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. baicalensis*, *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.

Морфология 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 высота створки/диаметр створки и такая зависимость наблюдается и у других представителей этого рода: *A. baicalensis*, *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.) Simonson (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.) Simonson (Wetzel *et al.*, 2014). Valves of *A. muzzanensis* have usually slightly spiral dextrorse 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, Torgan 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* Olszyński et Żelana-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); $\bullet$: separation valves, $\times$: valves in the colony, $\blacktriangle$: 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).

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
<i>Aulacoseira granulata</i>					
5–21	5–18		8–15	8–12	Zabelina <i>et al.</i> , 1951 (as <i>Melosira granulata</i>)
5–21	5–22		8–15	6–14	Skabichevsky, 1960 (as <i>Melosira granulata</i>)
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 <i>et al.</i> , 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

Table 2 (continued)

3.0–11.5	10–17		10–15		Manoylov <i>et al.</i> , 2009
5.7–22.8	20.0–26.6	0.8–3.7*	6–12	7–12	Genkal, Okhapkin, 2010
7.8–14.3	10.7–21.0		7–9	7–10	Genkal, Bondarenko, 2011
7.8–14.3	10.7–21.0		7–9	7–10	Genkal <i>et al.</i> , 2011a
7.1–17	9.3–22.8		7–11	7–14	Genkal, Trifonova, 2011
5.5–17.7	12–18		8–12	9–14	Popovskaya <i>et al.</i> , 2011
7.8–20.0	20–24.4		7–8		Genkal <i>et al.</i> , 2011b
5–23.3	10–21		10	6–12	Genkal, Romanov, 2012
3–30	4–24		7–15		Kiss <i>et al.</i> , 2012
6.2–8.4	12.6–13.4		13–14		Bazhenova <i>et al.</i> , 2013
5–20	7.8–17.8		8–9	7–11	Genkal, Okhapkin, 2013
6.6–18.8	13.3–20		8–12	8–12	Genkal <i>et al.</i> , 2013a
6.4–15.5	14.3–22.8		8–11	9–14	Genkal <i>et al.</i> , 2013b
14.3–23.3	10–17		7–8	7	Genkal, Afonina, 2014
7.1–7.8	17.8–25.5		8–10	8–10	Genkal, Lepskaya, 2013
4.3–6.0	11.3–16		7–9		Ector <i>et al.</i> , 2015
5–17	14.4–20		9–12	8–12	Genkal, Okhapkin, 2016
4.3–27.8	11.7–25.5		6–10	5–12	Genkal <i>et al.</i> , 2015
8.3–16.7	13.3–18.9		8–9	9	Genkal, Bilous, 2015
6.0–8.9	10–15.5		9–13	8–10	Genkal, Yarmoshenko, 2013
2–30	5–24		8–15	9–14	Kulikovskiy <i>et al.</i> , 2016
5.7–20.0	12–19.1		7–13	6–14	Chudaev, Gololobova, 2016
<i>Aulacoseira muzzanensis</i>					
12–14	6–8		11–13		Meister, 1912
12–25	4–8		12	20	Zabelina <i>et al.</i> , 1951(as <i>Melosira granulata</i> var. <i>muzzanensis</i>)
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	separation valves 12–13 and 17–21; thin structure valves in the colony 20, coarse structured valves 8–10	Krammer, Lange-Bertalot, 1991

			separation valves 13–15; thin structure valves in the colony 11–13, coarse structured valves 7–10	separation valves 12–13 and 17–21; thin structure valves in the colony 16–20, coarse structured valves 8–10	Krammer, 1991
9–24	5–13		7–15		Potapova, English, 2011

Note. * — based on measurements on negatives from the archive of S. I. Genkal.

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.

Fig. 2. (a) *Aulacoseira granulata*, relationship between valve diameter (axis X, μm) and mantle height to valve diameter ratio (axis Y), $\bullet$: Ivankovo reservoir, $\times$: Sestroretsky Razliv reservoir. (b) *A. islandica*, relationship between valve diameter (axis X, μm) and mantle height to valve diameter ratio (axis Y), $\bullet$: Amur River, $\times$: Khanka Lake.

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 *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 *et al.*, 2013; Genkal, Chekryzheva, 2016). In *A. granulata* the ratio of the mantle height to valve diameter is more than 0.8, and in *A. muzzanensis* it is 0.3–0.6 (Table 2). Measurement and calculation of this characteristic in the other populations of *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 *A. granulata* varies from 0.19 to 0.24. Krammer, Lange-Bertalot (1991: Taf. 20, Fig. 1) present a micrograph of *A. muzzanensis* with a ratio of mantle height to valve diameter of about 0.8. Noteworthy that measurements of *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).

Fig. 3. (a) *Aulacoseira baicalensis*, relationship between valve diameter (axis X, μm) and mantle height to valve diameter ratio (axis Y), $\bullet$: Middle Baikal, $\times$: Krasnoe Lake. (b) *A. subarctica*, relationship between valve diameter (axis X, μm) and mantle height to valve diameter ratio (axis Y), $\bullet$: Kurilskoe Lake, $\times$: Krasnoe Lake.

In *A. muzzanensis* separation valves and those in filaments can have the same number areolae in 10 μm as in *A. granulata*, as well as much more (16–21) (Table 2). However, according to the literature, such numbers of areolae were found in *A. granulata* too: Genkal (1992) and Genkal and Gorokhova (2008) reported 16 and Maystrova *et al.* (2007) reported 18. In illustrations of *A. granulata* (Florin, 1970: Fig. 21–23) the number of areolae in 10 μm ranges from 14 to 20. Measurements from micrographs indicate that the number of areolae in 10 μm on separation valves of *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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