Recent spread of *Raphidiopsis raciborskii* in the lake district south of the Alps

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ABSTRACT

In recent years, there has been a rise in cyanobacterial blooms, and climate warming is believed to be a key driver sustaining these changes. Climate change may affect the geographic distribution of potentially toxigenic species and cyanobacteria, leading to the appearance of new threats in previously unexposed areas. Recently, the potentially toxic cyanobacterium *Raphidiopsis* (*Cylindrospermopsis*) *raciborskii*, known for forming blooms, has increased its presence, particularly in temperate regions. In this work, we expanded the knowledge about the distribution of *R. raciborskii* in Northern Italy. Specifically, we reported new observations recorded during the last decade based on investigations carried out in the framework of scientific and government monitoring and large biogeographical surveys carried out on the whole Alpine Space area. The detection of *R. raciborskii* in Northern Italy highlights the importance of closely monitoring freshwater quality and implementing measures to prevent the spread of harmful organisms.

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Introduction

Raphidiopsis raciborskii (Woloszynska) (Aguilera *et al.*) is a cyanobacterium belonging to the order Nostocales. Like other members of Nostocales, this species can potentially fix atmospheric nitrogen by forming heterocytes (Yema *et al.*, 2016). Originally, this cyanobacterium was better known by the name *Cylindrospermopsis raciborskii* (Wołoszyńska) (Seenayya & Subba Raju) and distinguished from *Raphidiopsis* for the absence of heterocytes in this latter genus. A number of works have sustained this separation, *e.g.*, Li *et al.* (2016). Based on morphological and 16S rRNA gene comparisons, Moustaka-Gouni *et al.* (2009) suggested that *Raphidiopsis mediterranea* Skuja represented a non-heterocytous life-cycle stage of *C. raciborskii*. Successively, based on the analysis of 16S rRNA, 16S-23S ITS, and *cpcBA*-IGS sequences, and following the rule of priority, Aguilera *et al.* (2018) proposed the unification of the two genera in one unique genus, *Raphidiopsis*, which is the genus presently included in AlgaeBase (Guiry and Guiry, 2024), and also recognized in the Genome Taxonomy Database (GTDB) (Parks *et al.*, 2022). Nevertheless, the taxonomic characterization of this genus and its species is still the subject of debate and research (Komárek, 2020; Sha, 2025).

Raphidiopsis raciborskii is considered an invasive species originating from tropical countries (Sukenik *et al.*, 2012). Different primary dispersion centers were proposed, including African lakes and Australia (Padisák, 1997; Haande *et al.*, 2008) and America (Moreira *et al.*, 2015). In Europe, the first records of *R. raciborskii* were documented in Lake Kastoria, Greece (Skuja, 1937). Successively, since the 1970s, the presence of this species has been increasingly reported throughout the European continent

(Padisák, 1997; Sukenik *et al*., 2012; Antunes *et al*., 2015). In Italy, *R. raciborskii* was reported for the first time in blooms recorded in 1995 in Lake Trasimeno, in 2002 in Lake Albano, and in 2003 in Lake Cedrino (Manti *et al*., 2005) (Table 1A). Successively, several other observations of *R. raciborskii* in Central Italy, Sardinia, Sicily and Emilia Romagna were reported (Manfredini and Ghion, 2005; Mattei and Stefanelli, 2008; Mugnai *et al*., 2008; Messineo *et al*., 2009, 2010; Manganelli *et al*., 2014; Elia *et al*., 2019; Del Pasqua *et al*., 2024). In Northern Italy, reports on the presence of *R. raciborskii* were limited to a few observations in the eutrophic/hypereutrophic lakes Sartirana in 2007 and Castellaro in 2010 and 2012 (Manganelli *et al*., 2014) (Table 1A). It is interesting to observe that in 2009, a bloom of *Raphidiopsis mediterranea* Skuja was observed in Lake Annone ovest (Manganelli *et al*., 2014).

Raphidiopsis raciborskii is part of the group of cyanobacteria responsible for the formation of cyanoHABs (Harmful Algal Blooms caused by Cyanobacteria). The toxigenic strains of this species are able to synthesize a wide range of secondary metabolites, including the cytotoxic Cylindrospermopsin (CYN), the neurotoxic Saxitoxin (STX), and analogs (responsible for the Paralytic Shellfish Poisoning, PSP, in humans through consumption of contaminated shellfish from marine environment) (Vico *et al*., 2020; Santos-Silva *et al*., 2024). The two classes of toxins are never produced simultaneously and are always produced individually by strains developing on different continents. Strains producing CYN have been documented in Australia, New Zealand, and Asia (Vico *et al*., 2020). Exclusive STX producers have been identified in South America (González-Madina *et al*., 2022). No CYN or STX producers have been identified from strains isolated in Africa, North America, or most of Europe (Vico *et al*., 2020).

In this work, we will expand the knowledge about the geographical distribution of *R. raciborskii* in Northern Italy. Specifically, we will include new detections recorded during the last decade based on investigations carried out in the framework of scientific and government monitoring, and biogeographical surveys carried out on the whole Alpine Space area (Project Eco-AlpsWater).

Experimental approach

The new records of *Raphidiopsis raciborskii* were documented during the regular monitoring activities carried out by the Environmental Agencies of Northern Italy (Lombardy, Veneto, Trentino Alto Adige, and Friuli Venezia Giulia) and by investigations by research institutions (CNR of Verbania, Piedmont). The observations of the phytoplankton samples were carried out exclusively with inverted microscopes and using the Utermöhl method (*i.e*., "UNI EN 15204" and Wetzel and Likens, 2000).

Genetic (by analysis of environmental DNA, eDNA) and cyanotoxins (by LC-MS) analyses, including the determination of STX and CYN, the two most common toxins produced by *R. raciborskii*, were carried out on 59 samples from lakes and rivers throughout the Alpine region as part of the Alpine Space project Eco-AlpsWater. Metabarcoding analyses were performed using the V3-V4 region of the 16S rRNA marker. The field and laboratory methods and the bioinformatic analyses of the data have been reported by Salmaso *et al*. (2022, 2024), Domaizon *et al*. (2022), Cerasino *et al*. (2017), and Jablonska *et al*. (2024). The 16S rRNA sequences are reported in the Zenodo repository (https://zenodo.org/records/5822484), and the raw sequences are reported in the public ENA archives (study accession number PRJEB49047).

New evidence for the colonization of *Raphidiopsis raciborskii* in the southern perialpine region

New records of *Raphidiopsis raciborskii* were documented in Lombardy (lakes Comabbio and Mantova Superiore) and Veneto (Lake Frassino) but not in Friuli Venezia Giulia, Piedmont, Trentino Alto Adige and Valle d'Aosta (Table 1B, Figure 1).

Lake Comabbio is a small natural lake in Northern Italy that has only one emissary that connects it to Lake Varese after crossing the Palude Brabbia Nature Reserve (ZSC IT2010007). It is a eutrophic and polymictic low-depth lake with naturally high trophic levels mainly due to its morphology. In this lake, *R. raciborskii* was identified for the first time during a research survey

Table 1. A) First documentation of the presence of *Raphidiopsis* (*Cylindrospermopsis*) *raciborskii* in Italy. B) New records described in this work. Genetic analyses confirming the species determinations were performed only on strains collected in Lake Trasimeno (Mugnai *et al*., 2008).

(A)	Lake	Locality	Year	Reference	LM	Metab.
	Trasimeno	Central Italy, Umbria	1995	(Manti *et al*., 2005)	×	NA
	Albano	Central Italy, Latium	1995	(Manti *et al*., 2005)	×	NA
	Cedrino	Sardinia	2003	(Manti *et al*., 2005)	×	NA
	Valle Santa	Northern Italy, Emilia Romagna	2003	(Manfredini & Ghion, 2005)	×	NA
	Biviere di Gela	Sicily	2005	(Barone *et al*., 2010)	×	NA
	Lake Sartirana	Northern Italy, Lombardy	2007	(Manganelli *et al*., 2014)	×	NA
	Lake Castellaro	Northern Italy, Lombardy	2010	(Manganelli *et al*., 2014)	×	NA
	Lake Foschi Golf Club	Northern Italy, Emilia Romagna	2022	(Del Pasqua *et al*., 2024)	×	NA
	Canale Gallego	Northern Italy, Emilia Romagna	2022	(Del Pasqua *et al*., 2024)	x	NA
	Artificial lake (Paul Harris Park)	Northern Italy, Emilia Romagna	2023	(Del Pasqua *et al*., 2024)	x	NA
(B)	**Lake**	**Locality**	**Year**	**Reference**	**LM**	**Metab.**
	Frassino	Northern Italy, Veneto	2018	This work	×	×
	Mantova Superiore	Northern Italy, Veneto	2021	This work	×	×
	Comabbio	Northern Italy, Lombardy	2015	(Austoni *et al*., 2024)	×	NA

NA, not available; LM, light microscopy; Metab., identification of the genus, *Raphidiopsis* (*Cylindrospermopsis*), by metabarcoding (16S rRNA amplicon sequencing).

carried out by the CNR of Verbania in July 2015 (Austoni *et al*., 2024). The population identified in Lake Comabbio presented straight trichomes. Coiled trichomes were never observed. *R. raciborskii* average cell density was 2.5×10^{9} cell L^{-1} on July 24th (littoral zones) representing almost the total phytoplankton cell density. ELISA immunoassay analysis of the environmental samples detected concentrations of STX ranging from 0.27 to 0.36 µg L^{-1}, suggesting a possible association between *Raphidiopsis* and STX production, but further analysis via HPLC is necessary (Austoni *et al*., 2024) and this should be confirmed by LC-MS and genomic analysis of isolated strains.

In 2021, this species was detected for the first time in Lake Mantova Superiore during the regular monitoring activities carried out by ARPA Lombardia (Table 1B, Figure 1). Lake Mantova Superiore is classified as polymictic. It is located inside the Natural Reserve 'Valli del Mincio', and it is the largest of the three shallow fluvial eutrophic lakes in the province of Mantua, in Northern Italy. The three lakes are considered a wetland complex. In Lake Mantova Superiore, only straight trichomes were observed (Figure 2), and the average cell density of integrated samples was 1.1×10^{6} cell L^{-1} during the sampling campaigns of August 2021 and 2023 (2.1×10^{6} cell L^{-1} and 1.4×10^{5} cell L^{-1}, respectively).

Lake Frassino is located in Veneto (Northern Italy), about 1 km south of Lake Garda. It is a small shallow lake fed directly by local rainfall and small inlet streams. It is a eutrophic water body with high nutrient concentrations and high levels of primary production in an area dominated by agricultural and urban use (Barbato, 1987). Further, Lake Frassino has been included in the list of biotopes of the Natura 2000 network and in the sites of community importance (ZSC IT3210003). In this lake, *R. raciborskii* was found for the first time in 2018 during regular monitoring activities carried out by ARPA Veneto (Table 1B, Figures 1 and 3). Only straight trichomes were detected also in this lake. Maximum cell density in the integrated samples (0-6 m) was 3.7×10^{5} cell L^{-1} in late autumn 2018. In the following years, the maximum cell density values of *R. raciborskii* in the summer period were 1.4×10^{7} cell L^{-1} (2020), 7.0×10^{5} cell L^{-1} (2022) and 1.3×10^{8} cell L^{-1} (2023) (maximum value for the period from 2018 to 2023).

In the Alpine Region, two 16S rRNA sequences belonging to the genus *Raphidiopsis* (*Cylindrospermopsis*) were identified in the lakes Frassino and Mantova Superiore (Table 1B) as part of the metabarcoding survey carried out during the Eco-AlpsWater project (Salmaso *et al*., 2024). In the same framework, the PCR analyses by Jablonska *et al*. (2024) did not reveal the presence of *CYN* or *STX* genes in the samples collected in the same lakes. PCR analyses were not available for Lake Comabbio. Coherently, the LC-MS analysis of the samples from lakes Frassino and Mantova Superiore showed no measurable concentrations of CYN and STX (Salmaso *et al*., 2024).

Discussion and Conclusions

The investigations carried out in different lake typologies of the southern perialpine lake district allowed us to confirm and extend the knowledge about the presence of *R. raciborskii* in the Italian peninsula and Europe. This species was primarily found in shallow, human-affected, eutrophic lakes during the warmer months. In view of their great importance for tourism, drinking water supply, and as sources of biodiversity, it is worth highlighting the non-detection of *R. raciborskii* in the surveys carried out in the largest lakes south of the Alps (Garda, Maggiore, Como, Iseo, and Lugano).

With the exception of STX, which was detected in an envi-

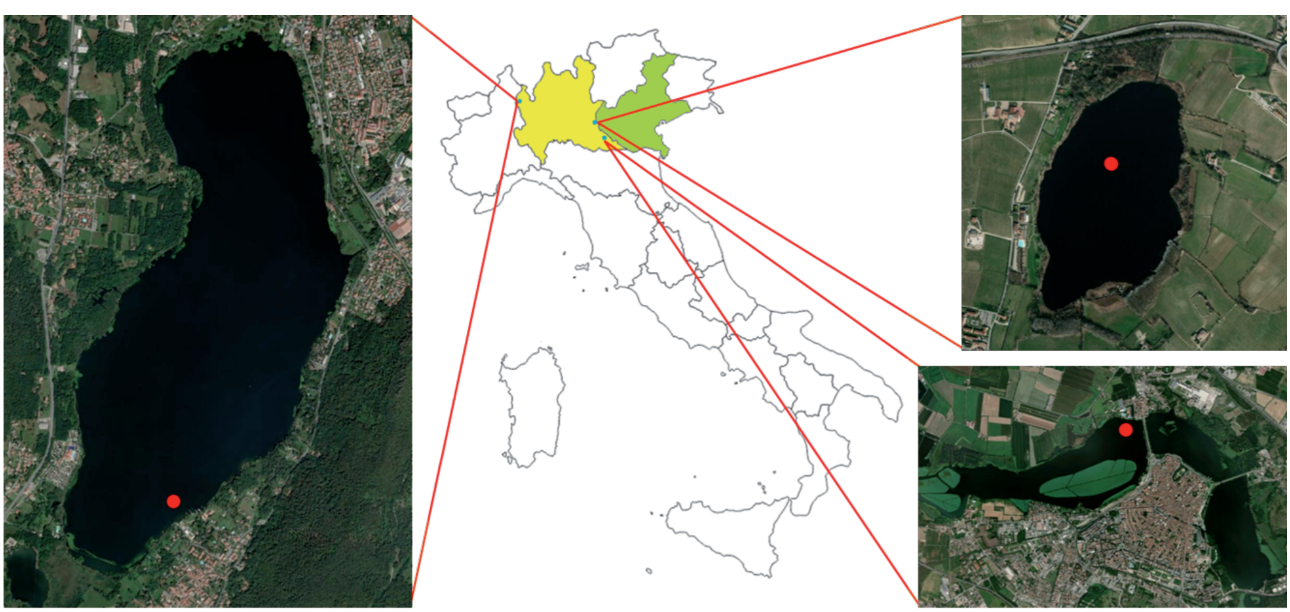

Figure 1. Map of the Italian regions in which cyanobacterium *Raphidiopsis raciborskii* was found. Red dots represent sites where phytoplankton samples containing *R. raciborskii* were collected. Left: Lake Comabbio (Lombardy); upper right Lake Frassino (Veneto); right below: Lake Mantova Superiore (Lombardy).

ronmental sample from Lake Comabbio (Austoni *et al*., 2024), here the analyzed samples tested negative for the presence of the two common cyanotoxins produced by selected strains of *R. raciborskii* (STX and CYN), as well as for selected genes that are part of the operons encoding these toxins. However, besides Lake Comabbio, confirmation of cyanotoxin production in *R. raciborskii* is needed in cases where measurable concentrations of CYN have been reported in environmental samples, *e.g.*, in North America (Florida) (Burns, 2008), Africa (Odokuma and Isirima, 2007; Mowe *et al*., 2014) and Europe (Manti *et al*, 2005; Kokociński *et al*., 2009; Messineo *et al*., 2010), especially when several potential CYN producers were reported simultaneously (*e.g.* Kokociński *et al*., 2009; Messineo *et al*., 2010). This would require combining normal surveillance activities with targeted investigations based on isolation of *Cylindrospermopsis / Raphidiopsis raciborskii* strains and analytical analyses and metagenomics and genome mining.

Figure 2. Light micrography of *Raphidiopsis raciborskii* from Lake Mantova Superiore (Lombardy, Italy). Scale bar: 20 µm. Photo by Manuela Marchesi.

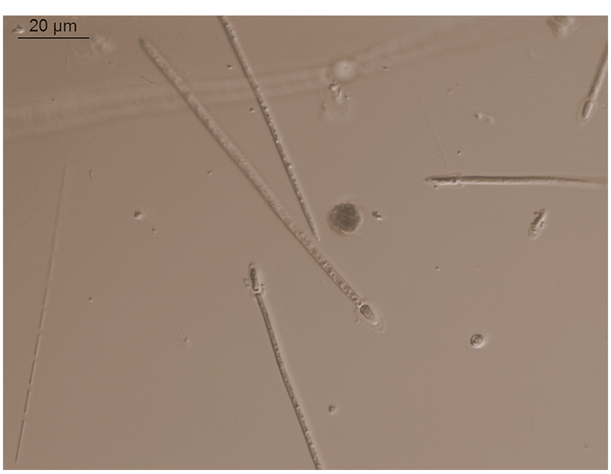

Figure 3. Light micrography of *Raphidiopsis raciborskii* from Lake Frassino (Veneto, Italy). Scale bar: 20 µm. Photo by Federica Giacomazzi.

With rising global temperatures and the potential spread of toxigenic strains, there is the potential for increased proliferation of cyanobacteria, including new strains of *R. raciborskii*. Early detection of these species is critical to monitoring their distribution and mitigating the ecological and potential health risks that they pose.

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