fig. 8. Abnormalities of a cutting edge of the rachidian tooth in *Viviparus viviparus* (*1, 2*) and *V. ater* (*3*). *1* and *2* from Molochnaya river, Terpen'e village; *3* — from fishpond in Nemeshaevo settlement.

Рис. 8. Аномалии режущего края рахидального зуба радулы *Viviparus viviparus* (*1, 2*) и *V. ater* (*3*). *1* и *2* из р. Молочная, с. Терпенье; *3* — из рыборазводного пруда в пгт Немешаево.

Conclusion

The present study shows the existence of moderate and similar ranges and patterns of radular variability in all involved species; it does not exceed the average level of indeterminate variability for the viviparids radula.

A set of abnormalities in radular teeth is revealed and illustrated: secondary splitting of the lateral denticles (1), their merging (2), transformation of denticles shape (3) or size (4) and finally addition or reduction of the denticles number (5). Usually the abnormalities appear in complex.

Sexual dimorphism in the radular characters of studied viviparids has not been registered.

Certain proportions of the rachidian tooth and some details of other teeth morphology reveal significant differences between the radulae of different species of studied viviparids. The quantitative evaluation of the radular variability suggests that the most reliable characters for the discrimination of closely related species are the dimensional parameters of cutting edge of the rachidian tooth. These parameters are useful for taxonomy on the generic level, i. e. to differentiate of the genera *Viviparus* and *Contectiana* but their reliability on specific level is limited.

The present study significantly improves the understanding of ranges and patterns of radular variability of European viviparids and thereby confirms the reliability of radular characters in the taxonomy of these snails. Thus certain morphological traits of the radula allow to differentiate some viviparid species more confidently, while using of the shell characters leads often to misidentification.

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References

Anistratenko V. V., Anistratenko O. Yu. Fauna Ukraine : In 40 vol. — Vol. 29: Mollusca. Fasc. 1. B. 1: Class Polyplacophora or Chitons, Class Gastropoda — Cyclobranchia, Scutibranchia and Pectinibranchia (part). — Kyiv : Veles, 2001. — 240 p. — Russian : *Анистратенко В. В., Анистратенко О. Ю.* Фауна Украины. 29. Моллюски. Класс Панцирные или Хитоны, класс Брюхоногие — Cyclobranchia, Scutibranchia и Pectinibranchia (часть).

Anistratenko V. V., Chernogorenko E. V. Fauna and ecology of the Gastropoda in the Middle Dnieper Basin // Vestnik zoologii. — 1989. — N 2. — P. 3–6. — Russian : *Анистратенко В.В., Черногоренко Е.В.* Фауна и экология брюхоногих моллюсков бассейна Среднего Днепра

Bandel K. The radulae of Caribbean and other Mesogastropoda and Neogastropoda // Zoologische Verhandelingen. — Leiden, 1984. — **214**. — 188 p.

Chernogorenko E. V. On the species composition of viviparides (Gastropoda, Viviparidae) in Europe and West Asia // Zoologicheskij Zhurnal. — 1988. —**67**, N 5. — P. 645–655. — Russian : *Черногоренко Е.В.* О видовом составе вивипарид (Gastropoda, Viviparidae*)* Европы и Западной Азии

Cleave H. J. van, Richey E. M. Studies on the radula in snails of the genus Viviparus // Transactions of the American Microscopical Society. — 1936. — **60**, N 2. — P. 223-229.

Cook P. A ciliary feeding mechanism in *V*iviparus viviparus (L.) // Proceedings of the Malacological Society. London. — 1949. — **27**. — P. 265–271.

Cooke A. H. Evolution in the molluscan radula // J. Conchology. — 1921. — **16**, N 5. — P. 145–150.

Datsenko L. N. Late-Cenozoic Viviparoidea of the SW part of East-European Platform : Thesis for degree of Doctor of Sciences in geological sciences. — Institute of Geological Sciences of the National Academy of Sciences of Ukraine. — Kyiv, 2008. – 417 p. — Manuscript. — Russian : *Даценко Л.Н.* Позднекайнозойские Viviparoidea юго-запада Восточно-Европейской платформы.

Falkner G., Bank R. A., Proschwitz T. von. Check-list of the non-marine Molluscan Species-group taxa of the States of Northern, Atlantic and Central Europe (CLECOM I) // Heldia (Munchner Malakologische Mitteilungen). — 2001. — N 4 (1/2). — P. 1–76.

Falniowski A. Embryonic shells of Viviparus — what they may tell us about taxonomy and phylogeny? (Gastropoda: Architaenioglossa: Viviparidae) // Malacologische Abhandlungen. — 1996. — **18**. — N 3. — S. 35–42.

Falniowski A., Mazan K., Szarowska M. Tracing the viviparid evolution: radular characters (Gastropoda: Architaenioglossa: Viviparidae) // Malacologische Abhandlungen. — 1996. — **18**. — N 4. — S. 43–52.

Golikov A. N., Starobogatov Ya. I. Systematics of prosobranch gastropods // Malacologia, 1975. — **15**, N 1. — P. 185–232.

Golikov A. N., Starobogatov Ya. I. Problems of phylogeny and system of the prosobranchiate gastropods // Systematics and fauna of gastropoda, Bivalvia and Cephalopoda / Ed. Ya. I. Starobogatov. — Trudy Zoologicheskogo Instituta Akademii Nauk SSSR. — 1989 (for 1988). — **187**. — P. 4–77. — Russian : *Голиков А. Н., Старобогатов Я.И.* Вопросы филогении и системы переднежаберных брюхоногих моллюсков.

Hammer Ø., Hurper D. A. T., Ryan P. D. PAST: Paleontological Statistics software package for education and data analysis // Paleontologica electronica. — 2001 — **4**, N 1. — P. 19.

Hickman C. S., McLean J. H. Systematic revision and suprageneric classification of Trochacean Gastropods // Natural History Museum of Los Angeles. County Science Series — 1990. — N 35. — VI +169 p.

Kerth K. Radula-Erzatz und Zähnchenmuster der Weinbergschnecke im Winterhalbjahr // Zoologische Jahrbücher Anatomie. — 1971. — **88**. — S. 47–62.

Krull H. Anatomische Untersuchungen an einheimischen Prosobranchieren und Beiträge zur Phylogenie der Gastropoden // Zoologische Jahrbücher (Abteilung Anatomie). — 1935. — **60** (3/4). — S. 399–464.

Levina O. V. Molluscs of the family Viviparidae inhabiting the water storage reservoirs of Dnieper river cascade // Hydrobiologicheskij Zhurnal. — 1992. — **28**, N 1. — P. 60–64. — Russian : *Левина О.В.* Моллюски семейства Viviparidae водохранилищ днепровского каскада.

Märkel K. Bau und Funktion der Pulmonaten-Radula // Zeitschrift für Wissenschaftliche Zoologie. — 1957. — **160**. — S. 213–289.

Pavluchenkova O. V. Morphological-functional and caryologic analysis of molluscs of the superfamily Viviparoidea (Gastropoda, Pectinibranchia) of Russian fauna and adjacent territories : Thesis for degree of Candidate of Sciences in biological sciences. — Zoological Institute of Russian Academy of Sciences. — St.-Petersburg, 1997. — 239 p. — Manuscript. — Russian : *Павлюченкова О.В.* Морфо-функциональный и кариологический анализ моллюсков надсемейства Viviparoidea (Gastropoda, Pectinibranchia) фауны России и сопредельных территорий.

Raup D. M. Geometric analysis of shell coiling: general problems // J. Paleontology. — 1966. — **40**, N 5. — P. 1178–1190.

Riedel F. Early ontogenetic shell formation in some freshwater gastropods and taxonomic implications of the protoconch // Limnologica. — 1993. — 23. — P. 349-368.

Rohrbach F. Ökologische und morphologische Untersuchungen an Viviparus (Bellamya) capillatus Frauenfeld und Viviparus (Bellamya) unicolor Olivier, unter Berücksichtigung anderer tropischer Formen in Hinblick auf phylogenetische Beziehungen // Archiv für Molluskenkunde. — 1937. — **69**. — S. 177–218.

Ryabceva Yu. S., Anistratenko V. V. Morphological traits of embryonic shells of the gastropod genus Viviparus (Gastropoda: Viviparidae) an attempt to discriminate closely related species inhabiting Ukraine // The Bulletin of the Russian Far East Malacological Society. — 2012. — **15/16**. — P. 117–128. — Russian : *Рябцева Ю.С., Анистратенко В.В.* Морфологические особенности эмбриональной раковины моллюсков рода Viviparus (Gastropoda: Viviparidae): попытка разграничения близких видов, обитающих в Украине

Sengupta M. E., Kristensen Th. K., Madsen H., Jørgensen A. Molecular phylogenetic investigations of the Viviparidae (Gastropoda: Caenogastropoda) in the lakes of the Rift Valley area of Africa // Molecular Phylogenetics and Evolution. — 2009. — **52**. — P. 797–805.

Shikov E. V., Zatravkin M. N. The comparative method of taxonomic study of Bivalvia used by Soviet malacologists // Malacol. Abhandlungen Staatl. Museum für Tierkunde. — 1991. — **15**, H. 2, N 17. — S. 149–159.

Simone L. R. L. Comparative morphology and phylogeny of representatives of the superfamilies of architaenioglossans and the Annulariidae (Mollusca, Caenogastropoda) // Arquivos do Museu Nacional (Rio de Janeiro). — 2004. — **64** (4). — P. 387-504.

Sitnikova T. Ya., Starobogatov Ya. I. Content and Systematic status of the group Architaenioglossa (Gastropoda, Pectinibranchia) // Zoologicheskij Zhurnal. — 1982. — **61**. — N 6. — P. 831–842. — Russian : *Starobogatov Ya. I.* Evolutionary transformations of the radulae // Evolution morphology of Molluscs (Regularities of morphological-functional transformations of the radular apparatus) / Ed. O. L. Rossolimo. — M. : Izd-vo Moscow Univer., 1990. — P. 48–91. — (Archives of Zoological Museum Moscow State University; Vol. 28). — Russian : *Старобогатов Я.И.* Эволюционные преобразования радул.

Thiele J. Handbuch der systematischen Weichtierkunde. Erster Band, Teil 1. — Jena : Gustav Fischer Verlag, 1929. — 376 S.

Troschel F. H. Das Gebiss der Schnecken zur Begründung einer Natürlichen Classification. Bd 1. — Berlin : Nicolaische Verlags-Buchhandlung, 1856–1863. — 252 S.

Troschel F. H., Thiele J. Das Gebiss der Schnecken zur Begründung einer Natürlichen Classification. Bd 2. — Berlin : Nicolaische Verlags-Buchhandlung, 1866–1893. — 409 S.

Trüb H., Ribi G. High fecundity of hybrids between the sympatric snail species Viviparus ater and V. contectus (Gastropoda: Prosobranchia) // Heredity. — 1997. — **79**. — P. 418–423.

Zhadin V. I. Study on ecology and variability of Vivipara fasciata Müll // Monographs of the Biological Volga Station. — 1928. — N 3. — 94 p. — Russian : *Жадин В. И.* Исследования по экологии и изменчивости Vivipara fasciata Müll.

Zilch A. Die Typen und Typoide des Natur–Museums Senckenberg, 14: Mollusca, Viviparidae // Archiv für Molluskenkunde. — 1955. — **84**, N 1/3. — S. 45–87.

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