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Two new fossil *Cyclotella* (Kützing) Brébisson species from Lake Ohrid, Macedonia/Albania

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Abstract: Lake Ohrid is the oldest existing lake in Europe and it is known for its high diversity with around 200 endemic or relict diatom species recognized. In order to understand this phenomenon, a large project on deep drilling was performed and a core with maximum sediment depth of 569 m which spans > 1.2 million years was recovered. Two new species of *Cyclotella* were discovered in the core samples, which are described here as *Cyclotella cavitata* sp. nov. and *Cyclotella sollevata* sp. nov. The species have been studied with light and scanning electron microscopes, their morphological features and their relevance to other members of the genus *Cyclotella* are discussed. *Cyclotella cavitata* sp. nov. is characterized by round to elliptical shape; elliptic and tangentially undulate central area with one to three papillae on the elevated side. Central fultoportulae are absent while marginal fultoportulae internally are located on slightly depressed costae, with short tube openings with two satellite pores surrounded by cowlings. Satellite pores are situated circumferentially. Internally the rimoportula is situated in the marginal area with a sessile labium. *Cyclotella sollevata* sp. nov. is characterized by round valves with convex or concave central area which is uneven, colliculate, with papillae and granules. Central fultoportulae are present with variable number (9–21), internally with short tube openings with two satellite pores, which are surrounded by cowlings; Internally marginal fultoportulae are located on depressed costae and have short tube openings with two satellite pores situated circumferentially, surrounded by cowlings. The rimoportulae are located in the marginal area with a sessile labium variably orientated. *Cyclotella sollevata* and *Cyclotella cavitata* have been observed only in the fossil sediments of Lake Ohrid. Comments on the position of rimoportula, used as synapomorphic character to separate *Lindavia* from *Cyclotella* sensu lato are provided.

Key words: *Cyclotella*, fossil, Lake Ohrid, new species, rimoportula

Introduction

The genus *Cyclotella* (Kützing) Brébisson is classified in the family Stephanodiscaceae Gleser & Makarova and represents one of the most frequently cited genera in this family (Houk et al. 2010). Species belonging to *Cyclotella* are commonly planktonic and mainly freshwater, a considerably lower number inhabit brackish and marine waters (Loginova 1990a, Round et al. 1990; Gleser et al. 1992). Species in *Cyclotella* have been also frequently recorded in many lacustrine deposits (Ognjanova–Rumenova 2001; Khursevich et al. 2001; Khursevich 2006; Khursevich & Kociolek 2008; Kociolek & Khursevich 2013). Loginova (1990b) reported that the first representatives from this genus are known from the Late Miocene. Similarly, Temniskova–Topalova et al. (1994) showed that the diversity of *Cyclotella* species in South Europe was higher during the Late Miocene. However, Wolfe & Siver (2009) identified centric diatoms resembling to *C. michiganiana* Skvortzow from Middle Eocene lacustrine sediments in the Northwest Territories, Canada.

Due to the dominance in the planktonic communities and their use in palaeoecological and biostratigraphic investigations, species in *Cyclotella* are of high importance (Cvetkoska et al. 2016; Jovanovska et al. 2016). Therefore, revisions of the genus occur frequently (Loginova 1990a; Håkansson 2002; Houk et al. 2010; Khursevich & Kociolek 2012). So far, several efforts to group the species based on their morphological features have been attempted. Lowe (1975) separated the genus into three groups, while Loginova (1990a) divided the *Cyclotella* species into 12 groups. Houk et al. (2010) distinguished three morphological groups within the genus *Cyclotella*. More recently, Khursevich & Kociolek (2012) proposed new morphological groups for *Cyclotella* species and provided a more detailed explanation of the morphological and structural characters of 12 groups. In their revision, however, no species from Lake Prespa or Lake Ohrid were included.

Lake Ohrid is known for presence of many endemic species, including centric diatoms (Jurilj 1954; Levkov et al. 2007; Levkov & Williams 2012). Most of the data for Lake Ohrid is related to its contemporary flora, but some reports include fossil diatoms (e.g. Roelofs & Kilham 1983; Cvetkoska et al. 2012, 2014). Roelofs & Kilham (1983) made the first observations on diatom assemblages in Core 9 from Lake Ohrid, where they identified several species of *Cyclotella* as dominant. Cvetkoska et al. (2012) observed two characteristic species complexes in core Co1202: *C. fottii* Hustedt and *C. ocellata* Pantocsek.

New core sequences were recovered in the spring of 2013 within the Scientific Collaboration on Past Speciation Conditions in Lake Ohrid (SCOPSCO) deep drilling campaign. The geochemical data indicates continuous existence of Lake Ohrid for about 2 million years (Lindhorst et al. 2015). The observations of core catcher samples showed presence of at least nine different species complexes in the core sequence with major shifts of species occurring at several depths (430 m, 320 m, 230 m and 80 m below the lake floor) (Wagner et al. 2014).

Detailed observations on samples from the lower part of the core sequence (ca. 400 and ca. 320 m b.l.f.) revealed the existence of two unknown species of *Cyclotella* and here we provide the descriptions of both. The species have been studied using light and scanning electron microscopy, the morphological features and their relevance to other members of the genus *Cyclotella* are discussed. The position of these two new species in the morphological groups proposed by Khursevich & Kociolek (2012) is elaborated. This paper is the initial contribution to a series of papers that will consider the taxonomy, speciation and evolution of *Cyclotella* sensu lato species in Lake Ohrid.

Material and methods

Lake Ohrid is located in a north–west trending tectonic graben between southwestern Macedonia and eastern Albania at an altitude of 693 m above sea level. It has a total surface area of 358 km^2, volume of 55.4 km^3 and maximum water depth of 293 m (Lindhorst et al. 2014). With a hypothesized age of 2 to 10 Ma (Stanković 1960; Dumurdzanov et al. 2004) it is thought to be the oldest lake in Europe. Lake Ohrid has highest index of endemic species when taking its surface area into account (Albrecht & Wilke 2008), with around 200 endemic diatom species (Levkov & Williams 2012).

The Scientific Collaboration on Past Speciation Conditions in Lake Ohrid (SCOPSCO) project was initiated in 2007 as an international initiative aiming to study the influence of major geological and environmental events on the biological evolution of lake taxa. An International Continental Deep Drilling (ICDP) campaign on Lake Ohrid was realized in the spring of 2013. A total of ~ 2100 m of sediment had been recovered from Lake Ohrid from four different sites. The "DEEP" site is located in the central part of Lake Ohrid at ~ 250 m water depth (Fig. 1). It is located in a basement depression with an estimated maximum sediment fill of 680 m. The geochemical measurements indicate that the sediment succession covers ca. 2 million years (Ma) in a quasi–continuous sequence (Lindhorst et al. 2015).

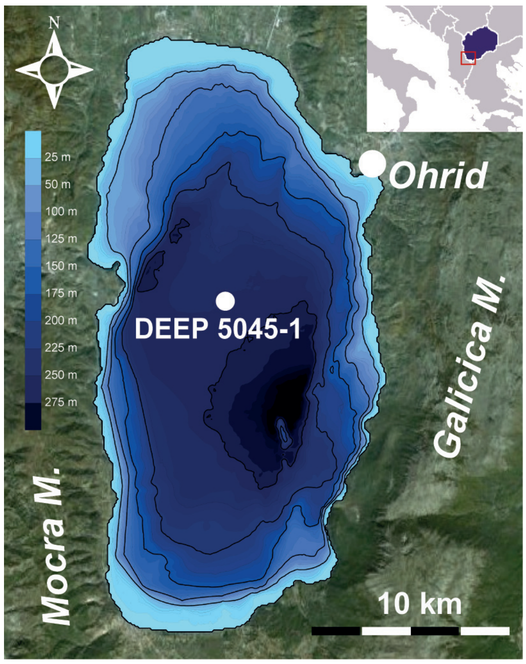

Fig. 1. Topographic map of Lake Ohrid and position of "DEEP" site coring location.

For diatoms, ca. 0.1 g wet sediment subsamples from a core catcher were taken and stored in Sterilin tubes at 4 °C. Samples were cleaned using a modification of Renberg's method for handling a large number of samples (Renberg 1990). Each sample was treated with cold H_2O_2 to oxidize organics

Fottea, Olomouc, 16(2): 218–233, 2016
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and 10% HCl to remove carbonates. Diatom slides were prepared using Naphrax® as a mountant. Slides were observed under oil immersion at 1500× magnification with a Nikon Eclipse 80i microscope, and diatom images were produced using a Nikon Coolpix P6000 camera. Scanning electron microscopy (SEM) was performed using a Cambridge S4 Stereoscan (Cambridge Instruments Ltd, Cambridge, UK) at the Friedrich Hustedt Study Centre for Diatoms (BRM) in Bremerhaven. Part of the SEM images were produced using the Field emission scanning electron microscope Philips, FEI XL30S FEG (FEI company, Hillsboro, Oregon) at the Utrecht University in Netherlands. SEM stubs were prepared using cleaned diatom material coated with gold–palladium (Polaron SC7640 sputter coater, Quorum Technologies, Ashford, UK). Holotype slides are deposited in the Macedonian National Diatom Collection (MKNDC) at the Faculty of Natural Sciences in Skopje, Republic of Macedonia. Isotype slides are deposited in the Friedrich Hustedt Study Centre for Diatoms (BRM), Bremerhaven, Germany and the Natural History Museum, London, United Kingdom (BM).

Results

Cyclotella cavitata **Tofilovska, Cvetkoska, Jovanovska, Ognjanova–Rumenova et Levkov sp. nov. (Figs 2–28)**

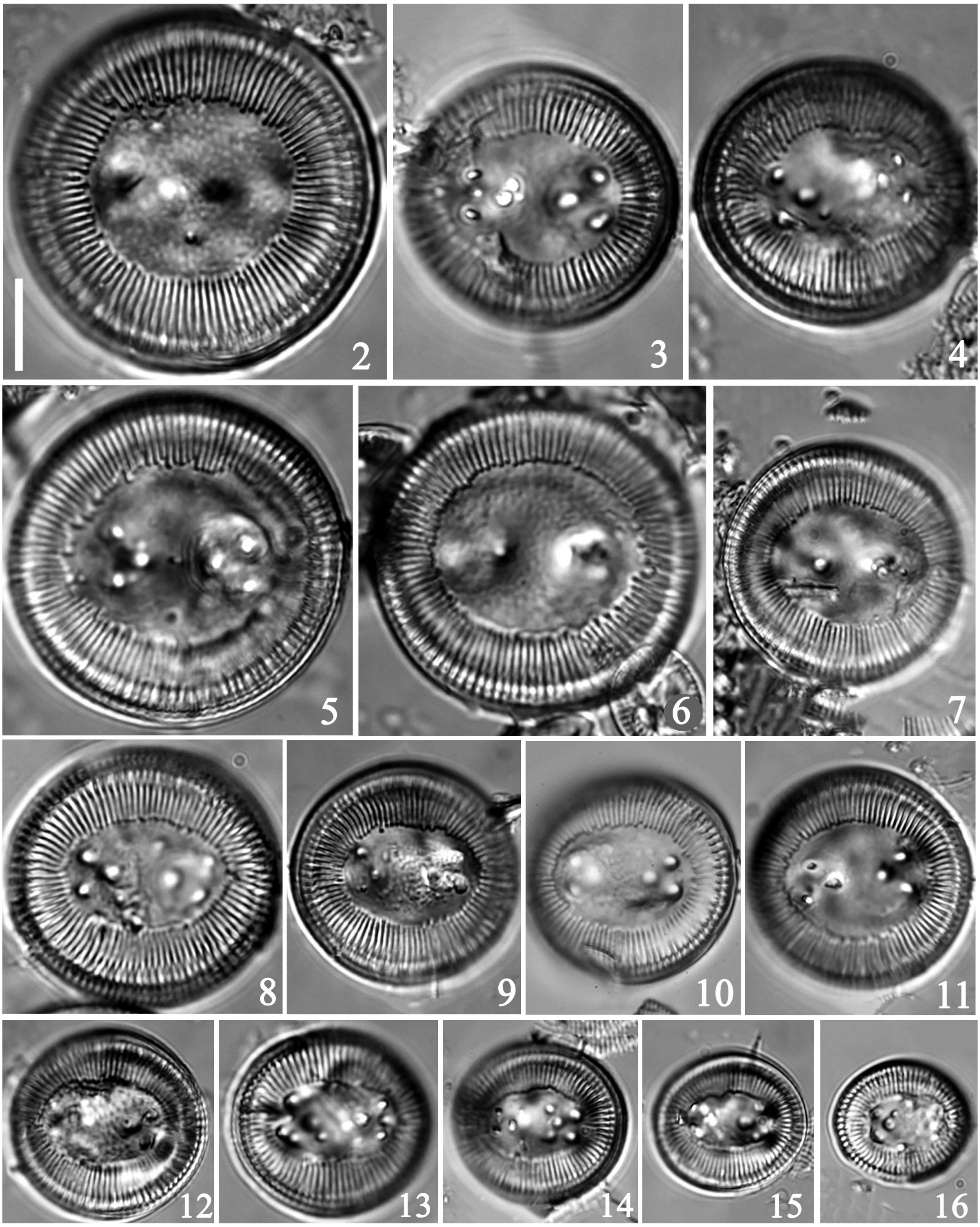
Description: Cells solitary. Valve shape round in larger specimens, becoming elliptical in medium and smaller specimens. Valve diameter with major axis between 13.8–41.0 μm and minor axis between 12.5–41.0 μm (Figs 2–16). Central area follows shape of valve outline, variable in size, its major axis 8.5–22.5 μm wide, its minor axis 6.0–19.0 μm wide. Central area tangentially undulate, slightly colliculate with 1–3 three papillae on elevated side. On depressed part of central area, 1–6 depressions present, which do not penetrate internally (Figs 17–20, 23–24). Papillae and depressions can be set in variable pattern. When 3 papillae, they form a triangle shape with apex towards center, same formed by depressions on other side (Figs 5, 8, 11, 19). Number of depressions increases, from largest (Fig. 17) to medium (Fig. 19) and smaller valves (Figs 18, 20). Striae placed at valve margins, with more or less equal length. Stria density varies from 11–18 in 10 μm (major axis), though in smaller valves stria density increases up to 20 in 10 μm. Striae bi– or tri–seriate on valve face, becoming multi–seriate towards valve mantle (Figs 19–20). Areolae adjust to interstriae with larger foramina, occluded with recessed cribrum–like structure (white arrow on Fig. 21). Internally areolae with alveolar openings (Figs 23–26). Alveoli occluded with central and marginal lamina forming tubular structure (Fig. 28). Alveolar apertures small, shorter than striae, with round shape, separated from each other by strongly thickened costae (Fig. 25). Striae separated by interstriae, with more or less same width as striae (Fig. 18). Spines and small granules present on interstriae at valve face/mantle junction and on mantle (Figs 17, 20). Central fultoportulae absent. External openings of marginal fultoportulae simple, round, located on interstriae on valve mantle (Fig. 19). Internally marginal fultoportulae located on slightly depressed costae, having short tube openings, with two satellite pores, covered with satellite pore covers running from the central tube, surrounded by cowlings (Figs 25, 26). Satellite pores are situated circumferentially. In larger valves, fultoportulae positioned at every second or third costa (Fig. 24), in smaller valves at every fourth or fifth costa (Fig. 23). External opening of valve face rimoportula simple, round, located at end of shortened stria, near elevated part of central area (white arrows on Figs 17, 19, 22). Internally rimoportula situated in marginal area with sessile labium (Figs 23, 27). Internal openings variably orientated (Figs 23, 24, 27).

Holotype: Here designated as circled specimen on slide MKNDC 007129/A. Holotype Fig. 10
Isotypes: BRM ZU10/61
Type locality: Lake Ohrid, site "DEEP", sediment core catcher from core 5045–1C–120A–CC at 321 m depth; Coordinates: N 41°02'57", E 20°42'54". Collection date: March–June 2013.
Etymology: The specific epithet is used to indicate the presence of several depressions in the central area.
Ecology and distribution: freshwater fossil, known only from type locality. In the type material it is very frequent.

Taxonomic notes: *Cyclotella cavitata* resembles *C. elymaea* Economou–Amilli (1991, figs 1–27), a fossil diatom from the Neogene deposits of northern Greece. The figures published of *C. elymaea* (op. cit.) show high valve morphological variability and different structural characteristics. The most similar specimens to *C. cavitata* are presented in Economou–Amilli (1991, figs 3–5, 18, 22, 23). However, *C. cavitata* differs from *C. elymaea* in a few morphological features such as valve shape (round throughout the whole life cycle in *C. elymaea* vs. elliptical, rarely round in *C. cavitata*); central area on the valve exterior is small, round with many small irregularly scattered depressions and without any papillae in *C. elymaea* and internal position of the marginal fultoportulae (located on unrecessed costae).

Cyclotella aegaea Economou–Amilli (1987, figs 1–26), described from Neogene deposits of Mytilinii, Samos Island, Greece, has a comparable valve size and similar ornamentation of the central area (with papillae on the elevated side) to the rounded forms of *C. cavitata.* However, it can be easily differentiated from *C. cavitata* by the following morphological features: in *C. aegaea* areolae are present in the central area; fultoportulae (0–3) are present on the valve face with three satellite pores and they are located at the elevated part of the central area. The marginal fultoportulae are placed on every valve mantle costa.

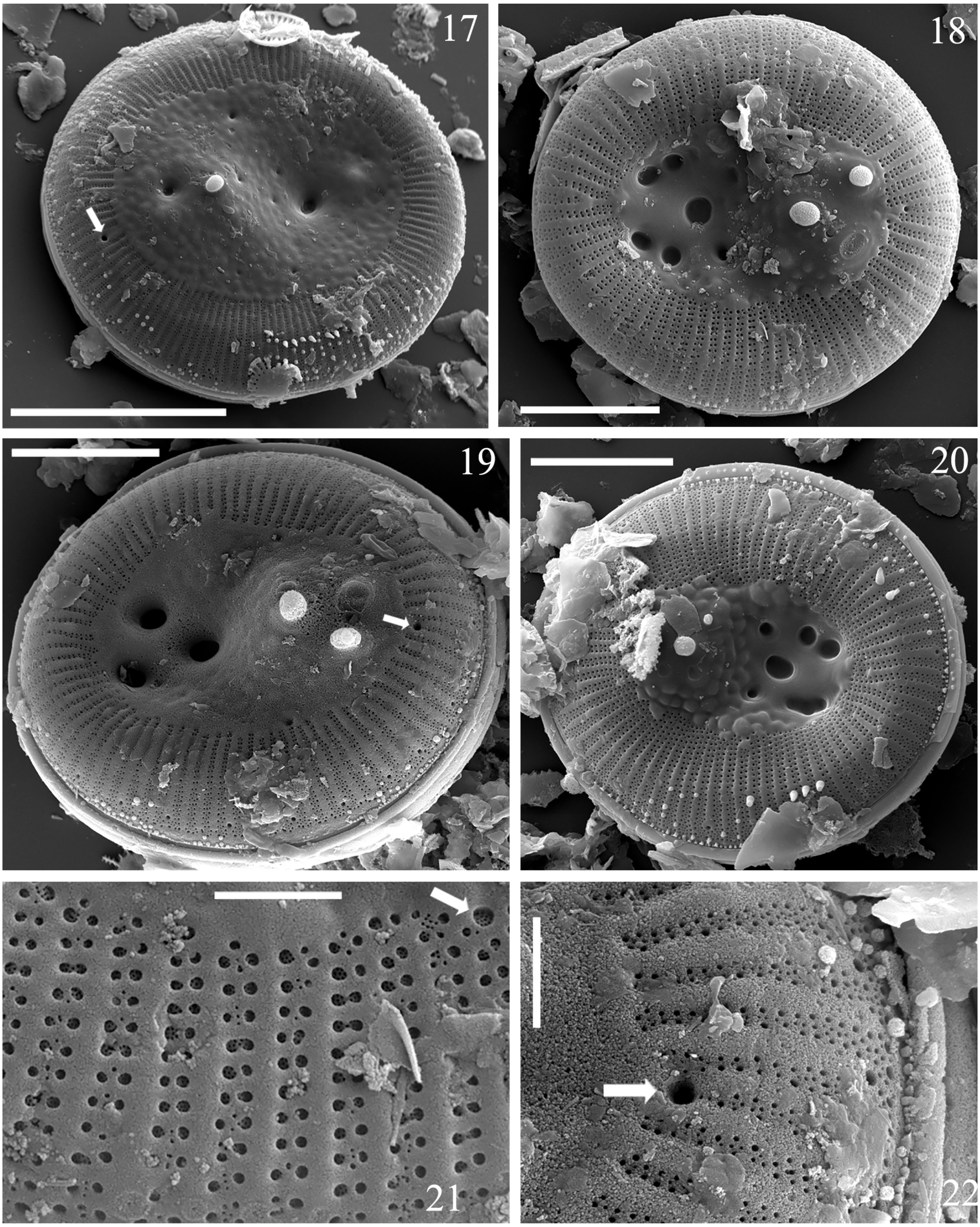
With respect to valve shape and the tangentia-



Figs 2–16. *Cyclotella cavitata*, LM valve views: (10) represents the holotype specimen, slide MKDNC 007129/A. Scale bar 10 μm.

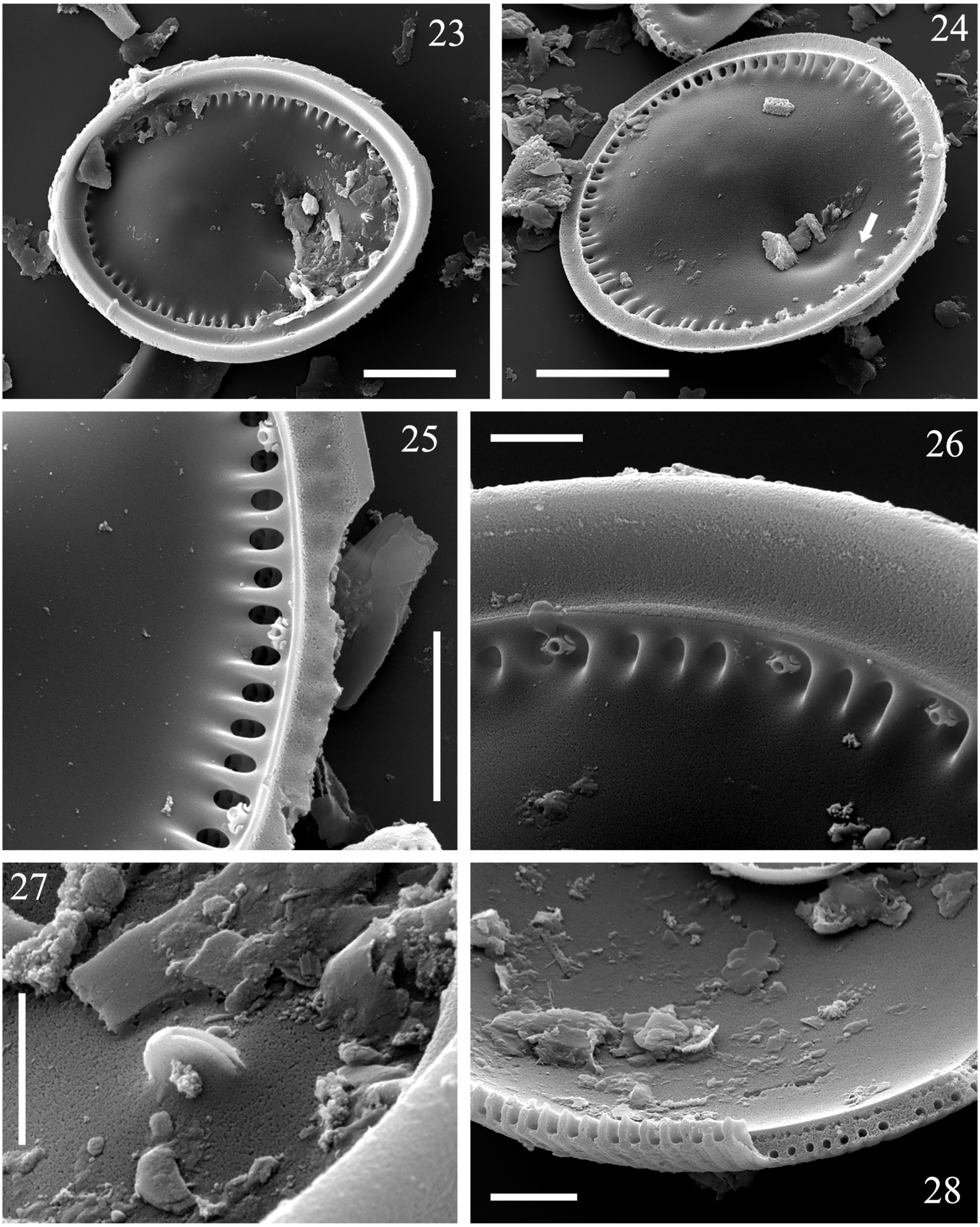
lly undulated central area, *Cyclotella cavitata* can be compared to *C. iris* BRUN & HÉRIBAUD (in HÉRIBAUD 1893), though several different ultrastructural features are observed between them. *Cyclotella iris* has unequal length of striae (SERIEYSSOL 1984; HOUK et al 2010) in contrast to the more or less equal length in *C. cavitata*. Papillae and depressions are absent in the central area of *C. iris*. Internally, the rimoportula in *C. iris* is positioned on a costa, in contrast to *C. cavitata* where it is placed on the marginal area of the valve face. *Cyclotella iris* also differs from *C. cavitata* in the number of satellite pores on the marginal fultoportulae (three in *C. iris*).

Cyclotella cavitata can easily be differentiated



Figs 17–22. *Cyclotella cavitata***,** SEM external valve views: (17–20) view of whole valve, showing variable pattern of the central area, (17) white arrow the rimoportulae, spines and granulates on valve mantle, (19) view of the marginal fultoportulae, and white arrow on the rimoportulae; (21) striae structure, white arrow on areolae occluded with cribrum–like structure; (22) white arrow on the rimoportulae. Scale bars 20 µm (17); 5 µm (18, 20); 10 µm (19); 1 µm (21, 22).

from *C. iris* var. *ovalis* Brun et Héribaud (in Héribaud 1893) in the size and shape of central area which is much smaller in *C. iris* var. *ovalis* and completely colliculate without papillae and depressions (see also Serieyssol 1984, figs 6–9, 20, 24, 37–42). Similar to the nominate variety, var. *ovalis* also has unequal length of striae. External opening of the rimoportula in *C. iris* var. *ovalis* is positioned on the mantle while internally is on a costa. *Cyclotella* cf. *iris* sensu Kusel–Fetzmann & Losert (2001, figs 5, 18–24) is more closely



Figs 23–28. *Cyclotella cavitata***,** SEM internal valve views: (23–24) view of whole valve, smaller and larger specimen respectively; (25) alveolar apertures; (26) showing the short tube openings of the marginal fultoportulae, positioned on depressed costa, with two satellite pores surrounded by cowlings; (27) view of the rimoportula, sessile labium; (28) alveoli occluded with central and marginal lamina derive tubular structure. Scale bars 5 µm (23, 25); 10 µm (24); 2 µm (26, 28); 1 µm (27).

related to *C. fottii* Hustedt and it clearly differs from *C. cavitata* by the valve outline, shape of the central area, position of the rimoportula, number of satellite pores on the marginal fultoportulae.

Cyclotella sp. sensu Ognjanova–Rumenova et al. (2008, figs 10: 1–5) was recorded from lacustrine deposits from Sofia Basin, Bulgaria, from the period of the Late Miocene–Early Pliocene. According to its morphological and ultrastructural features this taxon is more closely related to *C. iris* than to *C. cavitata*.

Fottea, Olomouc, 16(2): 218–233, 2016
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Both taxa can be easily differentiated by the shape of the central area (without papillae and depressions in *Cyclotella* sp.), position of the rimoportula (on costa in *Cyclotella* sp.), number of satellite pores (three in *Cyclotella* sp.) and striae morphology (striae have unequal length in *Cyclotella* sp.). *Cyclotella* sp. 1 sensu Ognjanova–Rumenova (2001, figs 8–10; 2005, fig. 2: 16–22; fig. 4: 1–5), a fossil diatom from Pelagonia Basin, Macedonia, is characterized by elliptical valve shape, radially undulate central area, three papillae on the elevated parts of the central area and three large depressions that do not penetrate the valve interior. However, the latter taxon differs from *C. cavitata* by the shape and ornamentation of the central area, the position of rimoportula (located on costa) and number of satellite pores of marginal fultoportulae (three).

Cyclotella cavitata differs from *C. fottii* with the respect to the valve outline and the size and shape of the central area. The latter species has circular valve shape, small, round central area without papillae and depressions. Additional differences can be noticed in the length of striae (*C. fottii* has branched and unequal striae), marginal fultoportulae (in *C. fottii* are situated on regular, not depressed costae) and number of rimoportulae (*C. fottii* has three to eight opposite to a single rimoportula in *C. cavittata*).

Cyclotella cavitata can also be compared to *C. minuta* (Skvortzow) Antipova (Antipova 1956) and *C. idahica* Khurcevich et Kociolek (in Kociolek & Khurcevich 2013, figs 1–9) only in the tangential undulation of the central area. *Cyclotella minuta*, in contrast to *C. cavitata*, has a larger central area without papillae and depressions, but with central fultoportulae. *Cyclotella idahica* also lacks papillae and depressions in the central area in contrast to *C cavitata*. Another main difference between these two species is the presence of high number of areolae and one central fultoportula in the central area of *C. idahica*.

***Cyclotella sollevata* Tofilovska, Cvetkoska, Jovanovska, Ognjanova–Rumenova et Levkov sp. nov. (Figs 29–49)**

Description: Cells solitary, valves round, diameter 11–30 µm. Valve face divided to central area and striated marginal area. Diameter of central area between 4–12 µm (Figs 29–49). Central area highly variable in shape, either convex (Figs 50–54) or concave (Figs 55, 56), consequently internally with distinct elevation or depression. Some valves with more elevated central area (compare Figs 50, 59 with Figs 51–54). Both convex and concave central area externally uneven, colliculate, with granules, papillae and simple, round openings of central fultoportulae (Figs 57–60, 63). Striae not branched, with more or less equal length; density from 14–20 in 10 µm. Striae bi– or tri–seriate on valve face, becoming multiseriate towards valve mantle (Figs 56, 59, 61). Areolae adjust to interstriae with larger foramina (Figs 51, 61, 62) occluded with recessed cribrum–like structure (white arrow on Fig 62). Internally, alveolar openings small, with round shape, positioned on marginal portion. Alveoli occluded with central and marginal lamina (Fig. 69). Strongly thickened, elongated costae separate alveolar apertures (Figs 66, 68). Internally, from valve margin a silica layer covers part of costae (double arrow on Fig. 64 and white arrow on Fig. 68). Interstriae separate striae, occasionally ornamented by small granulates (Figs 51, 52); spines positioned on valve face/valve mantle junction (Figs 57, 60). Central fultoportulae present in variable numbers (9–21). Externally fultoportulae with small round openings (Figs 50, 55, 58, 60, 63), internally having short tube openings with two satellite pores, covered with satellite pore covers running from the central tube, surrounded by cowlings (Fig. 67). Satellite pores are situated circumferentially. External openings of marginal fultoportulae simple, round, located on interstriae of valve mantle (white arrows on Figs 56, 61). Internally marginal fultoportulae located on depressed costae having short tube openings with two satellite pores, covered with satellite pore covers running from the central tube, surrounded by cowlings (Figs 68, 69). Fultoportulae positioned at every second, third or fourth costa (Fig. 70); in smaller valves at every fourth or fifth costa (Fig. 69). External opening of valve face rimoportulae simple, round, located at end of a shorten stria (white arrows on Figs 50, 60, 63). Internally rimoportula located in marginal area with a sessile labium variably orientated (Figs 64, 68–70).

Holotype: Here designated as circled specimen on slide MKNDC 007147/A. Holotype Figs 30, 31.
Isotypes: BRM ZU10/62
Type locality: Lake Ohrid, site "DEEP", sediment core catcher from core 5045–1C–120A–CC at 406 m depth; Coordinates: N 41°02'57", E 20°42'54". Collection date: March–June 2013.
Etymology: The specific epithet refers to the elevation of the central area, though the central area might be convex or concave.
Ecology and distribution: freshwater fossil, known only from type locality. In the type material it is very frequent.

Taxonomic notes: *Cyclotella sollevata* has unique set of characters which makes it easy to differentiate from other known species of *Cyclotella*. Morphologically, the most similar species is *C. armenica* Loginova et Pirumova (in Loginova et al. 1990, figs 7: 1–6) described from Late Pliocene sediments from Armenia. Both species have a central area that might be either convex or concave and presence of the central fultoportulae and multiseriate striae on the valve mantle. Differences between these two species can be noticed in the size of the central area (being larger externally and flat internally without distinct depression or elevation in *C. armenica*), number of central fultoportulae (one to several in

C. armenica opposite to 9–21 in *C. sollevata*), structure of fultoportulae (satellite pores are not covered with satellite pore covers running from the central tube in *C. armenica*), position of marginal fultoporulae (on every fifth to eighth costa in *C. armenica*) and position of the rimoportula (close to the costa in *C. armenica*).

In respect to the valve outline, *Cyclotella sollevata* slightly resembles *C. metochia* Ognjanova–Rumenova (2014, figs 11, 12, 14, 24, 28), a species described from the Neogene sediments of Metochia Basin, Kosovo. Yet, both species differ in the shape and ornamentation of the central area (*C. metochia* has small, flat and slightly coliculate central area), striae length (striae with unequal length present in *C. metochia*) and stria structure (biseriate striae composed of areolae with equal size in *C. metochia*).

Cyclotella praetemperei Khursevich (in Khursevich et al. 1999) sensu Kusel–Fetzmann & Losert (2001, figs 25–37) is comparable to *C. sollevata* with respect to a few morphological features. Both species, *C. sollevata* and *C. praetemperei*, have similar size, round shape of the valve and central area, and several central fultoportulae. However, differences can be noticed in the structure of the central area. The central area of *C. praetemperei* is smaller and slightly convex or concave, opposite to *C. sollevata* which has large and distinctly convex or concave central area. The central area appears similar in LM, though clearly differs on SEM, externally *C. praetemperei* lacks papillae and granules. Internally central fultoportulae have three satellite pores in *C. praetemperei vs*. two pores in *C. sollevata*. In contrast to *C. sollevata*, *C. praetemperei* has striae of unequal length. Internally, the rimoportula in *C. praetemperei* is positioned on the wall of alveolar opening, close to the costa, in contrast to the submarginal position of rimoportulae at *C. sollevata.* From the valve exterior, *C. baicalensis* Skvortzow & Meyer (1928, fig. 1: 3) differs from *C. sollevata* by the larger and elliptical shape of the central area, which is more finely colliculate and lacks papillae and depressions (Popovskaya et al. 2002). Also, in C. *baicalensis* the marginal fultoportulae are situated on every costa, opposite to *C. sollevata* where fultorportule are located on every 2–5 costa.

The fossil diatom *C. discostelliformica* Kociolek & Khursevich (2013, figs 25–39) appears similar in LM to *C. sollevata*, mainly in the valve shape and in the central area. Yet, they differ in the presence of areolae in the central area in *C. discostelliformica*. *Cyclotella sollevata* has a higher number of valve face fultoportulae and higher stria density than *C. discostellioformica.* Another difference is the number of satellite pores in the central and in the marginal fultoportulae, three in *C. discostelliformica vs*. two in *C. sollevata.*

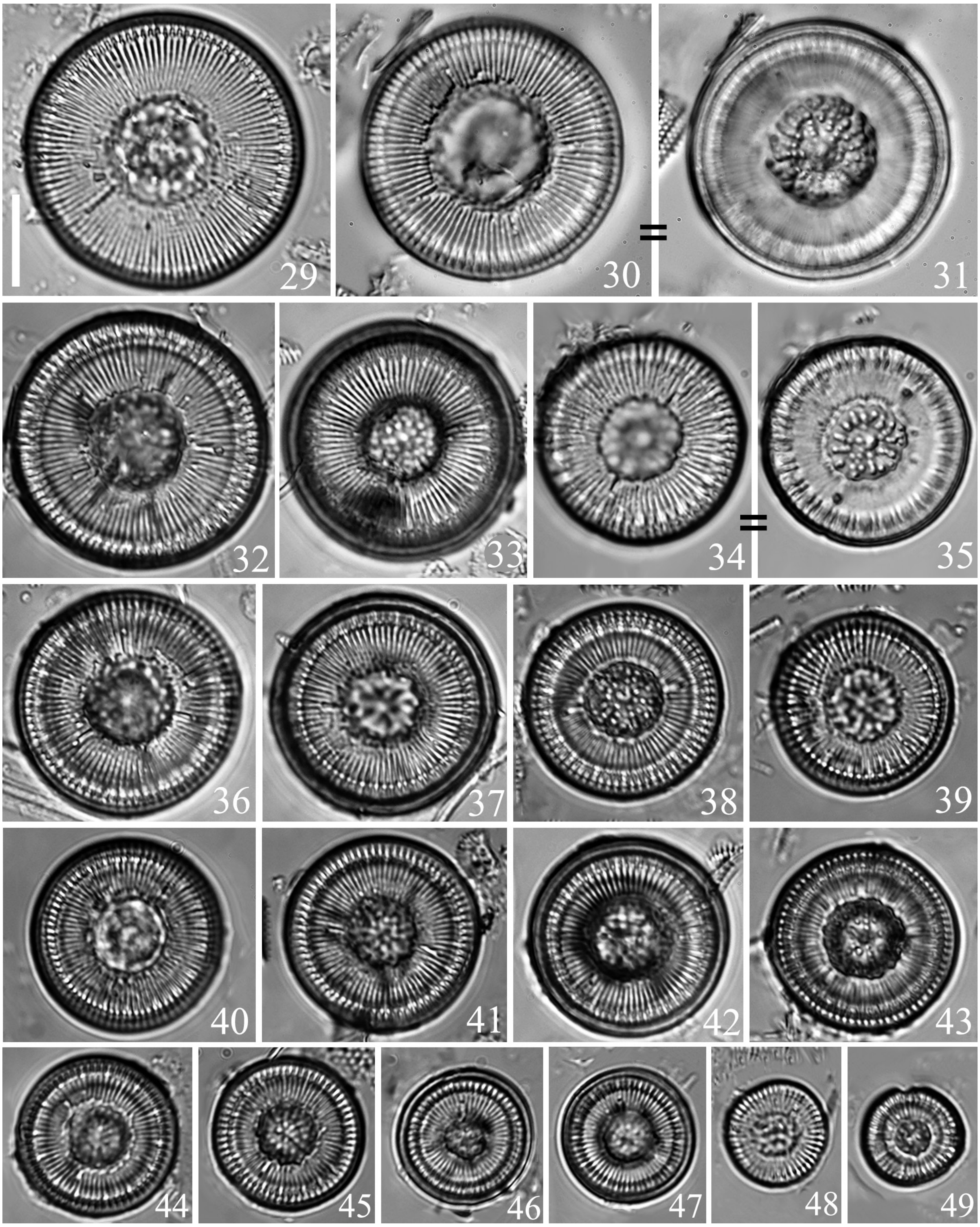
With respect to the valve outline and the central area, *C. sollevata* can be easily distinguished from other species known from Lake Ohrid, *C. fottii*, *C. bifacialis* Jurilj (1954), *C. ocellata* Pantocsek and *C. minuscula* (Jurilj) Cvetkoska (Cvetkoska et al. 2014).

Discussion

The genus *Cyclotella* is considered as heterogeneous and polyphyletic (Alverson et al. 2007). The species have high morphological variability with some being heterovalvar, thus identification is often problematic (Houk et al. 2010). Three morphologically distinct groups within the genus were first proposed by Lowe (1975) as the groups “meneghiniana”, “comta” and “stelligera”. Two of these groups, based on their distinctive features, have been transferred to the genera *Handmannia* M. Peragallo (in Handmann 1913) and *Discostella* Houk & Klee (2004). Later McFarland & Collins (1978) recognized the “striata” group, while Serieyssol (1981) added the “andancensis” group. Loginova (1990a) investigated more than 40 *Cyclotella* species and, based on several structural characteristics, the species were gathered into 12 groups. Houk et al. (2010) divided the genus *Cyclotella* in three groups based on 58 *Cyclotella* species. The groups were separated by: 1) species with central area lacking areolae and single rimoportula within a ring of marginal fultoportulae; 2) species with central area without areolae and at least one rimoportula not within a ring of marginal fultoportulae and 3) species with central area with areolae and at least one rimoportula not within a ring of marginal fultoportulae, but on the valve face.

More recently, Khursevich & Kociolek (2012) published a preliminary worldwide list of non–pennate diatoms, belonging to seven families, including Stephanodiscaceae. The majority were fossil diatoms, which included 42 extinct and 19 extant species of *Cyclotella* divided in 12 morphological groups. Several characters have been considered important for separating these groups: valve outline, stria morphology and structure, presence and location of the rimoportulae, position of the marginal fultoportulae, presence and location of valve face fultoportulae, number of satellite pores and presence of areolae in the central area and their occlusion. Based on these characters, *C. cavitata* might be placed into group 3 sensu Khursevich & Kociolek (2012) or “*andancensis*” group sensu Serieyssol (1981). This group is characterized by very small central area, striae with unequal length and rimoportula located on the inner end of one of the costae or on the costae (Khursevich & Kociolek 2012, p. 333). In *C. andancensis* Ehrlich (1966, figs 5: 11–13), as documented by Serieyssol (1981, fig. 2) the rimoportula is located on a costa. Khursevich & Kociolek (2012) included *C. elymaea* in this group, but this species has its rimoportula positioned submarginally and distantly from the valve mantle. In general, *C. cavitata* differs from the representatives of this group by the valve outline, size of the central area, position of the marginal fultoportulae (on the valve mantle in *C. andancensis*) and position of

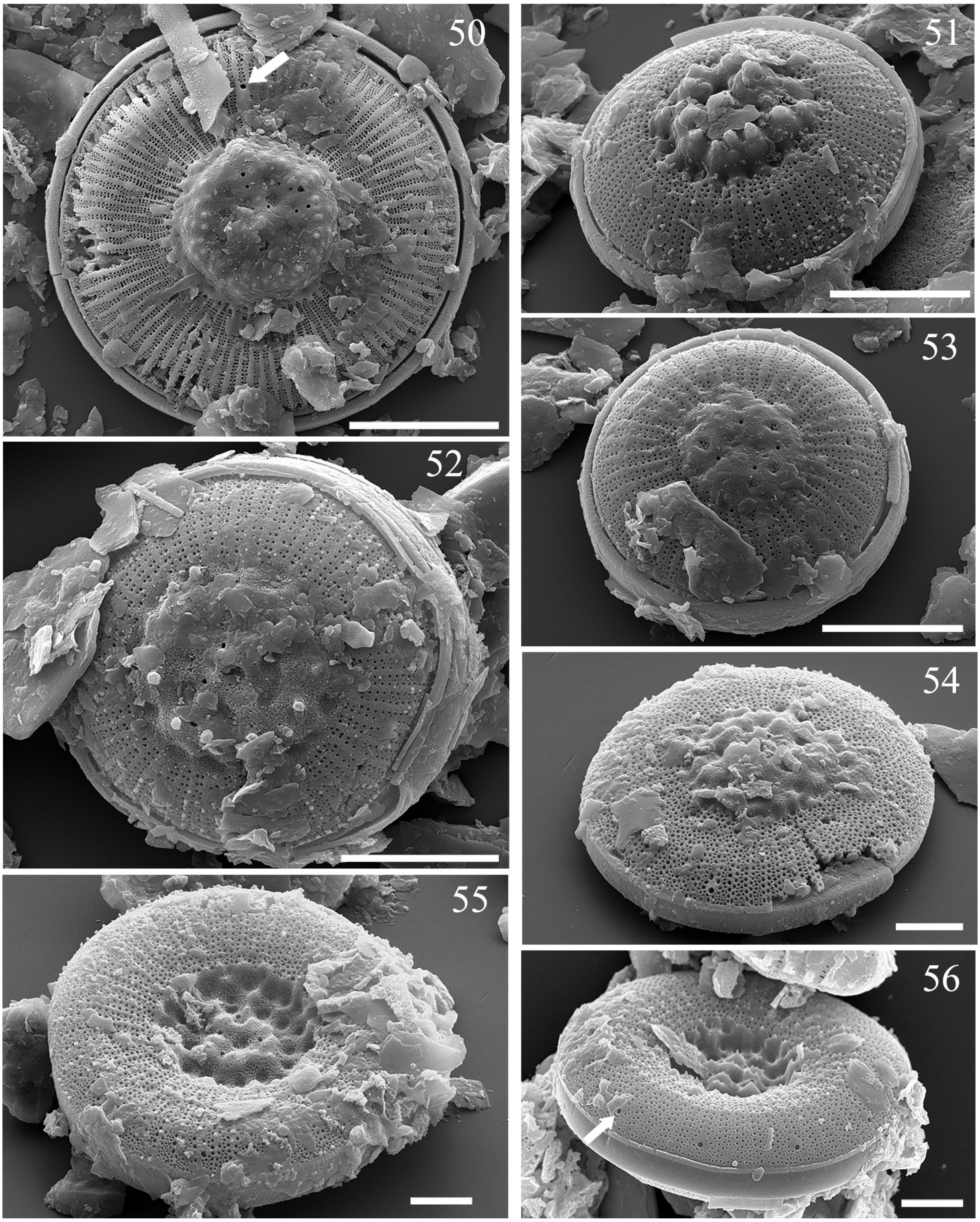
Fottea, Olomouc, 16(2): 218–233, 2016
DOI: 10.5507/fot.2016.003



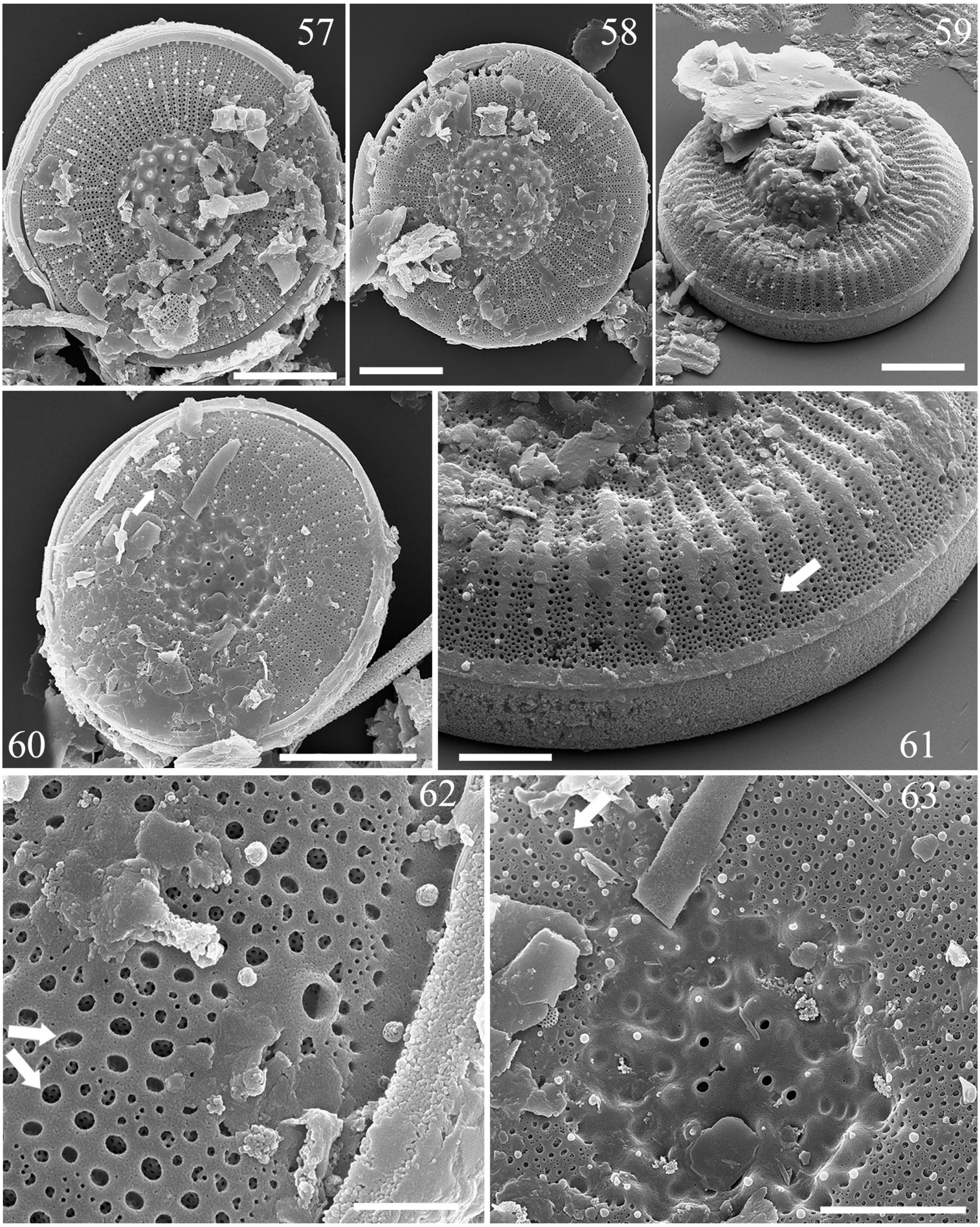
Figs 29–49. *Cyclotella sollevata*, LM valve views: (30, 31) represent the holotype specimen, slide MKDNC 007147/A. Scale bar 10 µm.

the rimoportula (on costa *C. andancensis*). *Cyclotella cavitata* can also be considered morphologically similar to group 2 sensu Khursevich & Kociolek (2012) or a group around *C. iris*. This group contains species with oval to rhomboid–elliptical valves, large central area without central fultoportula, marginal fultoportula with three satellite pores and rimoportula located on one of the recessed costae. However, apart from the morphological similarity exhibited in LM, *C. cavitata* possesses different ultrastructural features such as position of the rimoportula and number of satellite pores.

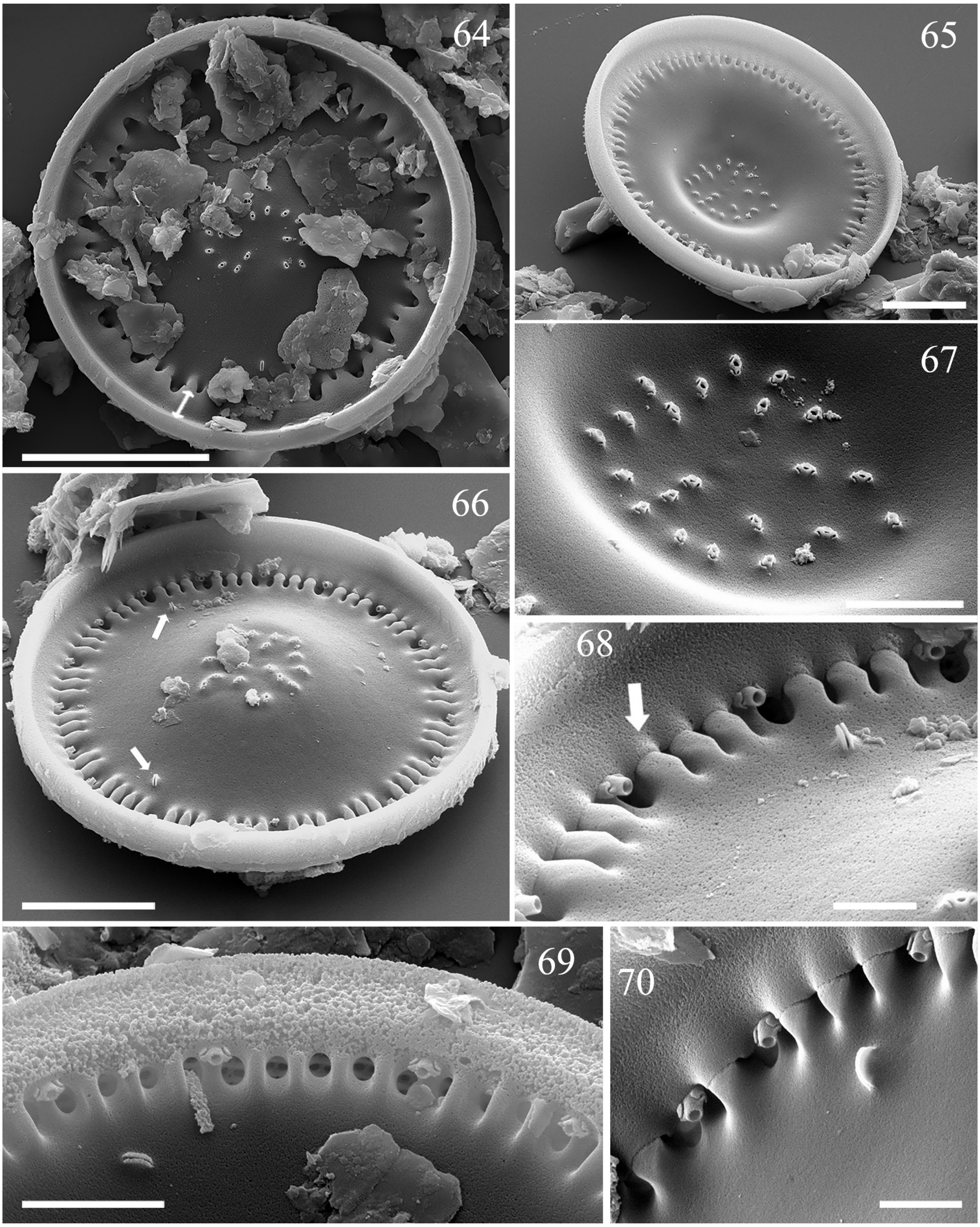
Cyclotella cavitata, which in LM appears quite different from *C. fottii*, shares many ultrastructural features with the latter species. Both are without valve



Figs 50–56. *Cyclotella sollevata***,** SEM external valve views: (50) valve with strongly convex central area, white arrow on rimoportulae; (51–54) valves with not strongly convex central area and different types of organization of the central area; (55–56) valves with concave central area, (56) white arrow on opening of one marginal fultoportula. Scale bars 10 µm (50); 5 µm (51–53); 2 µm (54–56).



Figs 57–63. *Cyclotella sollevata***,** SEM external valve views: (57) spines positioned on valve face/valve mantle junction; (58) showing papillae and simple, round openings of central fultoportulae; (59) valve with strongly convex central area; (60) valve with concave central area, white arrow on rimoportula at the end of a shorten stria; (61) striae structure, becoming multiseriate on the valve mantle. Marginal fultoportulae have round external opening (white arrow); (62) white arrows on larger areolae of the marginal rows of one stria, occluded with cribrum–like structure; (63) central coliculate area with granules (white arrow on rimoportula). Scale bars 5 μm (57–60); 2 μm (61, 63); 500 nm (62).



Figs 64–70. *Cyclotella sollevata*, SEM internal valve views: (64) double arrow on a silica layer that extends from the valve margin and covers part of the costae; (65) view on convex valve; (66) view of concave valve with two rimoportulae (white arrows); (67) central fultoportulae with two satellite pores with cowlings; (68) white arrow on a silica layer that extends from the valve margin and covers part of the costae; (69) alveolar apertures; (70) position of rimoportula. Scale bars 10 µm (64); 5 µm (65, 66); 2 µm (67, 69); 1 µm (68, 70).

face fultoportulae, the marginal fultoportulae are placed on recessed costae and have two satellite pores, covered with satellite pore covers running from the central tube, surrounded by cowlings and 1–4 rimoportulae which are sessile and located submarginally. These features are also present in *C. elymaea* from Northern Greece, but also in other species from Lake Ohrid (pers. observ.) erroneously identified as *C. iris* sensu Wagner et al. (2014). According to this, it is very likely that the species form a monophyletic group.

It is even harder to place *C. sollevata* in one of the groups proposed by Khursevich & Kociolek (2012). The most similar species to *C. sollevata* is *C. armenica*, which is grouped together with *C. ocellata* and *C. tripartita* Håkansson (1990, figs 1–4, 8–11, 13), or group 6 sensu Khursevich & Kociolek (2012). However, both *C. ocellata* and *C. tripartita* have a circumferential undulated central area with one to three valve face fultoportulae and marginal fultoportulae located on not recessed costae. In contrast, *C. armenica* has a distinctly convex or concave central area with many valve face fultoportulae and marginal fultoportulae are located on the recessed costae. It is possible that *C. sollevata* and *C. armenica* belong to the same group different than *C. ocellata*.

Cyclotella sollevata might also be placed in group 11 sensu Khursevich & Kociolek (2012) which is comprised mostly of species endemic to Lake Baikal. However, in contrast to *C. sollevata*, in this group the marginal fultoportulae are placed on almost every costa and are surrounded by cowlings with quite different shape.

Finally, both new species might be placed in the recently re–established genus *Lindavia* (Schütt) De Toni & Forti (1900) based on section *Lindavia* Schütt (1899). However, according to Nakov et al. (2015) *Lindavia* encompasses a broad range of taxonomic and morphological diversity and includes species with quite different ultrastructural features like the structure of alveolae, areolae, cribra, fultoportulae etc. According to authors, the only synapomorphic feature is the position of the internal and external openings of the rimoportula on the valve face close to or distant from a costa, but disassociated from the ring of marginal fultoportulae (Nakov et al. 2015, p. 251, 252). However, the authors only tentatively suggest that *Lindavia* represents a monophyletic genus, since they concluded that "future phylogenetic analyses may support the splitting of *Lindavia* into multiple genera" (Nakov et al. 2015, p. 253).

When creating the new combinations, Nakov et al. (2015) transferred *C. fottii*, *C. thienemanii* Jurilj and *C. minuscula* into the genus *Lindavia*. The position of the rimoportula as proposed synapomorphic character grouped all these species within *Lindavia*, however, the existing data show high variability of this character. For example, *C. fottii* doesn't have areolae or valve face fultoportulae (Levkov et al. 2007; Cvetkoska et al. 2012) and the rimoportula in some specimens is located on the valve mantle/face junction associated with a costa. In *C. minuscula* the position of the rimoportula is also variable. In some specimens the rimoportula is located on a costa (Cvetkoska et al. 2014, figs 73, 75), while in other specimens is located on the valve face (Cvetkovska et al. 2014, fig. 97; Levkov unpubl. data). In *C. thienemanii* the position of the rimoportula appears to be stable and located on the valve face distantly from the ring of marginal fultoportulae, due to which was previously transferred to *Puncticulata* by Levkov et al. (2007) and later to *Lindavia* by Nakov et al. (2015). Additionally, *C. thienemanii* shares another morphological feature of *Puncticulata/Handmania/Lindavia* (Levkov et al. 2007, fig. 9: 2), the presence of areolae in the central area.

Extensive SEM observations (e.g. Houk et al. 2010) show that the position of the rimoportula in *Cyclotella* (Kützing) de Brébisson sensu lato is variable. In one of the most frequent freshwater species *C. ocellata* Pantocsek the position of the rimoportula varies from at the valve face (Houk et al. 2010, fig. 200: 6; 201: 1) to the valve mantle associated to/at the base of the costa (op. cit., figs 201: 5, 6) or even it's located on a costa (op. cit., fig. 200: 3). Similar situation is present in *C. cretica* John & Economou–Amilli (1990, figs 1–23; Houk et al. 2010, figs 203: 5, 6), *C. polymorpha* Meyer & Håkansson (1996, figs 1–29; Houk et al. 2010, figs 205: 15, 16), *C. pseudocomensis* Scheffler (1994, figs 1–31; Houk et al. 2010, figs 219: 10–12) etc.

Driven by the given examples, it is rather questionable if the position of the rimoportula can be used as a "synapomorphy (defining character)" for *Lindavia*, as proposed by Nakov et al. (2015). Therefore, we strongly encourage future morphological and molecular studies to focus on defining a stable character that can be used as a synapomorphy for *Lindavia*. In doing so, detailed phylogenetic analyses are therefore preferable in order to test the ancestral species/genus for *Lindavia* in defining the plesyomorphic and potential synapomorphic characters. This, in turn, will retest the proposed hypothesis for double disassociation of the rimoportula from the ring of marginal fultoportulae, or more specifically, the separation of *Shionodiscus* Alverson, Kang & Theriot (in Alverson et al. 2006) from *Thalassiosira* Cleve (Cleve 1873) and *Lindavia* from *Cyclotella* sensu lato. The inconsistency of Nakov et al. (2015) in transferring species within *Lindiavia*, cannot be excluded as a potential bias in validating the position of the rimoportula as a synapomorphic character. In the end, detailed morphological and phylogenetic analyses on fossil and extant species are needed to prove the monophyly of the genus *Lindavia* as presented by Nakov et al. (2015). After redefinition of synapomorphic characters in *Cyclotella* sensu lato it might become necessary to transfer the newly described species to other genus different than *Cyclotella* sensu stricto.

The new species described in this study have been observed only from the fossil samples of Lake Ohrid "DEEP–5045–1" core. Several studies on the contemporary and fossil flora of lakes Ohrid and Prespa have been made in the last decades (see Levkov & Williams 2012) and these two species were not recorded. The preliminary observations of the core catcher samples from core 5045–1 (Wagner et al. 2014) show that both species have limited temporal distribution only in sediments from the lowermost part of the sequence (ca. 300–400 m). In the more recent sediments, *C. cavitata* and *C. sollevata* are replaced by other *Cyclotella* sensu lato species which are also not recorded in the contemporary diatom flora (e.g. Levkov et al. 2007; Cvetkoska et al. 2014). The ongoing analyses show that at least nine unknown *Cyclotella* species and one new genus (Jovanovska et al. 2016) are present in the core from Lake Ohrid. These species will be presented and discussed in the forthcoming studies, including their relations to the modern species with respect to the morphological phylogeny and evolution.

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