Vladinikolaevia, gen. nov. – a new enigmatic freshwater diatom genus (Cymbellaceae; Bacillariophyceae) from Mongolia

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Abstract: We studied a new freshwater cymbelloid diatom taxon collected from Mongolia with light and scanning electron microscopy. The monotypic genus *Vladinikolaevia* gen. nov., based on *V. mongolica* sp. nov, is described. The new genus is characterized by a combination of morphological features found in two well–known genera such as *Cymbella* and *Encyonema*. The raphe system is morphologically–similar to *Encyonema* but the presence of apical pore fields is similar to the genus *Cymbella* as presently circumscribed. There are other very interesting peculiarities found in *V. mongolica* sp. nov. that show it to be a distinct taxon. We discuss the morphology of this new genus in the context of valve morphogenesis and presence of primary and secondary valves. The description of this new genus from Mongolia supports our contention that Asia is home to many endemics, interesting and not yet described cymbelloid taxa.

Key words: Cymbellaceae, diatoms, new genus, new species, Vladinikolaevia, taxonomy

Introduction

Freshwater cymbelloid diatoms are characterized by their valves being asymmetrical about the apical axis, with or without apical pore fields (APF's), deflection of the raphe ends towards the dorsal or ventral margin, location and structure of the stigma(ta), and position and type of pore occlusions (Krammer 2002, 2003; Kulikovskiy et al. 2009, 2016; JÜTTNER et al. 2010b; KAPUSTIN et al. 2017). There was some reorganization of the group at the level of genus in the middle of the 19th century. Members of this group had originally been included in Cocconema Ehrenberg, Encyonema Kützing and Cymbella Agardh, which were separated by differences in growth habitat. Heiberg (1863) combined the three genera into Cymbella as he considered the growth habit character used to separate these taxa not sufficient for recognition at the genus level (KOCIOLEK & STOERMER 1988).

It was nearly 120 years later that the taxonomy and systematics of the group was again the focus of significant attention. Krammer (1982) re—split *Cymbella* into two subgenera, *Cymbella* and *Encyonema*, based on the ability to form stalks or mucilaginous tubes, respectively.

Encyonema was treated as a separate genus in KOCIOLEK & STOERMER (1988) in their analysis of the phylogenetic relationships among cymbelloid and gomphonemoid diatoms. They also found that Didymosphenia M. Schmidt in A. Schmidt et al., a genus with obvious gomphonemoid symmetry, was more closely related to Cymbella species, while the diatom genus Gomphocymbella O. Müller was more closely related to gomphonemoid diatoms. Reimeria was erected as a new genus by KOCIOLEK & STOERMER (1987) based on the type species Cymbella sinuata Gregory, but later shown to be morphologically more similar to gomphonemoid diatoms (SALA et al. 1993; LEVKOV & ECTOR 2010; KULIKOVSKIY et al. 2012, 2016).

Krammer & Lange-Bertalot (2000) treated *Cymbella* as three subgenera, *Cymbella*, *Encyonema* and *Cymbopleura* Krammer. Later, *Cymbopleura* was established as a separate genus (Krammer 1999, 2003). Krammer (2003) split *Gomphocymbella* and established two new genera, *Gomphocymbellopsis* Krammer (a genus that is part of the cymbelloid lineage) and *Afrocymbella* Krammer (for the gomphonemoid members, based on former *Gomphocymbella* taxa endemic to East African rift valley lakes), based on Kociolek & Stoermer's

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(1993) separation of the genus into two unrelated clades (Kociolek & Stoermer 1993; Krammer 2003).

Krammer (1997, 2003) contributed 6 new genera for the cymbelloid lineage (Pseudencyonema Krammer, Encyonopsis Krammer, Cymbellopsis Krammer, Delicata Krammer (now *Delicatophycus* M.J. Wynne 2019), Navicymbula Krammer, and Gomphocymbellopsis). Krsticiella was described by Levkov from ancient Lake Ohrid in 2007 and Kulikovskiy et al. (2012) described a few new species from Lake Baikal. JÜTTNER et al. (2010a) described *Oricymba* Jüttner, Krammer, Cox, Van de Vijver et Tuji based on the *Cymbella japonica* Reichelt in Kützing and later a few new species were described from Asia (Kulikovskiy et al. 2015, 2016; Zhang et al. 2015, 2016, 2018; RADHAKRISHNAN et al. 2018; Guo et al. 2021). Bahls (2015) described Kurtkrammeria Bahls on the basis a few species from the genus Encyonopsis. Kulikovskiy and his colleagues described Ochigma Kulikovskiy, Lange-Bertalot et Metzeltin, Khursevichia Kulikovskiy, Lange-Bertalot et Metzeltin and Celebesia Kapustin, Kulikovskiy et Kociolek (Kulikovskiy et al. 2012; Kulikovskiy & Kuznetsova 2016; Kapustin et al. 2017, respectively). Based on details of valve ultrastructure, we have gone from a single genus Cymbella (WILLIAMS et al. 1999; KAPUSTIN et al. 2017), to the group being comprised of 17 genera up to 2017. Later, Karthickia Kociolek, Glushchenko & Kulikovsky was described as an interesting genus from Southeast Asia (GLUSHCHENKO et al. 2019).

While this morphological diversity of freshwater cymbelloid diatoms has resulted in a large number of genera, the breakdown of a few groups within the Cymbellaceae proposed by Krammer (2003) is still intact. That is, we still recognize a group with apical pore fields (*Cymbella* and its relatives), a group without apical pore fields but with stigmata and ventrally–deflected external proximal raphe ends (*Encyonema* and its relatives), and a group without apical pore fields or stigmata, with dorsally–deflected external proximal raphe ends (*Cymbopleura* and its relatives). However, studies of the relationships among the expanded number of taxa

for the groups have not been undertaken. KOCIOLEK & STOERMER (1988), KEMARREC et al. (2011), KULIKOVSKIY et al. (2014) and NAKOV et al. (2014) have previously examined relationships of cymbelloid diatoms, and of the major subdivisions within this lineage, showing them to be more or less supported or equivocal in terms of representing natural groups.

A continuing study on the freshwater diatoms from Asia has yielded a taxon from Mongolia that resembles *Cymbella* in symmetry and the presence of apical pore fields, but exhibits a unique suite of features seen with both light and scanning electron microscopy. We present the species as new to science and describe a new genus, *Vladinikolaevia* gen. nov., and compare it with similar genera.

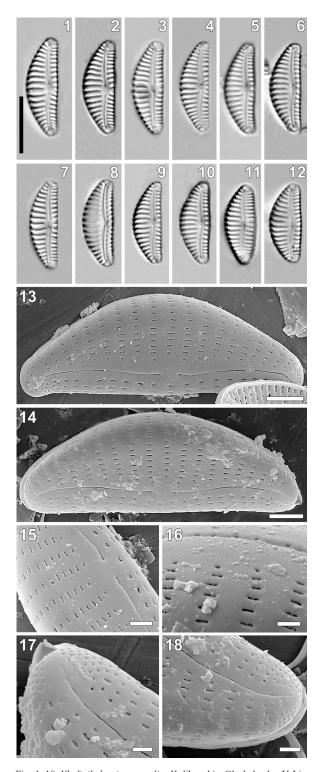
MATERIALS AND METHODS

Samples from Mongolia were collected by M.S. Kulikovskiy in 2015. It was collected from the Khövsgöl Lake, scraping of periphyton from stones and directly sampling benthos. A list of all samples examined in this study with their geographic position is presented in Table 1.

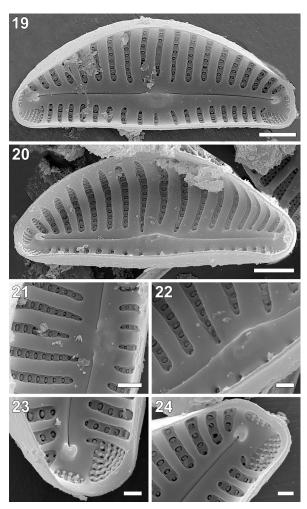
Samples were processed by means of a standard procedure involving treatment with 30% hydrogen peroxide (H_2O_2). Following treatment with H_2O_2 the samples were washed with deionized water. Permanent diatom preparations have been mounted in Naphrax® (Brunel Microscopes Ltd.). Light microscopic (LM) observations were performed with a Zeiss Axio Scope A1 microscope equipped with an oil immersion objective (×100, n.a. 1.4, differential interference contrast [DIC]) and an 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 an Eiko IB 3.

Table 1. List of collected samples.

Sample / Slide	Locality	Habitat	Coordinates	Altitude (m a.s.l.)	pН	WT (°C)	Conductivity (μS.cm ⁻¹)	Coll. date
02605	Khövsgöl Lake	benthos	50°59'22.8"N 100°42'30.4"E	1647	8.70	11.5	236	21.07.2015
MW-D 876s1	Khövsgöl Lake, Kheeguer Bay, central part	benthos	50°37'41.3"N 100°30'59.3"E	1647	8.78	16	234	22.07.2015
02685	Khövsgöl Lake	periphyton	50°47'12.9"N 100°31'50.2"E	1647	8.50	22	233	22.07.2015
02695	Khövsgöl Lake	periphyton	50°47'12.9"N 100°31'50.2"E	1647	8.58	12	234	21.07.2015
03009	Khövsgöl Lake	benthos	50°59'22.8"N 100°42'30.4"E	1647	8.70	11.5	236	21.07.2015



Figs 1–18. Vladinikolaevia mongolica Kulikovskiy, Glushchenko, Y. Liu et Kociolek sp. nov.: (1–12) LM, DIC; (13–18) SEM, external views, (13, 14) the whole valve, showing the distal raphe ends deflected to the ventral margin, (15) central area, showing the proximal raphe end and slit–like areolae, (16) valve margin, (17, 18) valves ends, showing the apical pore field on the both sides of the distal raphe end. Samples no 02605 (1, 2, 11), MW–D 876s1 (6, 9, 12), 02685 (7), 02695 (3, 4, 8), 03009 (5, 10). Figure 6 is of the holotype. Scale bars 10 μm (1–12), 2 μm (13, 14), 1 μm (15, 18), 0.5 μm (16, 17).



Figs 19–24. *Vladinikolaevia mongolica* Kulikovskiy, Glushchenko, Y. Liu et Kociolek sp. nov. Sample no MW–D 876s1. SEM, internal views: (19, 20) the whole valve; (21, 22) valve center, showing the elliptic projection covered the areola and intermissio; (23, 24) valve apex, showing the helictoglossa and bisected apical pore fields. Scale bars 2 μ m (19, 20), 1 μ m (21), 0.5 μ m (22–24).

RESULTS

Vladinikolaevia Kulikovskiy, Glushchenko, Y. Liu et Kociolek gen. nov. (Figs 1–24)

Description: Valves dorsiventral with a strongly convex dorsal margin and weakly concave or almost straight ventral margin, weakly convex in the middle. Externally, raphe lateral, undulate. Stigma lacking. Internally, raphe straight, internal proximal ends covered by a central flap; intermissio present. Externally, distal raphe ends curved towards the ventral margin, but do not bisect the porelli of the apical pore fields. The distal raphe ends terminate on the valve face. External proximal raphe ends curved slightly towards the dorsal margin. Striae uniseriate, with slit–like areolae. Apical pore fields are evident at both poles and on the ventral and dorsal sides of the valve. Areolae and porelli of the APF occluded internally.

Type species: *Vladinikolaevia mongolica sp. nov.* Kulikovskiy, Glushchenko, Y. Liu et Kociolek.

Etymology: Named in honor of Dr. Vladimir Alexandrovich Nikolaev (1938–2011), formerly of the Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg, for his many and varied contributions to our understanding of diatom taxonomy, systematics and evolution.

Vladinikolaevia mongolica Kulikovskiy, Glushchenko, Y. Liu et Kociolek sp. nov. (Figs 1–24)

Description: Valve dorsiventral with a strongly convex dorsal margin and weakly concave or almost straight ventral margin, weakly convex in the middle. Ends rounded, not protracted. Raphe lateral, undulate. Stigma is lacking. Length 13.9–17.6 μm, width 5.1–5.8 μm. Axial area linear, weakly expanded towards the central area. Dorsal striae parallel to weakly radiate in the middle of the valve becoming radiate towards the ends, 12-15 in 10 μm, ventral striae weakly radiate in the middle of the valve, almost parallel towards the ends, 14–16 in 10 μm. SEM: Externally, raphe undulate, distal raphe ends curved to the ventral margin, terminating on to the valve face (Figs 13, 14). Striae uniseriate, with slit-like areolae (Figs 13-18). APF are evident at both the ventral and dorsal sides of the valve, extending onto the valve face (Figs 17, 18). APF, with small and round porelli on both dorsal and ventral sides of the valve (Figs 17, 18). Internally, raphe straight, proximal ends small, straight to barely deflected dorsally (Figs 19, 21); intermissio present (Figs 19, 21). Interstriae are thickened (Figs 19–24). Helictoglossae slightly offset (Figs 19, 23, 24). Areolae and porelli of the APF occluded (Figs 23, 24).

Holotype (designated here): slide no. MW–D 876s1 (Fig. 6 represents the holotype), deposited in Diatom collection of the Department of Mycology and Algology, Faculty of Biology, M.V. Lomonosov Moscow State University (MW), Moscow, Russia.

Isotype: Slide no. MW–D 876s2, in collection of Maxim Kulikovskiy at the Herbarium of the Institute of Plant Physiology Russian Academy of Science, Moscow, Russia. **Type locality:** Khövsgöl Lake, Mongolia, benthos (50°37'41.3"N, 100°30'59.3"E).

Etymology: This species is named after the country where the type locality is located.

Ecology: The range of pH values (8.70–8.78) for these sampling sites indicates alkaline conditions. Conductivity ranged from 233–236 μS.cm⁻¹. This species was found in periphyton and benthos samples, and co–occurred with species of *Aulacoseira*, *Achnanthidium*, *Encyonema*, *Cymbopleura*, *Stephanodiscus*, and *Planothidium*.

Distribution: Type locality and sample numbers 02605, 02685, 02695, 03009.

DISCUSSION

Currently, the approach to freshwater cymbelloid diatom taxonomy and classification is based on the system developed by Krammer (2003), where certain morphological features have been identified as important (presence/absence of stigmata; presence/absence of apical pore fields; position of features relative to the 'dorsal' margin; Kociolek & Stoermer 1988; Krammer 2003; Cox & WILLIAMS 2006), though those hypotheses about the conservative nature of these features have not been put to formal testing. Other unique features or combinations of features have then been used to help diagnose other groups. The genus circumscriptions and descriptions of new genera have been made in reference to these 'important' features and the type species of the existing genera. Analyses of relationships within the group of apical pore field-bearing cymbelloid diatoms with molecular data are in a preliminary phase and have either confirmed the major genera recognized by Krammer or been equivocal with respect to them being monophyletic. However, taxon sampling of this lineage is severely limited relative to the size of the group, in terms of overall number of taxa (over 2,000 described species, varieties and forms; KOCIOLEK et al. 2021) and the number of genera represented in these analyses (less than 25% of the current described diversity at the level of genus.

In the context of Krammer's classification system, the one species we report on here from Mongolia differs from all other apical pore field—bearing freshwater cymbelloid diatoms. *Vladinikolaevia* gen. nov. as a genus share all morphological features special for cymbelloid diatoms. These are apical pore fields, dorsiventral symmetry, areolae with vola occlusion and raphe with distal and central raphe endings turned to dorsal side. Among many cymbelloid genera, previously described by us our new genus is similar to *Encyonema* in the shape of the valves and presence of the intermissio. However, *Encyonema* as a genus is characterized by absence of pore fields that is important delamination feature according to Krammer's circumscription.

Cymbella, Oricymba and Didymosphenia, all taxa with apical pore fields, have their pore fields uninterrupted by the external distal raphe ends, and the distal raphe ends are deflected towards the dorsal margin. Species of Oricymba and most species of Didymosphenia and Cymbella, have ventrally-placed stigmata that are quite distinct from one another (SCHMIDT 1899; KRAMMER 1982, 2002; Kociolek & Stoermer 1988; Jüttner et al. 2010a); in Vladinikolaevia, stigmata are absent. Many species of Cymbella and Didymosphenia have occluded areolae, with volae projecting into the lumen of the areolae (DAWSON 1973a, b; KOCIOLEK et al. 2000; Krammer 1982, 2002; Metzeltin & Lange-Bertalot 2014; OGNJANOVA-RUMENOVA et al. 2017). Exceptions to this can be found in C. cymbiformis Agardh, the type species of the genus, as well as C. lanceolata (Agardh) Agardh and C. schmimanski Krammer. In Oricymba striae are composed of slit–like areolae with dentate occlusions (JÜTTNER et al. 2010a; KULIKOVSKIY et al. 2015, 2016; ZHANG et al. 2015, 2016, 2018; RADHAKRISHNAN et al. 2018; Guo et al. 2021).

The Vladinikolaevia gen. nov. species is differentiated from dorsiventral freshwater, apical pore field-bearing or apical pore-free cymbelloid diatoms, as shown in Table 2. But we must note that our new genus is characterized such feature as curving of distal raphe endings to narrow ventral side (secondary side) and proximal raphe branches slightly turned to the wide dorsal side (primary side). This correspondence of wide dorsal side (primary side) and narrow ventral side (secondary side) arises during the ontogeny of cells belonging also to Encyonema (Mann 1981). However, *Encyonema* as a genus is characterized by absence of apical pore fields. In Cymbella proximal and distal raphe endings curved to the wide dorsal side that phylogenetically is the secondary side but this genus has pore fields (MANN 1981). In Vladinikolaevia gen. nov. we have what appears to be an intermediate morphological and phylogenetic stage between Cymbella and Encyonema. Further phylogenetic analyses are required to confirm this 'intermediate' systematic position of Vladinikolaevia gen. nov.

The discovery of an undescribed genus of freshwater cymbelloid diatom from Asia underscores Kociolek's (2019) report that this lineage has several endemic genera on the continent. KOCIOLEK (2019) noted Oricymba, Celebesia and several from Lake Baikal (Kulikovskiy et al. 2012; POMAZKINA & RODIONOVA 2014), for a total of 7 cymbelloid genera that are known only from Asia. Despite the importance of the region to the evolution of the lineage, there are almost no molecular sequence data for freshwater cymbelloid taxa from Asia (Kociolek 2019). Together with the previously described genus Karthickia, our new genus shows that during a comprehensive investigation of a previously poorly-studied area we can find new taxa with intermediate morphology between known and well-established taxa. These data demonstrate the key linkages between understanding diatom biodiversity, morphological diversity and phylogeny.

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Pore areolae elongated slit- occlusions like; internally areolae	Stigma absent	Apical pore present in both ends field	Distal raphe ventrally defle ends primary side)	Proximal dorsally deflects raphe ends secondary side)	Reference This study	Vladinikol
areolae elongated slit– like; internally areolae occluded by vola		ooth ends	ventrally deflected (to the primary side)	dorsally deflected (to the secondary side)		<i>tevia</i> gen. nov.
small slit-like foramina of the areolae externally, individual areola occluded internally by	present at the dorsal side (secondary side)	absent	dorsally deflected (to the secondary side)	ventrally deflected (to the primary side)	KOCIOLEK et al. 2019	Vladinikolaevia gen. nov. Karthickia Kociolek, Glushchenko et Kulikovskiy
areolae round, oval or elongated slit-like external openings with flap-like occlusions;	present at the ventral side (primary side) or absent	present in both ends	dorsally deflected (to the secondary side)	dorsally deflected (to the secondary side)	Krammer 2002; Kulikovskiy et al. 2016	<i>Cymbella</i> Agardh
small slit—like foramina of the arcolae exter- nally; internally arcolae opening	absent	absent	dorsally deflected (to the secondary side)	ventrally deflected (to the primary side)	Krammer 2003; Kulikovskiy et al. 2016	<i>Cymbopleura</i> (Krammer) Krammer
small slit—like or round foramina of the areolae externally; internally are- olae opening	present at the dorsal side (secondary side) or absent	absent	ventrally deflected (to the secondary side)	dorsally deflected (to the primary side)	Krammer 1997; Kulikovskiy et al. 2016	Encyonema Kützing
areolae open externally and internally by elongated slits and are partially occluded by dentate projections	present at the ventral side (primary side)	present in both ends	dorsally deflected (to the secondary side)	ventrally deflected (to the primary side)	JÜTTNER et al. 2010; KULIKOVSKIY et al. 2015	<i>Oricymba</i> Jüttner et al.
areolae open externally and internally	present at the ventral side (primary side) or absent	absent	dorsally deflected (to the secondary side)	dorsally deflected (to the secondary side)	Krammer 2003; Le Cohu et al. 2018	Delicatophycus M.J. Wynne

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