Cyclotella paleo–ocellata, a new centric diatom (Bacillariophyta) from Lake Kinneret (Israel)

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Abstract: Large, subfossil populations of an unknown centric, planktonic diatom were observed in a lake sediment core from Lake Kinneret (Israel), which is here described as *Cyclotella paleo–ocellata* sp. nov. The new taxon, which belongs to the *Cyclotella ocellata* species complex, is described and separated from other similar taxa (e.g., *Cyclotella ocellata, Cyclotella kuetzingiana, Cyclotella polymorpha, Cyclotella paraocellata*) based on a combination of the following morphological characters: valve diameter, number of orbiculi depressi (circular depressions), number of striae/10 µm, stria length, number and position of rimoportulae and the number of central and marginal fultoportulae. *Cyclotella paleo–ocellata* can be distinguished mainly by two prominent characteristics: (1) the number and the arrangement of the orbiculi depressi (4–8) which increase with the valve diameter and (2) the marginal fultoportulae, situated on each, every second or third costa. Since *Cyclotella paleo–ocellata* is at present only known from the subfossil bottom sediments of Lake Kinneret, its ecological preferences are inferred simply from the associated diatom flora.

Key words: Bacillariophyta, *Cyclotella paleo–ocellata*, Lake Kinneret, morphology, taxonomy

INTRODUCTION

The genus *Cyclotella* (Kützing) Brébisson is one of the most commonly occurring genera of the Stephanodiscaceae (Houk et al. 2010). Its species are centric and characterized by a distinct central area and a radially–striated marginal area (Håkansson 2002). Genera in the family of Stephanodiscaceae are a dominant component of the plankton in freshwaters worldwide. The genus *Cyclotella* often dominates species assemblages in paleolimnology, particularly in the circum–Mediterranean region, and can cause difficulties or loss of information in paleoenvironmental reconstructions due to the ongoing taxonomic uncertainty in this group (Håkansson 2002). The genus exhibits a high morphological variability that is still not completely understood, requiring more detailed analysis of recent and fossil diatom material.

Within the genus *Cyclotella*, it is possible to distinguish several groups of taxa that show a more or less similar morphology. One of these groups is the ‘species complex’ of *Cyclotella ocellata* Pantocsek, a term introduced by Hegewald & Hindáková (1997). Cvetkoska et al. (2012) recently reviewed the complex in detail. *Cyclotella ocellata* was first described by Pantocsek (1901, p. 104, fig.15: 318) as a flat valve with 3 “*margaritis majoribus*” (later named “orbiculi depressi” by Kiss et al. 1996) arranged in a triangular position in the central area with a ring of marginal striae.

As well as the high taxonomic variability within the taxon *C. ocellata* the ecological preferences are also still uncertain. According to several authors (e.g., Fritz et al. 1993; Van Dam et al. 1994; Kiss et al. 1996; Schlegel & Scheffler 1999; Cremer & Wagner 2003; Houk et al. 2010) *C. ocellata* seems to have an extremely broad tolerance of nutrient status, extending (in rare cases) from ultra–oligotrophic [e.g., Lake Ohrid (Cvetkoska et al. 2012)] to eutrophic [e.g., Lake Dagow (Schlegel & Scheffler 1999)]. Cremer & Wagner (2003) suggested that the *Cyclotella ocellata* complex must comprise several different species or ecological groups, exhibiting contrasting ecological preferences for nutrient status which may in part relate to the biogeographic region in which they grow. *Cyclotella ocellata* is known as a cosmopolitan taxon, often found in shallow lakes [e.g., Lake Las Madres (Kiss et al. 1996) and Laguna de Medina (Reed et al. 2001) in Spain], but can also dominate in very deep lakes such as Ohrid (Cvetkoska et al. 2012) or El'gygytgyn (Cremer & Wagner 2003), perhaps particularly those with a sandy or gravel lake bed (Houk et al. 2010). It also occurs in slow flowing rivers as plankton or periphyton (Krammer & Lange–Bertalot 1991; Ehrlich 1995; Houk et al. 2010).

Few diatom–based paleolimnological studies have been carried out previously in lake sediments of ancient Lake Kinneret. Pollingher et al. (1984) analysed the changing character of planktonic diatoms in Lake Kinneret over the last 5000 yrs and Ehrlich (1985) carried out a paleoecological assessment of recent environmental change in the diatom flora of five short cores. This included the description of two new planktonic species: *Cyclotella polymorpha* Meyer et Håkansson and *Stephanodiscus galileensis* Håkansson et Ehrlich (Håkansson & Ehrlich 1987; Meyer & Håkansson 1996). Ehrlich (1985) also observed a third unknown centric diatom which she denoted as *Cyclotella* sp. (Ehrlich 1985: plate 1, figs 13–14) without formal description.

Diatom–based paleolimnological studies on a longer timescale have not yet been accomplished in Lake Kinneret. During a drilling campaign which took place as part of the Collaborative Research Center (CRC) 806 "Our Way to Europe" (http://www.sfb806.uni–koeln.de), a 17.8 m long sediment core was recovered which spans the last c. 8200 yrs cal BP. The detailed diatom–based paleolimnological analysis of this sediment sequence forms part of a multi–proxy study of Holocene climate change and human impact in the Levant region. During a preliminary analysis of the diatom succession in the sediment sequence of Lake Kinneret, large populations of an unknown *Cyclotella* species are often recorded as abundant in assemblages dominated by the classic *Cyclotella ocellata* type.

Following detailed light and scanning electron microscopy observation, the unknown taxon could not be identified based on the currently available literature. Here, we describe this new taxon as *Cyclotella paleo–ocellata* sp. nov. and discuss its morphology and separation from other taxa within the *Cyclotella ocellata* complex, also attempting the first delimitation of its ecological preferences.

Materials and methods

Study site. Lake Kinneret (from Hebrew word *kinnṓr* = 'harp', reflecting the shape of the lake) is also known as the Sea of Galilee or Lake Tiberias and is located in the northern part of the Jordan Rift Valley in the North of Israel (32°48'08.12"N, 35°35'20.62"E; Fig. 1). It is situated, together with the Dead Sea basin, on the "Dead Sea Transform Fault (DSTF)". The DSTF currently forms a more than 1000 km long transform fault, connecting the divergent plate boundary along the Red Sea with the Alpine convergent zone in Turkey (Hurwitz et al. 2002). The modern and Holocene Sea of Galilee has evolved from ancient water bodies that filled the Kinneret tectonic depression in the northern Jordan basin during the Late Pleistocene (Hazan et al. 2004). The lake basin is mainly surrounded by volcanic igneous rocks (basalts in the Golan Heights), which were formed during the Oligocene, Miocene and Pleistocene and now form escarpments of up to 500 m in height around the lake.

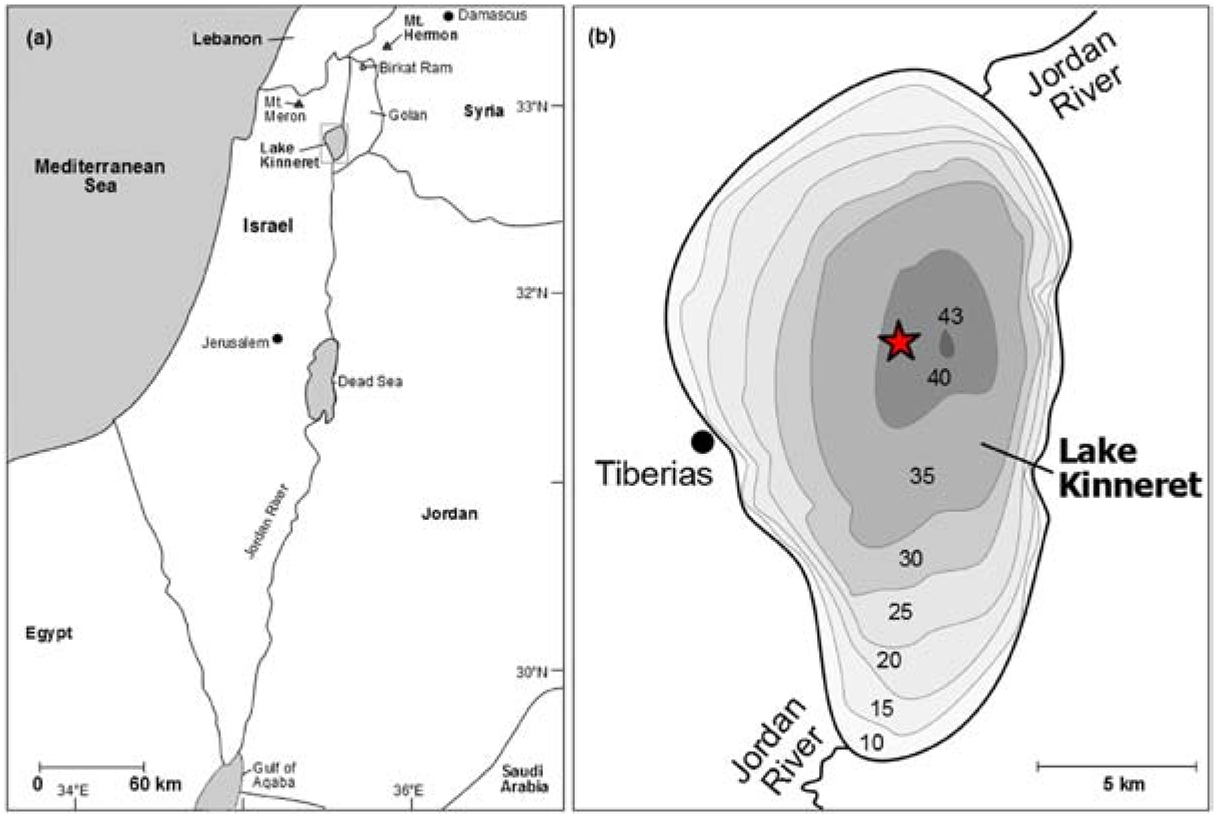


Fig. 1. (a) Location of Lake Kinneret in the North of Israel; (b) Bathymetrical map of the lake (interval of isobathic curves is 5 m). The drilling location is marked by a 'red star' (modified after Schiebel, 2013).

The lake is 22 (N–S) km long, 12 km (W–E) wide and up to 43 m deep, and is situated 210 m below sea level. The lake surface area is almost 167 km^2 and the catchment (total surface = 2730 km^2) extends to parts of the Upper Galilee in NE Israel, the Golan Heights, the Hermon range (with the peak of Mt. Hermon at 2814 m a.s.l.) and the southern Anti–Lebanon mountains (Baruch 1986). The lake is mainly fed from the north by the River Jordan, which also drains the lake southwards to the Dead Sea. The lake is warm and monomictic, being stratified with an anoxic hypolimnion from May to December and fully mixed from December to April (Gophen 2002). An overview of the main limnological parameters (i.e. chemical components of the lake water, composition of bottom sediments and secchi depth) are given in Table 1. Lake level fluctuates by up to 4 m depending on precipitation, evaporation and water abstraction by the National Water Carrier operation. The Kinneret area has a Mediterranean climate, characterized by mild, rainy winters and hot, dry summers (Baruch 1986).

Table 1. Table of typical annual limnological parameters for the epilimnion of Lake Kinneret based on the Lake Kinneret data base supplied by Ami Nishri (2014).

Chemical parameters		
pH	8.6	
Salinity (as Cl)	250	mg.l^{-1}
Silica (as SiO$_2$)	9	mg.l^{-1}
Soluble P (as PO$_4$)	2	µg.l^{-1}
Total Phosphorus	20	µg.l^{-1}
Nitrogen (as NO$_3$)	80	µg.l^{-1}
Pelagic bottom sediments		
Clay minerals	35	%
Calcium carbonate	55	%
Organic matter	5	%
Residual	3	%
Secchi depth	2.6	m

Field and laboratory methods. Two parallel sediment cores (core KI_10_I and KI_10_II) were recovered from a water depth of 38.8 m at the central, deepest part of the lake basin (32°49′13.8″N, 35°35′19.7″E; Fig. 1 'red star') in March 2010, using an UWITEC Universal Sampling Platform (http://www.uwitec.at) with a piston corer system. Sediment cores were transported for storage to the University of Bonn. The 17.8 m continuous master sequence covers approximately the last 8200 cal yrs BP (Schiebel 2013). This diatom study is based on analysis of taxa observed at various core depths between 4.5 m and 10.0 m, where the unknown species is abundant in the diatom flora.

All samples were prepared using standard techniques (Battarbee 1986): 0.2 g of wet sediment was treated with H_2O_2 (30%) and heated on a hotplate for several hours to oxidize organic matter. Afterwards a few drops of concentrated HCl (35%) were added to the hot sample residual to remove carbonates. Samples were washed with distilled water and centrifuged several times (1200 rpm for 7 min) to eliminate the acid residual and avoid dissolution during storage. The cleaned sample material is stored at 4 °C in a cooling chamber at the University of Bonn (Germany). A subsample from the cleaned, organic–free material was mounted in Naphrax™ for diatom community analysis using an Olympus BX53 light microscope (LM) at 1000× magnification, equipped with Differential Interference Contrast and an Olympus UC30 digital camera. For scanning electron microscopy (SEM), parts of the oxidized suspensions were filtered through a 1–µm Isopore™ polycarbonate membrane filter (Merck Millipore). The stubs were sputter–coated with a Gold–Palladium layer of 20 nm and studied using a ZEISS Ultra SEM microscope at 3 kV (Natural History Museum London, UK). Diatom terminology follows Ross et al. (1979), Kiss et al. (1996, 1999), Håkansson (2002) and Houk et al. (2010). The term 'orbiculi depressi' introduced by Kiss et al. (1996) is used to indicate the shallow central depressions.

Fifty non–dissolved valves were photographed and used for morphometric analysis of the following valve features: diameter (µm), length of the marginal striae (µm), number of striae in 10 µm, number of central fultoportulae, number of orbiculi depressi, number of rimoportulae and number of costae between the marginal fultoportulae.

Comparisons with other, similar *Cyclotella* taxa are based on Håkansson (1990a, 1990b, 2002), Kiss et al. (1996, 1999), Meyer & Håkansson (1996), Hegewald & Hindaková (1997), Genkal & Popovskaya (2008), Houk et al. (2010) and Cvetkoska et al. (2014).

Results

Cyclotella paleo–ocellata Vossel et Van de Vijver sp. nov. (Figs 2–18, 20–34)

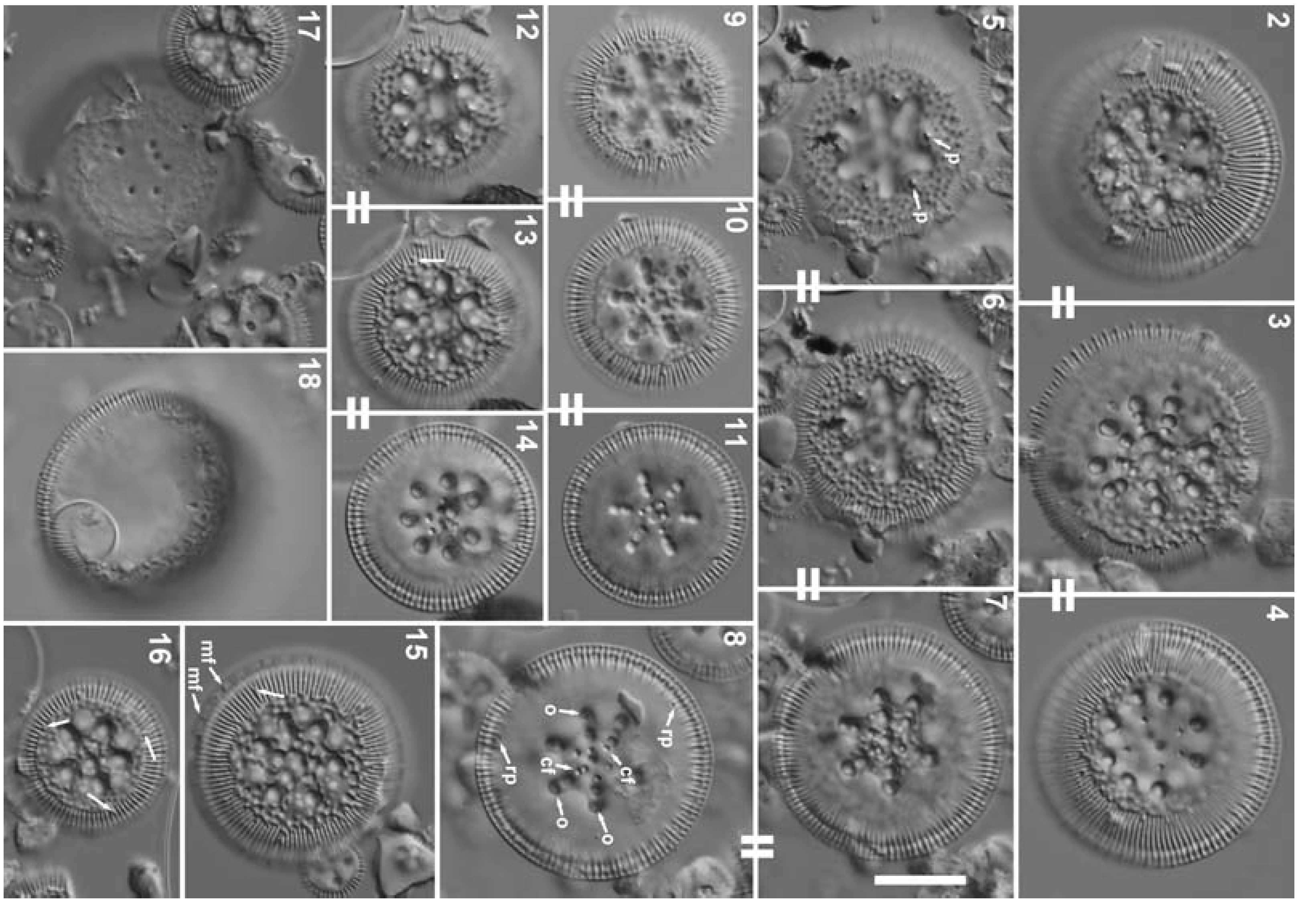
Description

Light microscopy (Figs 2–18): Valves circular, nearly flat. Valve diameter (n = 50): 14.1–28.7 µm. Three dome–shaped initial valves found (diameter 22.6–27.4 µm) (Figs 17, 18). Central area colliculate (Figs 2, 6, 13, 15), between ½ and ¾ of the valve diameter, clearly delimitable from marginal area. Orbicular depressions arranged concentrically in the central area (Figs 4, 14), presenting occasionally a star–

Table 2. Table of comparison between the morphology of *Cyclotella paleo–ocellata* and similar species belonging to the *Cyclotella ocellata*–complex.

	Cyclotella ocellata	***Cyclotella kuetzingiana***	***Cyclotella tripartita***	***Cyclotella rossii***	***Cyclotella pantanelliana***[a]	***Cyclotella polymorpha***	***Cyclotella paraocellata***	***Cyclotella paleo–ocellata***
Reference	KISS et al. (1999)	HOUK et al. (2010)	HÅKANSSON (1990a)	HÅKANSSON (1990b)	HOUK et al. (2010)	MEYER & HÅKANSSON (1996)	CVETKOSKA et al. (2014)	this study
Valve diameter (µm)	5–22	8–45	2–18	5–18	12–70	4.5–16	9–34	15–28
Central area	flat, smooth to colliculate	slightly undulate to nearly flat	colliculate, radially undulate	nearly flat, externally colliculate	concentrically (radially) undulate	circumferentially undulate, flat	flat, colliculate	flat, colliculate
Orbiculi depressi	3–6	none or short radial rows of depressions	none, 3 depressions with triangular punctate field	none, 2–8 radial punctated rows	radial series of depressions	variable	3–6	4–8
Number of striae (in 10 µm)	14–20	12–18	19–22	16–18	12–14	(18)20–22(24)	15–18	13–20
Striae lenght	unequal	unequal	unequal	equal	nearly equal	equal to unequal	unequal	equal
Central fultoportulae	1–5 (5)	1–5(7)	(1)2–3	2–3(5)	?	1–5(7)	3–5	1–8
Satellite pores on central fultoportula	2	2	2	2	?	2(3)	2–3	2
Marginal fultoportulae	on each 2–5 costae	on each (1)2–4(5) costae	on each (4)5–7 costae	on each 2–3(5) costae	on each costa	on each 2–5 costae	on each 3–5 costae	on each (1)2–3 costae
Satellite pores on marginal fultoportula	2	2	2	2	?	2	2	2
Rimoportulae	1	1	1	1	1–3?	1	3	1–3
Location of rimoportula in valve interior	close to costae	in the marginal area	separated from costae	separated from costae	?	in between costae/next to it	close to costae	close to costae

[a] no SEM observations in literature



Figs 2–18. Photographs of the type population of *Cyclotella paleo–ocellata* sp. nov. from the subfossil bottom sediments of Lake Kinneret (sample H44) taken under a light microscope (magnification 1000 times): (2–16) Vegetative cells. Several valves are photographed at different focus levels (indicated by '=') to show all morphological details; (17–18) Initial cells. Scale bar 10 µm. Used abbreviations: (cf) central fultoportula, (mf) marginal fultoportulae, (o) orbiculi depressi, (p) papilla, (rp) rimoportula, arrows on Figs 13, 15–16 = forked interstriae.

shaped pattern (Figs 3, 7, 11). Number of orbicular depressions variable, 4–8 (Fig. 19B). Papillae present in between the depressions, in number always equal to the number of orbicular depressions (‘p’; Fig. 5). Initial cells lacking any depressions or papillae (Figs 17, 18). Central fultoportulae easily visible by changing focus level, 2–8 (Fig. 19A) near the orbicular depressions (‘cf’; Fig. 8). Rimoportulae, 1–2(3) present near the marginal striae (‘rp’; Fig. 8). Marginal fultoportulae usually visible, separated by (0)1–2 costae (‘mf’; Fig. 15). Near the rimoportulae, three costae separating adjacent marginal fultoportulae. Marginal striae, 12–20 in 10 µm (Fig. 19C), almost equal in length, 2.4–5.6 µm, throughout the entire valve, never penetrating into the central area (Figs 2, 6, 10, 15). Some interstriae forked (‘arrows’; Figs 13, 15, 16).

Scanning electron microscopy (Figs 20–34):
Valve exterior: Valve face central area colliculate, covered by irregularly shaped, sized and scattered, usually rounded, hillock–like protuberances (Figs 20, 21, 24). Orbiculi depressi (circular depressions) occurring as large, shallow depressions never penetrating the valve wall (‘o’; Figs 20, 21, 23), gradually decreasing in size towards the center. Ball–like silica granules, looking like large papillae, positioned outwards between the orbicular depressions, decreasing in size towards the valve center when positioned in series on a ridge (‘p’; Figs 20, 21, 23). When absent, the papilla postament (‘pp’) visible as a round small depression where the silica granule (papilla) was originally located (Figs 20, 21). Silica granules show an irregular colliculate surface sculptured by a series of ridges and small hillocks (Figs 23, 24).

Externally striae multiseriate, usually composed of two (outer) rows of larger areolae and 1–2 (inner) rows of small areolae (Figs 20, 24, 26), the latter situated between the rows of larger areolae. Near the valve margin, striae merging due to shortening of the interstriae bearing a marginal fultoportula (‘mf’; Figs 24, 26). Interstriae of irregular width, slightly raised above the level of the striae (Fig. 24). Conical spinulae present on each interstria, near the central area (‘s’; Figs 24, 25). When absent, position of spinulae still visible as a shallow round depression (Figs 20, 24). Small granules (‘g’) scattered on the interstriae. A series of cylindrical, blunt spines present near the valve margin (‘ms’; Figs 20, 26 (‘arrows’), 27).

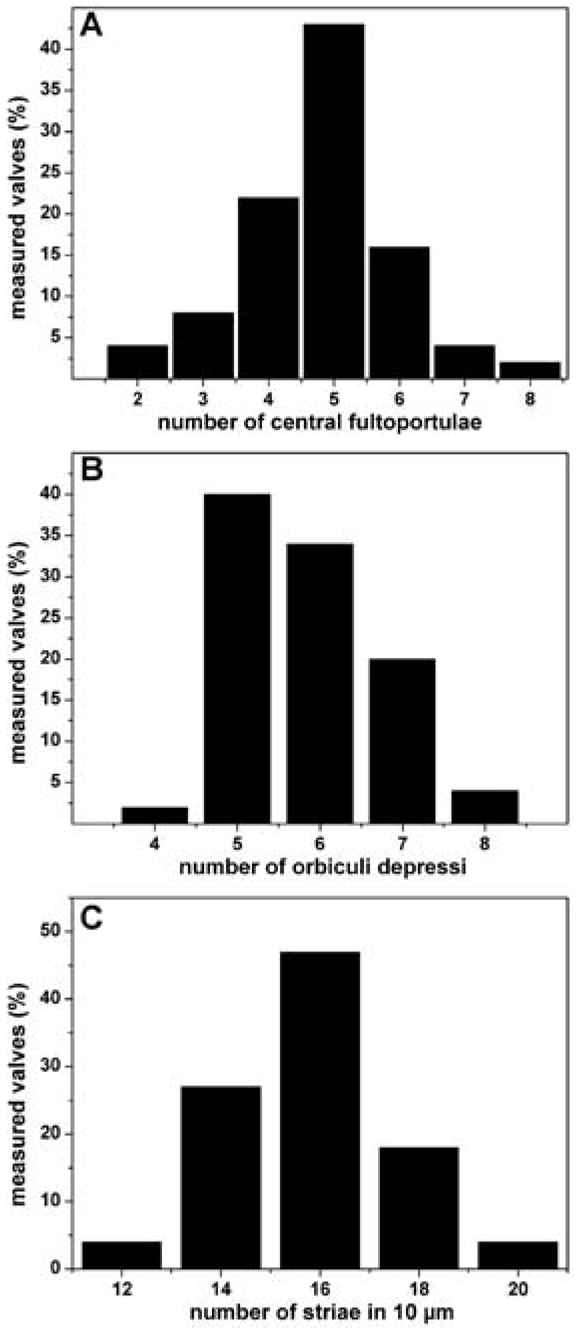
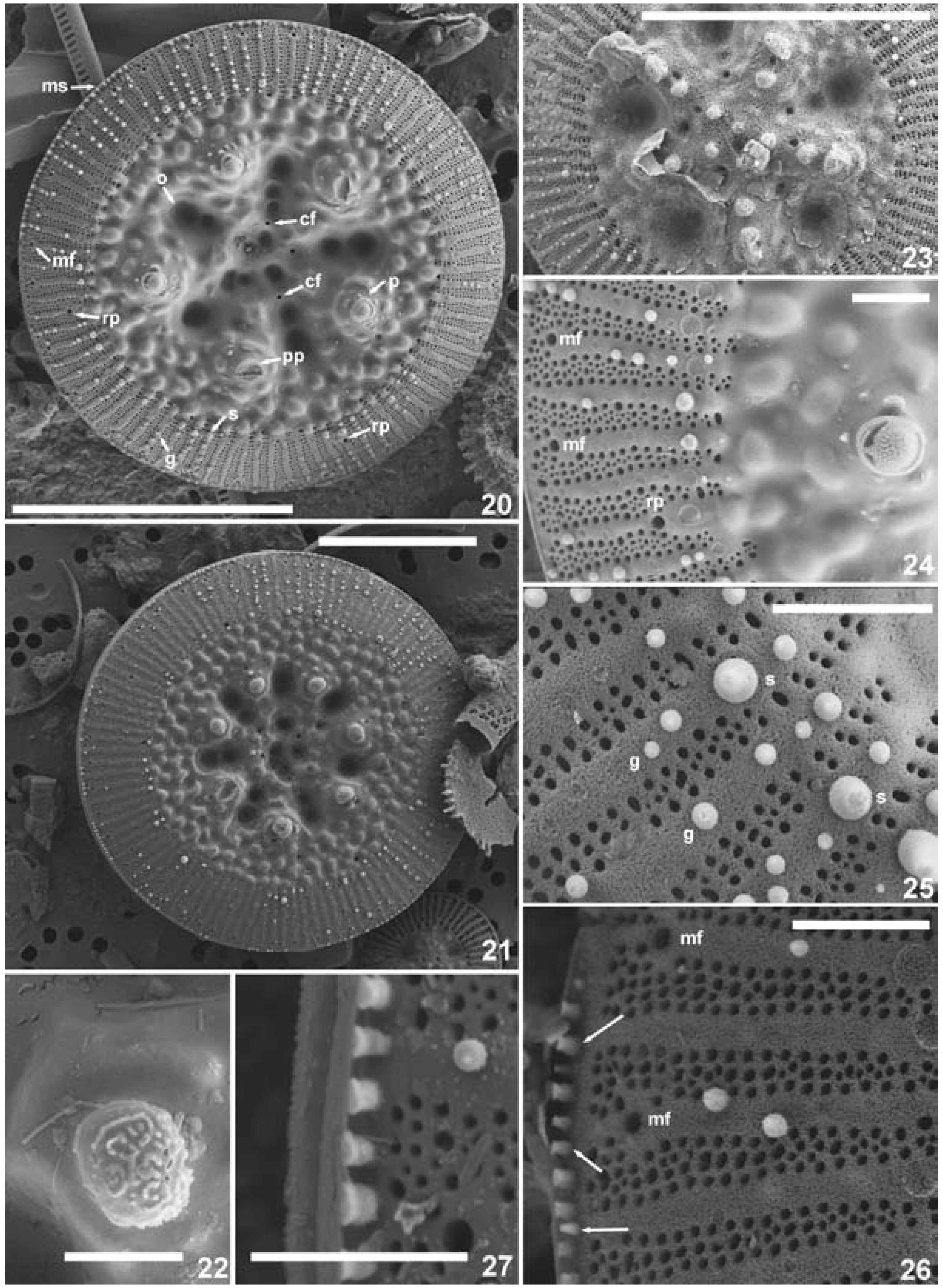
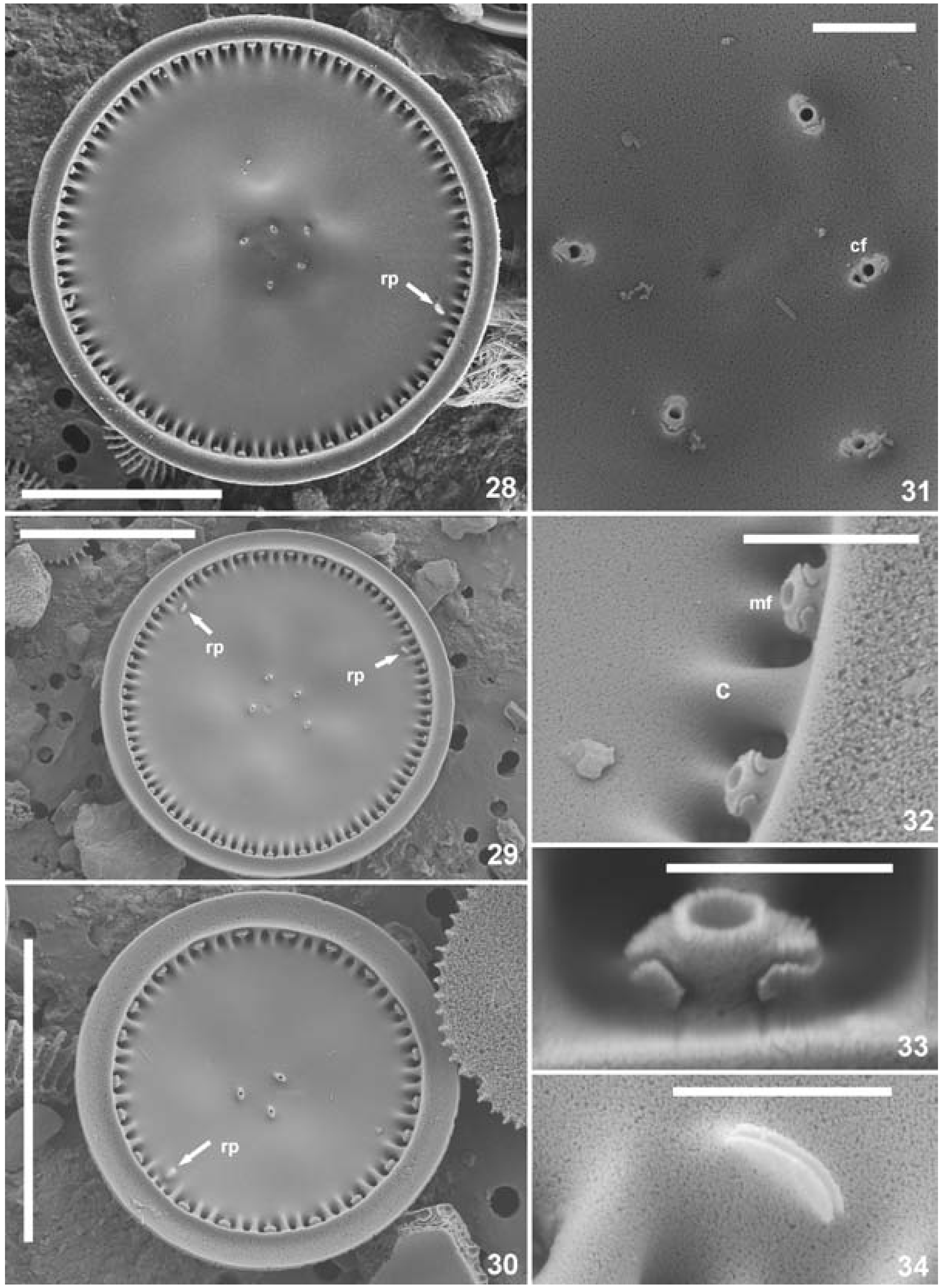


Fig. 19. Relation between measured valves of *Cyclotella paleo–ocellata* [in percentage; n = 50] and (A) the number of central fultoportulae; (B) the number of orbiculi depressi; and (C) the number of striae in 10 µm.



Figs 20–27. External scanning electron microscopy view of *Cyclotella paleo–ocellata* sp. nov. (type population, Lake Kinneret, sample H44): (20–21) External views of a complete valve face showing different organisations of the central area; (22) Detailed picture of a large silica granula (papilla) and its surface ornamentation; (23) Detailed external view of the central area showing radial rows of papillae and central fultoportulae; (24) Detailed external view of the central area and the marginal striae. Note the presence of spinulae, granulae, rimoportula and the marginal fultoportulae; (25) Detailed external view of the marginal striae with a clear indication of the spinulae and granulae. Note the different rows of areolae in the striae; (26) Detailed external view of the marginal striae. Note the presence of blunt spines on the valve margin (‘arrows’); (27) Detailed picture of blunt spines. Scale bars 10 µm (20, 21, 23), 1 µm (22, 24–27). Used abbreviations: (cf) central fultoportula, (g) granula (mf) marginal fultoportula, (ms) marginal spins, (o) orbiculi depressi, (p) papilla, (pp) papilla–postament, (rp) rimoportula, (s) spinula.



Figs 28–34. Internal scanning electron microscopy view of *Cyclotella paleo–ocellata* sp. nov. (type population, Lake Kinneret, sample H44): (28–30) Internal view of complete valves with different organization of the central area; (31) Detailed view of the central fultoportulae showing two satellite pores per fultoportula; (32) Detailed picture of the marginal area showing two marginal fultoportulae (with two satellite pores) separated by one thickened costa; (33) Detailed picture of a marginal fultoportula showing two setallite pores; (34) Detailed picture of a rimoportula as a sessile labium with a wide slit. Scale bars 10 µm (28–30), 1 µm (31, 32, 34), 1 µm (33). Used abbreviations: (c) costa, (cf) central fultoportula, (mf) marginal fultoportula, (rp) rimoportula.

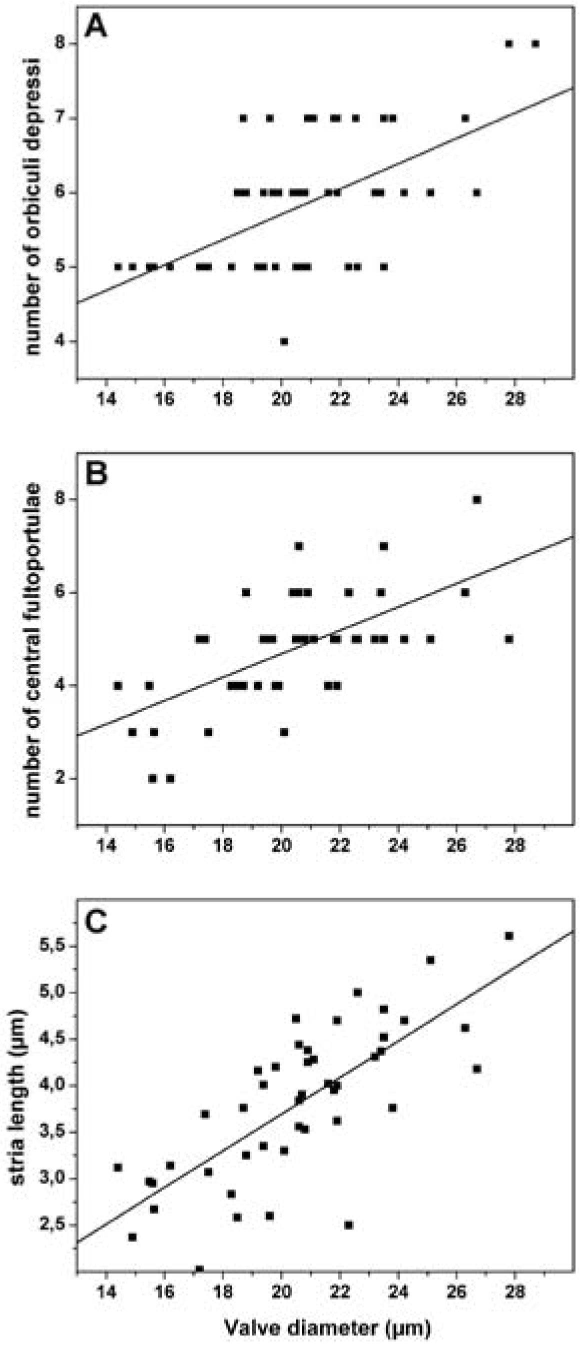


Fig. 35. Relation between the valve diameter (µm) of *Cyclotella paleo–ocellata* and (A) the number of orbiculi depressi ($r = 0.5955$; $p < 0.0001$); (B) the number of central fultoportulae ($r = 0.63352$; $p < 0.0001$); and (C) the stria length (µm) ($r = 0.74745$; $p < 0.0001$). A regression line is added to all graphs.

External openings of the central fultoportulae visible as small, rounded pores ('cf'; Figs 20, 21, 23). Marginal fultoportulae visible externally as small, rounded pores on each or every second or third interstria, usually shortening the interstriae near the valve margin (Figs 20, 24, 26). Rimoportula(e) positioned on the interstriae close to the central area, present as small, rounded pores ('rp'; Figs 20, 24). When rimoportula present, marginal fultoportula absent, separating two adjacent marginal fultoportulae by 3 interstriae (instead of 1–2).

Valve interior: Valve face more or less flat with a slightly undulating central area. Internal openings of the central fultoportulae present as short tubuli with two satellite pores ('cf'; Figs 28, 31). Near the valve margin interstriae (costae) composed of short stronger costae (ribs) without processes alternating thinner depressed costae bearing marginal fultoportulae, with small alveolar openings between them ('mf'; Figs 28, 30, 32). Internal openings of the marginal fultoportulae surrounded by two satellite pores (Figs 32, 33). Rimoportula(e) present externally as a small circular opening, internally as a sessile labium with a wide slit with a variable orientation, usually radial ('rp'; 28, 29, 30, 34).

Etymology: The specific epithet (*paleo–ocellata*) refers to the similarity with *Cyclotella ocellata* and the fact that, to date, the species has only been found in subfossil material from a sediment core.

Type locality: Lake Kinneret, Israel, sediment core KI10_II_4.8–5.8, sample H44 (Leg. Litt et al.; coll. date 03/2010).

Holotype (designated here): BR–4383 (Botanic Garden Meise, Belgium).

Isotypes (designated here): PLP–268 (University of Antwerp, Belgium); STIPB–Vossel–1 (Steinmann–Institute, Rheinische Friedrich–Wilhelms University of Bonn, Germany).

Associated diatom flora: *Cyclotella paleo–ocellata* is abundant over large parts of the sediment core (relative abundance often > 30 %), where *Cyclotella ocellata* is dominating the diatom flora. Other common taxa comprise various *Stephanodiscus* taxa including *S. galileensis*, *Amphora* taxa (e.g., *A. indistincta* Levkov and *A. ovalis* (Kützing) Kützing), unidentified *Staurosira* and *Staurosirella* taxa and *Aneumastus* taxa such as *A. stroesei* (Østrup) D.G.Mann et Stickle and *A. tusculus* (Ehrenberg) D.G.Mann et Stickle.

Discussion

Comparison with other taxa

Cyclotella paleo–ocellata belongs morphologically to the *Cyclotella ocellata* species complex, based on the presence of orbiculi depressi and papillae in the colliculate central area, and on the arrangement and position of marginal striae, rimoportulae and fultoportulae. Table 2 describes other taxa with which *C. paleo–ocellata* may be confused, demonstrating that the new taxon is quite distinct based on the measured set of morphological characteristics. It differs from similar *Cyclotella ocellata* Pantocsek and *Cyclotella kuetzingiana* Thwaites first of all in having marginal fultoportulae situated on each, every second or third costa.

Cyclotella ocellata has a similar stria density but a contrasting stria organization, exhibiting marginal striae of unequal length whereas in *C. paleo–ocellata* all marginal striae have a more or less equal length. Moreover, *C. ocellata* is usually smaller (valve diameter 5–22 µm vs. 15–28 µm in *C. paleo–ocellata*) with a lower number of orbiculi depressi (3–6 in *C. ocellata* vs. 5–8 in *C. paleo–ocellata*), a lower number of central fultoportulae (up to 5 vs. up to 8 in *C. paleo–ocellata*) and the marginal fultoportulae are positioned on each 2–5 costae whereas in *C. paleo–ocellata* this is limited to 1–3 costae. Kiss et al. (1996, 1999) discussed various biometrical ratios for *C. ocellata*. Figures 35 A–C show the same ratios for *C. paleo–ocellata*. All measured parameters are highly significant. Figure 35A shows clearly that larger valves have a higher number of orbiculi depressi ($r = 0.5955$, $p < 0.0001$), in contrast to *C. ocellata* where the number of orbiculi decreases with increasing valve diameter (Kiss et al. 1996). Hegewald & Hindaková (1997) made a similar observation in a study of a *C. ocellata* population from the Gallberg pond in NW–Germany (although the pictures shown in their publication clearly differ from the *C. ocellata* type species and appear to resemble more closely *C. polymorpha*), clearly indicating this important morphological difference between *C. ocellata* and *C. paleo–ocellata*. The number of central fultoportulae in relation to the valve diameter (Fig. 35B) shows a trend that is comparable to *C. ocellata*: larger valves tend to have a higher number of central fultoportulae ($r = 0.6335$, $p < 0.0001$) (Kiss et al. 1996). Finally, stria length significantly increases with valve diameter (Fig. 35C) in *C. paleo–ocellata* ($r = 0.7475$, $p < 0.0001$), a feature not analysed in *C. ocellata*. Genkal & Popovskaya (2008) analysed a *C. ocellata* population from Lake Khubsgul (southern Baikal basin, Mongolia). They observed larger valves (up to 40 µm) with a highly variable number of costae (2–8) between the marginal fultoportulae, a high number of central fultoportulae (1–13), which are often positioned very close to each other, and always 3–4 orbiculi depressi in the central area, regardless of the valve diameter. This combination of features has never been observed in *C. paleo–ocellata* and it is even highly likely that based on the differences between this taxon and the type species of *C. ocellata*, the Mongolian population may represents more than one taxon. *C. ocellata* and *C. paleo–ocellata* co–occur in our sediment samples but are easy to separate.

Cyclotella kuetzingiana Thwaites is similar to *Cyclotella paleo–ocellata* in the presence of depressions in the central area (see Håkansson 2002, figs 330–337; Houk et al. 2010, fig. 189: 1–6). However, *C. kuetzingiana* has a larger valve diameter (8–45 µm vs. 15–28 µm in *C. paleo–ocellata*) and marginal fultoportulae positioned on every 2–4(5) costae, while in *C. paleo–ocellata* the marginal fultoportulae are separated by (0)1–2 costae. Additionally, the central area depressions in *C. kuetzingiana* lack any pattern of arrangement. Valves sometimes have very few papillae (see Houk et al. 2010, fig. 188: 1–6, fig. 189: 1–5) and their number and arrangement is not equal as it is in *C. paleo–ocellata*. Also, no valves with more than seven central fultoportulae have been reported for *C. kuetzingiana* (Håkansson 2002; Houk et al. 2010). *Cyclotella kuetzingiana* var. *radiosa* Fricke has a similar radial arrangement of the central area depressions, but lacks any papillae, has smaller striae density (12–14 in10 µm), only one rimoportula and a large number of radially arranged valve face central fultoportulae (see Houk et al. 2010, fig. 192: 1–6).

Cyclotella tripartita Håkansson (1990a, p. 76, figs 1–4, 8–11, 13) has a smaller valve diameter (2–18 µm), fewer central fultoportulae (max 2–3 vs. 2–8 in *C. paleo–ocellata*) and there are 4–7 costae (instead of (0)1–2 in *C. paleo–ocellata*) between the marginal fultoportulae. Most definitively, *C. tripartita* lacks the typical orbiculi depressi. The central area is instead divided into six sections, three of them depressed having a triangular punctate field (Håkansson 1990a). The rimoportula is located at a rather large distance from the costae, contrary to *C. paleo–ocellata* where the rimoportulae are located immediately next to the costae.

Cyclotella rossii Håkansson (1990b, p. 267, figs 18–27, 46–49) has an equal number of costae between the marginal fultoportulae but is smaller (valve diameter 5–18 µm vs. 15–28 µm) with 2–3, sometimes 5, central fultoportulae. The species again lacks the typical orbiculi depressi but is characterized instead by 2–8 radial rows of puncta (Håkansson 1990b). The rimoportula in the valve interior is well separated from the costae, contrary to the new taxon.

Cyclotella pantanelliana Castracane (1886, p. 171) is larger (valve diameter up to 70 µm) with a lower number of marginal striae (only 12–14 in 10 µm) and lacks the typical orbiculi depressi, being characterized by radial series of large, coarse puncta, clearly penetrating the cell wall, which can be observed in LM during focus changing (Houk et al. 2010). Therefore, eroded valves of *C. paleo–ocellata* might look somewhat similar to *C. pantanelliana*. The arrangement of the marginal fultoportulae is also similar (separation by only 1 costa; Houk et al. 2010) and can produce some confusion. The marginal area of *C. pantanelliana* shows typical forked thinner costae between thickened ribs, which could also be confused with the forked interstriae of *C. paleo–ocellata*. However, no SEM observations have been made on the taxon of *C. pantanelliana* due to the fact that type material from Italy is no longer available.

Cyclotella polymorpha Meyer & Håkansson (1996, p. 64, figs 1–29) has a smaller valve diameter (4.5 µm – 16 µm) with a contrasting central area morphology which lacks the typical concentrically arranged orbiculi depressi. Both taxa are easy to distinguish by their characteristic central area: *Cyclotella polymorpha* shows a high variability of ornamentation patterns (i.e. radial rows of depressions with granulae on the raised area or 1–5 larger depressions having occasionally papillae in between (Houk et al. 2010) irregularly arranged in the central area in comparison to *C. paleo–ocellata*. Striae are usually of unequal length and usually penetrate deep into the central area. The central area is by this fact sometimes not clear to delimit in *C. polymorpha*, whereas it is easily in *C. paleo–ocellata.*

Cyclotella polymorpha becomes more abundant in the upper parts of the sediment sequence from Lake Kinneret and also occurs in the modern diatom flora. Its increase occurs at the expanse of *C. paleo–ocellata*, which is replaced completely at ca. 2500 cal yrs BP (Vossel unpublished).

Finally, *Cyclotella paraocellata* Cvetkoska, Hamilton, Ognjanova–Rumenova & Levkov (2014, p. 317, figs 1–23, 30–45) is rather similar to *C. paleo–ocellata* but can nevertheless be separated based on the lower number of orbiculi depressi (3–6), unequal stria length, a constant, higher number of rimoportulae (3 vs. 1–3 in *C. paleo–ocellata*) and a lower number of central fultoportulae (3–5). The central area of *C. paraocellata* is smaller than that of *C. paleo–ocellata* (40–50% vs. 50–75% of the valve diameter). The largest difference is the arrangement of the marginal fultoportulae, separated by 3–5 costae in *C. paraocellata* compared to (0)1–2 costae in *C. paleo–ocellata*. Although Cvetkoska et al. (2014) reported valves with twinned orbiculi depressi and papillae, the authors did not report any valves with multiple papillae arranged in a series.

Paleoecological remarks

It is remarkable that several new species of *Cyclotella* have evolved since the Miocene period in the Mediterranean region (Cvetkoska et al. 2014). *Cyclotella paleo–ocellata* in Lake Kinneret is a new example. The date of first appearance of *C. paleo–ocellata* is at present unknown, pending recovery of the pre–Holocene sediment record. It is not yet possible to identify the exact environmental preferences of *C. paleo–ocellata* since the taxon is only known from subfossil assemblages. Ecological preferences can be inferred instead based on its association with other taxa of known ecology. *Cyclotella paleo–ocellata* is often abundant where *C. ocellata* is dominating the diatom flora, together accounting for almost 90% of the assemblage. Several *Aneumastus* taxa such as *A. stroesei*, are also present but at very low abundance. These taxa are known to prefer oligotrophic lakes (Lange–Bertalot 2001).

As mentioned before, the broad ecological preference of *C. ocellata* makes ecological interpretations difficult. However, the period between 6500 and 3000 cal yrs BP is known as a humid phase (Litt et al. 2012), when the lake–level of Lake Kinneret was higher than at present (Hazan et al. 2005). *Cyclotella paleo–ocellata* has large, thick robust silica frustules, suggesting based on life habit preferences of similar taxa [e.g., cylotelloid species from Lake Malawi, Afrika (Huisman & Sommeijer 2002; Stone et al. 2011)] that it has an adaptive advantage in staying in suspension in deep turbulent open waters. Larger varieties of the *C. ocellata* complex often seem to occur in deeper open–water lakes [e.g., deeper phases of the Ioaninna sequence in Greece (Wilson et al. 2008)].

Both *Cyclotella paleo–ocellata* and *Stephanodiscus galileensis* disappear at c. 2500 cal yrs BP in the sediment record (Vossel, unpublished). Since this disappearance coincides with human–induced eutrophication indicated by a phase of forest clearance and the cultivation of olive trees identified in the pollen record (Schiebel 2013), it can be inferred that *C. paleo–ocellata* developed in an oligotrophic phase of lake development and has low tolerance of nutrient enrichment. Convincingly, the decrease of *Cyclotella paleo–ocellata* coincides with the rise of a range of centric taxa which are strong indicators for eutrophication, including *Cyclotella meneghiniana* Kützing, *C. polymorpha*, *Aulacoseira granulata* Ehrenberg and several small *Stephanodiscus* species including *S. hantzschii* Grunow, *S. minutulus* Kützing and *S. medius* Håkansson also indicating a clear shift from oligotrophic to more eutrophic conditions (Krammer & Lange–Bertalot 1991).

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