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## ***Pantocsekiella*, a new centric diatom genus based on morphological and genetic studies**

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The paper is dedicated for 100th death anniversary of the famous Hungarian diatomologist József Pantocsek (1846-1916).

### **Abstract**

Previous morphological studies showed that the description of the *Cyclotella* genus was too general and according to new morphological criteria new genera were established based on both recent and fossil taxa ( e.g. *Discostella*, *Handmannia*, *Puncticulata*, *Tertiarius*). Furthermore, previous molecular biological investigations proved that the *Cyclotella* genus was not monophyletic. Integrating the above mentioned knowledge the former *Cyclotella* genus has been split into 4 genera (*Cyclotella* s.s., *Discostella*, *Tertiarius* and *Lindavia*). Based on the position of rimoportula *Lindavia* genus was formed for involving the species of both the *Cyclotella ocellata* and *C. bodanica* lineages. Our morphological and molecular (genetic distance and phylogenetic analyses of *rbcL* and 18S rDNA sequences) investigations suggested that “*Lindavia/Cyclotella ocellata* group” could be raised from the *Lindavia* as a separate genus. Its distinctive morphological features are the followings: striae unequal in length, central area without areolae. We describe the new genus *Pantocsekiella* gen. nov. and we transferred several *Lindavia* taxa into it. We also provide an amended diagnosis for the genus *Lindavia*.

**Key words:** *Lindavia*, morphology, *Pantocsekiella* gen. nov., *rbcL*, taxonomy, 18S rDNA

### **Introduction**

The genus *Cyclotella* (BRÉBISSON 1838: 19) including many later described and morphologically diverse *Cyclotella* species was considered as a unitary genus for a long time (see for example KRAMMER & LANGE-BERTALOT 1991). Within the genus *Cyclotella* some different morphological groups were previously recognized by several authors: LOWE (1975), MCFARLAND & COLLINS (1978), SERIEYSSOL (1981), SERVANT-VILDARY (1986), LOGINOVA (1990). Later, more and more taxonomists believed that the genus description is too general and based on new morphological criteria (e.g. shape and position of rimoportula) several new genera were established on the basis of special characteristics of recent and fossil taxa as well. By this way the genera *Tertiarius* HÅKANSSON et KHURSEVICH (1997: 21), *Puncticulata* HÅKANSSON [2002: 21, 112 – later corrected as *Handmannia* PERAGALLO in Handmann (1913: 14) based on priority of description – see more detail in Khursevich & Kociolek 2012; and as *Lindavia* (SCHÜTT 1899a: 220) De Toni & Forti (1990: 553) regarding both *Handmannia* and *Puncticulata* illegitimate by NAKOV *et al.* 2015 based on the nomenclatural priority], and *Discostella* HOUK & KLEE (2004: 204–205) were established.

Using molecular methods MEDLIN & KACZMARSKA (2004) clearly showed that the order Centrales was not monophyletic and two main clades were separated. A recent study (ALVERSON *et al.* 2007) reconstructing the phylogenetic relationships within the order Thalassiosirales showed that the genus *Cyclotella* (KÜTZING)

BRÉBISSON (1838: 19) was not monophyletic. In their four-gene phylogenetic tree *Cyclotella ocellata* PANTOCSEK (1901: 104) and *C. bodanica* EULENSTEIN in GRUNOW (1878: 126) were clearly separated from the *C. meneghiniana* KÜTZING (1844: 50) group. Jung *et al.* (2010) pointed out that *C. bodanica* and *C. ocellata* belonged to *Discostella* or to a new genus from a genetic point of view, but they did not study them morphologically. KHURSEVICH & KOCIOLEK (2012) summed up and developed further these morphological groups and a complex diagnosis has been proposed based on the following key characteristics: a) the structure of alveolae, b) the structure, number and location of rimoportula and c) the structure of striae. Based on these criteria 12 morphological groups of *Cyclotella* taxa were differentiated. The 6th and 7th group has been taken for our paper and only species morphologically similar to *Cyclotella ocellata* are included. *Cyclotella ocellata* and *C. tripartita* HÅKANSSON (1990a: 78) are from group 6. The following characterization is given for these two species by KHURSEVICH & KOCIOLEK (2012): “These species have circular valves, with slightly or distinctly radially undulate central area. The latter with a pattern of three to nine larger lacunae (depressions) alternating with papillae (as in *C. ocellata*), or lacunae and papillae are arranged in 6–12 triangular sectors (as in *C. tripartita*), .... Near the center at least from one to several (up to 11) valve face fuloportulae with 2 satellite pores.... Usually one sessile rimoportula is present in the submarginal zone of the valve face or at the end of the central lamina. Alveolae simple. ....” *Cyclotella costei* DRUART et F. STRAUB (1988: 182), *C. gracilis* NIKITEEVA et LIKHOSHWAY (1994: 350), *C. kuetzingiana* THWAITES (1848: 169), *C. rossii* (GRUNOW) HÅKANSSON (1990b: 266–267), *C. schumannii* (GRUNOW) HÅKANSSON (1990b: 267) are from group 7. The characterisation is the following: “Valves circular to round, with the central area from nearly flat to more or less transversely undulate, having small and large lacunae (depressions), sometimes they lacking. Besides one to several (up to 5) valve face fuloportulae with 2 satellite pores are present near the center, ....and a single sessile rimoportula is positioned in the submarginal zone of the valve face. ... Striae of equal or unequal length. Alveolae simple. ...”

Previous studies showed that *C. ocellata* and related species form an independent group separately from the *C. meneghiniana* group [*C. meneghiniana* and related species e. g. *C. atomus* HUSTEDT (1937: 143), *C. distinguenda* HUSTEDT (1927: 320), *C. striata* (KÜTZING) GRUNOW in CLEVE et GRUNOW (1880: 119), *C. stylorum* BRIGHTWELL (1860: 96), *C. cryptica* REIMANN *et al.* (1963: 82), *C. gamma* SOVEREIGN (1963: 350)]. Since Håkansson (2002) drifted *Cyclotella bodanica* into the genus *Puncticulata*, Alverson (2014) featured these species as *Puncticulata ocellata* and *P. bodanica* (GRUNOW in SCHNEIDER) HÅKANSSON (2002: 119) in his phylogenetic tree.

NAKOV *et al.* (2015) transferred *C. ocellata* and related species together with several other centric diatoms (e.g. *Handmannia* species) to *Lindavia* genus on the bases of rimoportula position, but they raised that future phylogenetic analysis may support the splitting of *Lindavia* into some other genera.

We think that morphological features indicate that taxa transferred to *Lindavia* belong to two different genera. Based on current molecular information *Cyclotella/Lindavia ocellata* could be the congener of *Handmannia bodanica*. We used all 18S rRNA gene and *rbcL* sequences and morphological data from all available sources (clonal cultures, environmental samples, isolated cells, public database and previous publication) to show the distance between the two groups. Our results lead to the description of a new genus, *Pantocsekiella*. The additional aim of this study was to describe the valve morphology and ultrastructures of this new genus.

## Material and methods

Samples from several sources (Table 1.) were subjected to morphological and molecular investigation. The exception was Lake Balaton of which environmental sample was used only in morphological study.

**Sampling and sample processing:**—Phytoplankton samples were dipped ~20 cm below the water surface. From Lake Geneva, an integrated sample (between 0-20 m depths) was taken above the deepest point of the lake..

Two clonal cultures of *Lindavia (Handmannia) compta* (EHRENBERG) KOCIOLEK et KHURSEVICH emend GENKAL (2013: 347) isolated from Lake Stechlin and Lake Nehmitz (Germany) and one culture of a member of the *Cyclotella comensis* group (identified as *Cyclotella costei* DRUART & F. STRAUB 1988: 182–183, on morphological base) from Lake Geneva were established. Clonal cultures were established from single living cells isolated from unfixed material. For culturing conditions see KISTENICH *et al.* (2014). Molecular results of our previous studies (KISTENICH *et al.* 2014, DULEBA *et al.* 2015) were used for comparison; information about details of culturing, molecular methods and phylogenetic analyses are available therein.

Clonal cultures were divided to two subsamples: one for morphological observation and one for DNA analysis. Subsamples for morphological observations were centrifugated to concentrate the frustules that were cleaned with hydrochloric acid and hydrogen peroxide, subsequently washed in distilled water, filtered through a

3 µm-mesh polycarbonate membrane, fixed on SEM stubs and coated with gold. The subsamples for DNA analysis were processed in a short time or were preserved in absolute ethanol (Reanal).

**Morphological observations:**—Morphological observations were done by light microscopy (Olympus IX-70). In addition, the fine structure of the diatoms was observed with Zeiss EVO 10 and Hitachi S-2600N scanning electron microscopes. 30 SEM micrographs were taken for morphological analyses from clonal cultures of *Handmannia compta* from Lake Stechlin and Lake Nehmitz.

**Molecular methods:**—Molecular analyses were performed by various authors, therefore methods differed.

Genomic DNA of clone cultures S1 (Lake Stechlin) and NE1 (Lake Nehmitz) was extracted using a QIAGEN DNeasy® Plant Mini kit. For DNA amplification, we used the primers D512for and D978rev (ZIMMERMANN *et al.* 2011) for partial 18S rDNA regions (V4) and Wawrik for and Wawrik rev (WAWRIK *et al.* 2002) for partial *rbcL* DNA. Five microliters of template DNA were mixed with 30 µL ddH<sub>2</sub>O, 2.25 µL bovine serum albumin (BSA; 10 µg mL<sup>-1</sup>), 2.7 µL MgCl<sub>2</sub> (25 mM), 1.35 µL dNTPs (10 mM), 1.8 µL of forward and 1.8 µL of reverse primer (10 µM), 4.5 µL polymerase buffer (10×) and 0.6 µL Taq DNA polymerase (5U µL<sup>-1</sup>) for the polymerase chain reaction (PCR). Values in parentheses indicate the original concentrations of ingredients. PCR programmes were used according to ZIMMERMANN *et al.* (2011) and WAWRIK *et al.* (2002). PCR products were visualized in 2% agarose gel and relevant bands were cut out. Gel extraction and purification of PCR products was conducted by applying a QIAquick® Gel Extraction kit. Final products were sequenced twice (forward and reverse) with an ABI/Hitachi 3130xl Genetic Analyzer (Tokyo) using Sanger sequencing (Sanger *et al.* 1974) with PCR primers as sequence primers.

To extend sequences of the culture S1, additional PCRs were performed using 1F and 1528R primers (MEDLIN *et al.* 1988) for 18S rDNA and *rbcL*66F (ALVERSON *et al.* 2007) and dp7R (DAUGBJERG & ANDERSEN 1997). For *rbcL* reaction, the mixture contained 1.25 U DreamTaq™ DNA Polymerase (Thermo Scientific), 200 mM of each deoxynucleoside triphosphate (Fermentas), 1X DreamTaq Buffer (Thermo Scientific), 0.325 µM of each primer, 1 µL template in a total volume of 25 µL. PCR amplification used the following cycles: initial denaturation at 98 °C for 4 min, 32 cycles at 94 °C for 1 min, 56 °C for 30 sec, 72 °C for 1.5 min, and a final extension at 72 °C for 10 min. For 18S rDNA reaction, the mixture contained 0.05 U HotMaster Taq Polymerase (5Prime), 0.2 mM of each deoxynucleoside triphosphate (5Prime), 1X DreamTaq Buffer (5Prime), 0.2 µM of each primer, 1 µL template in a total volume of 50 µL. The heat protocol of this reaction was the following: initial denaturation at 94 °C for 5 min, 35 cycles at 94 °C for 1 min, 58 °C for 2 min, 72 °C for 2 min, and a final extension at 72 °C for 10 min. Sequencing reactions with 1F, 1528R (MEDLIN *et al.* 1988) Sk-155R (DULEBA *et al.* 2014) for 18S rDNA and *rbcL*66F (ALVERSON *et al.* 2007) and dp7R (DAUGBJERG & ANDERSEN 1997) for *rbcL* and capillary electrophoreses were performed by Biomi Ltd.

Cells were harvested from the *C. costei* culture by centrifugation. After lysing the cells, nucleic acids were co-precipitated using GenElute™-LPA (Sigma-Aldrich) according to the Manufacturer's instructions, and dissolved in TE buffer. Two gene fragments were amplified in PCR: partial *rbcL* and 18S rDNA. All PCRs were performed using the 1F and 1528R primers (MEDLIN *et al.* 1988) for 18S rDNA, DPrbcL1 and DPrbcL7 primers (DAUGBJERG & ANDERSEN 1997) for *rbcL* and according to the authors' specifications in a PCR thermal cycler (T personal, Biometra, Göttingen, Germany). Additional internal sequencing primers (528F for 18S rDNA, ELWOOD *et al.* 1985, NDrbcL6, DAUGBJERG & ANDERSEN 1997, 15R, 16F for *rbcL*, JONES *et al.* 2005) were used to retrieve the complete sequences of *rbcL*. Sanger sequencing was performed by GATC (Konstanz, Germany).

**Phylogenetic analysis:**—18S rDNA and *rbcL* sequences were aligned to sequences in National Center for Biotechnology Information (NCBI) GenBank database using basic local alignment search tool (BLAST, ALTSCHULE *et al.* 1990) in order to find sequences showing highest similarity with them. The search was performed in the Nucleotide collection database (nr/nt) using Standard Nucleotide BLAST program, megablast (highly similar sequences) algorithm with the default parameter settings.

Beside sequences from samples listed in Table 1, additional, unpublished and published sequences were used (Table 2). These included sequences of a clonal culture from Lake Balaton.

Within and between groups mean uncorrected p-distance values were calculated with MEGA 6 (TAMURA *et al.* 2013). Sequences from the same genus were treated as a group.

The *rbcL* sequences were aligned by codon to sequences downloaded from GenBank using Clustal W implemented in MEGA 6 (TAMURA *et al.* 2013). The 18S rDNA sequences were aligned by secondary structure using SILVA Incremental Aligner (SINA, PRUESSE *et al.* 2012, available at <http://www.arb-silva.de/aligner/>). 'Find best DNA models' option in MEGA6 was used to determinate the most appropriate substitution model for DNA sequence evolution of each gene. The models proposed by the software based on Bayesian Information Criterion were Tamura-Nei model with gamma distribution for 18S rDNA (TAMURA & NEI 1993) and General Time Reversible (GTR) model with gamma distribution and invariant sites for *rbcL* (RODRIGUEZ *et al.* 1990). Maximum likelihood phylogenetic analyses were run on single-gene datasets in MEGA 6 (TAMURA *et al.* 2013). Bootstrap test was performed in 500 replicates. Bayesian analyses were run on single and combined datasets. Data

were partitioned by genes. Posterior probability of distribution was estimated using Metropolis-coupled Markov Chain Monte Carlo (MCMC) as implemented in MrBayes 3.2 (RONQUIST *et al.* 2012). Two runs were started in which a cold and three heated chains were run. Samples were taken in every 100<sup>th</sup> cycle, 25% of the samples were discarded as burnin. The average standard deviation of split frequencies across independent analyses was used as convergence diagnostic, the analysis was continued until this value decreased below 0.01 or it was between 0.01 and 0.02, but it fluctuated around a value. For all parameters potential scale reduction factor (PSRF) was close to 1, average ESS values were higher than minimum ESS values in all analyses.

## Results

**Morphological investigation:**—Two clonal cultures of *Lindavia (Handmannia) comta* isolated from Lake Stechlin (Figs. 1, 2) and Lake Nehmitz (Figs. 3, 4) were newly investigated. Based on these cultures, frustules are disc-shaped; valves are circular, 6–12.9 µm in diameter. The central area of the valve face can be relatively small or large, not depending on the diameter; it is flat or slightly concentrically undulate, convex or concave, externally smooth to colliculate, sometimes radially wrinkled. Striation is fine, 7–9 striae are in 10 µm and unequal in length, central area is polygonal. The striation pattern has a complex alveolar structure; the internal alveolar openings are with alternating 3–7 thin costae between 2 thickened ribs. Each thickened costa bears a marginal fultoportula near the valve margin with two satellite pores positioned laterally. Areolae and central fultoportulae are arranged in radial rows or scattered. The central fultoportulae, externally with a small opening and internally with three satellite pores, are scattered among areolae or are inserted within the radial rows of areolae in the form of 1 ring. Isolated areolae are often present in the valve centre. 1–2 rimoportulae are situated on the valve face in the submarginal zone. The external openings are situated on a hyaline rib formed at the end of shortened stria internally with a sessile labium with a radial oblique or circumferential slit.

**Genetic investigation:**—From the clonal culture of *C. costei* full length of *rbcL* (1500 nt) and almost full length of 18S rDNA (1699 nt) were acquired. From the two *Lindavia (Handmannia) comta* cultures first partial sequences were gained [*L. comta* cultures: *rbcL*: 506 nucleotides (nt), 18S rDNA: 391 and 399 nt] but later sequences of the culture from Lake Stechlin were extended (*rbcL*: 1407 nt, 18S rDNA: 1667 nt).

**BLAST:** According to the BLAST search *rbcL* sequence of *C. costei* from Lake Geneva showed the highest similarity with *C. ocellata* strain LB8 (99%, 1427 identical nucleotides at the compared 1438 sites; our sequence proved to be too long compared to the ones in GenBank). Its 18S rDNA sequence also showed 99% similarity with *C. ocellata* (1685 identical nucleotides and two gaps at 1699 sites), but reached higher scores (99% similarity, 1688/1699 nt with two gaps) with a group of *Stephanodiscus* EHRENBERG (1845: 72) and *Cyclostephanos* ROUND ex THERIOT *et al.* (1987a: 346) sequences.

There was not any difference between the two cultures of *Lindavia (Handmannia) comta* (EHRENBERG) KOCIOLEK et KHURSEVICH emend GENKAL (2013: 347). NAKOV *et al.* in the compared regions of either 18S rDNA or *rbcL*. According to the BLAST search extended *rbcL* sequence of the *L. comta* from Lake Stechlin showed 98% similarity with four *Stephanodiscus* sequences (1372–1375 identical nt at 1407 sites) and *Lindavia (Handmannia) bodanica* (EULENSTEIN ex GRUNOW) KOCIOLEK et KHURSEVICH in KHURSEVICH et KOCIOLEK (2012: 339) NAKOV *et al.* (2015: 254) J98-1 strain (1371/1404 nt). Extended 18S rDNA sequence of *L. comta* from Lake Stechlin showed 99% (1642–1652/1667 with one gap) similarity several *Stephanodiscus* and *Cyclostephanos* sequences [including a *Stephanodiscus* strain later renamed as *Praestephanos triporus* (GENKAL & G.V. KUZMIN) TUJI & J.-S. KI in Tuji *et al.* (2014: 135)] and with *L. bodanica* J98-1 (1648/1667 nt with one gap) and *C. ocellata* LB8 (1645/1667 nt with one gap).

The p-distance values were calculated on two datasets. First, both short and long sequences (those of *C. costei* and *L. comta* cultures and the ones listed in Table 1) were also involved. Second, the short sequences were excluded, thus much longer regions could be compared. In general, the p-distance values were lower in longer region of the fewer sequences than in shorter region of the more sequences.

**Mean distances within groups:** Based on both of all and only the long *rbcL* the mean distance within the *Pantocsekiella* genus (all sequences: 0.29%, only the long ones: 0.84%) was lower than within other groups (all sequences: 0.96–6.48%, only the long ones: 0.95–7.50%).

Based on all 18S rDNA the mean distance of this group (0.49%) was relatively low value, two genera [*Bacterosira* Gran (1900: 114), *Stephanodiscus*, *Cyclostephanos*] showed lower (0–0.46%), five genera [*Shionodiscus*, *Lindavia (Handmannia)*, *Discostella*, *Skeletonema* GREVILLE (1865: 43), *Cyclotella*], showed higher values (0.55–2.80%). Considering only the long sequences, *Pantocsekiella* had higher value (0.58%) than *Stephanodiscus*, *Bacterosira* and *Cyclostephanos* (0.11–0.23%) and lower than *Shionodiscus*, *Discostella*, *Lindavia*, *Cyclotella*, *Skeletonema* (0.96–2.12%).

**Mean distances between groups:** The *rbcL* showed higher genetic distance between the proposed genus *Pantocsekiella* and *Lindavia (Handmannia)* than *Stephanodiscus* – *Lindavia (Handmannia)*, *Stephanodiscus* –

*Cyclostephanos* distances with and without short sequences. Based on 18S rDNA the *Pantocsekiella* – *Lindavia* (*Handmannia*) distance was higher than *Cyclostephanos* – *Pantocsekiella*, *Stephanodiscus* – *Pantocsekiella*, *Cyclostephanos*-*Stephanodiscus* distance in both analyses. (These distances are indicated with italic numbers on Table 3-4.).

**Phylogenetic analyses:** To improve the reliability of phylogenetic trees short sequences were excluded from these analyses. The phylogenetic tree based on single (Supplementary Figs 1-4.) and combined datasets (Fig. 5) showed that of the *Pantocsekiella ocellata* and *P. comensis* sequences formed a cluster clearly separated from the clade constituted by the *L. comta* and *L. bodanica* sequences.

The genus *Pantocsekiella* appeared to be monophyletic on all trees, therefore establishment of a new genus is reasonable. The closest relative of the *Pantocsekiella* genus was *Lindavia* (*Handmannia*) (Fig. 5, Supplementary Figs 1-4).

## New genus description

### *Pantocsekiella* K.T. KISS et ÁCS gen. nov.

**Type species:** *Cyclotella ocellata* PANTOCSEK (1901), Die Kieselalgen oder Bacillarien des Balaton, p 104, pl. 15, fig. 318.

**Diagnosis:**—Frustules are disc-shaped, solitary, seldom in short chains. Valves circular or slightly quadrangular, the valve face divided into a polygonal central area and a striated marginal one. The polygonal central area is more or less flat or radially undulate (3–5 undulation) or slightly tangentially undulated. The undulated forms with a pattern of three or more small or large alternating lacunae with or without papillae; this pattern is arranged in 6 or more triangular sectors, or the central area with numerous randomly located lacunae and small punctae which do not penetrate the cell wall. The central area can be relatively small or large, not depending on the diameter. The marginal part of the valve is structured by alveolate striae externally, separated by hyaline strips, striae are straight, unequal in length and a few of them are bifurcated. Simple alveolae are present within the marginal area internally. The inner aperture of the alveolae can be round or elongated. Costae are usually equal in length but those bearing a fuloportula are often shorter. The valve has one or a few rimoportulae situated in the submarginal zone on the costa or just below it (sessile internally and round aperture externally); the orientation of the lip varies. Generally, every third to fifth interstria bears a marginal fuloportula but it may occur on each to every 6th interstria. Their internal openings are surrounded by two satellite pores. Valve face fuloportulae (VFP: 1–4) are usually surrounded by two (1–3) satellite pores. In many cases the external openings of VFP are very difficult to observe, because many valves have some punctae irregularly arranged in the central part. Small granules are frequently observed on the interstriae near the margin and found sporadically on the whole valve face.

*Cyclotella* species differ from *Pantocsekiella* in arrangement of marginal fuloportulae and rimoportula(e). Rimoportula(e) of *Cyclotella* situated in the ring of marginal fuloportulae and striae (costae) are equal in length.

*Lindavia* species differ from *Pantocsekiella* in structure of central area. *Lindavia* species have areolae in central area and complex alveolar structure, *Pantocsekiella* and *Cyclotella* never.

#### **Systematic emplacement:**

Class Coscinodiscophyceae ROUND et CRAWFORD

Subclass Archaeogladiosphyceae NIKOLAEV et HARWOOD

Order Stephanodiscales NIKOLAEV et HARWOOD

Family Stephanodiscaceae GLESER et MAKAROVA

Genus *Pantocsekiella* K.T. KISS et ÁCS gen. nov.

**Etymology:**—The new genus has been named after József Pantocsek, the worldwide known famous Hungarian diatomologist, who originally described *Cyclotella ocellata*.

**Typus generis:** *Pantocsekiella ocellata* (PANTOCSEK) K.T. KISS et ÁCS, *comb. nov.*

*Pantocsekiella ocellata* (PANTOCSEK) K.T. KISS et ÁCS, *comb. nov.*

**Basionym:**—*Cyclotella ocellata* PANTOCSEK (1901), Die Kieselalgen oder Bacillarien des Balaton, p 104, pl. 15, fig. 318.

**Synonyms:**—*Cyclotella crucigera* PANTOCSEK 1901, p. 104, pl. 15, fig. 325; *Cyclotella kuetzingiana* var. *planetophora* FRICKE in SCHMIDT 1900, pl. 222, figs. 9–12; *Cyclotella tibetana* HUSTEDT 1922a, p. 117; pl. 9, fig. 19; *Cyclotella trichonidea* var. *parva* ECONOMOU-AMILLI 1979, p. 470, figs. 21–25. *Lindavia ocellata* (PANTOCSEK) NAKOV *et al.* 2015, p. 256.

**Type locality:**—Lake Balaton, Hungary.

**General description:**—Frustules are disc-shaped, valves are circular, rarely slightly quadrangular (in Lake Visovac). The polygonal central area of valve face is more or less flat or radially undulate, 3–5 undulation depending on number of orbiculi depressi (OD, Figs. 6–11). Usually, the structure of the central area and marginal area of the valve surface is different on valves with OD but frequently seems almost homogenous on small valves without OD. A slight tangential undulation of central area can be seen on quadrangular and triangular valves at tilted position (Fig. 6). The valve face has OD and papillae zero (Fig. 10) to five, besides OD there are relatively small punctae zero to eleven in number. The central part of the valve can be relatively small or large (2.5–7.3 µm), not depending on the diameter and contains different-sized and spaced colliculate protuberances. The marginal part of the valve is structured by alveolate striae externally, separated by hyaline strips, striae are straight, unequal in length and a few of them are bifurcated (Figs. 7, 9). Small granules are frequently observed on the interstriae near the margin and found sporadically on the striae (Figs. 6, 9, 11) or on the whole valve face. Simple alveolae are present within the marginal area internally. The inner aperture of the alveolae can be round or elongated. Costae are usually equal in length but those bearing a fultoportula are often shorter (Figs. 12–14). The valve has one or a few rimoportulae situated in the submarginal zone on the costa or just below it (sessile internally and round aperture externally); the orientation of the lip varies. Generally, every third to fifth interstria bears a marginal fultoportula (MFP) but it may occur on each to every 6th interstria. Their internal openings are surrounded by two satellite pores. Valve face fultoportulae (VFP: 1–4, Figs. 12, 13) are usually surrounded by two (1–3) satellite pores (Figs. 12–14). In many cases the external openings of VFP are very difficult to observe, because many valves have some punctae irregularly arranged in the central area.

## Nomenclatural changes

New nomenclatural combinations suggested in connection with the proposed new genus *Pantocsekiella* are proposed.

### *Pantocsekiella andancensis* (A. EHRLICH) K.T. KISS, ECTOR *et* ÁCS, *comb. nov.*

**Basionym:**—*Cyclotella andancensis* A. EHRLICH (1966). Ehrlich (1966) - Contribution à l'étude des gisements volcano-lacustres à diatomées de la région de Rochessauve et de Saint-Bauzile (Ardèche). Bull. Soc. Géol. France, ser. 7, 7, p. 316, pl. 5, fig. 11 -13.

**Synonyms:**— *Cyclotella andancensis* var. *bauzilensis* SERIEYSSOL (1980) *Cyclotella* species of late Miocene age from St. Bauzile, France. In: Ross, R. (Ed.) Proceedings of the Sixth Symposium on Recent and Fossil Diatoms. Otto Koeltz Science Publishers, Koenigstein, p. 29; figs. 22-28; *Cyclotella andancensis* var. *bipolairra* SERIEYSSOL (1980) *Cyclotella* species of late Miocene age from St. Bauzile, France. In: Ross, R. (Ed.) Proceedings of the Sixth Symposium on Recent and Fossil Diatoms. Otto Koeltz Science Publishers, Koenigstein, p. 30; figs. 29-36.

**Type locality:**— Deposits of the Montagne d'Andance, Saint-Bauzile, Ardèche, France.

### *Pantocsekiella arctica* (GENKAL *et* KHARITONOV) K.T. KISS, GENKAL *et* ÁCS, *comb. nov.*

**Basionym:**—*Cyclotella arctica* GENKAL *et* KHARITONOV (1996). *Cyclotella arctica* (Bacillariophyta) - a new species from Lake El'gygytgyn (Chukotka Peninsula). *Botanicheskii Zhurnal* **81** p. 69, pl. 1, figs. 1–8, pl. 2, figs. 1–3.

**Synonym:**—*Lindavia arctica* (GENKAL *et* KHARITONOV) NAKOV *et al.* 2015, p. 254.

**Type locality:**—Lake El'gygytgyn, Chukchi Peninsula, Russia.

### *Pantocsekiella azigzensis* (FLOWER *et al.*) K.T. KISS *et* ÁCS, *comb. nov.*

**Basionym:**—*Cyclotella azizzensis* FLOWER *et al.* (1990). A new species of *Cyclotella*, *C. azizzensis* sp. nov., described from modern material collected from upland lakes in Morocco. *Diatom Research* **5**, p. 254, figs. 1–12, 16–23.

**Synonym:**—*Lindavia azizzensis* (FLOWER *et al.*) NAKOV *et al.* 2015, p. 254.

**Type locality:**—Lake (Aguelmane) Azigza, Morocco.

***Pantocsekiella bavarica* (KLEE, ROL. SCHMIDT et JENS MÜLLER) K.T. KISS et ÁCS, *comb. nov.***

**Basionym:**—*Cyclotella bavarica* KLEE, ROL. SCHMIDT et JENS MÜLLER (1993) Alleröd diatom assemblages in prealpine hardwater lakes of Bavaria and Austria as preserved by the Laacher See eruption event. *Limnologia* **23**, p. 135, figs. 6 a-l, 7 a-e.

**Synonym:**—*Lindavia bavarica* (FLOWER *et al.*) NAKOV *et al.* 2015, p. 254.

**Type locality:**—Lake Starnberg, Bavaria, Germany.

***Pantocsekiella chantaica* (KUZMINA et GENKAL) K.T. KISS, GENKAL et ÁCS, *comb. nov.***

**Basionym:**—*Cyclotella chantaica* KUZMINA et GENKAL (1989). On new species of genus *Cyclotella* Kütz. (Bacillariophyta). *Biology of Inland Waters* **84**, p. 9, figs. 1–14.

**Synonym:**—*Lindavia chantaica* (KUZMINA et GENKAL) NAKOV *et al.* 2015, p. 254.

**Type locality:**—River Chantaika, Siberia, Russia.

***Pantocsekiella comensis* (GRUNOW in VAN HEURCK) K.T. KISS et ÁCS, *comb. nov.***

**Basionym:**—*Cyclotella comensis* GRUNOW in VAN HEURCK (1882). *Synopsis des Diatomées de Belgique. Atlas*, pl. 93, figs. 16, 17.

**Synonym:**—*Lindavia comensis* (GRUNOW in VAN HEURCK) NAKOV *et al.* 2015, p. 254.

**Type locality:**—Lake Como, Italy.

***Pantocsekiella costei* (DRUART et F. STRAUB) K.T. KISS et ÁCS, *comb. nov.***

**Basionym:**—*Cyclotella costei* DRUART et F. STRAUB (1988). Description de deux nouvelles Cyclotelles (Bacillariophyceae) de milieux alcalins et eutrophes: *Cyclotella costei* nov. sp. et *Cyclotellawuethrichiana* nov. sp. *Schweiz. Z. Hydrol.* **50**, p. 182-183, figs. 7–13.

**Synonyms:**—*Cyclotella comta* var. *unipunctata* FRICKE in SCHMIDT 1990, pl. 224, figs. 5–12; *C. operculata* var. *unipunctata* Hustedt 1922b, p. 235; *C. distinguenda* var. *unipunctata* (HUSTEDT) HÅKANSSON et J.R. CARTER 1990, p. 154; *C. cyclopuncta* HÅKANSSON et J.R. CARTER 1990, p. 155, figs. 6–8; *C. operculata* f. *minuta* GRUNOW in VAN HEURCK 1882, pl. 93, fig. 24, *Lindavia costei* (DRUART et F. STRAUB) NAKOV *et al.* 2015, p. 255.

**Type locality:**—Lake Paladru (archaeological site of Les Grands Roseaux), France.

***Pantocsekiella cretica* (J. JOHN et ECONOMOU-AMILLI) K.T. KISS et ÁCS, *comb. nov.***

**Basionym:**—*Cyclotella cretica* J. JOHN et ECONOMOU-AMILLI (1990). *Cyclotella cretica*, a new species of diatom from the island of Crete, Greece. *Diatom Research* **5**, p. 44, figs. 1–23.

**Synonym:**—*Lindavia cretica* (J. JOHN et ECONOMOU-AMILLI) NAKOV *et al.* 2015, p. 255.



**Type locality:**—Lake Kournas, Island of Crete, Greece.

***Pantocsekiella delicatula* (HUSTEDT) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella delicatula* HUSTEDT (1952). Neue und wenig bekannte Diatomeen. IV. *Botaniska Notiser* 1952, p. 376, figs. 34–36.

**Synonym:**—*Lindavia delicatula* (HUSTEDT) Nakov *et al.* 2015, p. 255.

**Type locality:**—Small groundwater Lake Seebachlacke near Kienberg-Gaming, Austria.

***Pantocsekiella elymaea* (ECONOMOU-AMILLI) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella elymaea* ECONOMOU-AMILLI (1991). *Cyclotella elymaea*, a new fossil species from the neogene basin of Kozani-Aeani-Servia, Northern Greece. *Diatom Research* 6: 224, figs. 1–27.

**Synonym:**—*Lindavia elymaea* (ECONOMOU-AMILLI) Nakov *et al.* 2015, p. 255.

**Type locality:**—In fossil Neogene sediment of the Kozani-Aeani-Servia basin, Greece.

***Pantocsekiella gordonensis* (H.J. KLING et HÅKANSSON) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella gordonensis* H.J. KLING et HÅKANSSON (1988). A light and electron microscope study of *Cyclotella* species (Bacillariophyceae) from central and northern Canadian lakes. *Diatom Research* 3, p. 70, figs. 51–52, 98–100.

**Type locality:**—Lake Gordon, Canada.

***Pantocsekiella gracilis* (NIKITEEVA et LIKHOSHWAY) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella gracilis* NIKITEEVA et LIKHOSHWAY (1994). *Cyclotella gracilis* sp. nov. from Pleistocene material of Lake Baikal, Russia. *Diatom Research* 9, p. 350, figs. 2–9.

**Synonym:**—*Lindavia gracilis* (NIKITEEVA et LIKHOSHWAY) Nakov *et al.* 2015, p. 255.

**Type locality:**—Underwater Academic Ridge of Lake Baikal (56° 26' ON, 107° 44' SE), Russia.

***Pantocsekiella granulata* (KULUMBAEVA et GENKAL in GENKAL et KULUMBAEVA) K.T. KISS, GENKAL et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella granulata* KULUMBAEVA et GENKAL in GENKAL et KULUMBAEVA (1990). About diatom algae (Centrophyceae) of Song-Köl Lake (Western Tian Shan). *Biologiya Vnutrennikh Vod (Biology of Inland Waters), Informatsii Biulleten* 86, p. 23, pl. 1, figs. 12–14, pl. 2, figs. 1–6 (in Russian).

**Type locality:**—Song-Köl Lake, Kyrgyzstan (USSR, lacus Sonkulj).

***Pantocsekiella hinziae* (HOUK, C. KÖNIG et KLEE) K.T. KISS, ECTOR et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella hinziae* HOUK, C. KÖNIG et KLEE (2015). *Cyclotella hinziae* sp. nov. – a small *Cyclotella* (Bacillariophyceae) from subalpine lake Schliersee (Bavaria, Germany). *Fottea* 15, p. 236, figs. 1–6, 19–37.

**Type locality:**—Lake Schliersee, Germany.

***Pantocsekiella hispanica* (K.T. KISS, E, HEGEWALD et ÁCS) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella hispanica* K.T. KISS, E. HEGEWALD et ÁCS (2002). *Cyclotella hispanica* a new dimorphic centric diatom species (Bacillariophyceae). *Algological Studies* **106**, p. 8, figs. 1–8, 10–18, 20, 23–47.

**Type locality:**—Lake Banyoles, Spain.

***Pantocsekiella horstii* (GENKAL et KULIKOVSKIY) K.T. KISS, GENKAL et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella horstii* GENKAL et KULIKOVSKIY (2012). *Cyclotella horstii* sp. nov. (Bacillariophyta) from Ivankovskoe reservoir (Volga reservoirs, Russia). *Phytotaxa* **59**, p. 56, figs. 2–34.

**Synonym:**—*Lindavia horstii* (GENKAL et KULIKOVSKIY) NAKOVet al. 2015, p. 255.

**Type locality:**—Ivankovskoe Reservoir (Volga Reservoirs Series), Russia.

***Pantocsekiella indistincta* (BENNETT et KOCIOLEK in KOCIOLEK et al.) K.T. KISS, ECTOR et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella indistincta* BENNETT et KOCIOLEK in KOCIOLEK et al. (2014). Diatoms of the United States 1: Taxonomy, ultrastructure and description of new species and other rarely reported taxa from lake sediments in the Western U.S.A. – In: LANGE-BERTALOT, H. et KOCIOLEK, J.P. (Eds.): *Bibliotheca Diatomologica* 61, p. 14, pl. 10, figs. 10–16, pl. 13, figs. 1–5.

**Type locality:**—Huntington North Reservoir, Utah, 39,348188, - 110,947762, USA.

***Pantocsekiella iranica* (NEJADSATTARI et al. in KHEIRI et al.) K.T. KISS, ECTOR et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella iranica* NEJADSATTARI et al. in KHEIRI et al. (2013). *Cyclotella iranica* sp. nov. (Bacillariophyta: Coscinodiscophyceae), a new diatom from the Karaj River, Iran. *Phytotaxa* **104**, p. 37, figs. 2–14.

**Synonym:**—*Lindavia iranica* (NEJADSATTARI et al. in KHEIRI et al.) NAKOVet al. 2015, p. 256.

**Type locality:**—Albourz, Karaj, Karaj River (epipelon), downstream of the Amir Kabir Dam, near the village of Aderan, elevation 1555 m, 35°53'N, 51°4'E, Iran.

***Pantocsekiella kuetzingiana* (THWAITES) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella kuetzingiana* THWAITES (1848). Further observations on the Diatomaceae with descriptions of new genera and species. *Ann. Magaz. Nat. Hist.*, 2nd series, 1, p. 169, pl. 11/D, figs. 1–5.

**Synonym:**—*Cyclotella krammeri* HÅKANSSON 1990b, p. 263, figs. 3–10, 35–41.

**Type locality:**—Krageholmssjön, Sweden.

***Pantocsekiella melnikiae* (GENKAL et BONDARENKO) K.T. KISS, GENKAL et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella melnikiae* GENKAL et BONDARENKO (2010). Diatom algae in mountain lakes of the Dzherginskiy reserve (the Baikal area). 1. Centrophyceae. *Diatom Research* **25**, p. 283, figs. 2–19.

**Synonym:**—*Lindavia melnikiae* (GENKAL et BONDARENKO) NAKOVet al. 2015, p. 256.

**Type locality:**—Lake Amut (north-eastern region of Lake Baikal), East Siberia, Russia.

***Pantocsekiella minuscula* (JURILJ) K.T. KISS et ÁCS, comb. nov. stat. nov.**

**Basionym:**—*Cyclotella thienemannii* var. *minuscula* JURILJ (1954). Flora i vegetacija Dijatomeja Ohridskog Jezera (Flora and vegetation of diatoms from Ochrida Lake in Yugoslavia). *Jugoslavenska Akademija Znanosti i Umjetnosti, Zagreb (Prirodoslovnih istraživanja)* **26**, p. 112, fig. 6d.

**Synonym:**—*Cyclotella minuscula* (JURILJ) CVETKOSKA et al. 2014, p. 328, figs. 65–99, *Lindavia minuscula* (JURILJ) NAKOV et al. 2015, p. 256.

**Type locality:**—Lake Ohrid, Republic of Macedonia.

***Pantocsekiella narochanica* (GENKAL et MIKHEEVA) K.T. KISS, GENKAL et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella narochanica* GENKAL et MIKHEEVA (2006). New for science species from the genus *Cyclotella* Kützing (Bacillariophyta). *International Journal of Algae* **8**, p. 77, pl. 1, figs. 1–6, pl. 2, figs. 1–6.

**Synonym:**—*Lindavia narochanica* (GENKAL et MIKHEEVA) NAKOV et al. 2015, p. 256.

**Type locality:**—Lake Naroch, Belarus.

***Pantocsekiella notata* (LOSEVA) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella notata* LOSEVA (1980). Some new data on the frustule structure of two representatives of the genus *Cyclotella* from Upper Pliocene deposits in Kama River. *Botanicheskii Zhurnal* **65**, p. 1620–1621, pl. 2, figs. 1–23.

**Synonym:**—*Lindavia notata* (LOSEVA) NAKOV et al. 2015, p. 256.

**Type locality:**—Kama River basin (Upper Pliocene deposits), Omara, Republic of Tatarstan, Russia.

***Pantocsekiella paleo-ocellata* (VOSSEL et VAN DE VIJVER) K.T. KISS, ECTOR et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella paleo-ocellata* VOSSEL et al. (2015). *Cyclotella paleo-ocellata*, a new centric diatom (Bacillariophyta) from Lake Kinneret (Israel). *Fottea* **15**, p. 65, figs. 2–18, 20–34.

**Synonym:**—*Lindavia paleo-ocellata* (VOSSEL et al.) NAKOV et al. 2015, p. 257.

**Type locality:**—Lake Kinneret, Israel, sediment core KI10\_II\_4.8–5.8, sample H44.

***Pantocsekiella palustris* (GENKAL et KULIKOVSKIY) K.T. KISS, GENKAL et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella palustris* GENKAL et KULIKOVSKIY (2008). New centric diatom species (Bacillariophyta) from the Polistovo-Lowatsky sphagnous tract (Rdeisk State Nature Reserve). *Botanicheskii Zhurnal* **89**, p. 773, pl. 2, figs. 1–10.

**Synonym:**—*Lindavia palustris* (GENKAL et KULIKOVSKIY) NAKOV et al. 2015, p. 257.

**Type locality:**—Swamp Rdeiskiy, region Novgorod, Russia.

***Pantocsekiella paraocellata* (CVETKOSKA et al.) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella paraocellata* CVETKOSKA et al. (2014). Observations of the genus *Cyclotella* (Kützing) Brébisson in ancient lakes Ohrid and Prespa and a description of two new species *C. paraocellata* sp. nov. and *C. prespanensis* sp. nov. *Nova Hedwigia* **98**, p. 317, figs. 1–23, 30–45.

**Synonym:**—*Lindavia paraocellata* (CVETKOSKA et al.) NAKOV et al. 2015, p. 257.

**Type locality:**—Lake Prespa, near village Krani, N 40°56'06", E 21°04'27", Republic of Macedonia.

***Pantocsekiella polymorpha* (B. MEYER et HÅKANSSON) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella polymorpha* B. MEYER et HÅKANSSON (1996). Morphological variation of *Cyclotella polymorpha* sp. nov. (Bacillariophyceae). *Phycologia* **35**, p. 64, figs. 1–29.

**Synonym:**—*Lindavia polymorpha* (B. MEYER et HÅKANSSON) NAKOV *et al.* 2015, p. 257.

**Type locality:**—Lake Kinneret, Israel.

***Pantocsekiella prespanensis* (CVETKOSKA *et al.*) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella prespanensis* CVETKOSKA *et al.* (2014). Observations of the genus *Cyclotella* (Kützing) Brébisson in ancient lakes Ohrid and Prespa and a description of two new species *C. paraocellata* sp. nov. and *C. prespanensis* sp. nov. *Nova Hedwigia* **98**, p. 323, figs. 52–64.

**Synonym:**—*Lindavia prespanensis* (CVETKOSKA *et al.*) NAKOV *et al.* 2015, p. 257.

**Type locality:**—Lake Prespa, near village Stenje, N 40°56'40"; E 20°54'15", Republic of Macedonia.

***Pantocsekiella pseudocomensis* (SCHEFFLER) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella pseudocomensis* SCHEFFLER (1994). *Cyclotella pseudocomensis* nov. sp. (Bacillariophyceae) aus norddeutschen seen. *Diatom Research* **9**, p. 356, figs. 1–31.

**Synonym:**—*Lindavia pseudocomensis* (SCHEFFLER) NAKOV *et al.* 2015, p. 257.

**Type locality:**—Großer Boberowsee, near Neuglobsow, Brandenburg, Germany.

***Pantocsekiella reczickiae* (KHURSEVICH et LOGINOVA) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella reczickiae* KHURSEVICH et LOGINOVA (1984). A new species of the genus *Cyclotella* (KÜTZ.) BRÉB. from the Lower Anthropogene ancient lacustrine deposits of Belarus and Latvia. – *Doklady Akademii nauk BSSR* **28**, p. 52, pl. 1, figs. 1-7, pl. 2, figs. 1-4.

**Synonym:**—*Lindavia reczickiae* (KHURSEVICH et LOGINOVA) NAKOV *et al.* 2015, p. 257.

**Type locality:**— Republic of Belarus and Latvia (Lower Pleistocene deposits).

***Pantocsekiella reczickiae* var. *diversa* (LOGINOVA) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella reczickiae* var. *diversa* LOGINOVA (1989). Two new taxa of the genus *Cyclotella* (Bacillariophyta). *Botanicheskii Zhurnal* **74**, p. 1781-1782, pl. 2, figs. 3-5, 8-12.

**Synonym:**—*Lindavia reczickiae* var. *diversa* (LOGINOVA) NAKOV *et al.* 2015, p. 258.

**Type locality:**—Krasnaya Dubrova, Rechitsa district, Byelorussian SSR..

***Pantocsekiella rossii* (Håkansson) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella rossii* HÅKANSSON (1990b). A comparison of *Cyclotella krammeri* sp. nov. and *C. schumannii* Håkansson stat. nov. with similar species. *Diatom Research* **5**, p. 266–267, figs. 18–27, 46–49.

**Synonym:**—*Lindavia rossii* (HÅKANSSON) NAKOV *et al.* 2015, p. 258.

**Type locality:**—Laxå, Sweden.

***Pantocsekiella schumannii* (GRUNOW in SCHNEIDER) K.T. KISS et ÁCS, comb. nov.**

**Basionym:**—*Cyclotella kuetzingiana* var. *schumannii* GRUNOW in SCHNEIDER (1878). Naturwissenschaftliche Beiträge zur Kenntniss der Kaukasuländer, auf Grund seiner Sammelbeute herausgegeben von Dr. Oscar Schneider. Dresden. Im Verlage der Burdach'schen Hofbuchhandlung. Veröffentlicht von der naturw. Gesellschaft 'Isis' zu Dresden, p. 127. Illustrated by Grunow in Van Heurck (1882). Synopsis des Diatomées de Belgique. Atlas. Ducaju et Cie., Anvers, pl. 94, figs. 2-3.

**Synonym:**—*Cyclotella schumannii* (GRUNOW) HÅKANSSON 1990b, p. 267, figs. 28-31; *Lindavia schumannii* (GRUNOW) NAKOV *et al.* 2015, p. 258.

**Type locality:**—Domblitten (diatomaceous earth - Kieselguhr von Domblitten), near Zinten (East Prussia), now Kornevo (Russia).

***Pantocsekiella strelnikovae* (GENKAL et YARISHINA) K.T. KISS, GENKAL et ÁCS, *comb. nov.***

**Basionym:**—*Cyclotella strelnikovae* GENKAL et YARUSHINA (2004). New species of the genus *Cyclotella* (Bacillariophyta) from the polar Ural Lakes. *Botanicheskii Zhurnal* **89**, p. 1498, pl. 1, figs. 1-6, pl. 2, figs. 1-6, pl. 3, figs. 1-6, Pl. 4, figs. 1-9.

**Synonym:**—*Lindavia strelnikovae* (GENKAL et YARUSHINA) NAKOV *et al.* 2015, p. 258.

**Type locality:**—Lake Upper Ingilor (Polar Ural), Russia.

***Pantocsekiella trichonidea* (ECONOMOU-AMILLI) K.T. KISS et ÁCS, *comb. nov.***

**Basionym:**—*Cyclotella trichonidea* ECONOMOU-AMILLI (1979). Two new taxa of *Cyclotella* Kützing from Lake Trichonis, Greece. *Nova Hedwigia* **31**, p. 468, figs. 1–20.

**Synonym:**—*Lindavia trichonidea* (ECONOMOU-AMILLI) NAKOV *et al.* 2015, p. 259.

**Type locality:**—Lake Trichonis, Greece.

***Pantocsekiella tripartita* (HÅKANSSON) K.T. KISS et ÁCS, *comb. nov.***

**Basionym:**—*Cyclotella tripartita* HÅKANSSON (1990a). *Cyclotella tripartita* nov. sp. (Bacillariophyceae) and the relationship to similar taxa. In: RICARD, M. (Ed.), Ouvrage dédié à la Mémoire du Professeur Henry Germain, p. 78, pl. 1, figs. 1–4.

**Synonyms:**—*Cyclotella comensis* sensu MANGUIN 1961, p. 268, pl. 1 (26), figs. 3, 4, pl. 5 (31), fig. 4; *C. kisselevii* Korotkevich 1959, p. 92, figs. 2–4, *Lindavia tripartita* (HÅKANSSON) NAKOV *et al.* 2015, p. 259.

**Type locality:**—Desperation Lake (68° 20 N, 158° 45 W), Alaska, USA.

***Pantocsekiella wuethrichiana* (DRUART et F. STRAUB) K.T. KISS et ÁCS, *comb. nov.***

**Basionym:**—*Cyclotella wuethrichiana* DRUART et F. STRAUB (1988). Description de deux nouvelles Cyclotelles (Bacillariophyceae) de milieux alcalins et eutrophes: *Cyclotella costei* nov. sp. et *Cyclotellawuethrichiana* nov. sp. *Schweiz. Z. Hydrol.* **50**, p. 186, figs. 1, 2, 4, 6, 14, 16.

**Synonym:**—*Lindavia wuethrichiana* (DRUART et F. STRAUB) NAKOV *et al.* 2015, p. 259.

**Type locality:**—Lake Le Loclat, near Neuchâtel, Switzerland.

**Discussion**

For the supplementary description of the type species of the genus *Pantocsekiella*, we relied pronouncedly on the findings of the studies in the recent decades beside our previous researches. These investigations presented the detailed electron microscope analyses of *Cyclotella ocellata* (the most important investigations are: LOWE 1975, GENKAL & KUZMIN 1979, GENKAL&ZAGORENKO 1987, KLEE & STEINBERG 1987, HÅKANSSON 1990b, HEGEWALD&HINDÁKOVÁ 1997, KNIE & HÜBENER 2007, CHEREPANOVA *et al.* 2010 and the references listed in the Table 4) showing the morphological features of the species, and proving the remarkable variability and heterovalvate character of the valve face structure. It is notable that specimens of the genus *Pantocsekiella* having small diameter resemble to each other from outside (e.g. *Cyclotella ocellata*: GENKAL & ZAGORENKO 1987, figs. p–s; *C. hispanica*: KISS *et al.* 2002, figs. 7, 8; *C. comensis*: SCHEFFLER & MORABITO 2003, figs. 18–20, 24).

When the former Centrales order was divided into two clades (Mediophyceae and Coscinodiscophyceae) based on molecular, cytological and morphological results, rimoportula and marginal fuloportula were important morphological features (MEDLIN & KACZMARSKA 2004), and therefore their differences should be correlated to the phylogenetic divergences.

Shape and position of rimoportula is characteristic to the *Cyclotella meneghiniana* group [including *C. atomus* HUSTEDT (1937: 143), *C. cryptica* REIMANN *et al.* (1963: 82), *C. choctawhatcheeana* PRASAD in PRASAD *et al.* (1990: 419), *C. distinguenda* HUSTEDT (1927: 320), *C. litoralis* C.B. LANGE et SYVERTSEN (1989: 343–344), *C. quillensis* L.W. BAILEY (1921: 159), *C. striata* (KÜTZING) GRUNOW in CLEVE et GRUNOW (1880: 119), see Fig. 5. in phylogenetic tree]; it is situated on the edge arising from the valve mantle costa internally. Marginal fuloportulae can be found also on costae that are identical. Previously *Cyclotella* involved the *Discostella* species that were later separated as a distinct genus based on both morphological (HOUK & KLEE 2004) and phylogenetic evidences (JUNG *et al.* 2010). The rimoportula of *Discostella* can be found also on the edge, on the costae, however, the marginal fuloportulae are situated between costae. The rimoportulae are usually sessile, rarely petiolate.

NAKOV *et al.* (2015) identified the rimoportula position as a synapomorphy for the *Cyclotella comta* and *C. ocellata* groups and they transferred all taxa showing this synapomorphy into the genus *Lindavia*. As they cited THERIOT *et al.* (1987b) “from a phylogenetic perspective, both areolae and fuloportulae on the valve face are problematic because both are plesiomorphic within Thalassiosirales”, but the cited paper does not contain such statement. We consider that the areolae on the valve face with domed cribrum are apomorphic characters, not plesiomorphic, because they did not appear in the *Pantocsekiella* yet. Based on the phylogenetic tree of Alverson (2014) those groups having these features (e.g. *Stephanodiscus*, *Cyclostephanos*) diverged later than those ones lacking areolae on the valve face (e.g. *Cyclotella sensu stricto*).

In *Handmannia* genus which were also transferred to *Lindavia* by NAKOV *et al.* (2015) the areolae in the central area of valve face are covered by domed cribrum and there are several valve face fuloportulae on several species (e.g. *H. comta* (EHRENBERG) KOCIOLEK&KHURSEVICH in KHURSEVICH&KOCIOLEK (2012: 339)), or there are only areolae (e.g. *H. glabriuscula* (GRUNOW) KOCIOLEK et KHURSEVICH in KHURSEVICH et KOCIOLEK (2012: 339)). Comparing the two species under SEM shows that *Pantocsekiella ocellata* does not possess these important characteristics of the *Handmannia (Puncticulata)* genus. Species of the “*Cyclotella ocellata* group” can have more than one valve face fuloportulae, but nothing else penetrate the central area of the valve face. KOCIOLEK & WILLIAMS (2015) pointed out that “it would follow that all the taxa to be included in that group should have the diagnostic feature(s)” and draw attention to the importance of monophyly for describing new genera.

Several studies searched for a barcode that can be used for diatom species identification [e.g. the V4 region of 18S rDNA, ZIMMERMANN *et al.* (2011) and a region at the 3' end of *rbcL*, HAMSHER *et al.* (2011)]. For precise identification an appropriate threshold is needed. Some authors tried to determine a threshold at species level on certain markers (e.g. LUDDINGTON *et al.* 2012), but it proved to be difficult (RIMET *et al.* 2014).

Establishing a threshold at genus level is more difficult because “genera form wider taxonomic groups than species do and include different lineages” (KERMARREC *et al.* 2014). Examining reference libraries KERMARREC *et al.* (2014) attempted to define inter-/intraspecific and inter-/intrageneric thresholds for assigning genus and species names to sequences from benthic communities. They tested the thresholds on mock community with known composition (mainly pennates). They obtained the best estimation of the real community composition using 99% sequence identity threshold for 18S rDNA at both levels, 99% species and 98% genus threshold for *rbcL*. The read selection criteria used for species was probably too strict for the assignment of genus names. Mean distance of *Pantocsekiella* group from all other genera studied was above 2% in the case of *rbcL*. This was true for pairwise distances. In the case of the long 18S rDNA the mean distance of *Pantocsekiella* from *Cyclostephanos* and *Stephanodiscus* was under 1% (0.89 % and 0.85 %, respectively). Pairwise distances of *Pantocsekiella* with most of *Stephanodiscus* and *Cyclostephanos* sequences as well as *Praestephanos triporus* were below 1% (0.56–0.84% in all sequences, 0.54–0.94 %). It should be considered that KERMARREC *et al.*

(2014) defined thresholds mostly based on pennates. According to KERMARREC *et al.* (2014), identity threshold applicable to all diatom taxa is difficult to establish because diatom lineages have not all evolved at the same rate. Investigating the 333 nt of 18S rDNA including V4 region of 26 genera in orders Thalassiosirales, Lithodesmiales and Cymatosirales Luddington *et al.* (2012) found intergeneric p-distance ranged from 0.001–0.235 (0.1–23.5%). In the analysis of all 18S rDNA sequences the mean distance of *Pantocsekiella* from *Lindavia* (*Handmannia*) (1.76 % in the 360 nt region) the sister group of *Pantocsekiella* (Fig. 5) fit into this range, but it was under the 2% threshold that Luddington *et al.* (2012) set for species identification. Comparing of *Cyclotella comensis* group to *Cyclostephanos delicatus* (GENKAL) CASPER & SCHEFFLER (1990: 311) and *Stephanodiscus alpinus* HUSTEDT (1942: 412) based on similar region of 18S rDNA Kistenich *et al.* (2014) also found intergeneric distance lower than 2% (0.74%). The *Pantocsekiella* – *Stephanodiscus* and *Pantocsekiella* – *Cyclostephanos* distance in our analysis with more sequences from both genera (1.10% and 1.25%, respectively) exceeded this value but remained under 2%.

In partial region (507 nt) of *rbcL* KISTENICH *et al.* (2014) detected 4.54–6.11% intergeneric distance. Although in the analysis of all *rbcL* sequences, *Lindavia* (*Handmannia*)– *Pantocsekiella* distance (4.30%) remained below this range, *Pantocsekiella* – *Stephanodiscus* distance (4.95 %) fell into it and *Pantocsekiella* – *Cyclostephanos* distance (6.36%) exceeded it. It should be noted that *Pantocsekiella* sequence from Lake Himód was shifted with 105 nt in 3' direction comparing to those of Kistenich *et al.* (2014), therefore the comparison was possible on the overlapping 402 nt region.

KI (2009) and JUNG *et al.* (2010) investigated the relationship of the genera *Cyclotella*, *Discostella* and *Stephanodiscus* using almost full-length of 18S rDNA (1689 and 1704 sites, respectively). The results of their p-distance and phylogenetic analyses showed the significant separation of the three genera. However, these studies extended to only the *C. meneghiniana* group within the *Cyclotella* genus. They excluded *C. ocellata* and *C. bodanica* because they considered these species as belonging to *Discostella* or a new genus (Jung *et al.* 2010). The corrected p-distance calculated using Kimura two-parameter model was 5.4±0.45 between *Stephanodiscus* and *Cyclotella*, 1.7±0.28 between *Stephanodiscus* and *Discostella* (KI 2009), the similarity between *Discostella* and *Cyclotella* was 94.4±0.5% (JUNG *et al.* 2010). The mean distance calculated with the same model on the long region (1564 nt) of 18S rDNA between *Cyclotella* and *Discostella* was 4.89%; between *Cyclotella* and *Stephanodiscus* it was 4.69% and between *Discostella* and *Stephanodiscus* 1.60%. The *Pantocsekiella*–*Lindavia* (*Handmannia*) distance with this method was 1.15%.

One *Stephanodiscus* strain investigated by KI (2009) has been recently transferred into the new genus *Praestephanos*, as *P. triporus* (TUJI *et al.* 2014). This genus was described based on morphological characters (position of rimoportulae and marginal fultoportulae, pattern of areolae) and its unique position on phylogenetic tree based on four markers (SSU and LSU rDNA, *rbcL* and *psbC*). *Praestephanos triporus* showed 0.56–1.12% pairwise p-distance in the short and 0.96–1.12% distance in the long region of 18S rDNA and 3.86–4.59 % pairwise p-distance in the short and 3.00–3.67% distance in the long region of *rbcL* from the members of *Pantocsekiella*.

The topology of both maximum likelihood and Bayesian inferred phylogenetic trees differed from previously published Thalassiosirales trees (ALVERSON *et al.* 2007, ALVERSON 2014). A main difference was the lack of monophyly of *Stephanodiscus* and within it *Cyclostephanos* species in the 18S rDNA tree suggesting that two genera cannot be distinguished by the studied region that may have not enough phylogenetic signal in this group of diatoms. The mean distance between these groups was low in the studied region (0.33) that was compared among all used sequences. This region that contained V4 subregion was found to show very low variation within the *Stephanodiscus* (ZIMMERMANN *et al.* 2011). The distance was also low in the long stretch (0.27). Most of the differences occurred only in one sequence. Comparing just *Cyclostephanos* and *Stephanodiscus* sequences six parsimony informative sites were found with MEGA software (at parsimony informative sites at least two different nucleotides occur each of them in at least two taxa). At these sites the substitutions were characteristic only to a group of sequences but none of the differences separated the two genera (e.g. at 188<sup>th</sup> position all *Cyclostephanos*, but *C. tholiformis* had guanine, *Stephanodiscus* sequences and *C. tholiformis* contained adenine; at 239<sup>th</sup> position all *Cyclostephanos* but along with *S. hantzschii* WTC21 contained cytosine instead of thymine). Based on the phylogenetic tree of ALVERSON (2014) *Stephanodiscus* and *Cyclostephanos* are closely related, relatively recently diverged genera that may explain the low intergeneric variation. In ALVERSON *et al.* (2007) the monophyly of *Cyclostephanos* and *Stephanodiscus* was proved based on combined dataset of 18S and 28S rDNA. The 18S rDNA alone may not suitable for separating these genera, just in combination with another gene e.g. 28S rDNA or as in our case with *rbcL*. Differences at four sites in the extended sequenced region of 18S rDNA separated *Lindavia* (*Handmannia*) from *Pantocsekiella*.

In the case of *rbcL* the monophyly of *Stephanodiscus* was confused by *Praestephanos triporus* grouping with *Stephanodiscus* sequences. This genus was established from species that drifted from *Stephanodiscus* (TUJI *et al.* 2014). The sequence used was also originally identified as *Stephanodiscus*.

Based on all above mentioned results, not only morphological but also molecular investigations clarified that the former *Cyclotella* genus was needed to be divided into several new genera, as did NAKOV et al (2015). *Cyclotella ocellata* and *C. bodanica* represented lineages separate from the *C. meneghiniana* group (ALVERSON et al. 2007). Previously the sequences of only two species *Cyclotella (Lindavia) ocellata* and *Cyclotella (Puncticulata/Handmannia/Lindavia) bodanica* were available beside the *Cyclotella meneghiniana* group. To investigate if *C. ocellata* belonged to the genus *Lindavia* we supplemented previous data with sequences of additional species (*Cyclotella comensis* group and *Handmannia radiosae*). Our results indicated that *Cyclotella ocellata* did not belong to either *Puncticulata (Handmannia/Lindavia)* or *Cyclotella* or other established genera (because of the high genetic distance). Therefore we propose the drift of the species into a new genus, *Pantocsekiella* as its generitype species.

Differential diagnosis of the three genera (Figs. 15–25):

*Cyclotella*: striae are of equal length, central area round (Figs. 15, 18); alveolae simple (Fig. 19); a single rimoportula (rarely two) arising near the margin from the valve mantle costa internally (Fig. 19) and opening by distinct round aperture or slit externally.

*Lindavia (Handmannia)*: striae of unequal length (Figs. 17, 20, 21), central area polygonal; presence of valve face fuloportulae and areolae or only areolae; areolae with internal domed cribra and external foramina (Figs. 20, 21); presence of a complex alveolar structure composed primary thick costae internally bearing marginal fuloportulae, secondary thin costae which can be forked (Fig. 21); sessile rimoportula on the valve face in the submarginal zone (Figs. 20, 21).

*Pantocsekiella*: striae of unequal length (Figs. 16, 22), central area polygonal; flat or radially or tangentially undulated; alveolae simple (Fig. 23); one or a few sessile rimoportulae are present in the submarginal zone of the valve face or at the end of the central lamina (Fig. 23). Internally no any structure (except VFP) penetrates the central part of cell wall.

In the literature uncertainty can be observed about the characterisation of “*Puncticulata comta*”, the “*Puncticulata*” genus and the “*Cyclotella ocellata*” group, their coherency or separation. LOWE (1975) rated the *Cyclotella* genus into three groups (*C. meneghiniana* group, *C. comta* group and *C. stelligera* group). Within the *C. comta* group (“...the *comta* group, includes *C. comta*, *C. antiqua*, *C. ocellata* and *C. michiganiana*”) “*Cyclotella comta* and *C. antiqua* are very closely related and may constitute a subgroup of the *comta* group.” This means that he did not consider *C. ocellata* to belong to the *comta* subgroup.

HÅKANSSON (2002) mentioned the following as the important characteristic of the genus *Puncticulata*: “Central area ... with both areolae and fuloportulae or areolae only or fuloportulae only.” The latter feature (fuloportulae only) can be observed on two species: *P. notata* (LOSEVA) HÅKANSSON (2002: 126) and *P. kurdica* (HÅKANSSON) HÅKANSSON (2002: 129). Regarding to their morphological properties these two species significantly differ from the other species of the genus. On SEM photographs the external valve face is confusingly similar to the *C. ocellata*. On *P. notata* recordings (HÅKANSSON 2002: figs. 475-478) 3-4 orbiculi depressi can be seen, on the internal side of the valve the structure of the alveolar chambers and costae actually resembles to that of the genus *Puncticulata* (HÅKANSSON 2002: figs. 479-481), but GENKAL&POPOVSKAYA (2008a: figs. 26-32) found similar alveolar chamber/costa structure in *C. ocellata*. On *P. kurdica* recordings (HÅKANSSON 2002, figs. 482-485) 4-6 orbiculi depressi can be seen; on the internal side of the valve the structure of the alveolar chambers and costae correspond with that of *C. ocellata* (HÅKANSSON 2002, figs. 487, 488), and the many valve face fuloportulae are also characteristic to *C. ocellata* (GENKAL&POPOVSKAYA 2008a). For all these reasons, we consider that *P. notata* and *P. kurdica* could not be classified to the *Puncticulata* genus.

This opinion is supported by the fact that KHURSEVICH & KOCIOLEK (2012) wrote the following among the characteristics of the genus *Handmannia*: “...presence of both areolae and valve face fuloportulae, or areolae only within the central area”. They did not ranked either *C. kurdica* or *C. notata* to the genus *Handmannia*, the latter was rated into the 12<sup>th</sup> *Cyclotella* group. NAKOV et al. (2015) synonymized those as *Lindavia* based on the nomenclatural priority.

## Identification key - Distinctive light microscopic characters of the three genera

1. Striae of equal length ... *Cyclotella*
  - Striae of unequal length ... 2
2. Central area with areolae ... *Lindavia (Handmannia)*
  - Central area without areolae ... *Pantocsekiella*



Amended diagnosis of *Lindavia* genus is based on several works where *Lindavia*, *Puncticulata*, *Handmannia* were morphologically characterized (SCHÜTT 1989a, b, DE TONI&FORTI 1900, HANDMANN 1913, HÅKANSSON 2002, KHURSEVICH&KOCIOLEK 2012, NAKOVET *et al.* 2015).

***Lindavia* (F. SCHÜTT) DE TONI et FORTI**

**Basionym:** *Cyclotella socialis* F. SCHÜTT (1899a), *Berichte der Deutschen Botanischen Gesellschaft* 17: 220. 1899. Figures: *Abbildungen der Jahrbücher für wissenschaftliche Botanik*, pl. 7: figs. 23–35, pl. 8: figs. 37, 40. 1899.

**Diagnosis:**—Frustules are disc-shaped, solitary, seldom in short chains. Valves circular or oval-elliptic or oblong-elliptic, with almost flat, concave or convex, or concentrically undulate, or tangentially undulate central area and a striated marginal zone. Central area slightly polygonal, with areolae and fultoportulae or only areolae. Loculate areolae (internally with domed cribra) form distinct radial rows, sometimes parallel rows or groups (without distinct order). Fultoportulae on the valve face with three satellite pores (rarely with two or four) are located in areolar rows, replacing one-several areolae in every row or sometimes in the slope of the central undulation. The marginal part of the valve is structured by long or short striae externally, separated by hyaline strips; striae are straight, more or less equal in length and a few of them are bifurcated. The striae of the marginal area are composed of small areolae, mostly increasing in numbers towards and onto the mantle. Complex alveolae are present within the marginal area internally. The inner aperture of the alveolae is elongated. Costae are usually equal in length but those bearing a fultoportula are often shorter and thick. There are secondary thin costae between thick ones, which can be forked-branched in some species. Fultoportulae situated on the mantle, externally with slightly thickened apertures on the slightly thicker interstriae, internally with two satellite pores. The valve has one or a few rimoportulae situated in the submarginal zone on the costa or just below it, or on the valve face (sessile internally and round or slit-like aperture externally); the orientation of the lip varies.

**Type species:** *Lindavia socialis* (F. SCHÜTT) DE TONI & FORTI (1900: 553).

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## Table & Figure captions

**TABLE 1.** Description of sampling sites and the type of samples included in morphological and molecular analyses. Abbreviations: Fr= France, Ge= Germany, md=maximal depth.

**TABLE 2.** Additional sequences used in phylogenetic analyses.

**TABLE 3.** Mean p-distances (expressed in percentage) of *rbcl* sequences between genera as groups. First number is the mean distance of all sequences, the comparison involved 415 positions. The second number in

parentheses represents the mean distance without short sequences, 1306 positions were included in the analysis. The number in parentheses after genus name indicates the number of species included in each group: the first number in the analysis with all sequences, the second number in analysis without short ones. Intergeneric distances lower than *Pantocsekiella*–*Lindavia* distance in both analyses are in italic.

**TABLE 4.** Mean p-distances (expressed in percentage) of 18S rDNA sequences between genera as groups. First number is the mean distance of all sequences, the comparison contained 360 positions. The second number in parentheses represents the mean distance without short sequences, 1564 positions were involved in the analysis. The number in parentheses after genus name indicates the number of species included in each group: the first number in the analysis with all sequences, the second number in analysis without short ones. In the case of *Cyclotella* 18S rDNA sequence of *C. stylorum* was not available hence 11 species could be evaluated in contrast the 12 species in the analysis of *rbcL*. Intergeneric distances lower than *Pantocsekiella*–*Lindavia* distance in both analyses are in italic.

**TABLE 5.** The variability of morphological elements of *Cyclotella ocellata*. (Diam) valve diameter in  $\mu\text{m}$ ; (striae) number of striae in 10  $\mu\text{m}$ ; (vfp) number of valve face fuloportulae; (sp-vfp): number of satellite pores of valve face fuloportulae; (mfp) arrangement of marginal fuloportulae; (sp-mfp) number of satellite pores of marginal fuloportulae; (rp) number of rimoportulae; note: (\*) according to measurements by microphotographs.

**FIGURES 1–4.** SEM micrographs of *Lindavia comta* (Figs. 1–2: culture isolated from Lake Stechlin, Figs. 3–4 culture isolated from Lake Nehmitz). Figs. 1, 3. External view of valve face, striae different in length, areolae in center scattered, valve face fuloportulae in ring; spinules on margin and granules in centre. Figs. 2, 4. Internal view of valve, areolae in center scattered, valve face fuloportulae in ring. Scale bar = 1  $\mu\text{m}$ .

**FIGURE 5.** Bayesian inferred phylogenetic tree of combined data constructed Tamura-Nei model (TAMURA & NEI 1993) with gamma distribution for 18S rDNA and GTR model (RODRÍGUEZ *et al.* 1990) with gamma distribution and invariant sites for *rbcL*. In two runs a cold and three heated chains were run for 700000 generations. The average standard deviation of split frequencies across independent analyses was 0.010198 in the last generation.

Posterior probability values are indicated at the nodes. Scale bar represents 0.05 substitutions per site.

**FIGURES 6–14.** SEM micrographs of *Pantocsekiella ocellata*: (6–11) external view; (12–14) internal view; (6). Valve with three OD and three papillae, interstriae ornamented with granules (from Lake Balaton); (7) valve with three OD and two papillae (from Lake Himód); (8) valve with three OD (twin OD-s) and three papillae (from Lake Visovac); (9) valve with seven OD and three papillae, interstriae ornamented with granules (from Lake Balaton); (10) valve with four OD without papillae (from Lake Dunaharaszti); (11) slightly quadrangular valve with three OD and three papillae, interstriae ornamented with granules (from Lake Visovac); (12) valve with one valve face fuloportula, costae are equal in length (from Lake Balaton); (13) valve with four valve face fuloportulae, costae bearing marginal fuloportulae are shorter (from Lake Balaton); (14) slightly quadrangular valve with two valve face fuloportulae and three rimoportulae, costae bearing marginal fuloportulae are shorter (from Lake Visovac). Scale bars: (14) 10  $\mu\text{m}$ ; (6, 7, 9, 11–13) 5  $\mu\text{m}$ ; (10) 2.5  $\mu\text{m}$ ; (8) 2  $\mu\text{m}$ .

**FIGURES 15–17.** LM micrographs of characteristic species for *Cyclotella* (*C. meneghiniana*), *Pantocsekiella* (*P. ocellata*) and *Lindavia* (*L. comta*) genera. Scale bars: Fig. 15: 10  $\mu\text{m}$ ; Figs. 16, 17: 5  $\mu\text{m}$ .

**FIGURES 18–23.** SEM micrographs of characteristic species for *Cyclotella*, *Lindavia* (*Handmannia*) and *Pantocsekiella* genera (outside and inside view). Figs. 18, 19. *C. meneghiniana*, white arrow: rimoportula. Figs. 20, 21. *L. comta*, white arrow: rimoportula, black arrow: domed cribra on inside view and foramina on outside view. Figs. 22, 23. *P. ocellata*, white arrow: rimoportula. Scale bars: Fig. 18: 10  $\mu\text{m}$ ; Figs. 19, 22, 23: 5  $\mu\text{m}$ ; Figs. 20, 21: 2  $\mu\text{m}$ .

**Supplementary Figure 1.** Bayesian inferred phylogenetic tree for 18S rDNA sequences constructed using Tamura 3-parameter model (TAMURA & NEI 1993) with gamma distribution. In two runs a cold and three heated chains were run for 900000 generations. The average standard deviation of split frequencies across independent analyses was 0.015144 in the last generation. Scale bar represents 0.03 substitutions per site. Available GenBank accession number of the used sequences is provided in the name of taxa. Posterior probability values are indicated at the nodes.

**Supplementary Figure 2.** Maximum likelihood phylogenetic tree constructed using Tamura 3-parameter model (TAMURA & NEI 1993) with gamma distribution. Scale bar represents 0.02 substitutions per site. Available GenBank accession number of the used sequences is provided in the name of taxa. Bootstrap values are indicated at the nodes.

**Supplementary Figure 3.** Bayesian inferred phylogenetic tree for *rbcL* sequences constructed using GTR model (RODRÍGUEZ *et al.* 1990) with gamma distribution and invariant sites. In two runs a cold and three heated chains were run for 900000 generations. The average standard deviation of split frequencies across independent



analyses was 0.008216 in the last generation. Scale bar represents 0.04 substitutions per site. Available GenBank accession number of the used sequences is provided in the name of taxa. Posterior probability values are indicated at the nodes.

**Supplementary Figure 4.** Maximum likelihood phylogenetic tree constructed using *rbcL* sequences constructed using GTR model (RODRÍGUEZ *et al.* 1990) with gamma distribution and invariant sites. Scale bar represents 0.02 substitutions per site. Available GenBank accession number of the used sequences is provided in the name of taxa. Bootstrap values are indicated at the nodes.

<b>Name of water/ closest town/type of water body</b>	<b>GPS/country</b>	<b>Area and depth</b>	<b>Trophic level</b>	<b>Sampling date</b>	<b>Sample</b>	<b>Target species</b>
Lake Geneva/Thonon-les-Bains/natural	N 46°27'E 6°32' Fr	Area: 581000 ha, md: 308 m	in re-oligotrophic phase	July 2009	clonal culture	<i>Cyclotella comensis</i> group ( <i>C. costei</i> )
Lake Stechlin/ Neuglobsow/natural	N 53°9'6" E 13°1'34" Ge	Area: 425 ha, md: ~68 m	oligotrophic	May 2011	clonal culture	<i>Lindavia (Handmannia)</i> <i>comta</i>
Lake Nehmitz/ Neuglobsow/natural	N 53°08'12" E 12°59'05" Ge	Area: 161 ha, md: ~18.6 m	mesotrophic	May 2011	clonal culture	<i>Lindavia (Handmannia)</i> <i>comta</i>



<b>Species</b>	<b>Culture</b>	<b>Sampling site</b>	<b>Reference</b>
<i>Cyclostephanos delicatus</i>	MD 11	Lake Ziegelinnen, Schwerin (Germany)	unpublished
<i>Cyclotella comensis</i> -group	NE 3	Lake Nehmitz, Brandenburg (Germany)	unpublished
<i>Cyclotella comensis</i> -group	JO 2	Jonsvannet (Trondheim, Norway)	unpublished
<i>Cyclotella comensis</i> -group ( <i>C. comensis</i> )	BG 2	Lake Baggersee (Austria)	KISTENICH <i>et al.</i> (2014)
<i>Cyclotella comensis</i> -group ( <i>C. costei</i> )	F1	Lake Fernsteinsee (Austria)	KISTENICH <i>et al.</i> (2014)
<i>Cyclotella comensis</i> -group ( <i>C. costei</i> )	GUL	Lake Gültzsee (Germany)	KISTENICH <i>et al.</i> (2014)
<i>Cyclotella comensis</i> -group ( <i>C. pseudocomensis</i> )	HS1	Lake Hausse (Germany)	KISTENICH <i>et al.</i> (2014)
<i>Cyclotella distinguenda</i> -group	BG 3	Lake Baggersee (Austria)	unpublished
<i>Cyclotella meneghiniana</i> -group	W 8	Warnow, Rostock (Germany)	unpublished
<i>Cyclotella ocellata</i>	BA0	Balaton (Hungary)	unpublished
<i>Cyclotella ocellata</i>	KK4	Kiesgrube-Krugsdorf	KISTENICH <i>et al.</i> (2014)
<i>Cyclotella ocellata</i>		Lake Dunaharaszti (Hungary)	DULEBA <i>et al.</i> (2015)
<i>Cyclotella ocellata</i>		Lake Himód (Hungary)	DULEBA <i>et al.</i> (2015)
<i>Cyclotella ocellata</i>		Lake Visovac (Croatia)	DULEBA <i>et al.</i> (2015)
<i>Lindavia (Handmannia) comta</i> -group	DM 1	Demenzsee, OVP (Germany)	unpublished
<i>Stephanodiscus alpinus</i>	SN 3	Schweriner Innensee (Seewarte) (Germany)	unpublished
<i>Stephanodiscus medius</i>	MD 9	Lake Ziegelinnen, Schwerin (Germany)	unpublished
<i>Stephanodiscus parvus</i> -group	HSP 7	Lake Hohen Sprenger (Germany)	unpublished
<i>Stephanodiscus parvus</i> -group	BA 2	Lake Balaton (Hungary)	unpublished

	<i>Pantocsekiella</i> (2/2)	<i>Lindavia</i> (2/2)	<i>Cyclotella</i> (12/12)	<i>Discostella</i> (4/4)	<i>Stephanodiscus</i> (12/10)	<i>Cyclostephanos</i> (6/5)	<i>Bacterosira</i> (2/2)	<i>Shionodiscus</i> (2/2)
<i>Lindavia</i> (2/2)	4.30 (3.41)							
<i>Cyclotella</i> (12/12)	8.48 (6.47)	7.60 (6.25)						
<i>Discostella</i> (4/4)	6.50 (5.26)	5.51 (5.03)	8.18 (6.65)					
<i>Stephanodiscus</i> (12/10)	4.95 (3.44)	3.45 (2.79)	7.51 (6.01)	4.74 (4.28)				
<i>Cyclostephanos</i> (6/5)	6.36 (4.02)	4.38 (3.25)	7.70 (5.92)	5.00 (4.16)	3.42 (2.17)			
<i>Bacterosira</i> (2/2)	5.81 (5.90)	5.48 (5.86)	8.45 (7.15)	5.30 (5.26)	4.34 (5.22)	3.95 (4.95)		
<i>Shionodiscus</i> (2/2)	10.12 (7.48)	8.98 (7.35)	10.43 (7.82)	9.58 (7.30)	8.98 (7.16)	9.22 (7.23)	8.73 (7.04)	
<i>Skeletonema</i> (6/6)	8.44 (6.29)	7.31 (6.04)	8.87 (6.96)	7.00 (5.79)	6.95 (5.60)	6.23 (5.39)	5.86 (5.65)	10.36 (7.80)

	<i>Pantocsekiella</i> (2/2)	<i>Lindavia</i> (2/2)	<i>Cyclotella</i> (11/11)	<i>Discostella</i> (4/4)	<i>Stephanodiscus</i> (12/10)	<i>Cyclostephanos</i> (6/5)	<i>Bacterosira</i> (2/2)	<i>Shionodiscus</i> (2/2)
<i>Lindavia</i> (2/2)	1.76 (1.13)							
<i>Cyclotella</i> (11/11)	7.70 (4.87)	8.66 (5.21)						
<i>Discostella</i> (4/4)	1.91 (1.81)	3.26 (2.28)	8.20 (4.73)					
<i>Stephanodiscus</i> (12/10)	1.10 (0.85)	1.39 (1.21)	7.79 (4.54)	2.31 (1.57)				
<i>Cyclostephanos</i> (6/5)	1.25 (0.89)	1.55 (1.21)	7.89 (4.54)	2.45 (1.56)	0.33 (0.27)			
<i>Bacterosira</i> (2/2)	2.52 (1.93)	2.71 (2.24)	6.94 (4.82)	2.78 (2.22)	1.94 (1.37)	2.18 (1.56)		
<i>Shionodiscus</i> (2/2)	2.52 (1.79)	2.71 (2.13)	7.89 (4.77)	2.60 (2.10)	1.94 (1.37)	2.18 (1.46)	1.11 (1.15)	
<i>Skeletonema</i> (6/6)	7.00 (5.48)	8.10 (5.96)	10.46 (7.51)	6.94 (5.53)	7.54 (5.53)	7.75 (5.68)	5.69 (5.27)	6.44 (5.45)

diam	striae	vfp	sp-vfp	mfp	sp-mfp	rp	References
6–25	13–15						KRAMMER & LANGE-BERTALOT 1991
3–33	10–20	1–3	2	on every costae	4–9 2	1–3	KOZURENKO <i>etal.</i> 1992
5–27	14–23	1–6	2	on every costae	2–7 2		KISS <i>et al.</i> 1996
5.6–25	14–20	0–5	2	on every costae	2–7 2	1	KISS <i>et al.</i> 1999
8–13	15–18	1–2	2	on every costae	2–4 2	1	ALFINITO <i>et al.</i> 2001
2–18		1–3	2	on every costae	(4)5– 2	1	HÅKANSSON 2002
2.5–43	10–19	1–7	2	on every costae	2–6 2	1–4	EDLUND <i>et al.</i> 2003
5.5–35.3	10–22	1–6					GENKAL & BONDARENKO 2004
3.4–44.2	11–25	1–13	1–3	on every costae	1–8 2	1–4	GENKAL & POPOVSKAYA 2008a
4.4–16.4	18–20						GENKAL & POPOVSKAYA 2008b
7.6–16.4	14–20						POPOVSKAYA & GENKAL 2008
3.5–24.3	12–30						GENKA <i>et al.</i> 2009
5–22	14–20	1–4 (5)	2	on every costae	2–5 2	1	HOUK <i>et al.</i> 2010
5.3–17.8	14–25	1–9	2*	on every costae *	4–6 2*	1*	GENKAL & YARUSHINA 2010
6–18.6	14–25						KHARITONOV & GENKAL 2010
8.8–22.2	12–14						GENKAL & BONDARENKO 2011
4–44	14–20	1–13	2	on every costae	3–6 2	1 (2)	KISS <i>et al.</i> 2012
5.5–19	19–22						SOLAK & KULIKOVSKIY 2013
5–19	16–18	1	2	on every costae	4–5 2	1	CVETKOSKA <i>et al.</i> 2014
2–44.2	10–30	0–13	1–3	on every costae	1–9 2	1–4	min-max from the table

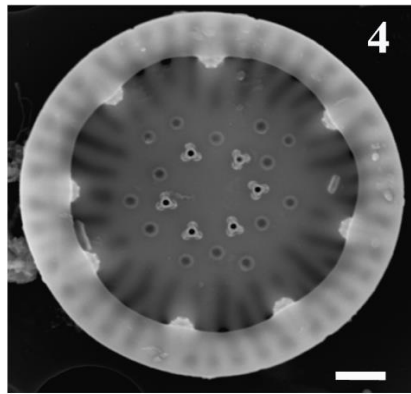
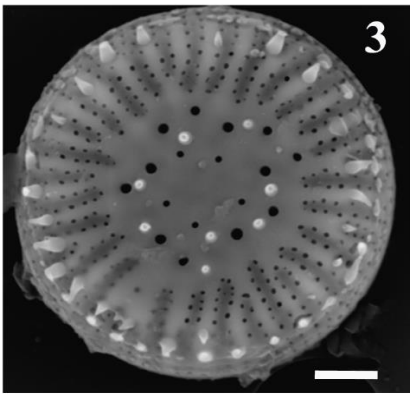
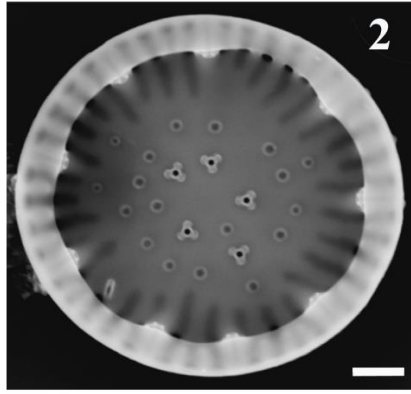
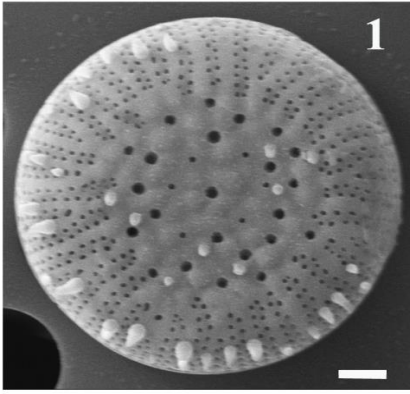




Figure 5.

