Cryptogamie, Algologie, 2018, 39 (3): 365-388

A putative species flock in the diatom genus *Gomphonema* Ehrenberg (Bacillariophyta: Gomphonemataceae) from Lake Baikal, Russia: description of six new species similar to *G. ventricosum* W. Gregory

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Abstract – We describe as new to science six new species of the diatom genus *Gomphonema* Ehrenberg from Lake Baikal, based on light and scanning electron microscope observations. The six species are morphologically similar to *G. ventricosum*, a northern European taxon known mostly from Scotland, Scandinavia and other Baltic countries, though it has been recognized also from North America. The six species are similar to *G. ventricosum* W. Gregory in the structure of the external occlusions over the areolae. The species also have prominent septa and pseudosepta, which distinguishes them from other species of the genus. They are distinguished from one another in the shapes and sizes of the valves. This group of closely related species may correspond to a species flock, a phenomenon in freshwater diatoms that is known from ancient lakes and flowing water systems. Further research is needed to confirm the monophyly of this group, and either support or challenge the idea of them representing a species flock.

Diatom / *Gomphonema* / new species / Lake Baikal / species flock

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doi/10.7872/crya/v39.iss3.2018.365

INTRODUCTION

Lake Baikal, a large, ancient lake system in Siberia, contains nearly 20% of the liquid freshwater on earth (Kozhov, 1963), has been estimated to be nearly 30 million years old (Mats, 1993) and supports a unique biota (Kozhova & Izmest'eva, 1998; Martens, 1997; Timoshkin, 1997). Since the earliest reports (Gutwinski, 1891) to recent treatments (Kulikovskiy *et al.,* 2011; Kociolek *et al.,* 2013) of the diatoms from Lake Baikal, nearly 1500 taxa have been reported (Kulikovskiy *et al.*, 2011, 2012a,b,c, 2013, 2014a,b, 2015a–e, 2016a,b; Kociolek *et al.*, 2013; Kulikovskiy & Kociolek, 2014; Kulikovskiy & Kuznetsova, 2014, 2016).

Within ancient lake systems, establishment of species flocks for a wide range of vertebrates, invertebrates and algae have been described. The term "species flock" is usually reserved for examples of monophyletic taxa that have invaded a habitat and quickly diversified and occupied numerous niches in that system. The term is usually reserved for examples where the geography is localized, the group is monophyletic and the resulting species from the adaptive radiation numerous. Perhaps the best-known example of this phenomenon is Darwin's finches in the Galapagos Islands (Grant, 1999), and such species flocks have been reported from freshwater rivers (e.g. Sullivan *et al.,* 2002) and ancient lakes. In the latter habitat type species flocks have been described for fishes (Meyer, 1993; Salzburger & Meyer, 2004; Kontula *et al.,* 2003), a wide variety of invertebrates (Martens & Schön, 1999; Schön & Martens, 2012; Martens *et al.,* 2008), and only putative examples exist for diatoms (Mann, 1999; Edlund & Soninkhishig, 2009; Seddon *et al.,* 2011). Application of the concept of "species flocks" to these diatom examples was justified by them meeting the conditions of limited geographic distribution and putative monophyly based on shared, unique morphological characteristics, but they lack an estimate of rate of evolution and the size of the purported "flock" has been relatively small (ca. 4 or so taxa). Kociolek *et al.* (2017) documented a number of examples of species flocks for freshwater diatoms, including gomphonemoid diatoms in Lake Baikal.

As part of our continuing effort to document the diatom gomphonemoid diatoms of Lake Baikal, including the genus *Gomphoneis* Cleve (Kociolek *et al.,* 2013) and *Gomphonema* (Kulikovskiy & Kociolek, 2014; Kulikovskiy *et al.,* 2015a), we have been treating endemics from the lake, including those described by previous workers such as Skvortzow (1937), Skvortzow & Meyer (1928), Skabitchevsky (1985), Kulikovskiy & Kociolek (2015), and newly described taxa (Kulikovskiy & Kociolek 2015).

A species commonly reported from Lake Baikal, and for which endemic subspecific taxa have been described, is *Gomphonema ventricosum* W. Gregory. First reports of this species from Lake Baikal was by Østrup (1908), and it was subsequently reported from the lake by Wislouch (1924), Skvortzow & Meyer (1928), Meyer (1930), Skvortzow (1937), Dawson (1973) Skabitchevsky (1985), Kociolek & Stoermer (1987), and Yoshitake *et al.* (2009). Several authors remarked about the variability in shape of this species in the lake, leading to the description of two subspecific taxa, *G. ventricosum* f. *curtum* Skvortzow & K.I. Meyer 1928 and *G. ventricosum* subsp. *baicalense* Skabichevsky 1985. Skvortzow (1971) proposed a new form found in the Yenisei River in Siberia: *G. ventricosum* f. *subcapitatum*. Other varieties of *G. ventricosum* have been described from Africa (Reichelt, 1904: var. *africana*), USA, Oregon (Cleve, 1894: var. *maxima*), Tasmania (Cleve, 1894: var. *tasmanica*) and Guatemala (Grunow *in* Van Heurck, 1880: var.

ornata). The typical forms of *G. ventricosum* belong to northern countries and for that reason Cleve (1894) wrote that is doubtful whether the varieties should not be considered as distinct species. Kociolek and Stoermer's treatment of *G. ventricosum* included illustrating the holotype of Gregory (1856) as well as reviewing and verifying many species reports from northern latitudes (Kociolek & Stoermer, 1987). They demonstrated the consistent nature of the outline of the valve and the characteristic rounded central area of this species. They concluded that *G. ventricosum*, a northern European taxon known mostly from Scotland, Scandinavia and other Baltic countries, is restricted in its distribution to Eurasia, and that it was unlikely to occur in the continental USA with most reports being species of *Gomphoneis* (Kociolek 2011). In their treatment of specimens from Lake Baikal (Stoermer collection 3910, currently housed at the Diatom Collection of the California Academy of Sciences), Kociolek & Stoermer (1987) illustrated and noted specimens with both similar and dissimilar outlines, but their specimens all show a rectangular to bow-tie-shaped central area. These specimens resemble the specimens reported from the lake by various authors. Dawson (1973) and Kociolek & Stoermer (1993) remarked on the unique nature of the valve ultrastructure of "*G. ventricosum*" from Lake Baikal as opposed to more "typical" as well as other groups within the genus. This includes the complex nature of the areolae, differing from the "C-shaped" areolae of the "typical" species of the genus.

In the present report, we use light and scanning electron microscope observations of populations of *Gomphonema* from Lake Baikal commonly referred to as G. *ventricosum*, to compare with published illustrations of the holotype and describe new species from the lake. We discuss this group of species in the context of other reported species flocks in Lake Baikal.

MATERIAL AND METHODS

Collections were made by M. Kulikovskiy at the southern part of Lake Baikal in 2011. Samples used in this publication were collected from a shallow-water part of Lake Baikal. Samples were collected from stones (Table 1). Water mineralization, pH and temperature measurements were performed using the Hanna Combo (HI 98129) device, Hanna Instruments, Inc., USA.

The samples were treated with 10% hydrochloric acid to remove carbonates and washed several times with deionized water for 12 h. Afterwards, samples were boiled in concentrated hydrogen peroxide (≈ 37%) to dissolve organic matter. They were washed again with deionized water four times at 12 h intervals. After decanting and filling with deionized water up to 100 ml, the suspension was spread onto coverslips and left to dry at room temperature. Permanent diatom preparations were mounted in Naphrax®. Light microscopic (LM) observations were performed with a Zeiss Axio Scope A1 microscope equipped with an oil immersion objective (x100, n.a. 1.4, differential interference contrast [DIC]) and Axio Cam ERc 5s camera (Zeiss). Valve ultrastructure was examined by means of a JSM-6510LV scanning electron microscope (IBIW, Institute for Biology of Inland Waters RAS, Borok, Russia). For scanning electron microscopy (SEM), parts of the suspensions were fixed on aluminum stubs after air-drying. The stubs were sputter coated with 50 nm of Au by means of a Eiko IB 3.

Table 1. Data for samples used in the current study.

Sample and slide number	*Sampling place*	*Coordinates*	*Conductivity, µS/cm*	*Temperature, °C*	*pH*	*Date*
18572	near village Boldakovo	N52º35.694' E107º17.142'	103	17	9.3	16.07.2011
18591	near village Murino	N51º29.244' E104º24.060'	48	17	9	20.07.2011
18571	near village Kultuk	N51º43.460' E103º43.096'	62	21.3	9.3	21.07.2011
18588	near village Boyarsk	N51º80.635' E109º48.351'	104	18	9.1	19.07.2011

All samples and slides are deposited in the collection of Maxim Kulikovskiy at the Herbarium of the Institute for Biology of Inland Waters, Russian Academy of Science (IBIW), Borok, Russia.

Terminology for valve features of this group follows that of Kociolek & Stoermer (1988c, 1993).

RESULTS

Gomphonema borealis Kulikovskiy, Kociolek & Solak, **sp. nov.** **Figs 1-22**

Description:

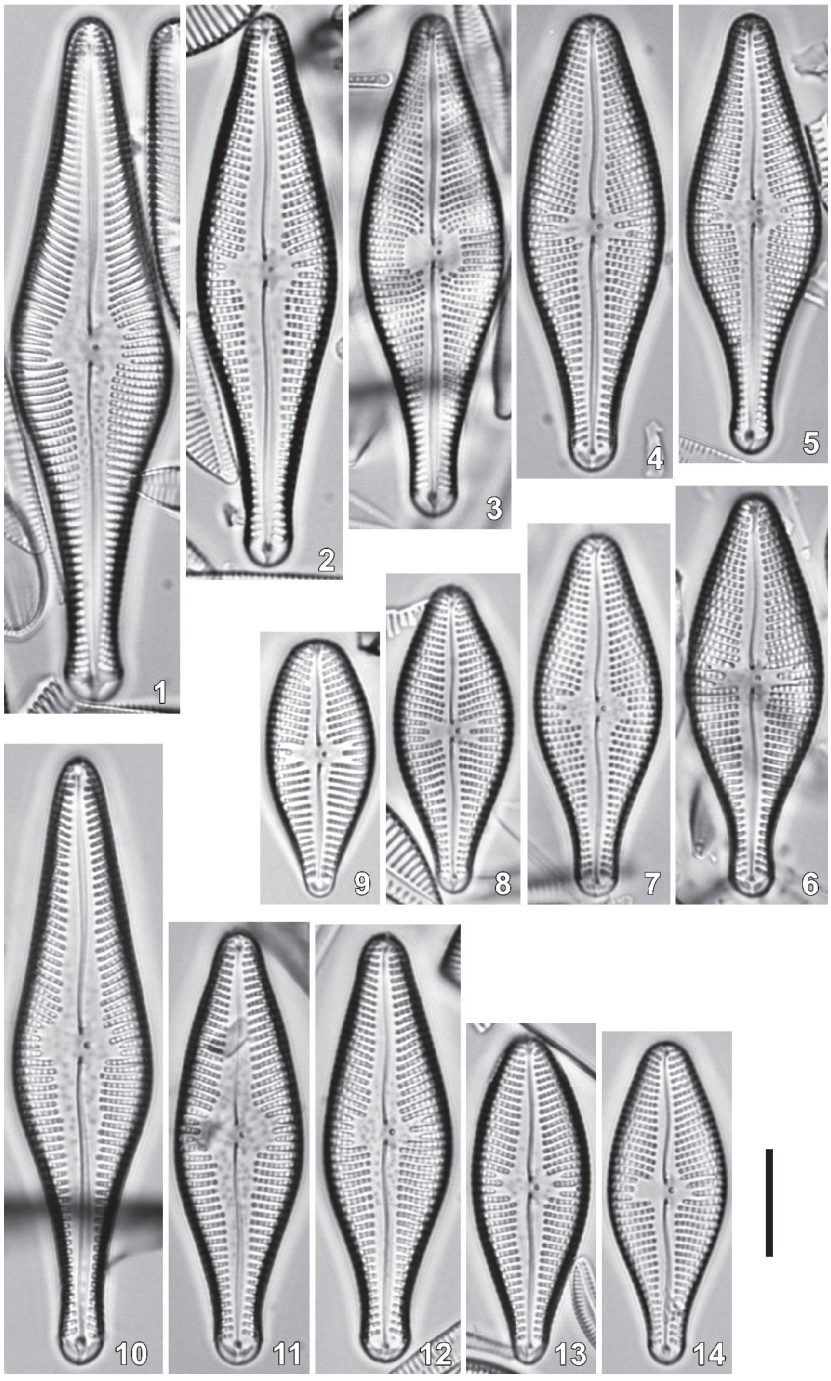
LM:Valves rhombic-lanceolate-clavate, broadest at the center tapering strongly towards the rounded footpole, tapering strongly to rounded headpole, which is slightly protracted in smaller specimens. Length 24-64 µm, breadth 10-15 µm. Axial area narrow at the poles, lanceolate, widening to the laterally expanded orbicular to rectangular, to bow-tie shaped central area. Raphe lateral, undulate, with external proximal raphe ends dilated and rounded. Striae distinctly punctate, uniseriate, dash-like in shape, radiate throughout the valve length, 13-15/10 µm. A single round stigma opening is present in the central area close to the proximal raphe ends. Bilobed apical pore field evident at the footpole.

SEM: Exterior of the valves with areolae with variously-shaped occlusions, appearing to be located in slight depressions on the valve face. Proximal raphe ends dilated, distal ends deflected onto the mantle at the headpole, bisecting the bilobed apical pore fields at the footpole, which is present almost exclusively on the mantle. Internally, the inwardly-projecting central nodule bears proximal raphe ends recurved at approximately 90 degrees and a single slit-like stigma opening. Helictoglossae, septa and pseudosepta are present at the apices.

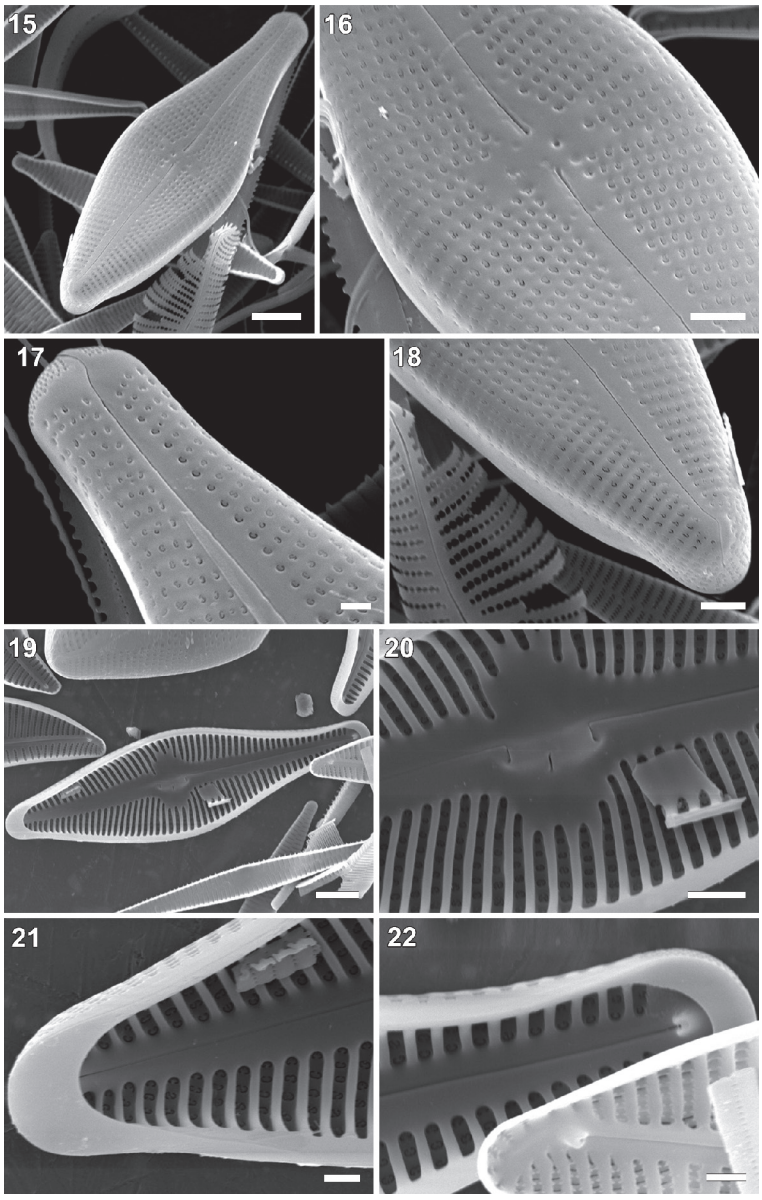
Holotype: Slide no 18572 (illustrated in Fig. 4) in collection of Maxim Kulikovskiy, I.D. Papanin Institute for Biology of Inland Waters (IBIW), Russian Academy of Sciences, 16.07.2011, leg. M.S. Kulikovskiy.

Type locality: Lake Baikal, near village Boldakovo, N52º35.694' E107º17.142'.

Etymology: Named for being a northern species.



Figs 1-14. *Gomphonema borealis* Kulikovskiy, Kociolek & Solak, sp. nov. LM. Size diminution series of two morphotypes, showing more robust (**1-9**) and slightly more linear (**10-14**) outlines. Figure 4 is of the holotype. Scale bar: 10 μm.



Figs 15-22. *Gomphonema borealis* Kulikovskiy, Kociolek & Solak, sp. nov. SEM. Valve exterior. **15.** General valve view, showing asymmetry about the transapical axis. **16.** Central portion of the valve with slightly dilated proximal raphe ends, round stigma opening and external pore occlusions. **17.** Footpole, with apical pore fields (APF's) positioned at the edge of the valve face and extending onto the mantle. Porelli of the APF's are morphologically distinct and physically separated from the valve face areolae. **18.** Headpole, with external distal raphe end deflected onto the valve mantle. Valve interior. **19.** General valve view, with pseudosepta and central nodule prominent. **20.** Central area of the valve with an internally-raised central nodule bearing recurved proximal raphe ends and a slit-like stigma opening. **21.** Headpole with pseudoseptum obscuring helictoglossa. **22.** Footpole, with a pseudoseptum and helictoglossa evident. Scale bars: 5 µm (Figs 15, 19); 2 µm (Figs 16, 18, 20); 1 µm (Figs 17, 21, 22).

Comments: Variability within this species shows some specimens being more robust (Figs 1-9) in outline that others (Figs 10-14).
Differential diagnosis: The rhombic-lanceolate shape of the valve distinguishes this species from the others described here, and the type of G. ventricosum (Kociolek & Stoermer, 1987), except *G. sibericum* (which is also rhombic-lanceolate in shape). *Gomphonema borealis* is distinguished from *G. sibericum* by being proportionately wider, while *G. sibericum* is more linear in outline.

Gomphonema sibericum Kulikovskiy, Kociolek & Solak, **sp. nov.** **Figs 23-43**

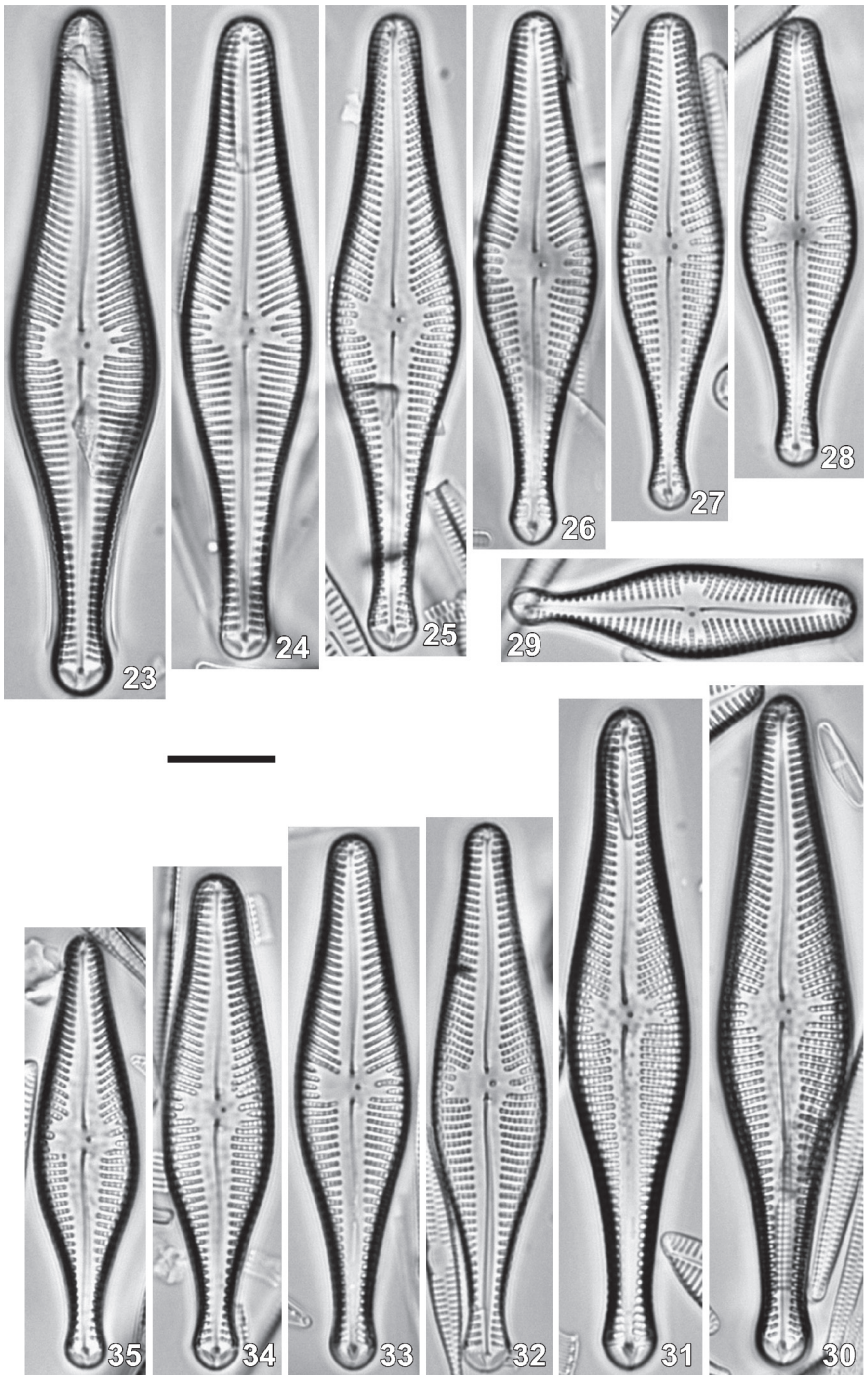
Description:

LM:Valves rhombic-lanceolate-clavate, tapering strongly to the poles, broadest towards the footpole, headpole, slightly protracted, rounded and a rounded footpole. Length 32-64 µm, breadth 8.0-13.8 µm. Axial area narrow at the poles, linear-lanceolate, widening to the laterally expanded irregularly- to bow-tie shaped central area. Striae around the central area shortened. Raphe lateral undulate, with external proximal raphe ends straight. Striae distinctly punctate, uniseriate, dash-like in shape, radiate throughout the valve length, 12-14/10 µm. A single round stigma opening is present in the central area close to the proximal raphe ends. Bilobed apical pore field evident at the footpole. Septa and pseudosepta are present at the apices.
SEM: Exterior of the valves with areolae with variously-shaped occlusions, with the areolae appearing flat on valve face or within depressions formed by silica outgrowths. Proximal raphe ends straight, distal ends deflected onto the mantle at the headpole, bisecting the bilobed apical pore fields at the footpole, which occur on the valve face and mantle. Internally, the inwardly-projecting central nodule bears proximal raphe ends recurved at approximately 90 degrees and a single slit-like stigma opening. Helictoglossae, septa and pseudosepta are present at the apices.
Holotype: Slide no 18591 (illustrated in Fig. 26) in collection of Maxim Kulikovskiy, I.D. Papanin Institute for Biology of Inland Waters (IBIW), Russian Academy of Sciences, 20.07.2011, leg. M.S. Kulikovskiy.
Type locality: Lake Baikal, near village Murino, N51º29.244' E104º24.060'.
Etymology: Named for the region in which it was found**.**
Comments: Variability in this species is expressed with some valves having a slightly more linear outline (Figs 30-35) than others (Figs 23-29).
Differential diagnosis: The rhombic-lanceolate shape of this species distinguishes it from the type of *G. ventricosum* (Kociolek & Stoermer 1987) and all other species treated here except *G. borealis*. *Gomphonema sibericum* differs from *G. borealis* being relatively more linear in outline.

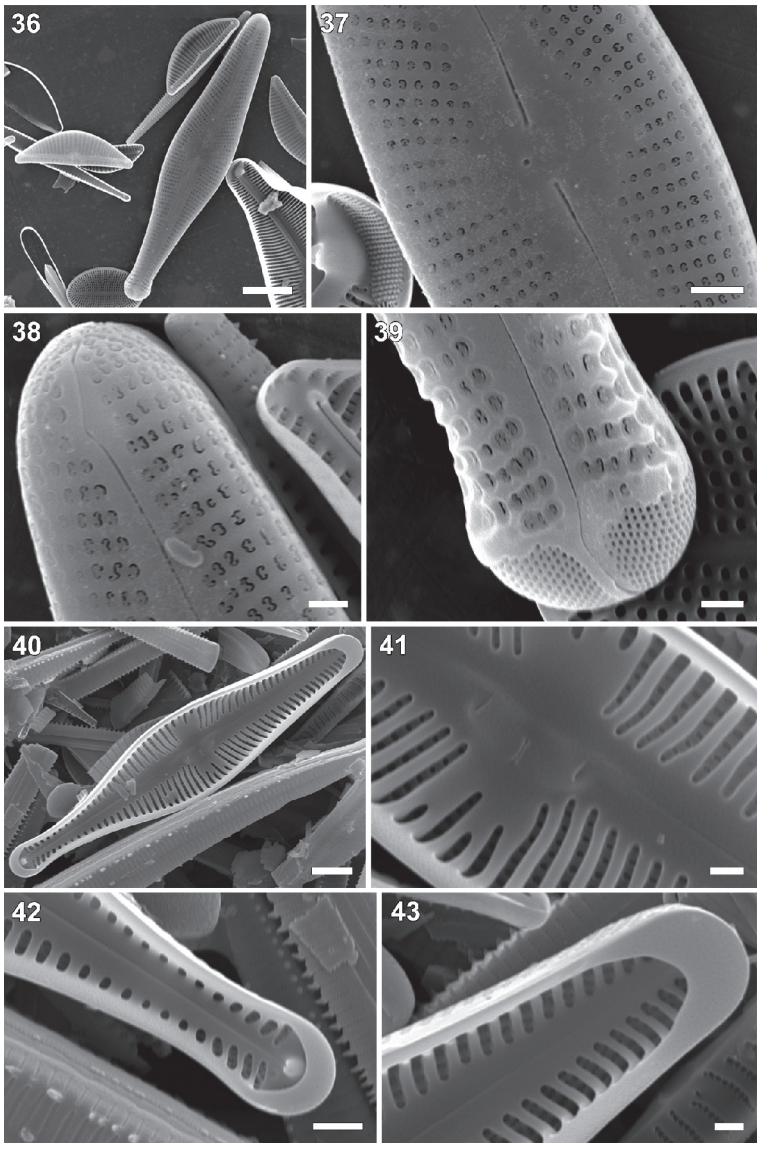
Gomphonema russicum Kulikovskiy, Kociolek & Solak, **sp. nov.** **Figs 44-66**

Description:

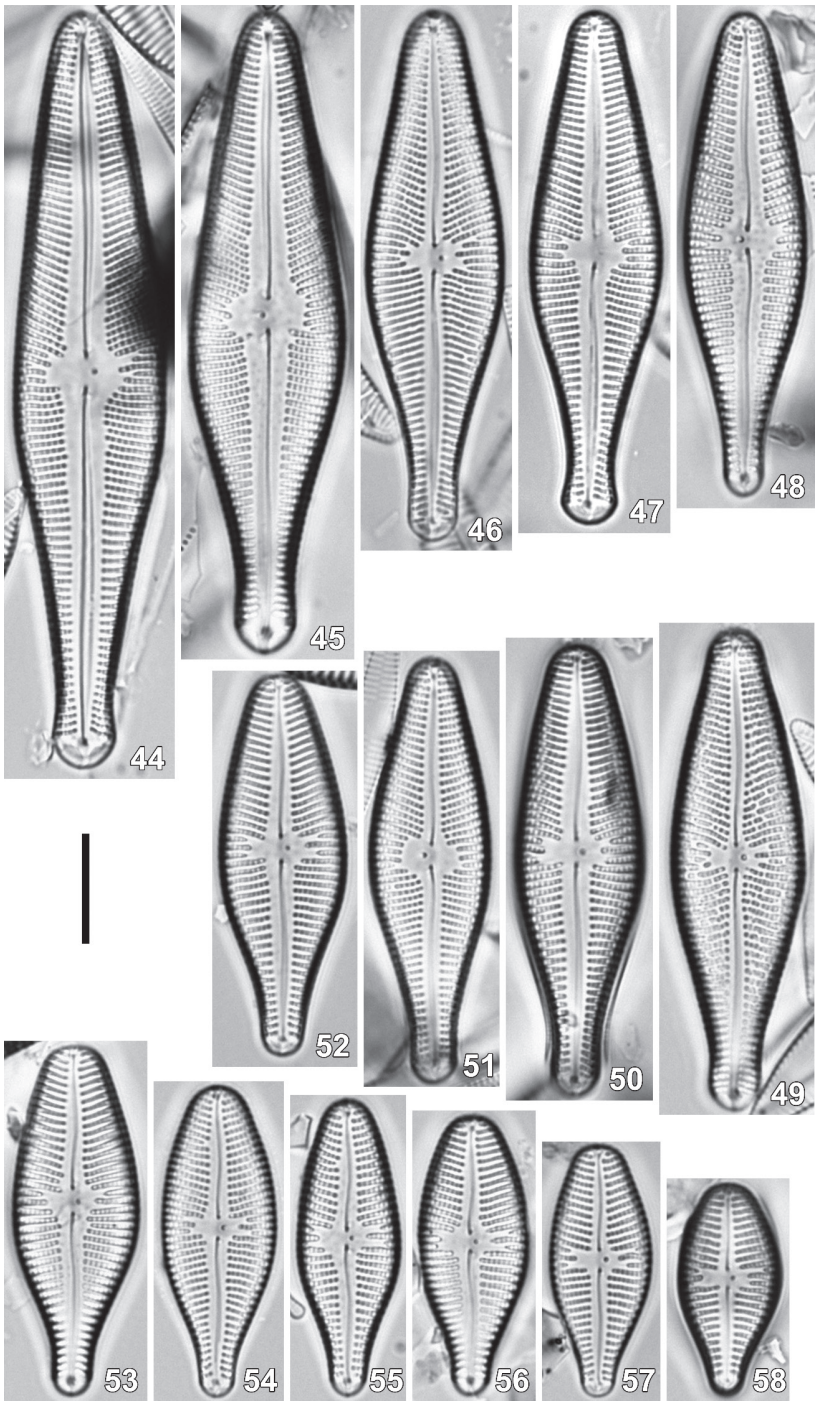
LM:Valves linear-lanceolate-clavate, headpole and footpole rounded. Length 19.5-69.0 µm, breadth 9.0-14.5 µm. Axial area narrow at the poles, lanceolate, widening to the laterally expanded orbicular to rectangular, to bow-tie shaped central area. Raphe lateral undulate, with external proximal raphe ends dilated and rounded. Striae distinctly punctate, uniseriate, dash-like in shape, radiate throughout the valve length, 13-15/10 µm. A single round stigma opening is present in the central area close to the proximal raphe ends. Bilobed apical pore field evident at the footpole. Septa and pseudosepta are present at the apices.



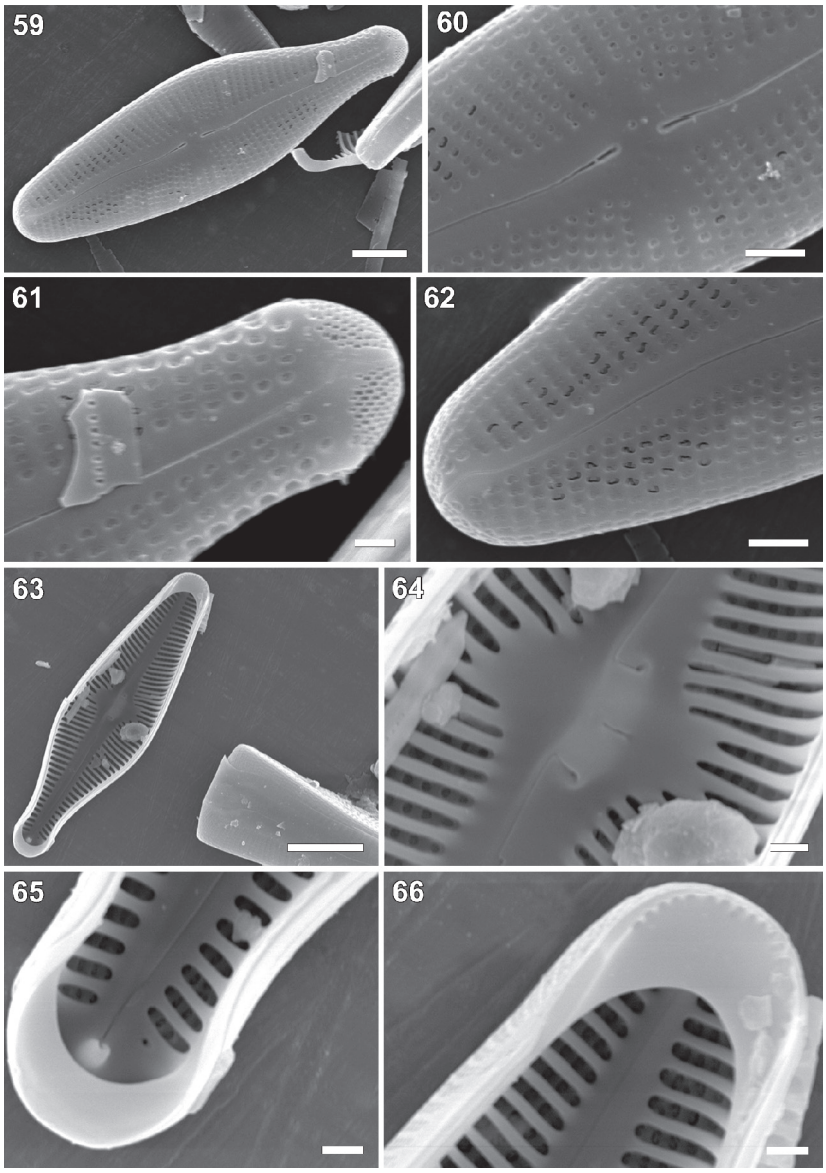
Figs 23-35. *Gomphonema sibericum* Kulikovskiy, Kociolek & Solak, sp. nov. LM. Size diminution series of two morphotypes, showing specimens with more broadly (**23-29**) and slightly more narrow (**30-35**) headpoles. Figure 26 is of the holotype. Scale bar: 10 μm.



Figs 36-43. *Gomphonema sibericum* Kulikovskiy, Kociolek & Solak, sp. nov. SEM. Valve exterior. **36.** General valve view, showing asymmetry about the transapical axis**. 37.** Central portion of the valve with small proximal raphe ends, round stigma opening and variously-shaped external pore occlusions. **38.** Headpole, with external distal raphe end deflected onto the valve mantle. **39.** Footpole, with APF's positioned on the valve face and extending onto the mantle. Bilobed APF is bisected by external distal raphe end. Porelli of the APF's are morphologically distinct and physically separated from the valve face areolae. Extra layers of silica give the valve an undulate to rugose appearance. Valve interior. **40.** General valve view, with pseudosepta and expanded central area evident. **41.** Central area of the valve with an internally-raised central nodule bearing recurved proximal raphe ends and a slit-like stigma opening. **42.** Footpole, with a pseudoseptum and helictoglossa evident. **43**. Headpole with pseudoseptum obscuring helictoglossa. Scale bars: 10 µm (Fig. 36); 5 µm (Fig. 40); 2 µm (Figs 37, 42); 1 µm (Figs 38, 39, 41, 43).



Figs 44-58. *Gomphonema russicum* Kulikovskiy, Kociolek & Solak, sp. nov. LM. Size diminution series of larger specimens in the series. Fig. 47 is of the holotype. Scale bar: 10 µm.



Figs 59-66. *Gomphonema russicum* Kulikovskiy, Kociolek & Solak, sp. nov. - SEM. Valve exterior. **59.** General valve view, showing asymmetry about the transapical axis. **60.** Central portion of the valve with dilated raphe ends, small, round stigma opening and variously-shaped external pore occlusions located in small depressions. **61.** Footpole, with APF's positioned on the valve face and extending onto the mantle. Bilobed APF is bisected by external distal raphe end. Porelli of the APF's are morphologically distinct and physically separated from the valve face areolae. **62.** Headpole, with external distal raphe end deflected onto the valve mantle. Valve interior. **63.** General valve view, with pseudosepta and expanded central area evident. **64.** Central area of the valve with an internally-raised central nodule bearing recurved proximal raphe ends and a slit-like stigma opening. **65.** Footpole, with a pseudoseptum and helictoglossa evident. **66.** Headpole with pseudoseptum obscuring helictoglossa. Scale bars: 10 µm (Fig. 63); 5 µm (Fig. 59); 2 µm (Figs 60, 62); 1 µm (Figs 61, 64-66).

SEM: Exterior of the valves with areolae with variously-shaped occlusions, appearing to be located in slight depressions on the valve face. Proximal raphe ends dilated, distal ends deflected onto the mantle at the headpole, bisecting the bilobed apical pore fields at the footpole, which is present almost exclusively on the mantle. Internally, the inwardly-projecting central nodule bears proximal raphe ends recurved at approximately 90 degrees and a single slit-like stigma opening. Helictoglossae, septa and pseudosepta are present at the apices.

Holotype: Slide no 18571 (illustrated in Fig. 47) in collection of Maxim Kulikovskiy, I.D. Papanin Institute for Biology of Inland Waters (IBIW), Russian Academy of Sciences, 21.07.2011, leg. M.S. Kulikovskiy.

Type locality: Lake Baikal, near village Kultuk, N51º43.460' E103º43.096'.

Etymology: Named for this species occurring in Russia.

Differential diagnosis: This species differs from *G. ventricosum* and other species described here by having linear-lanceolate valves, tapering gently to both poles, except *G.rimetiana*. *Gomphonema russicum* differs from *G. rimetiana* by having more angular valves.

Gomphonema rimetiana Kulikovskiy, Kociolek & Solak, **sp. nov.** **Figs 67-93**

Description:

LM: Valves linear-lanceolate-clavate, broadest at the center, tapering gently towards the rounded to broadly-rounded headpole, quickly to the constricted, rounded footpole. Length 22.5-56.5 µm, breadth 9-12.5 µm. Axial area narrow at the poles, lanceolate, widening to the laterally expanded, rectangular central area. Raphe lateral undulate, with external proximal raphe ends dilated and rounded. Striae distinctly punctate, uniseriate, dash-like in shape, radiate especially towards the headpole, becoming parallel towards the footpole, 12-15/10 µm. A single round stigma opening is present in the central area close to the proximal raphe ends. Bilobed apical pore field evident at the footpole. Septa and pseudosepta are present at the apices.

SEM: Exterior of the valves with areolae with variously-shaped occlusions, appearing to be located in slight depressions on the valve face. Proximal raphe ends dilated, distal ends deflected onto the mantle at the headpole, bisecting the bilobed apical pore fields at the footpole, which is present on the valve face and the mantle. Internally, the inwardly-projecting central nodule bears proximal raphe ends recurved at approximately 90 degrees and elongate single slit-like stigma opening. Helictoglossae offset from the main raphe branch, septa and pseudosepta are present at the apices.

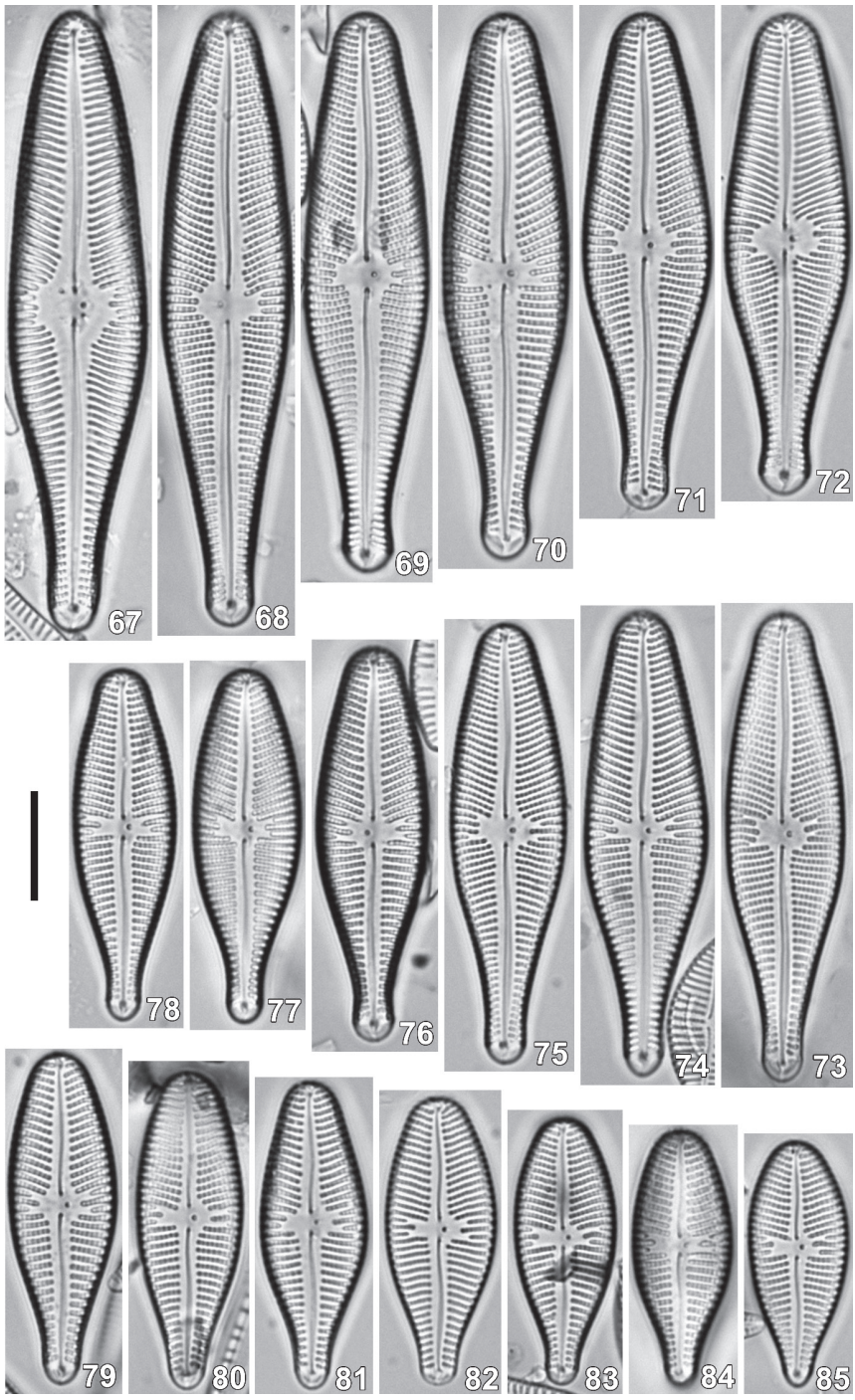
Holotype: Slide no 18588 (illustrated in Fig. 70) in collection of Maxim Kulikovskiy, I.D. Papanin Institute for Biology of Inland Waters (IBIW), Russian Academy of Sciences, 19.07.2011, leg. M.S. Kulikovskiy.

Type locality: Lake Baikal, near village Boyarsk, N51º80.635' E109º48.351'.

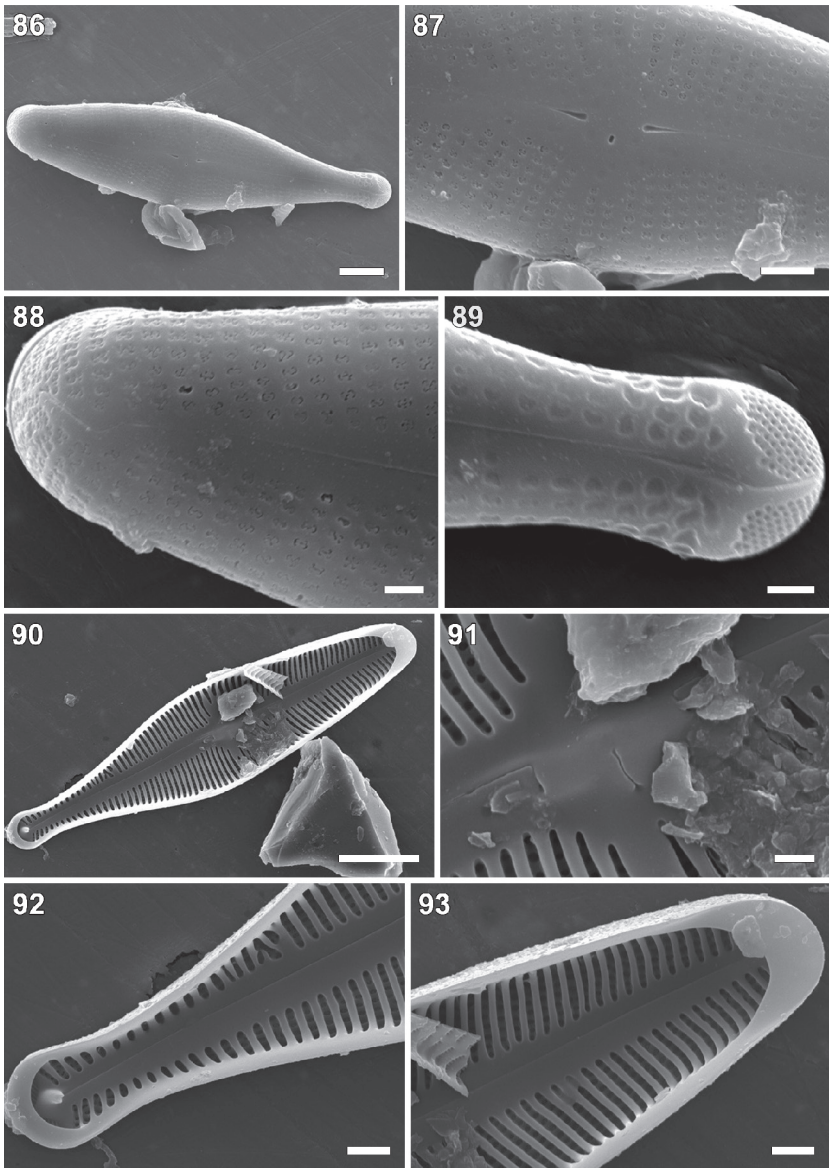
Etymology: Named in honor of Dr. Frédéric Rimet, and his contributions to our understanding of diatom phylogeny and ecology through the use of molecular data.

Comments: The more linear outline of this species makes it easy to identify from the others from Lake Baikal.

Differential diagnosis: This species is most similar to *G. russicum* but differs by having a more linear valve shape. The linear-lanceolate shape distinguishes this species from those that are more rhombic-lanceolate (*G. borealis*, *G sibericum*), and those that are more lanceolate (*G. jahniana*, *G. eriensioides*) in shape.



Figs 67-85. *Gomphonema rimetii* Kulikovskiy, Kociolek & Solak, sp. nov. LM. Size diminution series. Fig. 70 is of the holotype. Scale bar: 10 µm.



Figs 86-93. *Gomphonema rimetii* Kulikovskiy, Kociolek & Solak, sp. nov. SEM. Valve exterior. **86.** General valve view, showing asymmetry about the transapical axis. **87.** Central portion of the valve with dilated raphe ends, small, round stigma opening and variously-shaped external pore occlusions located in small depressions. **88.** Headpole, with external distal raphe end deflected onto the valve mantle. **89.** Footpole, with APF's positioned on the valve face and extending onto the mantle. Bilobed APF is bisected by external distal raphe end. Porelli of the APF's are morphologically distinct and physically separated from the valve face areolae. Valve interior. **90.** General valve view, with pseudosepta evident. **91.** Central area of the valve with an internally-raised central nodule bearing recurved proximal raphe end and a slit-like stigma opening. **92.** Footpole, with a pseudoseptum and helictoglossa evident. **93.** Headpole with pseudoseptum obscuring helictoglossa. Scale bars: 10 µm (Fig. 90); 5 µm (Fig. 86); 2 µm (Figs 87, 92, 93); 1 µm (Figs 88, 89, 91).

Gomphonema jahniana Kulikovskiy, Kociolek & Solak, **sp. nov. Figs 94-113**

Description:

LM: Valves broadly lanceolate-clavate, broadest just towards the footpole from the valve center, tapering to rounded headpole, and tapering more distinctly towards the rounded footpole. Length 26.5-51.0 µm, breadth 9.0-12.5 µm. Axial area narrowly to more broadly linear-lanceolate, widening to the laterally expanded orbicular to rectangular central area. Raphe lateral undulate, with external proximal raphe ends dilated and rounded. Striae distinctly punctate, uniseriate, dash-like in shape, radiate throughout the valve length, 13-14/10 µm. A single round stigma opening is present in the central area close to the proximal raphe ends. Bilobed apical pore field evident at the footpole. Septa and pseudosepta are present at the apices.

SEM: Exterior of the valves with areolae with variously-shaped occlusions, appearing to be located in slight depressions on the valve face. Proximal raphe ends dilated, distal ends deflected onto the mantle at the headpole, bisecting the bilobed apical pore fields at the footpole, which is present on the valve face and the mantle. Internally, the inwardly-projecting central nodule bears proximal raphe ends recurved at approximately 90 degrees and elongate single slit-like stigma opening. Helictoglossae offset from the main raphe branch, septa and pseudosepta are present at the apices.

Holotype: Slide no 18591 (illustrated in Fig. 96) in collection of Maxim Kulikovskiy, I.D. Papanin Institute for Biology of Inland Waters (IBIW), Russian Academy of Sciences, 19.07.2011, leg. M.S. Kulikovskiy.

Type locality: Lake Baikal, near village Murino, N51º29.244' E104º24.060'.

Etymology: Named in honor of Dr. Regine Jahn, Botanical Garden and Botanical Museum, Berlin, Dahlem, Germany, for her work on diatom biology and ecology, especially with regard to the genus *Gomphonema*.

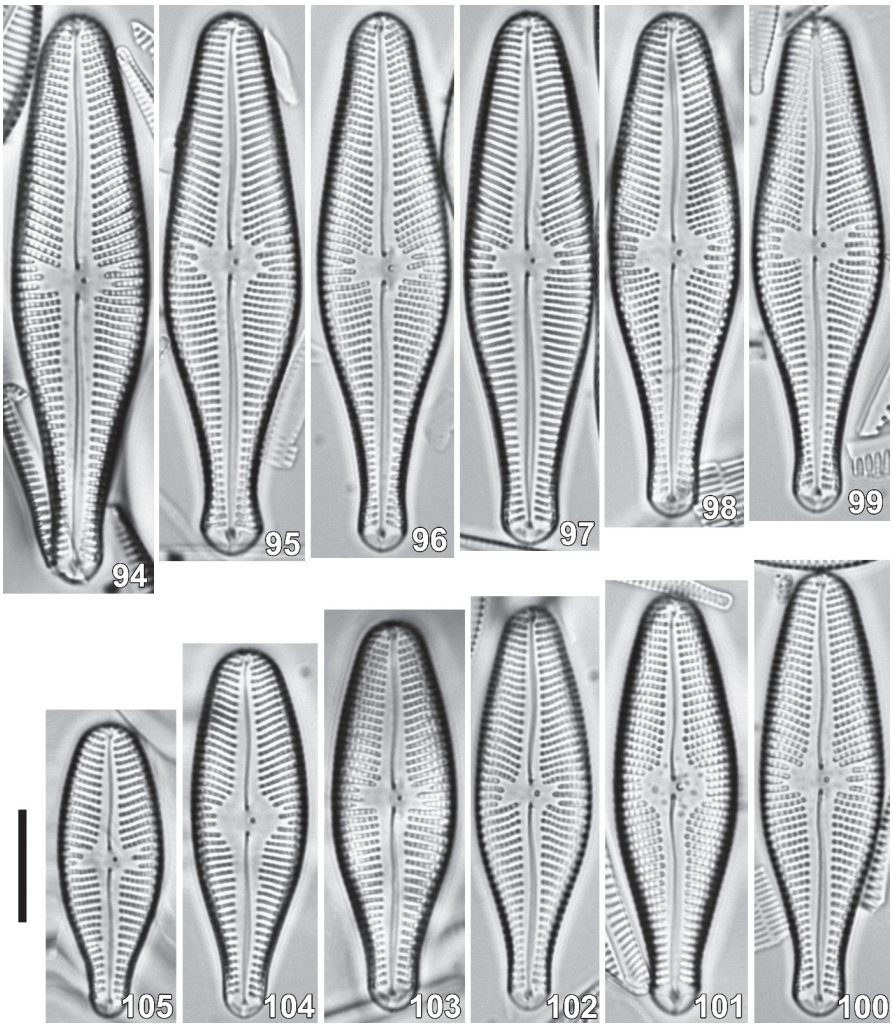
Differential diagnosis: *Gomphonema jahniana* and *G. eriensioides* both are lanceolate-clavate in shape, which distinguishes them from the taxa that are more rhombic-lanceolate (*G. borealis*, *G. sibericum*), those that are more linear-lanceolate (*G. russicum*, *G. rimetiana*) and *G. ventricosum*. *Gomphonema jahniana* is distinguished from *G. eriensioides* by having a headpole that is rounded but not protracted.

Gomphonema eriensioides Kulikovskiy, Kociolek & Solak, **sp. nov. Figs 114-126**

Description:

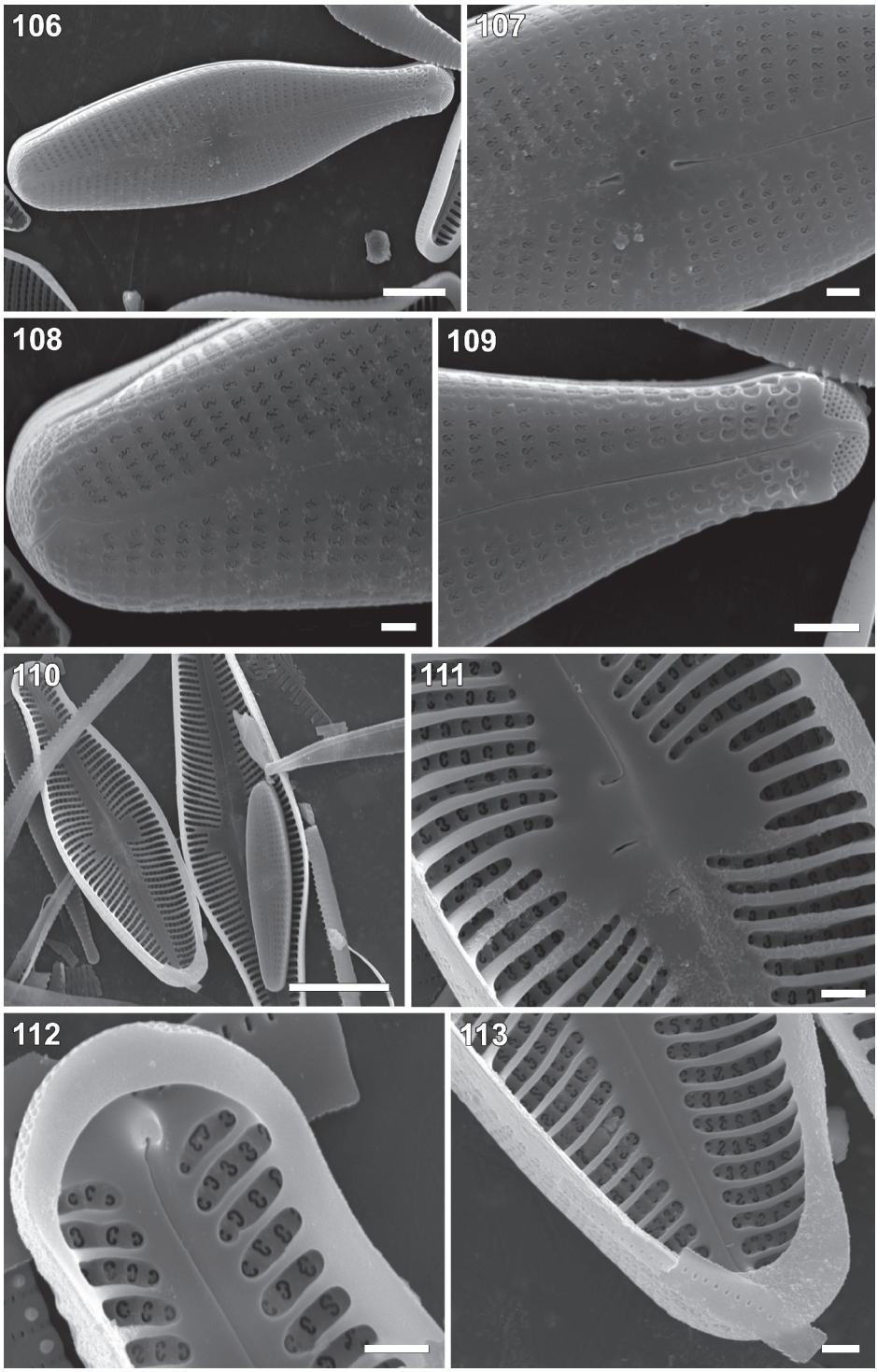
LM:Valves broadly lanceolate-clavate, broadest slightly towards the footpole from the central area, rounded, protracted headpole, and a broadly rounded footpole. Length 36.5-47.0 µm, breadth 11.0-12.5 µm. Axial area linear-lanceolate, widening to the slightly laterally expanded, rectangular central area. Raphe lateral undulate, with external proximal raphe ends dilated and rounded. Striae distinctly punctate, uniseriate, dash-like in shape, radiate throughout the valve length, 11.5-15.0/10 µm. A single round stigma opening is present in the central area close to the proximal raphe ends. Bilobed apical pore field evident at the footpole. Septa and pseudosepta are present at the apices.

SEM: Internally, the inwardly-projecting central nodule bears proximal raphe ends recurved at approximately 90 degrees and elongate single slit-like stigma opening. Helictoglossae offset from the main raphe branch, septa and pseudosepta are present at the apices.



Figs 94-105. *Gomphonema jahnii* Kulikovskiy, Kociolek & Solak, sp. nov. LM. Size diminution series. Fig. 96 is of the holotype. Scale bar: 10 µm.

Figs 106-113. *Gomphonema jahnii* Kulikovskiy, Kociolek & Solak, sp. nov. SEM. Valve exterior. **106.** General valve view, showing asymmetry about the transapical axis. **107.** Central portion of the valve with dilated raphe ends, small, round stigma opening and variously-shaped external pore occlusions. **108.** Headpole, with external distal raphe end deflected onto the valve mantle. **109.** Footpole, with APF's positioned on the valve face and extending onto the mantle. Bilobed APF is bisected by external distal raphe end. Porelli of the APF's are morphologically distinct and physically separated from the valve face areolae. Extra layers of silica give the valve an undulate to rugose appearance. Valve interior. **110.** General valve view, with pseudosepta evident. Interstriae are narrow. **111.** Central area of the valve with an internally-raised central nodule bearing recurved proximal raphe end and a slit-like stigma opening. Interstriae are quite narrow. **112.** Footpole, with a pseudoseptum and helictoglossa evident. Helictoglossa is offset from main axis of axial area. **113.** Headpole with pseudoseptum obscuring helictoglossa. Scale bars: 10 µm (Fig. 110); 5 µm (Fig. 106); 2 µm (Fig. 109); 1 µm (Figs 107, 108, 111-113).


106
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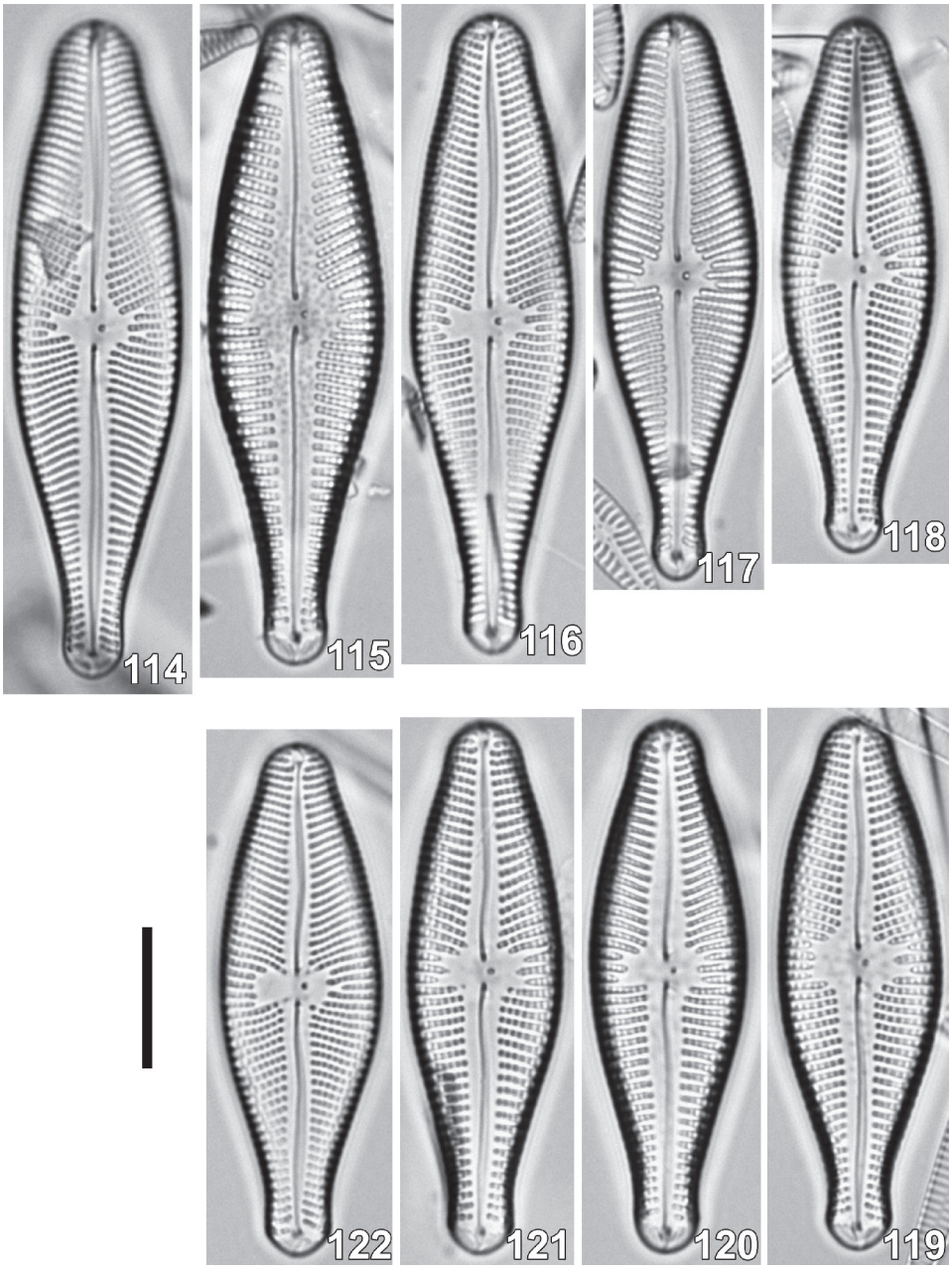

Fig 114-122. *Gomphonema eriensioides* Kulikovskiy, Kociolek & Solak, sp. nov. LM. Size diminution series. Fig. 115 is of the holotype. Scale bar: 10 μm.

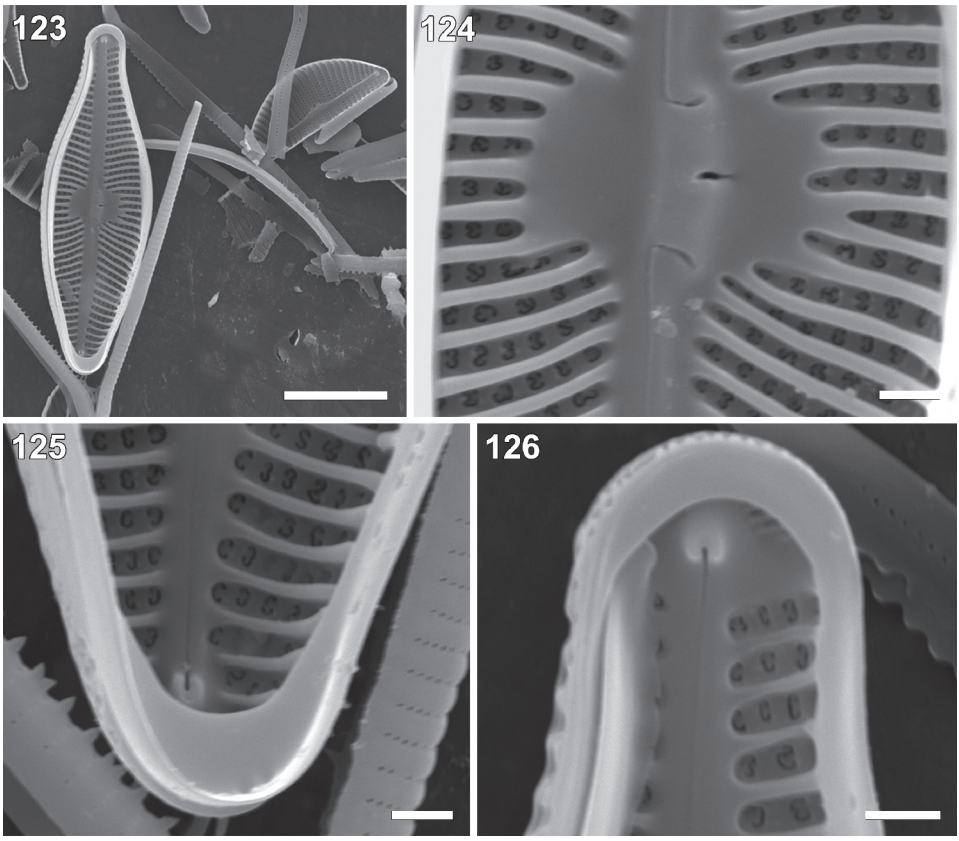

Fig 123-126. *Gomphonema eriensioides* Kulikovskiy, Kociolek & Solak, sp. nov. SEM. Valve interior. **123.** General valve view, with pseudosepta and central nodule evident. **124.** Central area of the valve with an internally-raised central nodule bearing recurved proximal raphe end and a slit-like stigma opening. Interstriae are quite narrow. **125.** Headpole with pseudoseptum and helictoglossa in view. **126.** Footpole, with a pseudoseptum and helictoglossa evident. Scale bars: 10 μm (Fig. 123); 1 μm (Figs 124-126).

Holotype: Slide no 18591 (illustrated in Fig. 115) in collection of Maxim Kulikovskiy, I.D. Papanin Institute for Biology of Inland Waters (IBIW), Russian Academy of Sciences, 19.07.2011, leg. M.S. Kulikovskiy.
Type locality: Lake Baikal, near village Murino, N51º29.244' E104º24.060'.
Etymology: Named for its superficial resemblance to *Gomphoneis eriense* (Grunow) Skvortzow & K.I. Meyer.
Comments: Specimens of this species appear similar to *Gomphoneis eriense*, a taxon known only from North America. *Gomphoneis eriense* has doubly-punctate striae and longitudinal lines on either side of the axial area (Kociolek & Stoermer, 1988b), distinguishing it easily from this new species of *Gomphonema*.
Differential diagnosis: *Gomphonema eriensioides* resembles *G. jahniana* in having lanceolate-clavate valves, a feature that distinguishes them from species with rhombic-lanceolate-clavate valves (such as *G. borealis* and *G. sibericum*) and those

with linear-lanceolate-clavate valves (*G. russicum* and *G. rimetiana*). *Gomphonema eriensioides* differs from *G. jahniana* by having protracted apices, a feature lacking in the latter taxon.

DISCUSSION

When compared with the holotype population of *Gomphonema ventricosum*, originally found by Gregory (1856) in Scotland (banks of the Spey River, near Elchies), presented by Kociolek & Stoermer (1987), specimens from Lake Baikal formerly assigned to that species appear quite distinct. The Lake Baikal specimens across the 6 new species described here differ from *G. ventricosum sensu stricto* by being proportionately broader, having striae that are more distinctly punctate, and a central area that is more irregular in its construction. These differences are evident more or less across the size diminution series for all species. In addition, each new species presented here has a distinct shape, separating them from each other as well as *G. ventricosum*. On the basis of our observations of historical material (Skvortzow & Meyer, 1928; Skabitchevsky, 1936; Kociolek & Stoermer, 1988a; Kulikovskiy & Kociolek, 2014) and material collected by us and the Darwin Initiative from around Lake Baikal (Kulikovskiy *et al.,* 2012b; Kociolek *et al.,* 2013), we conclude that there are no verifiable records of *G. ventricosum* from Lake Baikal.

There were two previously described subspecific taxa assigned to *Gomphonema ventricosum* from Lake Baikal, namely *G. ventricosum* f. *curta* Skvortzow (1937) and *G. ventricosum* subsp. *baicalense* Skabitchevsky (1985). Yoshitake *et al.* (2009) reported *G. ventricosum* f. *curta* from Lake Baikal, but the small specimens they illustrated could have come from several different taxa from the lake. Descriptions of these taxa are vague, the illustrations of them generalized, and type specimens are wanting, making a positive identification of either taxon nearly impossible. While Yoshitake *et al.* (2009) reported five different "types" of *G. ventricosum* from three lakes in eastern Asia, specimens from Lake Baikal appear different from those of Lake Hovsgol and Lake Kurilskoye. It appears to us that none of the five types illustrated by Yoshitake *et al.* (2009) are of Gregory's *G. ventricosum*. In addition, Skvortzow & Meyer (1928) reported *Gomphoneis eriense* from Lake Baikal. Based on their illustrations, it appears that their report of that species, and three subspecific taxa (Skvortzow & Meyer 1928), represent valves of *Gomphonema eriensoides*.

We suggest that the six new species described here may form part of a species flock endemic to Lake Baikal, or possibly the Baikal Rift Zone. It is possible that figures 24-26 in Yoshitake *et al.* (2009), from Lake Hovsgol, represent another new species of this group. While most other purported species flocks of diatoms (Mann, 1999; Edlund & Soninkhishig, 2009; Seddon *et al.,* 2011) are geographically constrained, the Lake Baikal species complex also does have what appears to be a synapomorphy diagnosing a monophyletic group (the interesting shape of the external areaolar occlusions that differ from the c-shaped flaps seen in most 'typical' *Gomphonema* species (Dawson, 1973; see discussion in Kociolek & Stoermer, 1993). This however needs to be confirmed by a formal phylogenetic analysis to determine if the group is monophyletic. Perhaps the best example of a species flock in freshwater diatoms is illustrated in the genus *Tetralunata* Hamsher *et al.* (2014), where nearly 20 species are found in or near Lake Toba, Sumatra. This genus is

found only on Sumatra in the vicinity of Lake Toba and was shown with a cladistics analysis be monophyletic (Hamsher *et al.,* 2014). *Tetralunata* taxa must have evolved quickly, since Lake Toba was formed by the eruption of a super volcano *ca* 75,000 years ago (Storey *et al.,* 2012; Roberts *et al.,* 2013). Kociolek *et al.* (2017) have detailed other putative examples of species flocks in freshwater diatoms, from river and lake systems, including some examples from fossil localities.

While the putative species flock described here is one of the largest species flocks yet described for diatoms, the relatively small number (6) as compared to many other examples of species flocks is noteworthy. Diatoms have fast generation times (2-3 times per day) and high rates of speciation (Theriot *et al.*, 2006), thus we might expect to see higher numbers of species in species flocks of diatoms. Six species (and certainly there will be more added to this list; rareness of some morphotypes in our samples did not allow us to describe them at this time) is modest compared to the tens or hundreds of species described from species flocks for other groups or organisms. It is possible that in addition to rareness of individuals for other taxa, morphological diversity of valves is too conservative to recognize other species in this species flock. Thus, it may be necessary to look for features related to sexual reproduction, physiology, and molecular sequence data to highlight other levels of diversity in the group (Kociolek *et al.*, 2017). Features other than morphology have been used to document diversity in other groups, including molecular data (Schön & Martens, 2012) and behavior (Stauffer *et al.,* 2002). The possibility of cryptic species being present in this group is worthy of future study to explore if species flocks in diatoms exist in numbers not indicated by frustular morphology alone, as has been suggested for other groups of diatoms (e.g. Amato *et al.*, 2007).

Acknowledgements. This work was supported by the Russian Foundation for Basic Research (17-04-00042_a) for sample preparing and LM and Russian Science Foundation (14-14-00555) for completing manuscript and SEM. We appreciate the helpful comments by Luc Ector and an anonymous reviewer.

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Mise en page et impression
bialec, nancy (France)
Dépôt légal n° 93320 - 20 août 2018