

**Variation of shell shape in *Solariella obscura*
(Vetigastropoda: Trochoidea)
in the Eurasian Arctic seas
and adjacent part of the Western Pacific Ocean**

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Solariella obscura (Couthouy, 1838) is a highly variable species, widely distributed in the seas of the Northern Hemisphere. We tested whether the forms (varieties) of *S. obscura*, recognized by shell sculpture, differ by shape-dependent conchological characters using principal component analysis and discriminant function analysis. We also tested differences between Atlantic and Pacific representatives of the species. A total of nine samples (265 specimens) from the Barents, the Kara and the Bering seas were measured by seven conchological parameters. Varieties of *S. obscura* did not differ significantly in studied characters. It conforms to morphological data of radula and stomach.

Key words: *Solariella obscura*, shell shape, variability, morphology, Arctic, Pacific Ocean.

**Изменчивость формы раковины *Solariella obscura*
(Vetigastropoda: Trochoidea)
в морях евразийской Арктики
и прилегающей западной части Тихого океана**

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Solariella obscura (Couthouy, 1838) широко распространен в морях северного полушария и характеризуется высокой изменчивостью морфологии раковины. Мы проверили, различаются ли формы (вариететы) *S. obscura*, выделенные по скульптуре, параметрами, определяющими форму раковины, с помощью анализа главных компонент и дискриминантного анализа. Мы также проверили различия между арктическими и тихоокеанскими представителями вида. Всего было промерено девять выборок *S. obscura* (265 экз.) из Баренцева, Карского и Берингова морей по семи конхологическим параметрам. Вариететы *S. obscura*, как и выборки из Арктики и Пацифики, не отличались друг от друга по исследованным конхологическим параметрам. Это согласуется с данными о морфологии радулы и желудка.

Ключевые слова: *Solariella obscura*, форма раковины, изменчивость, морфология, Арктика, Тихий океан.

Representatives of Trochoidea Rafinesque, 1815 are often characterized by a high intraspecific variation in shell morphology. This led to frequent taxonomic confusions, particularly descriptions of numerous conchological forms as separate taxa of species or subspecies level. Taxonomic status of such forms is often a subject of discussions.

Galkin [1955] tried to explain conchological variability in some trochoidean species from the Eurasian Arctic and the Northwestern Pacific seas. He recognized ecological (varieties) or geographical (subspecies) categories within the most variable species of Trochoidea [Galkin, 1955]. Particularly, for *Solariella obscura* (Couthouy, 1838), a species, widely distributed in temperate and Arctic waters of the Northern hemisphere, Galkin [1955] defined three varieties with different patterns of teleoconch sculpture. Also, he noted that distribution of the varieties in the ocean depends on a depth. According to Galkin [1955], typical form (Fig. 1B) has 2–3 spiral cords, crossed with several axial ribs or folds on the body whorl, and had been reported from the depth range of 3–335 m. *S. obscura* var. *intermedia* (Fig. 1A) has a shell, covered with a spiral sculpture or almost smooth, and lives at a depth of 6–90 m. Body whorl of *S. obscura* var. *bella* (Fig. 1C) has 3–4 ridges. The representatives of this form live at a depth of 39–513 m [Galkin, 1955]. All three forms are not discrete, and specimens with an intermediate pattern of sculpture sometimes occur sympatrically [Galkin, 1955; Warén, 1993]. Strongly sculptured specimens with a reticulate sculpture pattern (i.e., belonging to Galkin's «var. *bella*») had been suggested to have a higher spire, than snails with low sculpture or smooth specimens («var. *intermedia*») [Galkin, 1955; Warén, 1993]. However, this suggestion had never been tested statistically.

In the present paper, we tested whether the forms (varieties) of *S. obscura*, designated by Galkin [1955] based on shell sculpture, differ in shape-dependent conchological characters. We also tested differences between Atlantic and Pacific representatives of the species.

Material and methods

For the present study, collections of *S. obscura*, stored in the Zoological Institute of the Russian Academy of Sciences (ZIN) (S. Petersburg) and Laboratory of

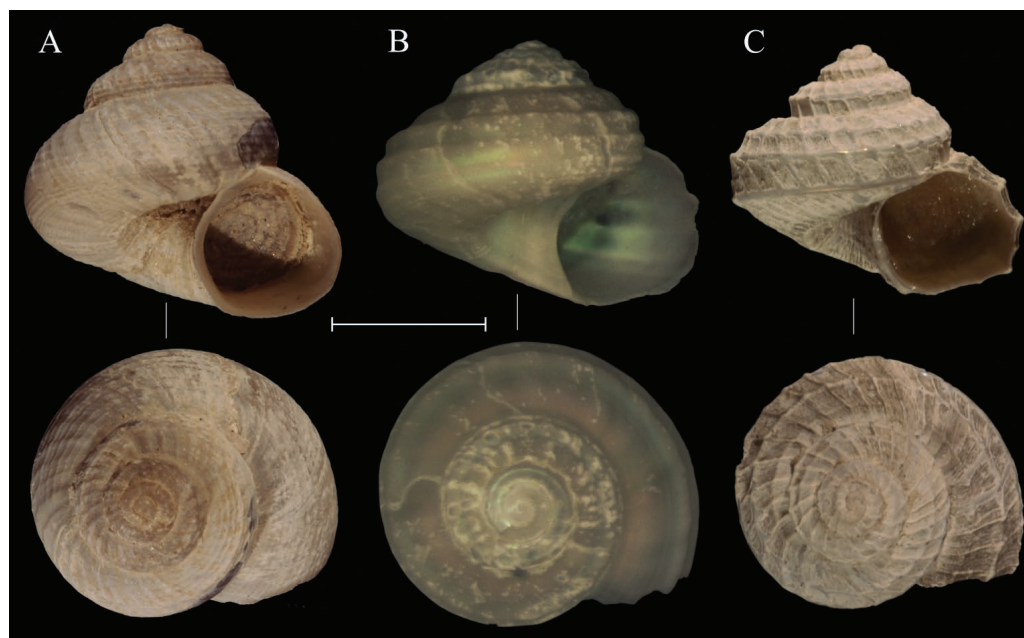


Fig. 1. Varieties of *Solariella obscura*: **A** – «var. *intermedia*», Barents Sea, Iokangskie Islands, 68°04.38' N, 39°34.70' E, ZIN 28/4289; **B** – typical form, Bering Sea, 29 m, 64°02.2' N, 170°04' W, ZIN 675/56388; **C** – «var. *bella*», Barents Sea, 154 m, 69°40.597' N, 34°06.184' E. Scale bar 3 mm.

Macroecology and Biogeography of Invertebrates of the S. Petersburg State University (LMBI) (S. Petersburg), were used. The samples were taken from the Eurasian Arctic and northwest Pacific (Barents, Kara and Bering Seas) (Table 1).

Shells were studied under the stereomicroscope MBS-10 with an eyepiece-micrometer. All specimens of *S. obscura* were divided into three varieties according to Galkin's diagnosis [Galkin, 1955; Krol, Nekhaev, 2016]. A total of nine samples (265 specimens) (Table 1) were measured for the following conchological parameters: shell height, body whorl height, aperture height, shell width, aperture width, umbilicus width, whorls number (Fig. 2A–C).

For testing differences between the conchological forms and geographical groups (Arctic (Barents and Kara seas) vs. Pacific (Bering Sea)) principal component analysis (PCA) and discriminant function analysis (forward stepwise method) with two data types were performed. For the discrimination, we firstly used direct data of seven measurements mentioned above. Secondly, we used principal component scores (except for axis 1, which is usually correlated with absolute size [Humphries et al., 1981; Vinarski et al., 2017]), the result of the principal component analysis. All statistical analyzes were performed with statistical packages PAST version 1.96 [Hammer et al., 2001] and STATISTICA version 12.

Table 1

Measurements of shells of *Solariella obscura*

	SH, mm	BWH, mm	AH, mm	AW, mm	SW, mm	UW, mm	WN
Typical form, Bering Sea, 29 m, 64°02.20' N, 170°04.20' W, ZIN 88/57652, n=30							
Mean	6.47	5.05	3.35	3.29	7.35	1.84	4.64
SD	0.67	0.48	0.24	0.27	0.62	0.27	0.24
Min	5.40	4.40	2.90	2.90	6.50	1.50	4.25
Max	7.70	6.00	3.90	3.90	8.70	2.50	5.10
«Var. <i>intermedia</i> », Kara Sea, 24 m, 71°41.481' N, 83°29.291' E, LMBI, n=30							
Mean	7.11	5.99	4.22	4.04	8.58	2.04	3.93
SD	1.28	0.80	0.46	0.48	1.04	0.30	0.34
Min	3.20	3.80	2.80	2.60	5.80	1.50	3.25
Max	9.10	7.60	5.20	4.90	10.70	2.50	4.60
«Var. <i>intermedia</i> », East Kamchatka, near Ust-Kamchatsk, 20 m, 56°09.68' N, 162°28.52' E, ZIN 54/4797, n=25							
Mean	4.62	3.93	2.87	2.82	5.95	1.56	4.01
SD	0.88	0.72	0.46	0.45	0.98	0.42	0.38
Min	3.10	2.65	2.00	2.00	4.15	1.00	3.25
Max	6.60	5.55	3.80	3.80	7.90	3.10	4.50
«Var. <i>intermedia</i> », Kara Sea, 17 m, 73°49' N, 70°32' E, ZIN 36/4779, n=30							
Mean	6.16	5.13	3.71	3.57	7.42	1.71	4.43
SD	0.81	0.62	0.38	0.38	0.94	0.31	0.25
Min	5.20	4.50	3.30	3.10	6.50	1.00	4.00
Max	8.40	6.60	4.80	4.50	9.90	2.40	5.00
«Var. <i>intermedia</i> », Barents Sea, 15 m, 69°12' N, 56°50' E, ZIN 85/31660, n=30							
Mean	8.56	6.51	4.30	4.23	9.65	2.70	5.17
SD	0.93	0.62	0.42	0.40	0.90	0.48	0.20
Min	7.00	5.50	3.50	3.70	8.30	2.00	4.80
Max	10.70	8.00	5.10	5.20	12.00	4.00	5.60
«Var. <i>intermedia</i> », Barents Sea, Iokangskie Islands, 68°04.38' N, 39°34.70' E, ZIN 28/4289, n=30							
Mean	6.82	5.41	3.59	3.57	7.87	1.90	4.61
SD	0.93	0.62	0.35	0.36	0.84	0.33	0.29
Min	5.50	4.40	3.00	3.00	6.50	1.50	4.20
Max	8.50	6.60	4.30	4.30	9.70	2.60	5.10

Table 1 (Continued)

	SH, mm	BWH, mm	AH, mm	AW, mm	SW, mm	UW, mm	WN
«Var. <i>intermedia</i> », Barents Sea, 25 m, 68°26.05' N, 38°13.39' E, LMBI, n=30							
Mean	3.53	2.89	2.26	2.15	4.52	0.95	3.47
SD	1.28	0.99	0.84	0.76	1.65	0.21	0.33
Min	2.40	2.00	1.50	1.50	3.15	0.60	3.10
Max	7.70	6.70	5.20	4.90	10.20	1.70	4.50
«Var. <i>intermedia</i> », Barents Sea, 56 m, 69°08' N, 47°52' E, ZIN 88/4350, n=30							
Mean	5.50	4.43	2.89	2.89	6.58	1.58	4.36
SD	0.68	0.49	0.27	0.25	0.68	0.24	0.29
Min	3.90	3.20	2.30	2.30	5.00	1.20	3.90
Max	6.90	5.50	3.30	3.30	7.90	2.20	5.00
«Var. <i>bella</i> », Barents Sea, 292 m, 72°00' N, 43°10' E, ZIN 13/4700, n=30							
Mean	4.31	3.30	2.23	2.29	4.83	1.20	3.98
SD	0.92	0.69	0.45	0.48	1.01	0.32	0.42
Min	2.00	1.65	1.25	1.20	2.50	0.50	2.75
Max	5.75	4.40	3.10	3.10	6.60	1.75	4.75

Note. SD – standard deviation; SH – shell height, mm; BWH – body whorl height; AH – aperture height; AW – aperture width; SW – shell width; WN – whorls number; UW – umbilicus width.

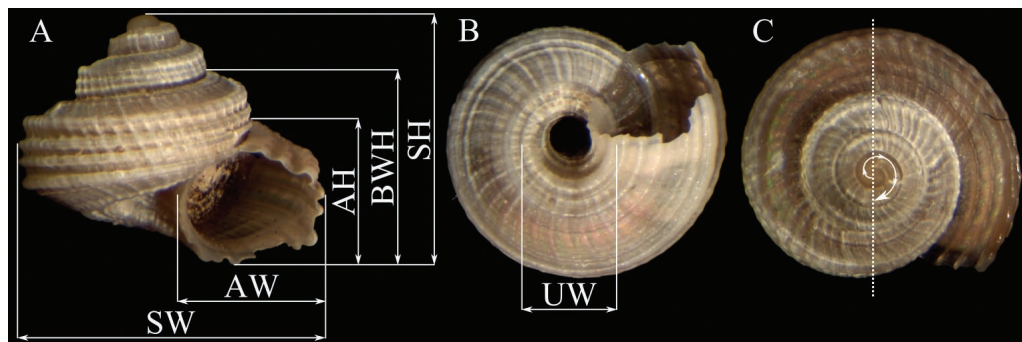


Fig. 2. Scheme of shell measurements (A–B) and counting of whorls number (C). Shell of «var. *bella*». SH – shell height; BWH – body whorl height; AH – aperture height; AW – aperture width; SW – shell width; UW – umbilicus width; spiral arrow indicates the first whorl, whorls number of the shell = 3.9.

Results

Results of measurements of *Solariella obscura* are presented in the Table 1 for samples and in Fig. 3 for varieties. Box plots of shell height (Fig. 3A), body whorl height (Fig. 3B), aperture height (Fig. 3C), shell width (Fig. 3D) and umbilicus width

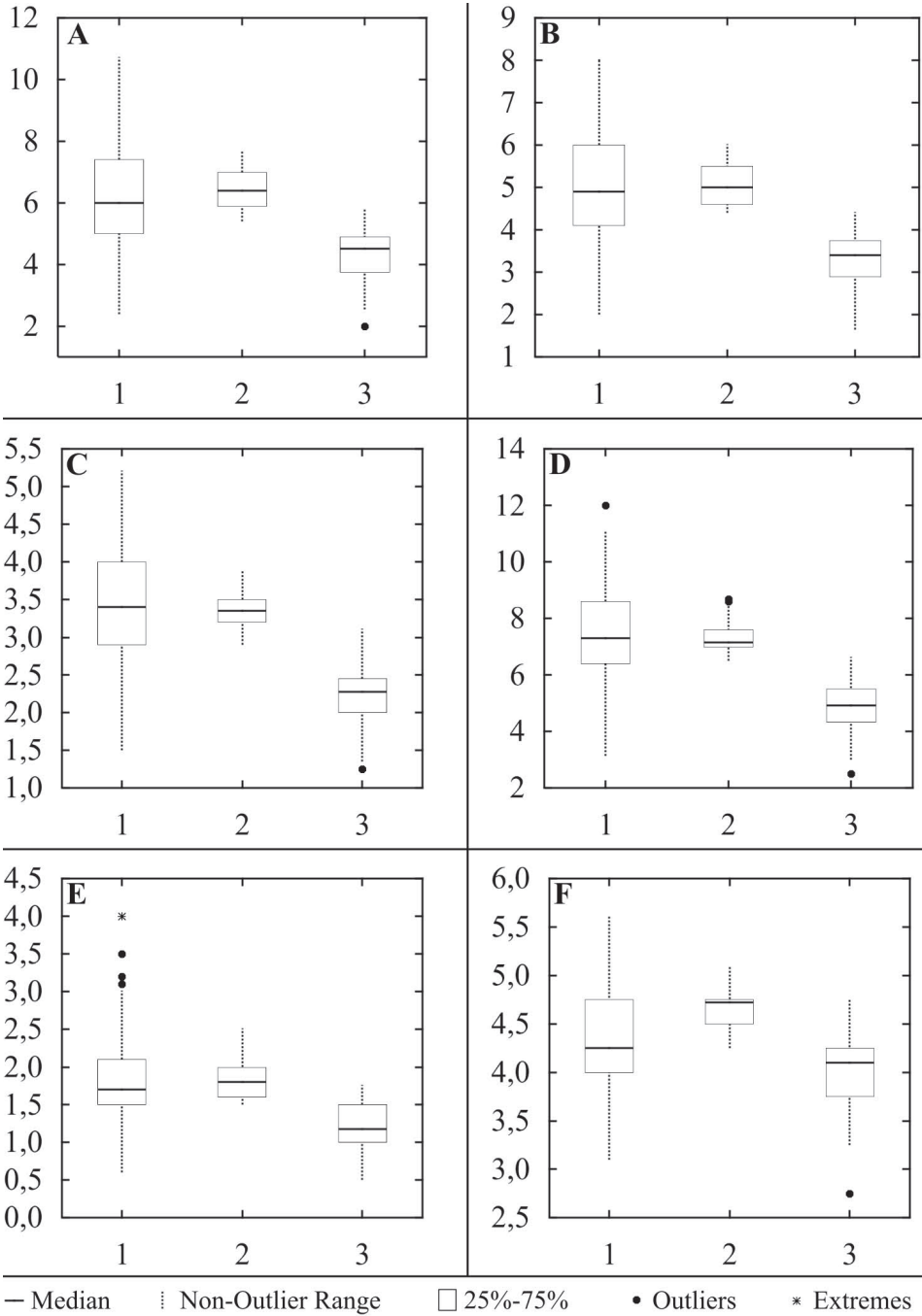


Fig. 3. Box plots of conchological parameters: **A** – shell height; **B** – body whorl height; **C** – aperture height; **D** – shell width; **E** – umbilicus width; **F** – whorls number. 1 – «var. *intermedia*», 2 – typical form, 3 – «var. *bella*».

(Fig. 3E) indicate that «var. *intermedia*» and typical form ranges overlapped with each other, while «var. *bella*» ranges were not overlapped with other two varieties. In the box plot of whorls number (Fig. 3F) ranges of «var. *intermedia*» were partially overlapping with other two varieties, but ranges of «var. *bella*» and typical form did not overlap. This indicates that general pattern of distribution of absolute shell measurements is not different in all three conchological forms.

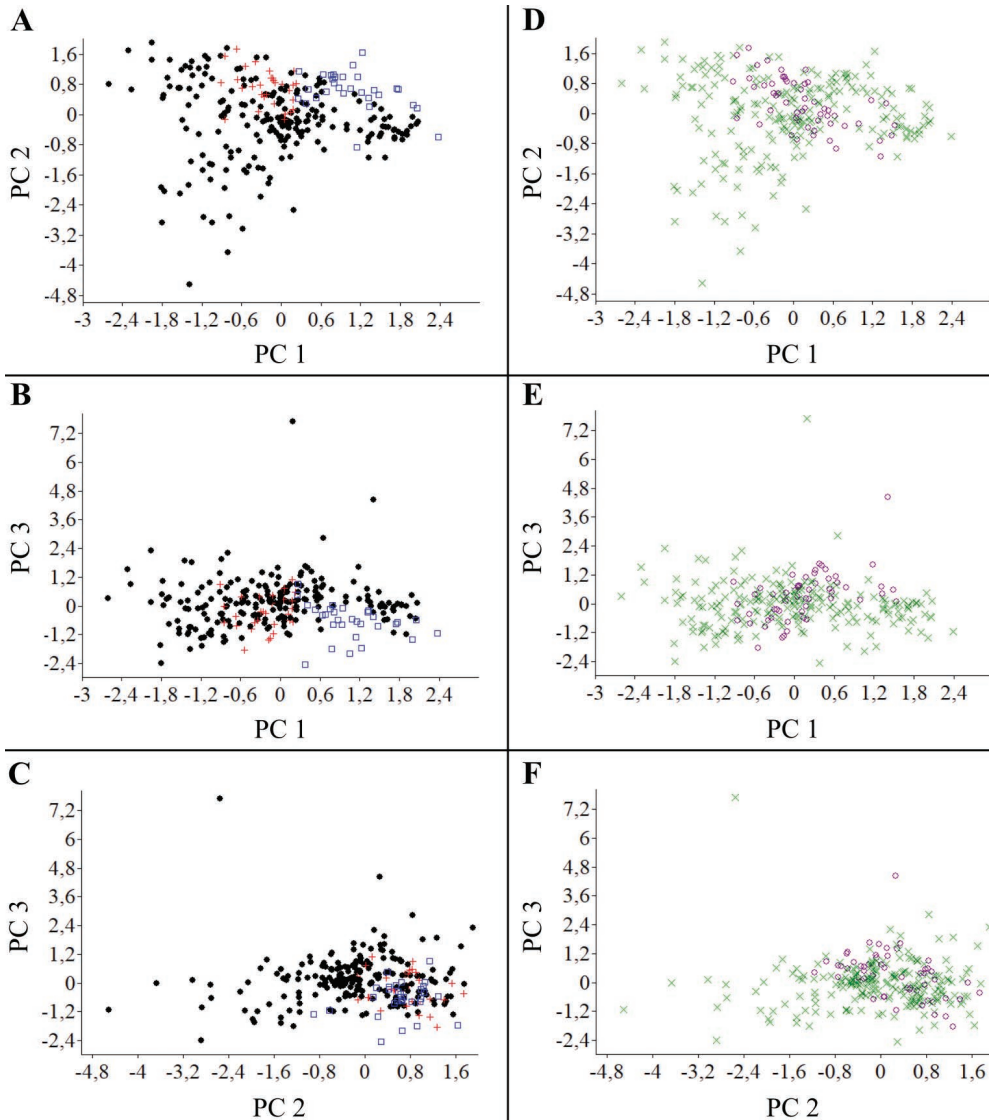


Fig. 4. PCA scatterplots: **A–C** – varieties of *Solariella obscura*; typical form – red crosses, «var. *intermedia*» – black dots, «var. *bella*» – blue squares; **D–F** – geographic groups; Arctic – green crosses, Pacific – violet circles.

The first axis of principal component analysis explained 95.66% of the variance. The bulk of remaining variance is explained by axis 2 (2.09%) and axis 3 (0.86%). Varieties of *S. obscura* were not segregated in separate clusters in the scatterplot of PCA. Nevertheless, individuals of «var. *intermedia*» were compactly grouped and were slightly separated from the rest of the shells (Fig. 4A–C). Arctic and Pacific samples of *S. obscura* were also not segregated in separate clusters (Fig. 4D–F).

Discriminant function analysis, performed with varieties and geographical groups of *S. obscura*, had not demonstrate significant differences neither when absolute values of shell measurements, nor when values of PCA coordinates were used (Table 2, 3).

Table 2

The results of discriminant function analysis (grouped by varieties of *Solariella obscura*)

Group (observed)	Percent correctly classified, %	Group (predicted)		
		Typical form p=0.77	«Var. <i>intermedia</i> » p=0.11	«Var. <i>bella</i> » p=0.11
Analysed by conchological parameters (Wilks' $\lambda=0.72$, $F(4.52)=23.45$, $p<0.05$)				
Typical form	0	0	30	0
«Var. <i>intermedia</i> »	97.56	1	200	4
«Var. <i>bella</i> »	60.00	0	12	18
Total	82.26	1	242	22
Analysed by principal components (Wilks' $\lambda=0.80$, $F(4.52)=15.60$, $p<0.05$)				
Typical form	3.33	1	28	1
«Var. <i>intermedia</i> »	97.07	0	199	6
«Var. <i>bella</i> »	16.67	0	25	5
Total	77.36	1	252	12

Table 3

The results of discriminant function analysis (grouped by geographic groups)

Group (observed)	Percent correctly classified, %	Group (predicted).	
		Arctic p=0.79	Pacific p=0.21
Analysed by conchological parameters (Wilks' $\lambda=0.97$, $F(2.26)=3.84$, $p<0.05$)			
Arctic	99.05	208	2
Pacific	1.82	54	1
Total	78.87	262	3
Analysed by principal components (Wilks' $\lambda=0.96$, $F(2.26)=5.02$, $p<0.05$)			
Arctic	99.05	208	2
Pacific	1.82	54	1
Total	78.87	262	3

Discussion

The results of multivariate analysis demonstrate that tested forms of *S. obscura*, distinguished based on the shell sculpture, do not differ in shell shape. Also, differences were not observed between the western (Barents and Kara seas) and the eastern (Bering Sea) populations. These results correspond to the evidence of investigations of radula [Galkin, 1955; Warén, 1993] and stomach [Krol, Nekhaev, 2016], which also did not demonstrate evident differences between representatives of different conchological forms.

Some authors [e.g., Høisæter, 1986] had considered a presence of one more species of the genus, *Solariella laevis* Friele, 1886, in the northern Atlantic. Warén [1993] synonymized *S. laevis* with *S. obscura*. The former species conforms to Galkin's definition of *S. obscura* var. *intermedia*. Therefore, our investigation also confirms conspecificity of both forms.

High level of variation of the shell sculpture did not correlate with other morphological characters, as had also been reported in other gastropod taxa [Wigham, 1975; Golikov, 1980; Rex et al., 1988; Nekhaev, 2016]. Usually, this variation is explained by the influence of environmental factors as wave activity, substrate, water temperature or depth-related conditions [Wigham, 1975; Rex et al., 1988; Urabe, 2000]. The geographical pattern of variation of shell sculpture had been reported for some Arctic gastropod species [Golikov, 1980]. However, all conchological forms of *S. obscura*, designated by Galkin, occur sympatrically in the Arctic and Pacific seas (this study) and in the Atlantic Ocean [Warén, 1993; Dornellas, Simone, 2015]. Hence, the ecological explanation of shell variation, offered by Galkin [1955] is unlikely.

Acknowledgements

We are grateful to Boris Sirenko, Raisa Pikalova and Alexey Merkuljev (S. Petersburg, Russia) for their valuable help during the work with collections of ZIN. We also express our gratitude to Yuri Kantor (Moscow) who reviewed our manuscript. The study is supported by Russian Scientific Foundation under the grant No. 18-74-00010 (study of ZIN collections, statistical analysis) and Grant Council of the President of Russia under the grant No. MK-4797.2018.4 (study of recent material from the Barents Sea).

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Published online December 27, 2018