Morphology and taxonomy of Aulacoseira muzzanensis (Bacillariophyta)

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Abstract. Morphological investigation of wild populations of Aulacoseira granulata shows significant variability of its quantitative morphological characteristics: valve diameter and height; number of rows of areolae and number of areolae in 10 µm on the valve mantle; and number of spines and their length on separation valves. Low values of mantle height to valve diameter ratio and large numbers of areolae in 10 µm, typical for A. muzzanensis, are also found in populations of A. granulata. The valve height/diameter ratio decreases as the valve diameter increases, and such relationships also occur in other taxa of this genus (A. baikalensis, A. islandica, and A. subarctica). No correlation is found between valve diameter and number of spines in separation valves. Our investigations confirm the correctness of referring A. muzzanensis to the synonymy of A. granulata, and based on original and published data, we suggest emendation of the diagnosis of A. granulata.

Keywords: Aulacoseira, Aulacoseira granulata, diatoms, frustule morphology, scanning electron microscopy, taxonomy.

Mорфология и таксономия Aulacoseira muzzanensis (Bacillariophyta)

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Резюме. Изучение морфологии панциря в природных популяциях Aulacoseira granulata показало значительную изменчивость количественных признаков: диаметра створки и ее высоты, числа рядов ареол и ареол в 10 мкм на загибе створки, числа и длины шипов на разделительных створках. Небольшие значения отношения высоты створки к ее диаметру и высокие числа ареол в 10 мкм, характерные для A. muzzanensis, встречаются и в популяциях A. granulata. Показано, что с увеличением диаметра створки уменьшается отношение высоты створки/диаметр створки и такая зависимость наблюдается и у других представителей этого рода: A. baikalensis, A. islandica, A. subarctica. Не выявлено корреляции между диаметром створки и числом шипов у разделительных створок. Наши исследования подтверждают корректность сведения A. muzzanensis в синонимику к A. granulata и на основе оригинальных и литературных данных предлагается расширить диагноз A. granulata.

Ключевые слова: Aulacoseira, Aulacoseira granulata, диатомовые, морфология панциря, сканирующая электронная микроскопия, таксономия.

Melosira muzzanensis F. Meist. was described in 1912 (Meister, 1912). Then, a new combination for M. granulata was suggested — M. granulata var. muzzanensis (F. Meist.) Hust. (Hustedt, 1930). This combination is the variety included in the first
Russian systematic report of diatom algae (Zabelina et al., 1951). Later, M. granulata var. muzzanensis was changed to Aulacoseira muzzanensis (F. Meist.) Krammer (Krammer, 1991), but the systematic position of this species remains in question. Melosira granulata var. muzzanensis was mentioned in some publications in the 1960s (Ermolaeva, 1967; Kuzmin, Elizarova, 1967), but a monograph by Skabichevsky (1960) referred this variety to the synonymy of M. granulata (Ehrenb.) Ralfs. In work on Centrophyceae this variety is described as a synonym of Aulacoseira granulata (Ehrenb.) Simon- sen (Davydova, Moiseeva, 1992).

The independent taxonomic status of A. muzzanensis was recognized in other publications (Krammer, 1991; Krammer, Lange-Bertalot, 1991; Algae..., 2009; Potapova, English, 2011). Notably, Krammer and Lange-Bertalot (1991) believe that A. muzzanensis differs from A. granulata by a lower mantle height to valve diameter ratio (h/d) and a greater number of areolae in a row on the valve mantle. However, one more combination, A. granulata var. australiensis (Grunow) Moro was described based on the difference from the type variety in the valve diameter, position of areolae on the valve face and the number of spines on the separating spines (Moro, 1991).

There are other species similar to A. muzzanensis. One is A. gessneri (Hust.) Simon- sen (Wetzel et al., 2014). Valves of A. muzzanensis have usually slightly spiral dextrorose rows of areolae on the valve mantle, which have never been observed in A. gessneri and clearly separate these species. A species similar to A. muzzanensis, A. brasiliensis Tremarin, T organ et T. Ludwig (Tremarin et al., 2012), has been recently described. It differs from A. muzzanensis by the length of spines, position of areolae on the valve face and mantle, and the position and structure of rimoportulae. Even more recently, A. pseudomuzzanensis Olsyński et Żelazna-Wieczorek was described by Olszyński et Żelazna-Wieczorek (2018). This species differs from A. muzzanensis by the number of areolae in 10 µm on the mantle, position of areolae on the valve face, and structure of rimoportula.

The aim of this study is to investigate the morphological variability in populations of A. granulata and specify the systematic position of A. muzzanensis.

Material and methods

This study used SEM micrographs of valves of A. granulata from Cheboksar (July 1981), Ivankovo (August 1991) and Sestroretsk Razliv reservoirs (August 2016); A. islandica from the Amur River (March 1997) and Lake Khanka (March 1993); A. baicalensis from Middle Baikal (May 1984); A. subarctica from lakes Krasnoe (August 2004) and Kurilskoe (August 1967).

Diatom frustules were treated from organic matter by cold burning (Balonov, 1975) with sulphuric acid and potassium dichromate. Cleaned specimens were dried on stubs, coated with gold using an EIKO–IB–3 sputter coater, and examined using a JSM–25S scanning electron microscope operating at 15 kV.
Results and discussion

In the population from the Cheboksar Reservoir, the range of variability of quantitative morphological characteristics, including mantle height/diameter (h/d) ratio, is similar in separation valves and valves in the filament (Table 1). These features correspond to the published data on *A. granulata* and *A. muzzanensis*, except for the separation valves by the number of areola rows in 10 µm and areolae in 10 µm, and fine-structure valves in the filament of *A. muzzanensis* by the number of areola rows in 10 µm and areolae in 10 µm (Table 2). Unfortunately, no information is available on the number of spines on separation valves. Kiss *et al.* (2012) reported 2–4 long spines for *A. granulata*. In valves from the Cheboksar Reservoir population, we recorded 1 to 7 spines, including long and more short ones (Fig. 1b). There were usually more longer spines, and we found no relationship between their number and the valve diameter (Fig. 1c). In their quantitative morphological characteristics, the valves from the Ivankovo Reservoir and Sestroretsk Razliv (Table 1) also corresponded to published data (Table 2), except for maximum values of valve diameter in the population from the highly eutrophic Sestroretsk Razliv (37.1 µm).

![Fig. 1. (a) Aulacoseira granulata, relationship between the valve diameter (axis X, µm) and mantle height to valve diameter ratio (axis Y); ●: separation valves, ×: valves in the colony, ▲: valves from Lago di Muzzeno (Krammer, 1991). (b) A. granulata, relationship between valve diameter (axis X, µm) and long and more short spines (axis Y). (c) A. granulata, relationship between valve diameter (axis X, µm) and long spines (axis Y).](image-url)
### Table 1

The variability of morphological features of *Aulacoseira granulata*

| Valve diameter, µm | Valve height, µm | Mantle height to valve diameter ratio | Number of areolae rows in 10 µm | Number of areolae in 10 µm | Waterbody                      |
|-------------------|-----------------|--------------------------------------|-------------------------------|----------------------------|--------------------------------|
| 6.7–26.7          | 7.1–21.1        | 0.33–2.48                            | 6–11                          | 4–12                       | Cheboksar Reservoir (separation valves) |
| 6.7–24.4          | 10.0–21.1       | 0.41–3.14                            | 6–10                          | 5–11                       | Cheboksar Reservoir (valves in the colony) |
| 6.8–25.0          | 12.8–25.7       | 0.56–2.94                            | 8–12                          | 6–12                       | Ivankovo Reservoir               |
| 14.4–37.1         | 10.0–18.9       | 0.30–0.92                            | 6–8                           | 5–10                       | Sestroretsk Razliv Reservoir     |

### Table 2

The variability of morphological features of *Aulacoseira granulata* and *A. muzzanensis* according to published data

| Valve diameter, µm | Valve height, µm | Mantle height to valve diameter ratio | Number of areolae rows in 10 µm | Number of areolae in 10 µm | References                  |
|-------------------|-----------------|--------------------------------------|-------------------------------|----------------------------|-----------------------------|
| **Aulacoseira granulata** | | | | | |
| 5–21              | 5–18            |                                      | 8–15                          | 8–12                       | Zabelina *et al.*, 1951 (as *Melosira granulata*) |
| 5–21              | 5–22            |                                      | 8–15                          | 6–14                       | Skabichevsky, 1960 (as *Melosira granulata*) |
| 2–21              |                 |                                      | 8–15                          | 8–12                       | Davydova, Moiseeva, 1992     |
| 4–30              | 5–24            | > 0.8                                | 7–15                          | 5–12                       | Krammer, Lange-Bertalot, 1991 |
| 3.5–19.5          | 11–20           |                                      | 8–12                          | 9–16                       | Genkal, 1992                 |
| 10–21             | 12.8–24         |                                      | 7–8                           | 6–8                        | Genkal, Yeshko, 1998         |
| 3–30              | 4–24            |                                      | 7–15                          |                            | Houk, 2003                   |
| 7–20              | 7.7–13.3        |                                      | 10–14                         | 7–14                       | Genkal, Mikheyeva, 2006      |
| 3.6–27.7          | 12–16.8         | 0.3–5.4*                             | 8–20                          | 8–15                       | Genkal, Trifonova, 2006       |
| 4.3–18.8          | 10.0–26.6       |                                      | 9–15                          | 8–18                       | Maystrova *et al.*, 2007      |
| 10.0–24.4         | 13–21           | 0.4–3.2*                             | 9–12                          | 10–12                      | Genkal, Golokolenova, 2008    |
| 3.9–20.7          | 3.6–21.6        | 0.2–4.3*                             | 8–15                          | 9–16                       | Genkal, Gorokhova, 2008       |
| 6.4–12.1          | 13.3–17.9       |                                      | 8–16                          | 5–14                       | Genkal, Kulikovskiy, 2008     |
| 2.7–27.0          | 7.8–24          | 0.5–5.3*                             | 6–15                          | 5–14                       | Genkal, Trifonova, 2008       |
| 6.6–14.4          | 16.6–23.5       |                                      | 8–10                          | 8–10                       | Popovskaya, Genkal, 2008      |
| Length | Width | Slope | Reference |
|--------|-------|-------|-----------|
| 3.0–11.5 | 10–17 | | Manoylov et al., 2009 |
| 5.7–22.8 | 20.0–26.6 | 0.8–3.7* | Genkal, Okhapkin, 2010 |
| 7.8–14.3 | 10.7–21.0 | 7–9 | Genkal, Bondarenko, 2011 |
| 7.8–14.3 | 10.7–21.0 | 7–9 | Genkal et al., 2011a |
| 7.1–17 | 9.3–22.8 | 7–11 | Genkal, Trifonova, 2011 |
| 7.5–17.7 | 12–18 | 8–12 | Popovskaya et al., 2011 |
| 7.8–20.0 | 20–24.4 | 7–8 | Genkal et al., 2011b |
| 5–23.3 | 10–21 | 10 | Genkal, Romanov, 2012 |
| 3–30 | 4–24 | 7–15 | Kiss et al., 2012 |
| 6.2–8.4 | 12.6–13.4 | 13–14 | Bazhenova et al., 2013 |
| 5–20 | 7.8–17.8 | 8–9 | Genkal, Okhapkin, 2013 |
| 6.6–18.8 | 13.3–20 | 8–12 | Genkal et al., 2013a |
| 6.4–15.5 | 14.3–22.8 | 8–11 | Genkal et al., 2013b |
| 14.3–23.3 | 10–17 | 7–8 | Genkal, Afonina, 2014 |
| 7.1–7.8 | 17.8–25.5 | 8–10 | Genkal, Lepskaya, 2013 |
| 4.3–6.0 | 11.3–16 | 7–9 | Ector et al., 2015 |
| 5–17 | 14.4–20 | 9–12 | Genkal, Okhapkin, 2016 |
| 4.3–27.8 | 11.7–25.5 | 6–10 | Genkal et al., 2015 |
| 8.3–16.7 | 13.3–18.9 | 8–9 | Genkal, Bilous, 2015 |
| 6.0–8.9 | 10–15.5 | 9–13 | Genkal, Yarmoshenko, 2013 |
| 2–30 | 5–24 | 8–15 | Kulikovskiy et al., 2016 |
| 5.7–20.0 | 12–19.1 | 7–13 | Chudaev, Gololobova, 2016 |

**Aulacoseira muzzanensis**

| Length | Width | Slope | Reference |
|--------|-------|-------|-----------|
| 12–14 | 6–8 | 11–13 | Meister, 1912 |
| 12–25 | 4–8 | 12 | 20 | Zabelina et al., 1951(as Melosira granulata var. muzzanensis) |
| 8–25 | 4–8 | 0.3–0.6 | separation valves 13–15; thin structure valves in the colony 11–13, coarse structured valves 7–10 | Krammer, Lange-Bertalot, 1991 |
| 8–25 | 4–8 | 0.3–0.6 | separation valves 12–13 and 17–21; thin structure valves in the colony 20, coarse structured valves 8–10 | |
A certain relationship was observed in all *A. granulata* populations (Fig. 1a, 2a) — with increasing valve diameter, the mantle height to valve diameter ratio decreases and the h/d ratio typical for *A. muzzanensis* (0.3–0.8), is found in large-diameter valves (Fig. 1a, 2a). Such correlation occurs in other representatives of the genus *Aulacoseira* (Fig. 2b, 3a, b). Skabichevsky (1960) also noted that *A. granulata* narrow cells have longer valves and its cells with a larger diameter are shorter.

According to the diagnosis of Krammer and Lange-Bertalot (1991) *A. muzzanensis* is characterized by shorter valves, a lower h/d ratio and a larger number of areolae in 10 µm than *A. granulata* (Table 2). According to the published data the first two
characteristics correspond with \textit{A. granulata} (Table 2), but the valve diameter and the height of its mantle significantly vary in a manner that may be due to seasonal, long-term or interpopulational variability (Genkal, 1990, 2007; Kiss \textit{et al.}, 2013; Genkal, Chekryzheva, 2016). In \textit{A. granulata} the ratio of the mantle height to valve diameter is more than 0.8, and in \textit{A. muzzanensis} it is 0.3–0.6 (Table 2). Measurement and calculation of this characteristic in the other populations of \textit{A. granulata} has shown similar results (Table 1). Measurements from published micrographs (Florin, 1970: Fig. 21–23) show that the mantle height to valve diameter ratio in \textit{A. granulata} varies from 0.19 to 0.24. Krammer, Lange-Bertalot (1991: Taf. 20, Fig. 1) present a micrograph of \textit{A. muzzanensis} with a ratio of mantle height to valve diameter of about 0.8. Noteworthy that measurements of \textit{A. muzzanensis} from micrographs (Krammer, 1991: Fig. 3, 4, 6, 8, 10, 10a, 11, 11a, 12, 13, 16) have shown that in this species population from the type locality the h/d ratio varies quite a bit — from 0.3 to 1.06 — and this ratio depends on the valve diameter as in other representatives of the genus (Fig. 1a, 2, 3).

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{fig3}
\caption{(a) \textit{Aulacoseira baicalensis}, relationship between valve diameter (axis X, \(\mu\)m) and mantle height to valve diameter ratio (axis Y), \(\bullet\): Middle Baikal, \(\times\): Krasnoe Lake. (b) \textit{A. subarctica}, relationship between valve diameter (axis X, \(\mu\)m) and mantle height to valve diameter ratio (axis Y), \(\bullet\): Kurilskoe Lake, \(\times\): Krasnoe Lake.}
\end{figure}

In \textit{A. muzzanensis} separation valves and those in filaments can have the same number areolae in 10 \(\mu\)m as in \textit{A. granulata}, as well as much more (16–21) (Table 2). However, according to the literature, such numbers of areolae were found in \textit{A. granulata} too: Genkal (1992) and Genkal and Gorokhova (2008) reported 16 and Maystrova \textit{et al.} (2007) reported 18. In illustrations of \textit{A. granulata} (Florin, 1970: Fig. 21–23) the number of areolae in 10 \(\mu\)m ranges from 14 to 20. Measurements from micrographs indicate that the number of areolae in 10 \(\mu\)m on separation valves of \textit{A. muzzanensis}
can differ even on one valve of the colony (14 and 18: Krammer, 1991: Fig. 11a), which indicates a wider range of variability of this characteristic coinciding with that of A. muzzanensis. Skabichevskiy (1960) also noted variations in the number of rows and areolae on the valve mantle and attributed it to cell age — old frustules have 11.2 rows of pores in 10 µm and 6.7 pores in a row and young ones have 13.2 rows and 13.3 pores.

In our opinion the results of our investigations and data from the literature confirm the correctness of referring Melosira granulata var. muzzanensis to the synonym of Aulacoseira granulata and make it possible to refine the diagnosis of the latter.

Aulacoseira granulata (Ehrenb.) Simonsen, 1979, Bacillaria, 2: 58, emend. Genkal (Plate I)

≡ Gallionella granulata Ehrenb., 1843, Abh. Königl. Akad. Wiss. Berlin, 1841: 415. ≡ Melosira granulata (Ehrenb.) Ralfs in Pritchard, 1861, A History of Infusoria, including the Desmidiaceae and Diatomaceae, British and Foreign, 4th ed.: 820.
≡ M. granulata var. angustissima (Ehrenb.) O. F. Müll., 1899, Hedwigia, 38(6): 315, pl. 12, fig. 28.
≡ M. muzzanensis F. Meist., 1912, Beitr. Kryptogamenfl. Schweiz 4(1): 41, 232, pl. 1, fig. 10. ≡ M. granulata var. muzzanensis (F. Meist.) Hust., 1930, Die Süßwasser-Flora Mitteleuropas, Heft 10: 88, fig. 7. ≡ Aulacoseira muzzanensis (F. Meist.) Krammer, 1991, Nova Hedwigia, 52(1–2): 98.
≡ A. granulata var. australiensis (Grunow) Moro, 1991, Arq. Biol. Technol. 34(2): 355.

Frustule from low to high, cylindrical with several bands. Valves straight or bent along central axis, round, flat, 2.0–37.1 µm in diameter. Valve face areolae arranged randomly, sometimes only along margin, or are structureless. Mantle with longitudinal straight or inclined areola rows 6–20, and transverse undulate rows (4–20 in 10 µm). Circular groove shallow, narrow, ringleist not wide. Linking spins along margin small, bifurcated, teardrop-shaped, branching, elongated and pointed; separation valves with long coarse spines of different lengths (1–7), overlying similarly shaped structureless parts (grooves) of adjacent valve mantle. Auxospores spherical.

Aulacoseira granulata var. australiensis has a range of variability of quantitative features (valve diameter 18–31 µm, height 11–17 µm, 8–16 striae in 10 µm, 8–16 areolae in 10 µm) coinciding with those of A. granulata var. granulata (Table 2). According to the diagnosis, areolae on the valve face of A. granulata var. australiensis are located over the entire surface; however, they are absent in the type variety in the author’s opinion (Moro, 1991). This statement is untrue, and areolae in A. granulata var. granulata are distributed over the entire surface (Krammer, Lange-Bertalot, 1991: Taf. 17, Fig. 7–10; Houk, 2003: Tab. XXV, Fig. 14, 15). One of the features that differentiates A. granulata var. australiensis from the type species is a smaller number of spines in the latter (2–3) compared to A. granulata var. australiensis (3–4). However, according to our data, their number may vary from 1 to 7 (Fig. 1b). In our opinion, in view of the above, A. granulata var. australiensis belongs to the group A. granulata var. granulata.
Plate I. *Aulacoseira granulata*, SEM (Ivan’kovo Reservoir, 16 VII 1981, sample 817, IBIW).  
1–10 — external view, the separation valves, variations in the number of spines and their length;  
11 — valves in the colony. Scale bars: 1, 2, 4, 6–8 — 5 µm; 6, 8, 12–14 — 10 µm.
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References

*Algae of Ukraine: Diversity, Nomenclature, Taxonomy, Ecology and Geography*. Vol. 2. *Bacillariophyta*. 2009. Ruggell: 413 p.

Balonov I. M. 1975. Preparation of algae for electron microscopy. *Metodika izucheniya boigeotsenozov* [Methods for the study of biocenoses]. Moscow: 87–89. (In Russ.).

Bazhenova O. P., Genkal S. I., Shakhval V. E., Bragina E. A. 2013. Centric diatom algae (Centrrophyceae) of the Bukhtarma reservoir (the Irtys River, Kazakhstan). *Algologia* 23(3): 308–317. (In Russ.). https://doi.org/10.15407/alg23.03.308

Chudaev D. A., Gololobova M. A. 2016. *Diatomovye vodorosli ozera Glubokogo (Moskovskaya oblast)* [Diatom algae in Glubokoe Lake (Moscow Region)]. Moscow: 447 p. (In Russ.).

Bethge H. 1925. *Melosira* und ihre Planktonbegleiter. *Pflanzenforschung* 3: 1–82.

Davydova N. N., Moiseeva A. I. 1992. Genera: *Aulacosira* Thw. *Diatomovye vodorosli SSSR (iskopae-my i sovremenny)* [The diatoms of the USSR (fossil and recent)]. Vol. II. Fasc. 2. St. Petersburg: 76–85. (In Russ.).

Ermolaeva L. M. 1967. Phytobenthos in Ponds of Bolshechehensk District. *Proceedings of Omsk Medical Institute* 77: 42–46. (In Russ.).

Florin M.-B. 1970. The fine structure of some pelagic fresh water diatom species under the scanning electron microscope. I. *Svensk Botanisk Tidskrift* 64: 51–64.

Genkal S. I. 1990. Morphology of centric diatoms: aspects of seasonal variability in the frustules. *Flora i produktivnost pelagicheskikh i litiralnykh phitotsenozov vodoemov basseina Volgi* [Flora and productivity of pelagic and littoral phytocoenoses of the Volga basin reservoir]. Leningrad: 237–253. (In Russ.).

Genkal S. I. 1992. *Atlas diatomovukh vodorosley planktona reki Volgi* [Atlas of the diatom algae of the plankton in the Volga River]. St. Petersburg: 128 p. (In Russ.).

Genkal S. I. 2007. Morphology, taxonomy, ecology and distribution of small-sized species of the genus *Stephanodiscus* (Bacillariophyta). 2. *Stephanodiscus makarovae*. *Botanicheskii zhurnal* 92(2): 241–248. (In Russ.).

Genkal S. I., Afonina E. A. 2014. Additions to the flora of centric diatom algae of the Velikaya River (Pskov Region). *Botanicheski Zhurnal* 99(11): 1238–1242. (In Russ.). https://doi.org/10.1134/S1234567814110032

Genkal S. I., Bilous O. P. 2015. Centric diatoms (Centrrophyceae) of the Lower Portion of the Southern Bug River (Ukraine). *International Journal on Algae* 17(4): 339–350. https://doi.org/10.1615/InterJAlgae.v17.i4.20

Genkal S. I., Bondarenko N. A. 2011. Diatom algae in mountain lakes of the Dzherginskiy Reserve (the Baikal area). 1. Centrrophyceae. *Povolzhskiy Ecologicheskiy Zhurnal* 2: 127–136. (In Russ.).

Genkal S. I., Bondarenko N. A., Shur L. A. 2011a. *Diatomovye vodorosli ozera yuga i severa Vostochnoy Sibiri* [Diatoms of lakes from south and north parts of Eastern Siberia]. Rybinsk: 72 p. (In Russ.).

Genkal S. I., Chekryzheva T. A. 2016. On morphology, taxonomy, ecology and distribution of *Cyclorella rossii* Håkansson (Bacillariophyta). *Nova Hedwigia* 102(3–4): 399–421. https://doi.org/10.1127/nova_hedwigia/2015/0316

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Genkal S. I., Chekryzheva T. A., Komulainen S. F. 2015. *Diatomovye vodorosli planktona Ladozhskogo oзera i vodoemov ego basseyna* [Diatom algae in waterbodies and watercourses of Karelia]. Moscow: 202 p. (In Russ.).

Genkal S. I., Golokolenova T. B. 2008. Centric diatom algae of the Tsimlyansk reservoir. *Povolzhskiy Ekologicheskii Zhurnal* 3: 178–189. (In Russ.).

Genkal S. I., Kulikovskiy M. S. 2008. Centrophyceae (Bacillariophyta) from Polistovo-Lovatsky sollognous tract (Rdeisky State Nature Reserve). *Botanicheskii zhurnal* 93(5): 1200–1209. (In Russ.).

Genkal S. I., Kulikovskiy M. S., Kuznetsova I. V. 2013a. New data to Centrophyceae (Bacillariophyta) of Lake Baikal, Russia. *Algologia* 23(1): 3–9. (In Russ.). https://doi.org/10.15407/alg23.01.003

Genkal S. I., Kulikovskiy M. S., Mikheeva T. M., Kuznetsova I. V., Luk’yanova E. V. 2013b. *Diatomovye vodorosli planktona reki Svisloch i ee vodokhranilishch* [Diatoms in plankton of the Svisloch River and its reservoirs]. Moscow: 236 p. (In Russ.).

Genkal S. I., Lepskaya E. V. 2013. Materials to the flora of centric diatom algae in Lake Nerpichye (the Kamchatka River Estuary). *Investigations of Aquatic Biological Resources of Kamchatka and the Northwest Pacific Ocean* 31: 62–73. (In Russ.).

Genkal S. I., Kulikovskiy M. S., Kuznetsova I. V. 2011b. New data on the flora of diatom algae (Centrophyceae) in waterbodies of Sakhalin Island. *Inland Water Biology* 4: 408–418. https://doi.org/10.1134/S1995082911030084

Genkal S. I., Okhapkin A. G. 2010. Diatoms (Centrophyceae) in the Kama reservoir phytoplankton. *Povolzhskiy Ekologicheskii Zhurnal* 3: 254–262. (In Russ.).

Genkal S. I., Okhapkin A. G. 2013. Centric Diatoms (Centrophyceae) in the lower reaches of the Oka River (Russian Federation). *Hydrobiological Journal* 49(3): 41–57. https://doi.org/10.1615/HydrobJ.v49.i3.40

Genkal S. I., Okhapkin A. G. 2016. Plankton Centrophyceae (Bacillariophyta) of the Klyaz’ma River (Russian Federation). *Hydrobiological Journal* 52(2): 35–48. https://doi.org/10.1615/HydrobJ.v52.12.40

Genkal S. I., Romanov R. E. 2012. Centric diatom (Centrophyceae, Bacillariophyta) in waters in the Lake Kraseo in conditions of climatic fluctuations and eutrophication. *Contemporary Problems of Ecology* 5(4): 399–412. https://doi.org/10.1134/S199542551204004X

Genkal S. I., Trifonova I. S. 2006. Materials on the flora of Bacillariophyta of the Narva river and Narva reservoir (North-Western Russia). 1. Centrophyceae. *Algologia* 91(5): 693–697. (In Russ.).

Genkal S. I., Trifonova I. S. 2008. Electron-microscopy study of centric diatoms in phytoplankton of the Lake Kraseo. *Mnogoletnie izmeneniya biologicheskikh soobshchestv mezotrofnogo ozera v usloviyakh klimaticeskikh fluktatsii i eutrofirovaniya* [Long-term changes of biological communities in mesotrophic lake in conditions of climatic fluctuations and eutrophication]. St. Petersburg: 35–41. (In Russ.).

Genkal S. I., Trifonova I. S. 2011. Centric diatoms (Centrophyceae, Bacillariophyta) in plankton of the Neva Bay of the Gulf of Finland. *Algologia* 21(1): 106–110. (In Russ.).

Genkal S. I., Yarmoshenko L. P. 2013. Centric diatoms (Bacillariophyta) of the cooling pond of the Khmelnitskiy nuclear power station (Ukraine). *Hydrobiological Journal* 49(1): 51–63. https://doi.org/10.1615/HydrobJ.v49.i1.60

Genkal S. I., Yeshko T. A. 1998. Materials to flora of Bacillariophyta of the water bodies of Karelia (Russia). *Konchezero Lake I. Centrophyceae. Algologia* 8(1): 11–13. (In Russ.).
Genkal, Trifonova. Morphology and taxonomy of Aulacoseira muzzanensis

Houk V. 2003. Atlas of Freshwater Centric Diatoms with a Brief Key and Descriptions. Part I. Melosiraaceae, Orthoseiraceae, Paraliaceae and Aulacoseiraceae. Czech Phycology Supplement, Volume 1. Olomouc: 27 p.

Hustedt F. 1930. Bacillariophyta (Diatomeae) Zweite Auflage. Die Süßwasser-Flora Mitteleuropas. Heft 10. Jena: 466 p.

Kiss K. T., Genkal S. I., Ector L., Molnar L., Duleba M., Biro P. 2013. Morphology, taxonomy and distribution of Stephanodiscus triporus (Bacillariophyceae) and related taxa. European Journal of Phycology 48(4): 363–379. https://doi.org/10.1080/09670262.2013.843204

Kiss K. T., Klee R., Ector L., Ács É. 2012. Centric diatoms of large rivers and tributaries in Hungary: morphology and biogeographic distribution. Acta Botanica Croatica 71(2): 311–363. https://doi.org/10.2478/v10184-011-0067-0

Krammer K. 1991. Morphology and taxonomy in some taxa of the genus Aulacoseira Thwaites (Bacillariophyceae) II. Taxa in the A. granulata-, italic- and lirata-groups. Nova Hedwigia 53: 477–496.

Krammer K., Lange-Bertalot H. 1991. Bacillariophyceae 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. Süßwasserflora von Mitteleuropa. Bd 2/3. Stuttgart, Jena: 576 S.

Kulikovskiy M. S., Glushchenko A. M., Genkal S. I., Kuznetsova I. V. 2016. Opredelitel diatomovykh vodorosley Rossii [Identification book of Diatoms from Russia]. Yaroslavl: 804 c. (In Russ.).

Kuzmin G. V., Elizarova V. A. 1967. Phytoplankton in the Sheksna Reach of The Rybinsk Reservoir in 1963-1965. Proceedings of the Institute for Biology of Inland Waters 15: 104–133. (In Russ.).

Manoylov K. M., Ognjanova-Rumenova N., Stevenson R. J. 2009. Morphotype variations in subfossil diatom species of Aulacoseira in 24 Michigan Lakes, USA. Acta Botanica Croatica 68(2): 401–419.

Maystrova N. V., Genkal S. I., Scherbak V. I., Semenyak N. Ye. 2007. Centrophyceae in the upper section of the Kanev water reservour (Ukraine). Algologia 17(4): 467–475. (In Russ.).

Meister F. 1912. Die Kieselalgen der Schweiz. Beitr. zur Kryptogamenflora der Schweiz 4/1. Bern: 1–254.

Moro R. S. 1991. Morphology of Aulacoseira granulata (Ehrenberg) var. australiensis (Grunow) nov. comb. unser light microscopy. Arquivos de Biologia e Tecnologia 34(2): 353–359.

Olszynski R. M., Zelazna-Wieczorek J. 2018. Aulacoseira pseudomuzzanensis sp. nov. and other centric diatoms from post iron ore mining reservoirs in Poland. Diatom Research 33(2): 155–185. https://doi.org/10.1080/0269249X.2018.1509886

Popovskaya G. I., Genkal S. I. 2008. Materials to the flora of diatom algae (Centrophyceae) from lakes of the Baikal Region and Transbaikalia. Inland Waters Biology 1: 311–319. (In Russ.). https://doi.org/10.1134/S1995082908040019

Popovskaya G. I., Genkal S. I., Likhoshway Ye. V. 2015. Diatoms of the plankton of Lake Baikal: Atlas and Key. Second Edition, Revised and Expanded. Novosibirsk: 180 p.

Potapova M., English J. 2011. Aulacoseira muzzanensis. Diatoms of North America. The source for diatom identification and ecology. https://diatoms.org/species/aulacoseira_muzzanensis (Date of access: 20 IX 2019).

Skabichevsky A. P. 1960. Planktonnye diatomeye vodorosli presnykh vol SSSR. Sistematika, ekologiya i rasprostranenie [Planktonic diatom algae of the USSR freshwaters. Systematics, ecology and distribution]. Moscow: 350 p. (In Russ.).

Tremarin P. I., Veiga Ludwig. T. A., Torgan, L. C. 2012. Ultrastructure of Aulacoseira brasiliensis sp. nov. (Coscinodiscophyceae) and comparison with related species. Fottea 12(2): 171–188. https://doi.org/10.5507/fot.2012.013

Wetzel C. E., Ector L., Bicudo D. C. 2014. Type analysis of Aulacoseira gessneri (Hustedt) Simonsen (Bacillariophyceae) from South America. Nova Hedwigia, Beiheft 143: 381–390.
Algae of Ukraine: Diversity, Nomenclature, Taxonomy, Ecology and Geography. Vol. 2. Bacillariophyta. 2009. Ruggel: 413 p.

[Balonov] Балонов И.М. 1975. Подготовка водорослей к электронной микроскопии. Методика изучения биоциенозов внутренних водоемов. М.: 87–89.

[Bazhenova et al.] Баженова О. П., Генкал С. И., Шаховал В. Е., Брагина Е. А. 2013. Центрические диатомовые водоросли (Centrophyceae) Бухтарминского водохранилища (р. Иртыш, Казахстан). Альгология 23(3): 308–317. https://doi.org/10.15407/alg23.03.308

Bethge H. 1925. Melosira und ihre Planktonbegleiter. Pflanzenforschung 3: 1–82.

[Chudaev, Gololobova] Чудаев Д. А., Гололобова М. А. 2016. Диатомовые водоросли озера Глубокое (Московская область). М.: 447 с.

[Davydova, Moiseeva] Давыдова Н. Н., Моисеева А. И. 1992. Роды: Aulacosira Thw. Диатомовые водоросли СССР (ископаемые и современные). Т. II. Вып. 2. СПб.: 76–85.

[Ernolova] Эрнолева Л.М. 1967. Фитобентос прудов Большереченского района. Вопросы гигиены: труды Омского медицинского института 77: 42–46.

Florin M.-B. 1970. The fine structure of some pelagic fresh water diatom species under the scanning electron microscope. I. Scensk Botanisk Tidsskrift. 64: 51–64.

[Genkal] Генкал С. И. 1990. Морфология панциря центрических диатомей: аспекты сезонной изменчивости. Флора и продуктивность пелагических и литоральных фитоценозов водоемов бассейна Волги. Л.: 237–253.

[Genkal] Генкал С. И. 1992. Amphac диатомовых водорослей планктона реки Волги. СПб.: 128 с.

[Genkal] Генкал С. И. 2007. Морфология, таксономия, экология и распространение мелкоразмерных видов Stephanodiscus (Bacillariophyta). 2. Stephanodiscus makinovae. Ботанический журнал 92(2): 241–248.

[Genkal, Afonina] Генкал С. И., Афонина Е. А. 2014. Дополнение к флоре центрических диатомовых водорослей (Centrophyceae) реки Великая (Псковская область). Ботанический журнал 99(11): 1238–1242. https://doi.org/10.1134/S1234567814110032

Genkal S. I., Bilous O. R. 2015. Centric diatoms (Centrophyceae) of the Lower Portion of the Southern Bug River (Ukraine). International Journal on Algae 17(4): 339–350. https://doi.org/10.1615/IntAlgae.v17.i4.20

[Genkal, Bondarenko] Генкал С. И., Бондаренко Н. А. 2011. Диатомовые водоросли горных озер Дзержинского заповедника (Прибайкалье) 1. Centrophyceae. Поволжский экологический журнал 2: 127–136.

[Genkal et al.] Генкал С. И., Бондаренко Н. А., Щур Л. А. 2011а. Диатомовые водоросли озер юга и севера Восточной Сибири. Рыбинск: 72 с.

Genkal S. I., Chekhryzheva T. A. 2016. On morphology, taxonomy, ecology and distribution of Cyclotella rossii Håkansson (Bacillariophyta). Nova Hedwigia 102(3–4): 399–421. https://doi.org/10.1127/nova_hedwigia/2015/0316

[Genkal et al.] Генкал С. И., Черкышева Т. А., Комулайнен С. Ф. 2015. Диатомовые водоросли водоемов и водотоков Карелии. М.: 202 с.

[Genkal, Golokolenova] Генкал С. И., Голокolenова Т. Б. 2008. Центрические диатомовые водоросли Цимлянского водохранилища. Поволжский экологический журнал 3: 178–189.

[Genkal, Gorokhova] Генкал С. И., Горокова О. Г. 2008. Материалы к флоре диатомовых водорослей (Centrophyceae) в водоемах Самарской Луки. Известия Самарского научного центра Российской академии наук 10(5/1): 206–216.
Генкал С. И., Куликовский М. С. 2008. Центрические диатомовые (Bacillariophyta) Полистово-Ловатского сфагнового массива (Государственный природный заповедник «Редьский»). Ботанический журнал 93(8): 1200–1209.

Генкал С. И., Куликовский М. С., Кузнецова И. В. 2013а. Материалы к флоре Centrophyceae (Bacillariophyta) озера Байкал (Россия). Альгология 23(1): 3–9. https://doi.org/10.15407/alg23.01.003

Генкал С. И., Куликовский М. С., Михеева Т. М., Кузнецова И. В., Лукьянова Е. В. 2013б. Диатомовые водоросли планктона реки Свислочь и ее водохранилищ. М.: 236 с.

Генкал С. И., Куликовский М. С., Михеева Т. М., Кузнецова И. В., Лукьянова Е. В. 2013а. Материалы к флоре центрических диатомовых водорослей оз. Нерпичье (эстуарий р.Камчатка). Исследования водных биологических ресурсов Камчатки и северо-западной части Тихого океана 31: 62–73.

Генкал С. И., Михеева Т. М. 2006. Материалы к флоре диатомовых водорослей (Centrophyceae, Bacillariophyta) реки Неман и ее притоков. Ботанический журнал 91(3): 420–424.

Генкал С. И., Мотылкова И. В., Коновалова Н. В. 2011б. New data on the flora of diatom algae (Centrophyceae) in waterbodies of Sakhalin Island. Inland Water Biology 4: 408–418. https://doi.org/10.1134/S1995082911030084

Генкал С. И., Охапкин А. Г. 2010. Диатомовые водоросли (Centrophyceae) в фитопланктоне Камских водохранилищ. Поволжский экологический журнал 3: 254–262.

Генкал С. И., Охапкин А. Г. 2013. Centric Diatoms (Centrophyceae) in the lower reaches of the Oka River (Russian Federation). Hydrobiological Journal 49(3): 41–57. https://doi.org/10.1615/HydrobJ.v49.i3.40

Генкал С. И., Охапкин А. Г. 2016. Plankton Centrophyceae (Bacillariophyta) of the Klyaz'ma River (Russian Federation). Hydrobiological Journal 52(2): 35–48. https://doi.org/10.1615/HydrobJ.v52.i2.40

Генкал С. И., романов Р. Е. 2012. Centric diatom (Centrophyceae, Bacillariophyta) in watercourses and Boilies of water in Southeast of West Siberian Plain and Polar Ural. Contemporary Problems of Ecology 5(4): 399–412. https://doi.org/10.1134/S199542551204004X

Генкал С. И., Трифонова И. С. 2006. Материалы к флоре Bacillariophyta реки Нарва и Нарвского водохранилища (Северо-Запад России). I. Centrophyceae. Ботанический журнал 91(5): 693–697.

Генкал С. И., Трифонова И. С. 2008. Электронно-микроскопическое исследование центрических диатомей планкtonа оз. Красного. Микологические исследования в условиях климатических флуктуаций и эвтрофирования. СПб.: 35–41.

Генкал С. И., Трифонова И. С. 2011. Центрические диатомовые водоросли (Centrophyceae, Bacillariophyta) планктона Невской губы Финского залива. Альгология 21(1): 106–110.

Генкал С. И., Ярмощенко Л. Р. 2013. Centric diatoms (Bacillariophyta) of the cooling pond of the Khmelnitskiy nuclear power station (Ukraine). Hydrobiological Journal 49(1): 51–63. https://doi.org/10.1615/HydrobJ.v49.i1.60

Генкал С. И., Иешко Т. А. 1998. Материалы к флоре Bacillariophyta водоемов Карелии. Кончезеро. I. Centrophyceae. Альгология 8(1): 11–13.

Houk V. 2003. Atlas of Freshwater Centric Diatoms with a Brief Key and Descriptions. Part I. Melosira ceae, Orthoseira ceae, Paralia ceae and Aulacoceira ceae. Czech Phycology Supplement, Volume 1. Olomouc: 27 p.

Hustedt F. 1930. Bacillariophyta (Diatomeae) Zweite Auflage. Die Süßwasser-Flora Mitteleuropas. Heft 10. Jena: 466 p.

368
Kiss K. T., Genkal S. I., Ector L., Molnar L., Duleba M., Biro P. 2013. Morphology, taxonomy and distribution of *Stephanodiscus triporus* (Bacillariophyceae) and related taxa. *European Journal of Phycology* 48(4): 363–379. https://doi.org/10.1080/09670262.2013.843204

Kiss K. T., Klee R., Ector L., Ács É. 2012. Centric diatoms of large rivers and tributaries in Hungary: morphology and biogeographic distribution. *Acta Botanica Croatica* 71(2): 311–363. https://doi.org/10.2478/v10184-011-0067-0

Krammer K. 1991. Morphology and taxonomy in some taxa of the genus *Aulacoseira* Thwaites (Bacillariophyceae) II. Taxa in the *A. granulata-, italica- and lirata*-groups. *Nova Hedwigia* 53: 477–496.

Krammer K., Lange-Bertalot H. 1991. *Bacillariophyceae 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. Süßwasserflora von Mitteleuropa*. Bd 2/3. Stuttgart, Jena: 576 S.

Kulikovskiy et al. Куликовский М. С., Глущенко А. М., Генкал С. И., Кузнецова И. В. 2016. Определитель диатомовых водорослей России. Ярославль: 804 с.

Kuzmin, Elizarova Кузьмин Г. В., Елизарова В. А.1967. Фитопланктон Шекснинского плеса Рыбинского водохранилища в 1963-1965 гг. ИАиИ института биологии внутренних вод 15: 104–133.

Manoylov K. M., Ognjanova-Rumenova N., Stevenson R. J. 2009. Morphotype variations in subfossil diatom species of *Aulacoseira* in 24 Michigan Lakes, USA. *Acta Botanica Croatica* 68(2): 401–419.

Maystrova et al. Майстрова Н. В., Генкал С. И., Щербак В. И., Семенюк Н. Е. 2007. Центrophyceae верхней части Каневского водохранилища (Украина). *Альгология* 17(4): 467–475.

Meister F. 1912. Die Kieselalgen der Schweiz. *Beitr. zur Kryptogamenflora der Schweiz* 4/1. Bern: 1–254.

Moro R. S. 1991. *Morphology of Aulacoseira granulata* (Ehrenberg) var. *australis* (Grunow) nov. comb. unser light microscopy. *Arquivos de Biologia e Tecnologia* 34(2): 353–359.

Olszynski R. M., Zelazna-Wieczorek J. 2018. *Aulacoseira pseudomuzzanensis* sp. nov. and other centric diatoms from post iron ore mining reservoirs in Poland. *Diatom Research* 33(2): 155–185. https://doi.org/10.1080/0269249X.2018.1509886

Popovskaya, Genkal Поповская Г. и., Генкал С. И. 2008. Материалы к флоре диатомовых водорослей (Centrophyceae) озер Прибайкалья и Забайкалья. *Биология внутренних вод* 1: 311–319. https://doi.org/10.1134/S1995082908040019

Popovskaya G. I., Genkal S. I., Likhoshway Ye. V. 2015. *Diatoms of the plankton of Lake Baikal: Atlas and Key. Second Edition, Revised and Expanded*. Novosibirsk: 180 p.

Potapova M., English J. 2011. *Aulacoseira muzzanensis*. Diatoms of North America. The source for diatom identification and ecology. https://diatoms.org/species/aulacoseira_muzzanensis (Дата обращения: 20 IX 2019).

Skabichevsky] Скаччьевичский А. П 1960. Планктонные диатомовые водоросли пресных вод СССР. Систематика, экология и распространение. Москва: 350 с.

Tremarin P. I., Veiga Ludwig. T. A., Torgan, L. C. 2012. Ultrastructure of *Aulacoseira brasiliensis* sp. nov. (Coscinodiscophyceae) and comparison with related species. *Fottea* 12(2): 171–188. https://doi.org/10.5507/fot.2012.013

Wetzel C. E., Ector L., Bicudo D. C. 2014. Type analysis of *Aulacoseira gessneri* (Hustedt) Simonsen (Bacillariophyceae) from South America. *Nova Hedwigia, Beiheft* 143: 381–390.

Zabelina et al.] Забелина М. М., Киселев И. А., Прошкина-Лавренко А. И., Шешукова В. С. 1951. Определитель пресноводных водорослей СССР. Выпуск 4. Диатомовые водоросли. М.: 619 с.