

New and rare *Psammothidium* species (Bacillariophyta, Achnanthidiaceae) from Northeastern Siberia

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Abstract – Three rare *Psammothidium* species were found in recently surveyed lakes of Northeastern Siberia, Russia. One of these species found in lakes of the Kolyma Lowland, is new for science and is formally described here as *Psammothidium onufrii* sp. nov. It is morphologically similar to the brackish-water species *Achnanthes punctulata*, but it lacks a central area on rapheless valve and possesses a large central area on the raphe valve. *Psammothidium onufrii* is characteristic for tundra thermokarst lakes with moderate mineral content. *Psammothidium sacculum* previously reported from a few subarctic and arctic locations was found in several lakes of the Kolyma Lowland and of the Magadan District. The frustule ultrastructure of this species is documented for the first time here. The third species, known as *Achnanthes obliqua* (W. Gregory) Hustedt and transferred here to *Psammothidium*, is a morphologically distinct and relatively rare diatom occasionally reported from northern regions of Eurasia and Western North America. In Northeastern Siberia it was found in sediments of relatively large shallow lakes with low to moderate mineral content. Detailed morphological characterization of the three *Psammothidium* species will facilitate their detection in environmental surveys and their use in paleoenvironmental reconstructions.

Diatoms / lakes / morphology / new species / *Psammothidium* / Siberia / taxonomy

INTRODUCTION

The genus *Psammothidium* established by Bukhtiyarova & Round (1996) comprises monoraphid, mostly freshwater diatoms and is placed in the family Achnanthidiaceae based on such morphological characters as non-coaxial proximal internal raphe ends and simple internally occluded areolae. A character that sets this genus apart from all other representatives of the family is the frustule flexure with a convex external surface of the raphe valve and a concave external surface of rapheless valve, which is presumably an adaptation to epipsammic growth habit. The genus includes several taxa common and often abundant in rivers and lakes around the world, but new *Psammothidium* species continue to be discovered at a steady pace with most new species found in cold-water lakes (Potapova, 2012, 2014; Bukhtiyarova & Stanislavskaya, 2013; Enache *et al.*, 2013; Kopalová *et al.*, 2016; Blanco *et al.*, 2017). *Psammothidium* species are commonly reported in paleolimnological studies conducted in the Arctic (Pienitz, 2018) where they often constitute a relatively large proportion of diatom assemblages in lake sediments and are, therefore, important for paleoenvironmental reconstructions. In addition to

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commonly reported *Psammothidium* species such as *P. altaicum*, *P. bioretii*, *P. curtissimum*, *P. daonense*, *P. helveticum*, *P. marginulatum*, *P. rossii*, *P. scoticum*, *P. subatomoides*, and *P. ventrale*, examination of diatom samples collected in 2012–2013 from lakes in Northeastern Siberia revealed one unknown and two rare and insufficiently studied species of this genus. The goal of this study is to provide detailed morphological descriptions and basic ecological information for these three *Psammothidium* species, which could help in their identification and use in applied research.

MATERIAL AND METHODS

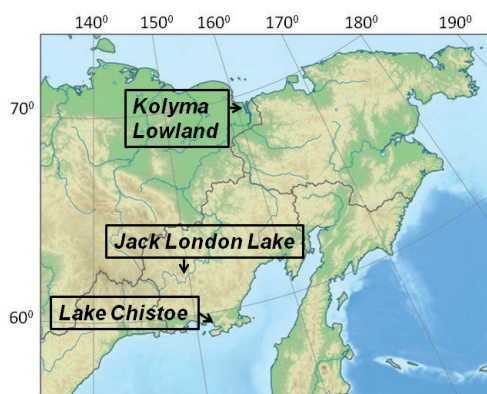


Fig. 1. Map of the Northeastern Siberia showing locations of the study areas.

Diatom samples used in this study were collected in 2012–2013 from three areas in Northeastern Siberia, Russia (Fig. 1). The first is the Kolyma Lowland in the northeastern part of Yakutia (or Sakha Republic) located at approximately 69°N, 161°E and covering both tundra and northern taiga zones. The region has a continental climate with mean annual air temperatures ranging from -13 to -9°C and mean annual precipitation about 200–300 mm (Andreev, 2001). This area is within the zone of continuous permafrost and is underlain by the ice-rich loess Pleistocene deposits partially reworked by thermokarst

and thermo-erosion (Veremeeva & Gubin, 2009). In addition to thermokarst lakes, much of the area is covered by polygonal bogs. Diatom samples were collected June 16–July 8, 2012 from 79 sampling sites around the delta of Kolyma River at the distance of 30–100 km from the coast of Arctic Ocean. The three *Psammothidium* species that are the focus of this paper were found in 12 of these samples listed in Table 1. Two other sampling locations are lakes in the Magadan Region (Table 1). The Jack London Lake (62°05'19"N, 149°29'34"E) is an alpine lake situated within the southern part of the Chersky mountain range at the altitude of 805 m a.s.l. This area has a harsh continental climate with very cold winters, mean annual air temperature around -12°C and mean annual precipitation about 350 mm. The lake is 8.7 km long, 1.6–3.5 km wide, with surface area of 14.4 km², up to 50 m deep and a sandy bottom. The lake watershed is occupied by alpine tundra, larch forest and bogs (Andreev, 2001). Lake Chistoe (59°32'N 151°50'E) is at a distance of approximately 8 km from the Sea of Okhotsk. The climate of this area is maritime subarctic with mean annual air temperatures of approximately -2.8°C and mean annual precipitation about 450 mm. The lake is located in a forested intermontane basin filled with non-marine quaternary sediments. The area of the lake is 40 km²,

Table 1. Studied diatom samples and records of *Psammothidium* species.

<i>Sampling locality</i>	<i>Sample number</i>	<i>Coll. date</i>	<i>Latitude, N</i>	<i>Longitude, E</i>	<i>pH</i>	<i>EC, $\mu S\ cm^{-1}$</i>	<i>Substrate</i>	<i>Species</i>
Yakutia, Lakes of Kolyma Lowland	ANSP RU000384	16 Jun 2012	68.74440	161.39395	7.6	72	Grass, silt	<i>P. sacculum</i>
	ANSP RU000388	16 Jun 2012	68.75997	161.40114	7.5	86	Silt, moss	<i>P. sacculum</i>
	ANSP RU000392	19 Jun 2012	68.76553	161.40173	6.7	92	Moss	<i>P. sacculum</i>
	ANSP RU000424	3 Jul 2012	69.41101	159.81657	7	84	Silt, grass	<i>P. obliquum</i>
	ANSP RU000427	3 Jul 2012	69.39997	159.81122	7	447	Grass	<i>P. onufrii</i>
	ANSP RU000431	3 Jul 2012	69.38292	159.80510	6.6	40	Moss	<i>P. obliquum</i>
	ANSP RU000441	6 Jul 2012	69.58131	158.51685	7.5	110	Grass	<i>P. sacculum</i>
	ANSP RU000443	6 Jul 2012	69.53046	158.64317	7.4	200	Grass, silt	<i>P. onufrii</i>
	ANSP RU000444	6 Jul 2012	69.51713	158.62695	7.1	190	Grass, silt	<i>P. obliquum</i>
	ANSP RU000445	6 Jul 2012	69.51721	158.62419	7.6	169	Grass, silt	<i>P. obliquum</i> <i>P. onufrii</i>
	ANSP RU000450	6 Jul 2012	69.52952	158.59978	7.1	143	Grass, moss	<i>P. onufrii</i>
	ANSP RU000456	7 Jul 2012	69.53950	158.89545	7	48	Silt	<i>P. obliquum</i>
	ANSP RU000552	1 Aug 2013	62.07684	149.55353	6.8	20	Sand, silt	<i>P. sacculum</i>
	ANSP RU000480	4 Aug 2012	59.56772	151.85200	8.4	13	Silt	<i>P. obliquum</i>

the average depth is 5-6 m. Bottom sediments are grey silt and sand (Andreev, 2001).

Diatom samples were collected by squeezing mosses and aquatic plants, scraping rocks, or siphoning the upper layer of silty sediments. The samples were treated by 30% hydrogen peroxide and potassium dichromate, then rinsed several times with distilled water. The permanent diatom slides were prepared with Naphrax mounting medium. The slides were examined with a Zeiss AxioImager A1 light microscope (LM) equipped with an AxioScopeMRm digital camera. For scanning electron microscopy (SEM) examination diatom slurries were dried on aluminum stubs, sputter-coated with Pt-Pd and observed with Zeiss Supra 50 scanning electron microscope under 10 kV accelerating voltage. Conductivity and pH were measured in the field with ExStikII conductivity/pH meter (Extech Instruments). Terminology follows Round *et al.* (1990).

RESULTS

Psammothidium onufrii sp. nov.

Figs 2-10, 24-29

Description. Valves elliptic to lanceolate, 4-5.5 μm wide, 7.5-15 μm long. Axial area very narrow, linear on both valves. Central area large, symmetric and transversely elliptic to rectangular on raphe valve; absent or very small on rapheless valve. Raphe straight, filiform, without terminal raphe fissures. Distal raphe ends straight, slightly expanded, internally form helictoglossae. Proximal raphe ends T-shaped, positioned in shallow grooves on external valve surface and appearing expanded in LM; internally bent in opposite directions. On raphe valve striae radiate, 28-32 in 10 μm , with approximately 40 areolae in 10 μm . On rapheless valve striae almost parallel to slightly radiate in the middle, becoming radiate towards ends, 26-31 in 10 μm , with approximately 30-35 areolae in 10 μm . Internal areolae openings round to transversely rectangular. External areolae openings round to transversely elliptic on raphe valve, round to slit-like on rapheless valve.

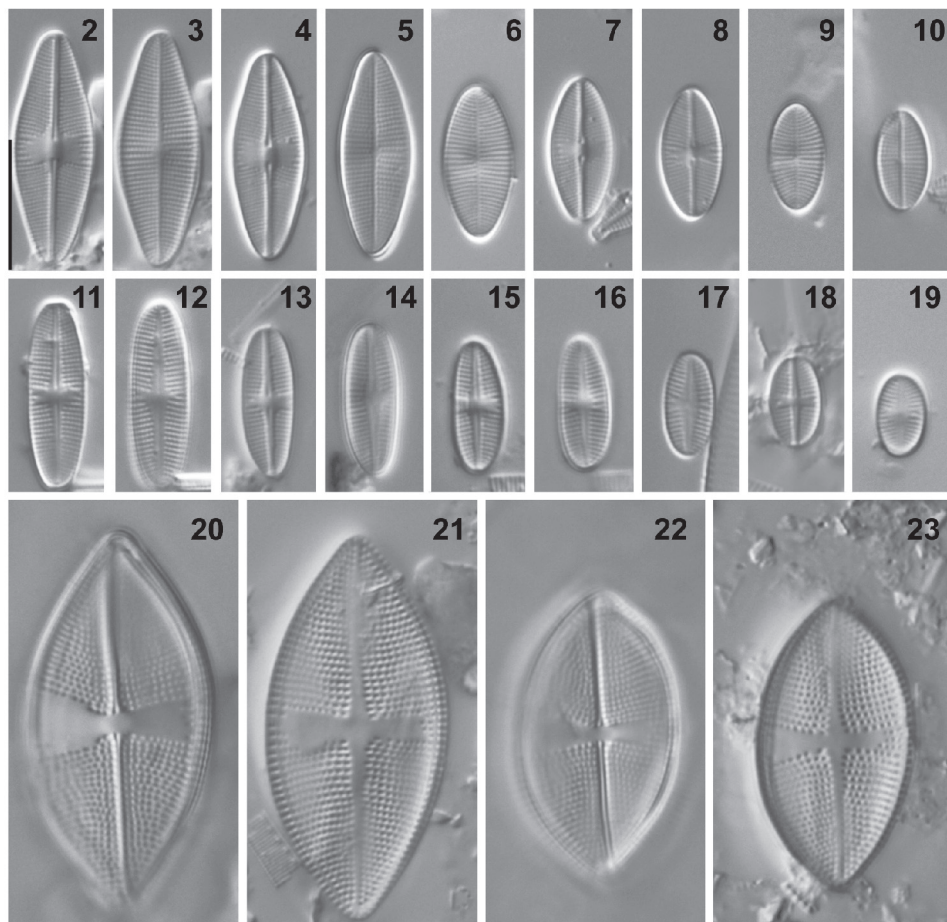
Holotype. Circled specimen on slide ANSP GC 36363, deposited at the Diatom Herbarium of the Academy of Natural Sciences of Philadelphia (Figs 2 and 3).

Isotypes. Circled specimens on slides ANSP GC 36364 deposited at the Diatom Herbarium of the ANSP and CANA 127982 deposited at the Canadian Museum of Nature.

Type locality. Unnamed lake, Kolyma Lowland, Yakutia, Russia. 69.530N, 158.643E. Sample ANSP RU000443 collected July 6, 2012 by M. Potapova.

Etymology. The species is named after Zimnyak Onufri, a Kolyma Lowland resident and enthusiast, in recognition of his invaluable help in organizing the 2012 collection trip to this remote area.

Distribution. *Psammothidium onufrii* has only been found in four lakes in the Kolyma Lowland (Table 1). These lakes had circumneutral water (pH 7.1-7.6) of moderate mineral content (conductivity 143-447 $\mu\text{S/cm}$). This species reached the highest relative abundance (1.8%) in a sediment sample from its type locality, a shallow thermokarst lake, approximately 700 m long and 500 m wide with water pH of 7.4 and conductivity of 200 $\mu\text{S/cm}$.



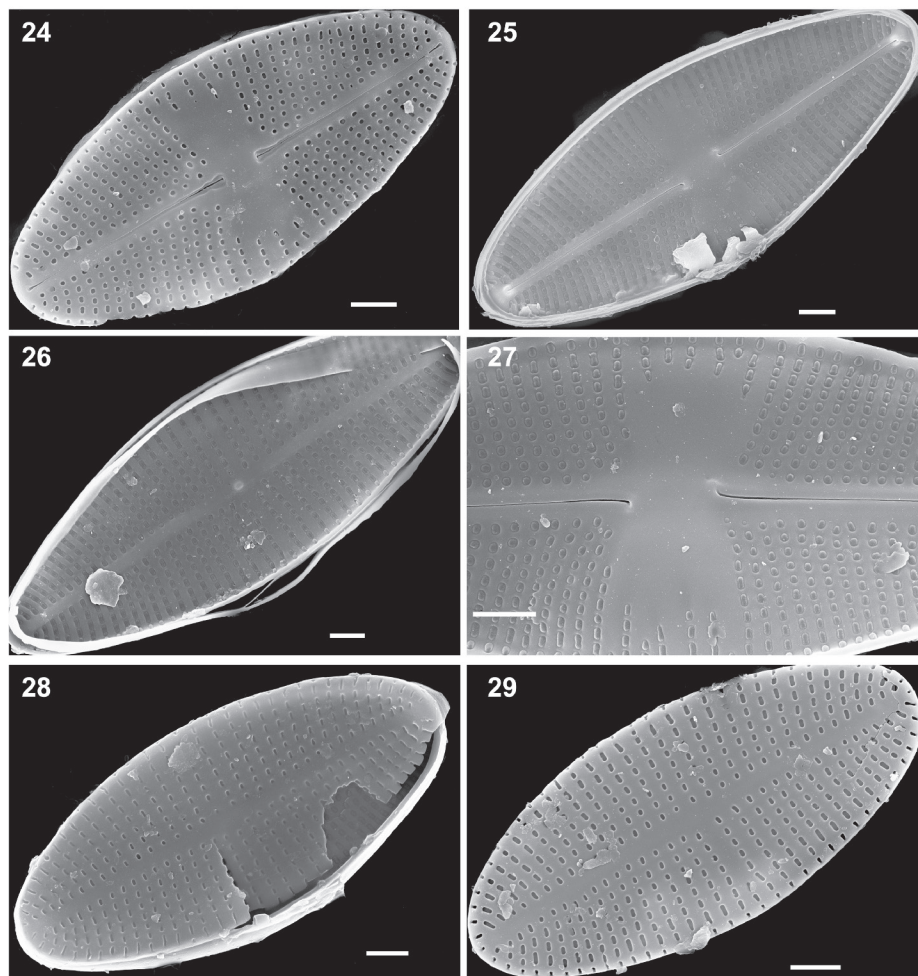
Figs 2–23. *Psammothidium* species from Northeastern Siberia, LM. **2–10.** *Psammothidium onufrii* sp. nov. Type population, sample ANSP RU000443 from an unnamed lake. Fig. 2 shows the raphe valve and Fig. 3 the rapheless valve of the holotype specimen from slide ANSP GC 36363. **11–19.** *Psammothidium sacculum*, sample ANSP RU000384 from an unnamed lake. **20–23.** *Psammothidium obliquum*, sample ANSP RU000480 from Chistoe Lake. Scale bar = 10 μ m.

***Psammothidium sacculum* (J.R. Carter) Bukhtiyarova**

Figs 11–19, 30–33

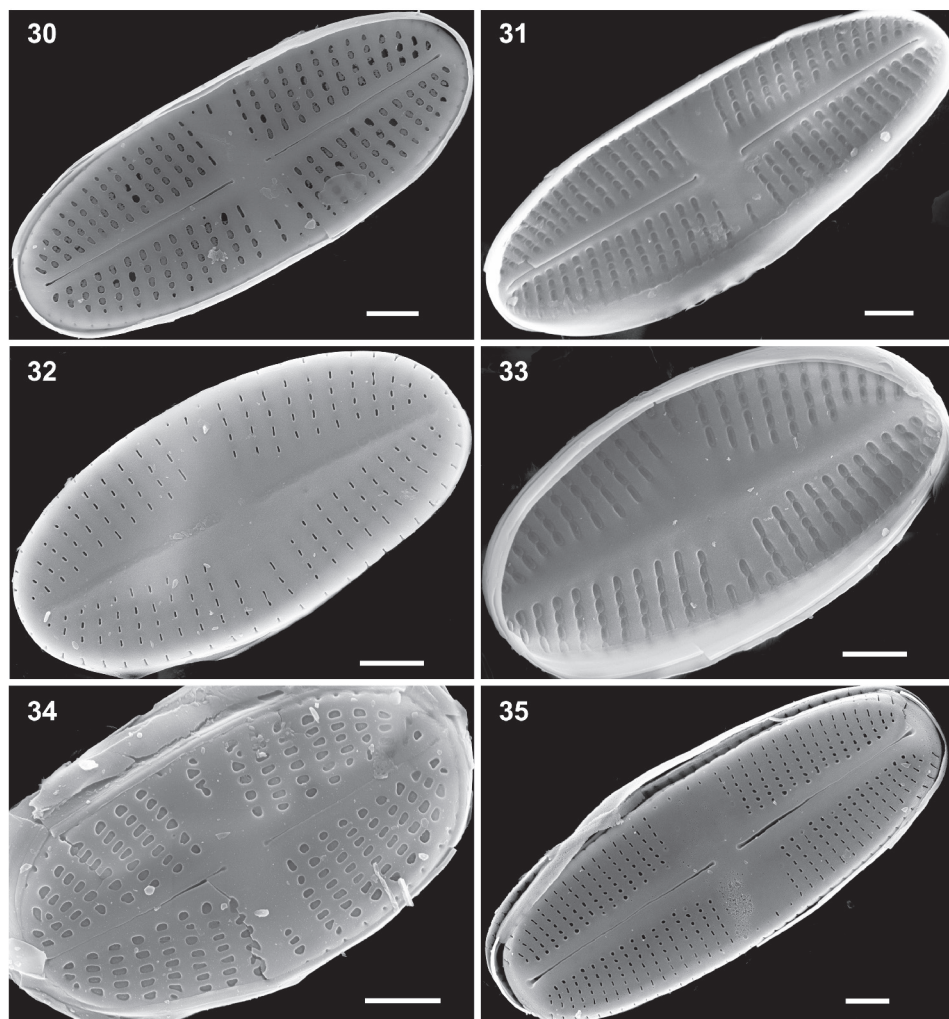
Basionym. *Achnanthes sacculus* J.R. Carter in Carter & Bailey-Watts, *Nova Hedwigia* 33(3/4), p. 535, pl. 24, fig. 6. 1981.

Morphology. In studied samples the valves of *P. sacculum* vary in width from 3.7 to 4.8 μ m, and in length from 6.1 to 14.9 μ m. The shorter valves are elliptic, while the longer ones are linear-elliptical and often slightly asymmetrical (Figs 13, 15). The raphe valve has a narrow axial area and transversely rectangular central area bordered by a few striae of various lengths (Figs 11, 13, 15, 18, 30, 31). The raphe is straight, without terminal raphe fissures, with simple and very slightly expanded distal and proximal ends (Fig. 29). The rapheless valve has a rhombic axial area that varies in width and is continuous with the central area, which is often



Figs 24–29. *Psammothidium onufrii* sp. nov., SEM. Type population, sample ANSP RU000443 from an unnamed lake. **24.** External view of a raphe valve showing expanded central area, T-shaped proximal raphe ends positioned in shallow grooves, straight and slightly expanded distal raphe ends and round to transversely elliptic areolae openings. **25, 27.** Internal views of raphe valves showing non-coaxial proximal raphe ends, helictoglossae at the distal raphe ends and occluded areolae openings. **26.** Internal view of a rapheless valve showing straight and narrow axial area and occluded areolae openings. A plain open girdle band is attached to the valve. **28, 29.** External views of rapheless valves showing straight and narrow axial area and areolae openings ranging in shape from rounded to transapically elongated and slit-like. Scale bars = 1 μ m.

slightly asymmetric and transversely expanded (Figs 12, 14, 16, 17, 19, 32, 33). Striae on both valves are radiate, 24–30 in 10 μ m, with approximately 40 areolae in 10 μ m. External areolae openings on raphe valve are mostly transversely rectangular-elliptic (Fig. 30). This character distinguishes *P. sacculum* from two similar and sometimes co-occurring species *P. microscopicum* (Cholnoky) S. Blanco (= *P.*



Figs 30–35. Three species of *Achnanthidiaceae* from Northeastern Siberia, SEM. **30–33.** *Psammothidium sacculum*, sample ANSP RU000384. **30.** External view of a raphe valve showing transversely rectangular central area, straight raphe with simple and very slightly expanded distal and proximal ends and transversely rectangular-elliptic areolae openings. **31.** Internal view of a raphe valve showing non-coaxial proximal raphe ends and occluded areolae openings. **32.** External view of a rapheless valve showing rhombic axial/central area and slit-like areolae openings. **33.** Internal view of a rapheless valve showing rhombic axial/central area and occluded areolae openings. A plain open girdle band is attached to the valve. **34.** *Psammothidium microscopicum*, sample ANSP RU000552 from the Jack London Lake, external view of a raphe valve showing apically elongated areolae openings. **35.** *Rossithidium petersenii*, sample ANSP RU000424, external view of a raphe valve showing small circular areolae near the raphe that gradually become slit-like near valve margin and much larger central area compared to *P. sacculum*. Scale bars = 1 μm .

curtissimum (J.R. Carter) Aboal) and *Rossithidium petersenii* (Hustedt) Aboal. *Psammothidium microscopicum* has apically elongated external areolae openings (Fig. 34), while *R. petersenii* has small circular areolae near the raphe that gradually

become slit-like near valve margin (Fig. 35). On rapheless valve of *P. sacculum* the external areolae openings are narrow transapically oriented slits (Fig. 32). Internal areolae openings are transversely rectangular and often almost confluent on rapheless valve. There is one row of areolae on the mantle, one areola per stria.

Distribution In the studied area, *Psammothidium sacculum* was found in four lakes of the Kolyma Lowland and in the Jack London Lake. These lakes had circumneutral water (pH 6.7-7.6) of relatively low mineral content (conductivity 20-110 $\mu\text{S}/\text{cm}$). This species reached the highest relative abundance (0.9%) in the sample RU000384 collected from a thermokarst lake with forested watershed, approximately 200 m in diameter with water pH of 7.6 and conductivity of 72 $\mu\text{S}/\text{cm}$.

Psammothidium obliquum (W. Gregory) Potapova comb. nov.

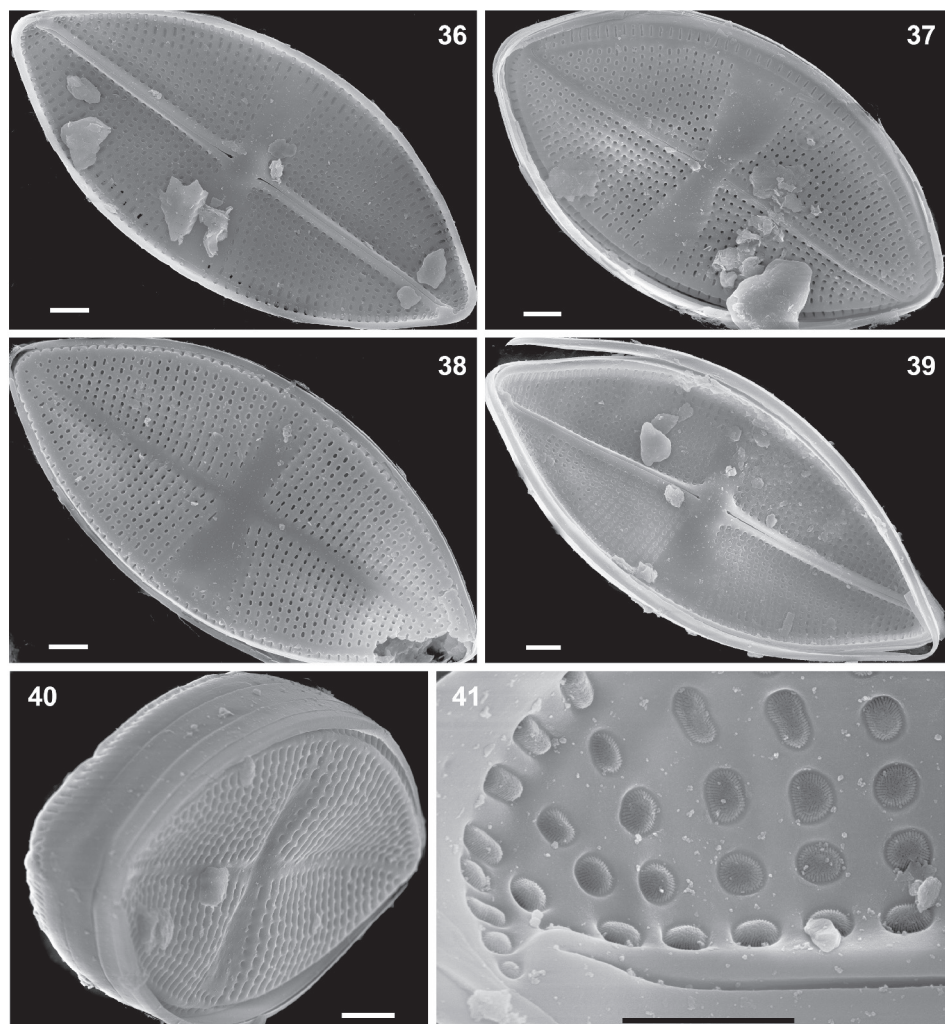
Figs 20-23, 36-41

Basionym. *Stauroneis obliquum* W. Gregory, Notice of some new species of British Fresh-water Diatomaceae. *Quarterly Journal of Microscopical Science*, new series, London 4: p. 10; pl. 1, fig. 35. 1856.

Synonyms. *Staurosigma obliqua* (W. Gregory) Rabenhorst 1864, *Navicula obliqua* (W. Gregory) Cleve 1891, *Schizonema obliquum* (W. Gregory) Kuntze 1898, *Eucoconeis onegensis* Wislouch & Kolbe 1916, *Achnanthes obliqua* (W. Gregory) Hustedt 1924, *Achnanthes onegensis* (Wislouch & Kolbe) Jousé 1939.

Morphology. The valves of *P. obliquum* in studied material are elliptic-lanceolate with slightly protracted apices, 12-14 μm wide and 22-30 μm long (Figs 20-23). The frustule is bent in a way characteristic for the genus *Psammothidium*, so that the external surface of the rapheless valve is in general concave, although the rapheless valve has a rather complex relief with depressions near both valve apices and depressed central area (Fig. 40). The raphe is oblique to the apical plane of the valve (Figs 20, 22, 36, 37) and has slightly expanded proximal ends and distal ends slightly turned to opposite sides (Fig. 37). Internal proximal raphe ends are turned to opposite sides as in all Achnanthidiaceae, and distally raphe branches end in helictoglossae (Figs 36, 39). The sternum of the rapheless valve is not oblique, runs from one valve apex to another and is only slightly curved (Figs 21, 23, 38). The axial area is narrow linear and central area is an asymmetrical, wedge-shaped fascia on both valves. It almost reaches the valve margin and is bordered by short striae. The striae are radiate, 19-22 in 10 μm on raphe valve and 16-20 on rapheless valve. There are approximately 20 areolae in 10 μm along the stria. External areolae openings are isodiametric near the raphe and become slightly transapically elongated towards the valve margins (Figs 37, 38). Internal areolae openings are circular to elliptic; they are occluded by hymens bearing perforations arranged in a pattern characteristic for Achnanthidiaceae (Fig. 41). There is one row of elongated areolae on the valve mantle, one areola per stria (Fig. 37).

Distribution. In the studied area, *Psammothidium obliquum* was found in five tundra lakes of the Kolyma Lowland where it was always found at low relative abundance (<0.5%) and in the Lake Chistoe, where it was reaching the relative abundance of 1.5%. These lakes had circumneutral to slightly alkaline water (pH 6.6-8.4) of relatively low mineral content (conductivity 13-190 $\mu\text{S}/\text{cm}$).



Figs 36–41. *Psammothidium obliquum*, SEM, sample RU000480, Chistoe Lake. **36, 39.** Internal views of raphe valves showing oblique raphes with non-coaxial proximal raphe ends and occluded areolae openings. In Fig. 39 an open plain girdle band is attached to the valve. **37.** External view of a raphe valve showing fascia-type asymmetric central area, oblique raphe with slightly bent distal and drop-like expanded proximal ends and areolae openings that vary in shape from almost circular near the raphe to slit-shaped towards the valve margin. A silica ridge is separating the row of elongated mantle areolae from the stria areolae on the valve face. **38.** External view of a rapheless valve showing a slightly sigmoid narrow axial area, fascia-like central area and areolae openings. **40.** External view of a frustule showing the relief of the rapheless valve and the girdle bands. Note the depressed central area and bent valve apices. **41.** Internal view of an apical portion of the raphe valve showing proximal raphe ends and internal areolae occlusions with a characteristic pattern of perforations. Scale bars = 2 µm in Figs 38–40, 1 µm in Fig. 41.

DISCUSSION

Morphological characters of the three species presented here are typical for the genus *Psammothidium*, but each species belongs to a different group of species within this diverse genus. *Psammothidium onufrii* is similar in valve size and outline, striae density and orientation and in most ultrastructural features to a diatom known as *Achnantes punctulata* Simonsen ex F. Hinz, Simonsen & R.M. Crawford and as invalidly published *Psammothidium punctulatum* (Simonsen) Bukhtiyarova & Round (Table 2). This latter species was described (Simonsen, 1959) and mostly reported from brackish waters (e.g., Snoejis & Kasperovičienė, 1996; Hay *et al.*, 2003) and occasionally from rivers and streams (Patrick & Freese, 1961; Bukhtiyarova & Round, 1996). Unlike *A. punctulata*, which has a distinct one-sided central area on both valves, *P. onufrii* either has an extremely small and hardly noticeable symmetrical central area (Figs 3, 5) or no central area at all (Figs 6, 9, 10, 28, 29) on the rapheless valve and has a large transapically elliptical “butterfly-shaped” and symmetrical central area of raphe valve (Figs 2, 4, 7, 8, 24, 25, 27). Occasionally, there is one shortened stria inserted between two middle striae on one side of the rapheless valve (Fig. 29), but this stria arrangement does not produce a central area reaching the valve margin as in *A. punctulata* (figs 54–56 in Bukhtiyarova & Round, 1996). Similarly to many other *Psammothidium* species, *P. onufrii* has a straight external raphe slit without terminal raphe fissures and proximal raphe ends positioned in a distinct drop-like depression or a groove on the external valve surface (Fig. 24). The T-shaped external proximal raphe ends (Fig. 24) have not been previously reported in this genus, possibly because their small size.

Based on morphological similarity, *P. onufrii* may be related to *A. punctulata*. Another similar species has been illustrated by Lange-Bertalot & Krammer (1989, pl. 40, fig. 18) from a marine sample from Lysekil, Sweden. This latter undescribed species has a symmetrical central area on the raphe valve, but this area is much smaller than in *P. onufrii*. The striae and areolae are much denser in this diatom than in both *A. punctulata* and *P. onufrii*. *Psammothidium kryophilum* (J.B. Petersen) E. Reichardt is another species that shares several characters with *P. onufrii* (Table 2). It has, however, considerably lower striae density (20–24 in 10 μm), curved distal raphe ends and small circular external areolae openings (Reichardt, 2004; Wetzel *et al.*, 2015).

Achnanthes sacculus (correct spelling: *saccula*) was described by Carter in Carter & Bailey-Watts (1981) from the Shetland archipelago, and has never been studied with SEM. Lange-Bertalot & Krammer (1989, pl. 27, figs 20 and 20') published LM photographs of the holotype specimen, which is approximately 4 μm wide and 10 μm long and is slightly asymmetric similarly to the specimens from Siberian samples (Figs 11–16). They also published two SEM photographs of rapheless valves (pl. 37, figs 5, 6 in Lange-Bertalot & Krammer, 1989) of a diatom tentatively identified as “*Achnanthes* species aff. *saccula* und aff. *fulla* Carter and aff. *okamurae* Skvortzov”. These photographs show elliptic valves with small circular areolae, rhombic axial area and an interrupted marginal ridge, characteristic for *Psammothidium scoticum* (Flower & Jones) Bukhtiyarova & Round, the species unknown before 1989, but widely distributed in both Eurasia and North America. The SEM photographs presented here are, therefore, the first evidence of the ultrastructure of *P. sacculum*. Although the size and striation pattern of this species make it similar to a number of other *Achnanthidiaceae*, the larger valves of *P. sacculum* have a slight, but distinct asymmetry. Together with a relatively narrow

Table 2. Comparison of *Psammothidium onufrii* with similar species (*Achnanthes punctulata*, *P. kryophilum*) and *P. sacculum* with similar species (*P. levanderi*, *P. microscopium*, *Rossthidium petersenii*). RV – raphe valve; RLV – rapheless valve.

Species (data source)	Valve width (μm)	Valve length (μm)	Valve shape	RV: striae density (in 10 μm)	RV: central area	RLV: striae density	RLV: central area
<i>P. onufrii</i> (this study)	4-5.5	7.5-15	elliptic to lanceolate	28-32	transversely elliptic to rectangular, symmetric	26-31	absent or very small
<i>A. punctulata</i> (Simonsen, 1959; Patrick & Freese, 1961; Lange-Bertalot & Krammer, 1989; Krammer & Lange-Bertalot, 1991; Hinz et al., 2012)	4-7.5	7.5-22	elliptic to lanceolate	18-28	transversely rectangular or elliptic, strongly asymmetric	18-28	transversely rectangular, one-sided
<i>P. kryophilum</i> (Petersen, 1924; Lange-Bertalot & Krammer, 1989; Reichardt, 2004)	3.8-5.5	7.4-19	elliptic to elliptic-lanceolate	20-24	transversely rectangular	20-24	absent
<i>P. sacculum</i> (Carter & Bailey-Watts, 1981; Krammer & Lange-Bertalot, 1991; this study)	3.7-4.8	6-15	lanceolate	24-30	transversely rectangular, narrow	24-30	rhombic, continuous with axial area
<i>P. levanderi</i> (Hustedt, 1933; Krammer & Lange-Bertalot, 1991; Blanco et al., 2017; Heudre et al., 2017)	4.0-5.2	6-11	elliptic	22-28	transversely rectangular, narrow	22-28	rhombic to elliptic, continuous with axial area
<i>P. microscopium</i> (Cholnoky, 1959; Krammer & Lange-Bertalot, 1991; Blanco, 2016)	~3.5	5.5-7	elliptic	26-30	transversely rectangular, narrow	18-20	narrowly rhombic, continuous with axial area
<i>Rossthidium petersenii</i> (Hustedt, 1937; Lange-Bertalot & Ruppel, 1980; Krammer & Lange-Bertalot, 1991; Potapova, 2010)	4-5	8.5-42.5	linear-elliptic	27-36	transversely rectangular, wide	27-33	transversely rectangular

central area on the raphe valve, this makes them distinguishable, for example, from *Rossithidium petersenii* (Fig. 35). The relatively short valves of this latter species may be confused with longer valves of *P. sacculum* if the larger central area on the raphe valve and perfectly symmetrical outline are not taken into account. On the other hand, the relatively short valves of *P. sacculum*, when observed with LM, are extremely similar to *P. microscopicum* that has been recently shown to be conspecific with *P. curtissimum* (Blanco, 2016), a species commonly reported from cold-water lakes (e.g., Pienitz, 2018). There is a considerable overlap in most morphological characters observable with LM between these two species, such as size and shape of the valve, shape of the central and axial area and striae density and orientation (Table 2), and only the shape of external areolae openings, a character requiring SEM observation, sets these two species apart.

Psammothidium levanderi (Hustedt) Bukhtyarova is another species similar to *P. sacculum* in size and striation pattern (Hustedt, 1933; Heudre *et al.*, 2017). It has, however, elliptic valves and a very wide lanceolate to elliptic axial area on rapheless valve (Table 2).

Potentially conspecific with *Psammothidium sacculum* is *Achnanthes bergianii* Cleve-Euler described from Stockholm, Sweden (Cleve-Euler, 1953). The illustrations (fig. 556 in Cleve-Euler, 1953) show a diatom similar in size and other characters to *P. sacculum*, although the range of valve width (3.5–9 µm) is far exceeding that of *P. sacculum* and striae density (23 in 10 µm) is considerably lower compared to *P. sacculum*. The identity of *A. bergianii* is however impossible to establish as the type material is missing. *Psammothidium sacculum* appears to have a wide distribution in colder lakes of the Northern Hemisphere (Shinneman *et al.*, 2009; Pienitz, 2018), but none of the earlier reported occurrences have been documented by photographs.

Psammothidium obliquum comb. nov. has been originally described as *Stauroneis obliqua* from Loch Leven, Scotland (Gregory, 1856). The placement in *Stauroneis* was obviously due to the conspicuous transverse central area present on both valves. In 1916 this same diatom has been described again as *Eucoconeis onegensis* from the bottom sediments of Lake Onega (Onezhskoe Lake) in Russia by Wislouch & Kolbe (1916) who mentioned its extreme similarity to *Stauroneis obliqua*. Interestingly, Wislouch & Kolbe mentioned that they also found *S. obliqua* in the same locality, and the only character distinguishing these two taxa in their opinion was the presence of raphe on both versus one valve per frustule. They even expressed a suspicion that perhaps *S. obliqua* “does not exist at all”, but were uncertain about this because some frustules appeared to have raphe on both valves. Wislouch & Kolbe described several valves in which the raphe was “less developed” on one valve compared to another, and hypothesized that *Eucoconeis onegensis* evolved from *Stauroneis* by losing the raphe on one valve. In the light of the current knowledge of the evolution of monoraphid diatoms (Cox, 2006) it is clear that in some specimens of *P. obliquum* raphe slit is incompletely infilled by silica on the “rapheless” valve and this vestigial raphe may create an appearance of a biraphid diatom.

Wislouch & Kolbe (1916) also discussed the difficulty of generic placement of their new species. They admitted that it did not fit the description of any known genera and they eventually “had to place it in *Eucoconeis*”, at the same time acknowledging dissimilarity between this new diatom and all other known species of *Eucoconeis*. The placement of this genus in *Psammothidium* versus *Eucoconeis* may still be disputed as *P. obliquum* has distal raphe ends slightly curved in opposite directions similarly to all known species of *Eucoconeis*. Many representatives of

Psammothidium, however, also have distal raphe ends bent to opposite sides. In *P. helveticum*, for example, these bent raphe ends are quite long and obviously extend beyond the position of helictoglossae on the internal valve surface and thus are blind grooves on the valve surface or terminal raphe fissures (Bukhtiyarova & Round, 1996). But even in the type species of the genus, *Psammothidium marginulatum* (Grunow) Bukhtiyarova & Round the distal raphe ends are slightly bent to opposite sides. Such characters of *Eucocconeis* as the concave raphe valve, sigmoid twist of the valve and small areolae almost confluent on the internal valve surface are not present in *P. obliqua*, however. Its areolae are remarkably coarse and their internal openings are distant (Figs 36, 39). In fact, *P. obliqua* is rather morphologically similar to *P. harveyi* (Reimer) Potapova, a diatom known only from North America (Potapova, 2012). Although *P. harveyi* is much smaller in size than *P. obliquum* and its raphe-sternum is not oblique, it also has a fascia-like asymmetric central areas on both valves and coarse areolae. Moreover, the valve shape of *P. harveyi* and *P. obliquum* is remarkably similar.

The modern distribution of *Psammothidium obliquum* appears to be limited to northern Eurasia (Davydova, 1985; Krammer & Lange-Bertalot, 1991) and Alaska (Foged, 1981). In Northeastern Siberia it was previously reported from Lake Elgygytgyn (Kharitonov & Genkal, 2012) and other lakes of Chukotka Peninsula (Kharitonov, 2010). This species has been recorded in the Miocene deposits of Japan (Tanaka & Nagumo, 2006), the Pliocene of the west coast of Kamchatka Peninsula, Russia (Gleser *et al.*, 1974, pl. 75, fig. 15) and the Holocene sediments of two alpine lakes in Western North America (Johnson *et al.*, 2018). It is possible that the distribution range of this species has contracted in response to climate change and/or human impacts as such a distinct and robust diatom is unlikely to be missed in modern samples.

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