UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

KAOLI PEREIRA CAVALCANTE

DINOFLAGELADOS EPICONTINENTAIS NO SUL DO BRASIL: ESTUDOS TAXONÔMICOS E ECOLÓGICOS

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Orientadora: Prof.ª Dr.ª Luciana de S. Cardoso
Coorientadores: Prof. ª Dr. ª Thelma A.V. Ludwig
Prof. Dr. António J. de B. F. M. Calado

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a coisa mais fina do mundo.
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SUMÁRIO

RESUMO

Os dinoflagelados são um grupo de micro-organismos eucariontes aquáticos bastante diverso em forma, nutrição e hábitat. Apesar da maior diversificação deste agrupo no ambiente marinho, cerca de 20% das espécies conhecidas são encontradas em água doce, e são um importante componente do plâncton em diferentes corpos de água ao redor do mundo. Uma ampla revisão taxonômica tem sido realizada recentemente, com substanciais mudanças no tradicional conhecimento sobre os dinoflagelados. Em contraste, os estudos com dinoflagelados epicontinentais no Brasil são escassos, difusos e limitados a poucas regiões, onde há poucos especialistas no assunto. Face à carência de informações básicas sobre dinoflagelados no país, a proposta desta tese é reunir um conjunto de estudos taxonômicos e ecológicos, de caráter exploratório, envolvendo dinoflagelados epicontinentais encontrados na região sul do Brasil. Os três primeiros estudos são relacionados ao processo de invasão biológica realizado por espécies *Ceratium* no sul do Brasil. O capítulo 1 registrou as primeiras ocorrências de espécies de *Ceratium* em três reservatórios do Estado do Paraná e oito mananciais localizados no Rio Grande do Sul. As espécies foram encontradas a partir de dezembro de 2011 e foram persistentes ao longo do tempo na maioria dos ambientes. *Ceratium furcoides*, a principal espécie colonizadora de ambientes brasileiros, ocorreu na maioria das amostras do Paraná e Rio Grande do Sul. *C. hirundinella*, até então nunca confirmada com precisão no território brasileiro, ocorreu somente em um ambiente, no extremo sul do Brasil. A identificação e a morfologia das espécies foram discutidas, baseadas em análises de microscopia de luz e eletrônica de varredura. No capítulo 2, a abundância e a variação morfológica de *C. furcoides* foram avaliadas durante sua fase inicial de colonização em dois reservatórios subtropicais no Rio Grande do Sul, com o objetivo de explorar quais foram os fatores ambientais relacionados à ocorrência, persistência e formação de florações deste dinoflagelado naqueles ambientes. A biomassa de *C. furcoides* apresentou, em ambos os reservatórios, forte variação sazonal, na qual estações quentes foram marcadas por um aumento na densidade e redução do tamanho das células, enquanto nas estações frias ocorreu redução na densidade e aumento significativo no volume celular. A dinâmica populacional de *C. furcoides* foi relacionada, principalmente, a uma combinação de condições ótimas de temperatura, matéria orgânica e pH e, secundariamente, à disponibilidade de nutrientes. A partir destes resultados e das informações sobre a autoecologia desta espécie disponíveis na literatura, discutiu-se os possíveis fatores relacionados ao sucesso de colonização de *C. furcoides* em reservatórios subtropicais brasileiros. No capítulo 3, estudos morfométricos foram realizados com as mesmas populações estudadas no capítulo anterior, com o objetivo de verificar a variação sazonal no volume celular de *C. furcoides* e quais são as dimensões lineares mais correlacionadas com o volume celular destas populações. O volume celular foi significtivamente diferente entre os meses e as estações do ano (ANOVA, $p<0,05$). Doze dimensões foram medidas por célula, e todas elas foram significativamente correlacionadas ao volume celular. Análises de regressão mostraram que a largura do corpo celular foi a medida mais representativa do volume celular naquelas populações. Estes resultados são um passo fundamental na facilitação de trabalhos de rotina durante programas de monitoramento desta espécie invasora. O capítulo 4 compreende o primeiro estudo florístico sobre dinoflagelados epicontinentais no Estado do Paraná. Quarenta e três ambientes foram amostrados entre 2010 e 2015 e 21 táxons de dinoflagelados foram encontrados. Os táxons foram descritos e ilustrados baseados em análises de microscopias de luz e eletrônica de varredura. Comentários taxonômicos, nomenclaturais e de distribuição conhecida para o Brasil foram feitos. Neste estudo, duas novas combinações nomenclaturais foram propostas, e quatro táxons foram registrados pela primeira vez em águas continentais brasileiras. Finalmente, no capítulo 5, foram investigados fatores ambientais e espaciais que estruturaram as populações de dinoflagelados em 18 reservatórios do estado do Paraná. As maiores biomassas de dinoflagelados foram encontradas em reservatórios com maior tempo de residência, estratificação térmica durante os meses quentes do ano e períodos de mistura completa. Turbulência, transparência da água, pH, condutividade e densidade do fitoplâncton foram os fatores ambientais mais relacionados à variação da biomassa de dinoflagelados. Partição de variância (RDAp) apresentou que os componentes espacial e ambiental foram significativos em explicar a variação da biomassa de dinoflagelados, com o componente ambiental apresentando um sinal mais forte que o espacial. Doze táxons de dinoflagelados foram encontrados neste estudo e dados de autoecologia foram apresentados, acrescentando novas informações ecológicas sobre as populações de dinoflagelados que ocorrem em reservatórios subtropicais. Os resultados obtidos nestes estudos, em conjunto, expressam a mais extensa contribuição para o conhecimento sobre dinoflagelados no sul do Brasil, e fornecem um consistente arcabouço de informações sobre morfologia, distribuição, ocorrência, sazonalidade e fatores ambientais relacionados aos dinoflagelados, que servem de base para o desenvolvimento desta linha de pesquisa no Brasil.

ABSTRACT

Dinoflagellates are a group of aquatic eukaryotic microrganisms, very diverse in morphology, nutritional strategies and habitat. Despite the higher diversification of this group in the marine environment, about 20% of the known species are found in freshwaters and are an important component in plankton of many distinct water bodies around the world. Recently, a comprehensive taxonomic revision has been carried out, with significant changes in traditional knowledge on the dinoflagellates. In contrast, studies about freshwater dinoflagellates in Brazil are scarce, diffuse and limited to few regions where there are the few experts in this field. Given the lack of basic information about dinoflagellates in this country, the purpose of this thesis is to gather a set of exploratory taxonomic and ecological studies on freshwater dinoflagellates found in southern Brazil. The three first studies are related to the biological invasion process performed by *Ceratium* spp. in southern Brazil. Chapter 1 recorded the first occurrences of *Ceratium* in three reservoirs from State of Paraná and eight watersheds from Rio Grande do Sul. The species were found from December 2011 and were persistent over time in the majority of environments. *Ceratium furcoides,* the main species colonizing Brazilian environments, occurred in the majority of samples from Paraná and Rio Grande do Sul. *C. hirundinella,* until now never precisely confirmed in Brazil, occurred only in one environment, in southermost Brazil. Identification and morphology of the species were discussed based on light and scanning electron microscopy analysis. In Chapter 2, abundance and morphological variation of *C. furcoides* were evaluated during its initial phase of colonization in two subtropical reservoirs from Rio Grande do Sul, in order to explore the environmental factors related to occurrence, persistence and bloom formation of this dinoflagellate in those environments. Biomass of *C. furcoides* showed, in both reservoirs, strong seasonal variation, in which warm seasons were featured by an increase of cell density and decrease in cell size, while it occurred reduction in density and significant increase in cell volume in cold seasons. Population dynamics of *C. furcoides* was related primarily to a combination of optimal conditions of temperature, organic matter and pH and secondarily to nutrient availability. Based on these findings and the autecological information of this species found in literature, it discussed the possible factors related to colonization success of *C. furcoides* in Brazilian subtropical reservoirs. In Chapter 3, morphometric studies were performed in the same populations analyzed in the previous chapter, in order to verify seasonal variation in cell volume of *C. furcoides* and the linear dimensions more related to cell volume in those populations. Cell volume was significantly different among months and seasons (ANOVA, $p<0.05$). Twelve dimensions were measured by cell and all of them were significantly correlated to cell volume. Regression analysis showed that body width was the most representative dimension of cell volume in those populations. These results are a fundamental step in facilitating routine work during monitoring programs of this invasive species. The Chapter 4 comprises the first floristic study about freshwater dinoflagellates in State of Paraná. Forty three water bodies was sampled between 2010 and 2015, and 21 dinoflagellate taxa were found. Taxa were described and illustrated based on light and scanning electron microscopy analysis. Taxonomic, nomenclatural comments and geographical distribution in Brazil were made. In this study, two new nomenclatural combinations were proposed and four taxa were recorded for the first time in Brazilian freswaters. Finally, in Chapter 5, environmental and spatial factors structuring dinoflagellate populations were investigated in 18 reservoirs from Paraná. Higher dinoflagellate biomasses were found in reservoirs with high retention time, thermal stratification during warm months and complete mixing periods. Turbulence, water transparency, pH, conductivity and phytoplankton density were the environmental factors more related to dinoflagellate biomass variation. Variation partitioning (pRDA) showed that both spatial and environmental components significantly explained biomass variation in dinoflagellates, with environmental fraction had a stronger signal than spatial one. Twelve dinoflagellate taxa were found in this study, and autecological data were provided, adding new ecological informations about dinoflagellate populations that occur in subtropical reservoirs. Together, the results of these studies represent the most extensive contribution for the knowledge on freshwater dinoflagellates in southern Brazil and provide a consistent framework of data about morphology, distribution, occurrence, seasonality and environmental factors related to dinoflagellates, which serve as basis for the development of more dinoflagellate researches in Brazil.

Apresentação

Dinoflagelados são organismos eucariontes, unicelulares ou coloniais, bastante diversos em forma, nutrição e hábitat. Dentre as particularidades que definem este grupo, destacam-se a presença de dois flagelos distintos entre si: um longitudinal, inserido na região posterior da célula, e um flagelo transversal helicoidal, que circunda a célula; um núcleo celular típico (conhecido como dinocário), no qual os cromossomos são permanentemente condensados, com pouca ou nenhuma histona associada ao DNA (Spector 1984). Dinoflagelados também possuem um envoltório celular constituído por vesículas achatadas sob a membrana plasmática, que podem ser vazias (em dinoflagelados "nus" ou "atecados") ou preenchidas por placas de celulose em várias espessuras, formando um mosaico de placas justapostas na superfície celular (dinoflagelados "tecados") (Taylor 1987). A presença e estrutura destas vesículas nos dinoflagelados são uma característica compartilhada com ciliados e apicomplexos e os inclui no supergrupo Alveolata, portanto filogeneticamente distante de todos os outros grupos considerados dentro de "algas" (Baldauf 2008).

Estima-se que os dinoflagelados surgiram há pelo menos 245 milhões de anos (Fensome et al. 1996), mas registros fósseis permitem datar a divergência entre os dinoflagelados e os apicomplexos há 650 Ma (Medlin 2012). Eles possuem um vasto registro fóssil e têm alto potencial na bioestratigrafia (Fensome et al. 1993, Carty 2014). Por isso, dinoflagelados fósseis foram intensamente estudados pelos palinólogos. As formas atuais, contudo, foram estudadas do ponto de vista zoológico (Dinozoa, Dinoflagellida, Dinoflagellata) ou botânico (Dinophyta, Pyrrophyta, Dinophyceae), a depender da escola de formação de cada pesquisador (Taylor 1976). Isto é reflexo da vasta diversidade nutricional que occore nos dinoflagelados, onde cerca de metade das espécies é autotrófica e a outra metade não possui plastídeos (Moestrup & Daugbjerg 2007). Desta forma, o mesmo grupo de organismos foi classificado de maneiras diferentes, sendo regidos por dois códigos nomenclaturais independentes (*International Code of Zoological Nomenclature*, ICZN e *International Code of Nomenclature for algae, fungi and plants*, ICN). Fensome et al. (1993) propuseram uma classificação com o objetivo principal de harmonizar as terminologias utilizadas entre palinólogos, ficólogos e protozoólogos, mas recentes descobertas têm modificado substancialmente a noção sobre relações filogenéticas entre os táxons de dinoflagelados, e a classificação do grupo requer ampla revisão (Moestrup & Daugbjerg 2007). Independente da abordagem científica escolhida, a pesquisa em dinoflagelados deve levar em consideração toda a versatilidade inerente a este complexo grupo biológico, de história evolutiva antiga. Nesta tese, os dinoflagelados são observados sob o ponto de vista botânico, portanto incluidos na Divisão Dinophyta.

Apesar da maior diversificação e adaptação de dinoflagelados ao ambiente marinho, cerca de 20% do número estimado de espécies são predominantemente epicontinentais (Moestrup & Daugbjerg 2007). Dinoflagelados de água doce são frequentemente menos abundantes e mais delicados do que as formas marinhas. Consequentemente, poucos especialistas têm dado atenção a estes organismos, acarretando em um relativo desconhecimento sobre a diversidade e os fatores que influenciam sua ocorrência (Grigorszky et al. 2003).

Até o início da década de 1990, cerca de 200 espécies distribuídas em 30 gêneros de dinoflagelados eram conhecidas para ambientes dulcícolas (Popovský & Pfiester 1990). O sistema de classificação tradicional é essencialmente baseado na morfologia externa da célula, levando em consideração a presença de teca, posição e deslocamento do cíngulo e do sulco, e em características citológicas básicas, as quais podem ser facilmente observadas em microscopia de luz, tais quais presença, forma e número de plastídeos, presença de estigma e de corpos de acumulação. Para os táxons tecados, a forma, número e disposição das placas tecais foi o principal critério utilizado na classificação (Huber-Pestalozzi 1950, Bourrely 1970, Popovský & Pfiester 1990, Carty 2014).

Recentemente, com o avanço de técnicas moleculares combinadas com análises refinadas de ultraestrutura, amplas revisões foram e estão sendo realizadas, clarificando o conhecimento evolutivo e as relações filogenéticas entre os táxons de dinoflagelados (Moestrup & Daugbjerg 2007). Muitas destas revisões resultaram em alterações taxonômicas e nomenclaturais, especialmente decorrentes do desmembramento de grandes gêneros (Daugbjerg et al. 2000, Flø Jørgensen et al. 2004, Craveiro et al. 2009, 2011, Calado 2011, Ki et al. 2011), redefinição em níveis de famílias (Lindberg et al. 2005, Calado et al. 2009, Moestrup et al. 2009, Mertens et al. 2015) e proposições de novos táxons, especialmente aqueles raros e de morfologia delicada (Hansen et al. 2007, Moestrup et al. 2008, Daugbjerg et al. 2014, Pandeirada et al. 2014, Takahashi et al. 2015).

O conhecimento sobre dinoflagelados epicontinentais no Brasil

A maioria dos trabalhos supracitados envolvem a taxonomia de dinoflagelados de água doce com base em populações de regiões temperadas. O conhecimento sobre táxons tropicais e subtropicais ainda é escasso. Na América do Sul, importantes estudos morfológicos com dinoflagelados epicontinentais foram realizados na Argentina (Boltovskoy 1973a, b, 1975, 1976, 1984, 1989, 1999, 2003).

No Brasil, o conhecimento é difuso e limitado, restrito a poucas regiões. Especialistas sempre foram e ainda são escassos no país. Quase todos os trabalhos com foco florístico ou taxonômico publicados são baseados em observações em microscopia de luz e ilustrados com desenhos. Detalhes ultraestruturais e da morfologia externa de populações brasileiras de dinoflagelados, são, então, praticamente desconhecidos. A primeira citação de uma espécie de dinoflagelado continental em território brasileiro foi feita por Möbius (1889), o qual descreveu uma nova forma taxonômica, *Peridinium tabulatum* Ehrenberg f. *brasilianum* ‘*brasiliana’* Möbius, encontrada na Laguna Rodrigo de freitas, cidade do Rio de Janeiro. Este táxon é atualmente considerado sinônimo da espécie estuarina *Bismatrum subsalsum* (Ostenfeld) Faust et Steidinger (Popovský & Pfiester 1990, Menezes & Teixeira-Júnior 2001). Outros registros de dinoflagelados epicontinentais foram realizados nas primeiras décadas do século XX, em listas de espécies da “fauna de protozoários”, nos Estados de Mato Grosso (Daday 1905), Rio de Janeiro (Prowazek 1910, Cunha 1913, 1916), Rio Grande do Sul (Cunha 1918) e São Paulo (Kleerekoper 1939). Novos registros só ocorreram a partir do final da década de 60, com ilustrações e algumas proposições de novos táxons (Bicudo & Bicudo 1967, 1969, Bicudo & Skvortzov 1968, 1970, Bicudo & Ventrice 1968, Uherkovich & Schmidt 1974, Uherkovich 1976, 1981, Uherkovich & Rai 1979, Uherkovich & Franken 1980). A partir da década de 1990, estudos direcionados à composição de dinoflagelados de água doce foram pontualmente realizados nas regiões norte (Menezes et al. 1995, Albuquerque & Menezes 1997, Meyer et al. 1997), centro-oeste (Menezes & Fernandes 1990), sudeste (Menezes 1994, 1995, Domingos & Menezes 1998, Borics et al. 2005, Bicudo 2011, 2013) e sul (Cardoso & Torgan 2007, Cardoso et al. 2010) do país, compondo a principal base do conhecimento sobre dinoflagelados de água doce neste país. Duas destas pesquisas resultaram na proposição de espécies novas para a ciência (Meyer et al. 1997, Borics et al. 2005).

Enquanto o Rio Grande do Sul é um dos estados brasileiros com maior conhecimento acerca da flora de dinoflagelados (Torgan et al. 2003, Cardoso & Torgan 2007, Cardoso et al. 2011), tais estudos são praticamente inexplorados nos outros estados que compõem a região Sul do Brasil. Em Santa Catarina, não há registros de espécies de dinoflagelados epicontinentais. No Paraná, muitos trabalhos foram realizados para outros grupos de algas, principalmente diatomáceas (Tremarin et al. 2009), porém sobre dinoflagelados continentais especificamente não há qualquer publicação. Nas listagens de fitoplâncton, geralmente em trabalhos ecológicos, Dinophyceae é representada em nível de classe ou gênero (*eg*. Train et al. 2000, Rodrigues & Bicudo 2001, Moro et al. 2003, Rodrigues et al. 2005, Borges et al. 2008). Apenas um táxon identificado em nível específico foi confirmado para o Estado paranaense até o início do presente estudo: *Peridinium gatunense* (Odebrecht et al. 2011).

Desde 1990, dinoflagelados do gênero *Ceratium* Schrank, raramente reportados no continente sul-americano, têm invadido corpos d'água desta região, com rápida expansão geográfica e algumas vezes em densas florações (Boltovskoy et al. 2013). No Brasil, até o início desta tese (março/2012), *Ceratium hirundinella* (O.F. Müller) Dujardin e *C. furcoides* (Levander) Langhans haviam sido registradas em reservatórios do sudeste (Ferrareze & Nogueira 2006, Santos-Wisniewski et al. 2007, Matsumura-Tundisi et al. 2010) e do semi-árido nordestino (Oliveira et al. 2011). Florações de *Ceratium*, embora não sejam nocivas, são problemáticas para o tratameno de água, porque a decomposição da biomassa produzida na floração pode gerar depleção de oxigênio na água e a consequente mortandade de peixes (Matsumura-Tundisi et al. 2010).

Estudos ecológicos sobre dinoflagelados epicontinentais

Pouca atenção é dada, também, à importância dos dinoflagelados na comunidade fitoplanctônica, sua distribuição e os fatores controladores destes em diferentes sistemas epicontinentais (Grigorszky et al. 2003). Em diversos locais do mundo, algumas espécies de dinoflagelados provocam florações em água doce, relacionadas a características ecofisiológicas e estratégias reprodutivas que permitem o seu crescimento em condições desfavoráveis a outras algas, e se tornam importantes constituintes da estrutura da comunidade ao longo do ano (Pollingher 1988). A ecologia de tais espécies foi intensamente estudada nestes ambientes (*e.g.* Dottne-Lindgren & Ekbohm 1975, Heaney & Talling 1980, Cantonati et al. 2003, Flaim et al. 2003, Alster et al. 2006, Zohary et al. 2012), em detrimento da maioria das espécies de dinoflagelados, cujas relações ecológicas são pobremente conhecidas.

No Brasil, a maioria das pesquisas sobre a ecologia do fitoplâncton continental determinam dinoflagelados em níveis taxonômicos genéricos ou supra-genéricos. Destacam-se alguns estudos, importantes na elucidação da variação espacial, temporal e distribuição sazonal de dinoflagelados em sistemas brasileiros. Oda & Bicudo (2006) estudaram a autecologia de *Peridinium gatunense* Nygaard e *Parvodinium umbonatum* (Stein) Carty em um reservatório raso oligotrófico de São Paulo. Cardoso & Torgan (2005, 2007) acessaram a autoecologia, diversidade, densidade e distribuição dos dinoflagelados em diferentes habitats associados à Laguna dos Patos, Rio Grande do Sul, durante dois hidroperíodos distintos. Gomes et al. (2010) investigaram a distribuição espacial e temporal de *Parvodinium umbonatum* de um lago oligotrófico raso do Distrito Federal. Cardoso et al. (2010) avaliaram a variação da biomassa de dinoflagelados planctônicos em relação às variáveis ambientais em três reservatórios no Rio Grande do Sul, com diferentes graus de trofia. Este trabalho foi o único realizado com dinoflagelados em reservatórios subtropicais do Brasil. Finalmente, Silva et al. (2012) e Nishimura et al. (2015) realizaram os primeiros estudos autoecológicos sobre a espécie invasora *Ceratium furcoides*, relacionando fatores ambientais à sua abundância em reservatórios tropicais no sudeste do Brasil.

Estrutura da tese

Face à carência de pesquisas sobre dinoflagelados realizadas no Brasil, em contraponto ao avanço do conhecimento sobre a biodiversidade de dinoflagelados em outras regiões do mundo, nesta tese apresenta-se um conjunto de estudos taxonômicos e ecológicos, de caráter exploratório e essencialmente baseado em reservatórios da região sul do Brasil. Os resultados foram divididos em cinco capítulos, estruturados como manuscritos publicados, submetidos ou a serem submetidos para publicação em revistas científicas. Os capítulos estão formatados segundo as normas das revistas para as quais serão encaminhados. As revistas científicas selecionadas para cada artigo encontram-se indicadas na primeira página dos capítulos.

O Capítulo 1 registra as primeiras ocorrências de espécies de *Ceratium* no sul do Brasil e revisa a distribuição conhecida, bem como os padrões de dispersão daquelas espécies em sistemas epicontinentais brasileiros.

No Capítulo 2, a autoecologia de *Ceratium furcoides* foi avaliada em dois reservatórios do Rio Grande do Sul, durante a fase inicial de colonização da espécie. Os resultados obtidos neste estudo são, então, comparados com a literatura a fim de se discutir os gatilhos ambientais e ecofisiológicos que tornam esta espécie uma eficiente invasora nos sistemas aquáticos subtropicais brasileiros.

O Capítulo 3 compõe-se de uma nota científica, baseada no mesmo conjunto de dados do capítulo anterior, demonstrando relações entre medidas lineares de células de *C. furcoides* e o seu volume celular, com o objetivo de facilitar estimativas de biovolume em trabalhos de monitoramento desta espécie invasora.

O Capítulo 4 é um estudo taxonômico amplo de espécies de dinoflagelados epicontinentais em 41 corpos de água localizados no Estado do Paraná e dois ambientes amostrados em Santa Catarina. Atualização nomenclatural, novos registros e revisão da distribuição geográfica para o Brasil foram realizados.

Finalmente, no Capítulo 5, padrões espaciais e ambientais de populações de dinoflagelados, ocorrendo em 18 usinas hidrelétricas do Estado do Paraná, foram verificados em um estudo ecológico de 2 anos e meio de amostragem. Neste, informações sobre a autoecologia das espécies encontradas foram adicionadas.

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Capítulo 1.

Primeiro registro de espécies invasoras de *Ceratium* Schrank, 1793 (Dinophyceae) no sul do Brasil, com notas sobre padrões de dispersão em ambientes brasileiros

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First record of expansive *Ceratium* Schrank, 1793 species (Dinophyceae) in Southern Brazil, with notes on their dispersive patterns in Brazilian environments

Kaoli Pereira Cavalcante[1]*, Juliana Conte Zanotelli[2], Carla Cristine Müller[2], Karen Dornelles Scherer[2], Juliana Karl Frizzo[2], Thelma Alvim Veiga Ludwig[3], Luciana de Souza Cardoso[1]

1. Universidade Federal do Rio Grande do Sul, Instituto de Biociências. Departamento de Botânica. Avenida Bento Gonçalves, 9500, Prédio 43433, CEP 91501–970, Porto Alegre, Rio Grande do Sul, Brazil.
2. Companhia Riograndense de Saneamento. Avenida Antônio de Carvalho, 2667 – Laboratório, Bairro Jardim Carvalho, CEP 91430–001, Porto Alegre, Rio Grande do Sul, Brazil.
3. Universidade Federal do Paraná, Departamento de Botânica. Laboratório de Ficologia. Centro Politécnico, Caixa Postal 19031, Jardim das Américas, CEP 81531–980, Curitiba, Paraná, Brazil.

*Corresponding author: kaolicavalcante@gmail.com

ABSTRACT

Ceratium Schrank is a planktonic dinoflagellate ubiquitous in temperate and subtropical freshwater environments from Northern Hemisphere. Over the past two decades, *Ceratium* species have been recorded in South American water bodies, with expansive behavior and fast colonization. This study registered *C. furcoides* (Levander) Langhans and *C. hirundinella* (O. F. Müller) Dujardin for the first time in South Brazil. *Ceratium furcoides* was found in samples from States of Paraná and Rio Grande do Sul and *C. hirundinella* occurred only in the southernmost Brazil. No co-occurrence of these species was detected on samples. The morphological variation, as well as the dispersal patterns of these species in Brazilian environments, is discussed based on LM and SEM analyses.

Ceratium Schrank is a freshwater dinoflagellate genus with only seven species currently recognized (Hickel 1988a; Popovský and Pfiester 1990; Temponeras *et al.* 2000). The features that define the genus include thick thecal plates, an elongated apical horn formed by apical (’) plates, 1–3 antapical horns formed by postcingular (’’’) and antapical (’’’’) plates, and six cingular plates (three in dorsal view), and its known Kofoidian plate formula is Po 4’ 5–6’’ 6c ?S 5–6’’’ 2’’’’ (Temponeras *et al*. 2000; Carty 2003; Bicudo and Menezes 2006; Gómez *et al.* 2010). Gómez *et al.* (2010) have redefined the *Ceratium* circumscription, which currently comprises only the freshwater species, and have created the new genus *Neoceratium* Gómez, Moreira *et* López-García to accommodate all the marine species related to the former. The main difference between both genera, from a morphological standpoint, is cingular number of plates - five (two in dorsal view) - in *Neoceratium* (Gómez *et al.* 2010). *Neoceratium* is a debated name for not being in complete accordance with Botanical Nomenclature rules (Calado and Huisman 2010; Gómez 2010). However the distinction between *Ceratium* and *Neoceratium* seems to be undoubted, considering morphological and molecular analyses (Gómez *et al.* 2010).

Ceratium is a common bloom-forming genus in lakes and reservoirs during boreal summer in temperate regions (Pollingher 1988; Carty 2003). Despite the non-toxicity of these blooms (Carty 2003), the aggregated smell and taste to the water and oxygen depletion resulting from massive cell collapse can cause economical and landscape impact (Pollingher 1988; Van Ginkel *et al.* 2001; Hart and Wragg 2009).

Ceratium species are stress-tolerant, due to their swimming abilities which enable diurnal vertical migrations to more favorable light and nutrients microhabitats, and resting cysts formation, which germinate in mixing periods. Moreover, their grazing resistance assures survival during strong zooplankton grazing-pressure (Pollingher 1988; Olrik 1994). *Ceratium hirundinella* (O. F. Müller) Dujardin is the ecologically best-known species (Pollingher 1988), though many records of the species are not documented by figures or morphological information and may correspond, fully or partially, to similar species, such as *C. furcoides* (Levander) Langhans, as discussed by Calado and Larsen (1997).

In Brazil, there were no *Ceratium* records until 2000s. Bicudo and Menezes (2006) cited *Ceratium* with basis on a publication in 1963. However, this paper presented a list of freshwater algae genera with sanitary importance, but not necessary that found in Brazilian waters (Branco *et al.* 1963). This mention can not be taken as a citation of *Ceratium* for Brazil. Moreover, for about 50 years, no other report of this conspicuous alga was made. Since 2003, *C. furcoides* and *C. hirundinella* have been found in several Brazilian aquatic systems. Ferrareze and Nogueira (2006) documented the occurrence of *C. hirundinella* in Paranapanema river basin, São Paulo. *Ceratium furcoides* was registered for the first time in Furnas reservoir, Minas Gerais, by Santos-Wisniewski *et al.* (2007), and more recently in Billings reservoir, São Paulo, by Matsumura-Tundisi *et al.* (2010). Finally, *C. furcoides* and *Ceratium* cf. *hirundinella* were detected by Oliveira *et al.* (2011) in two Brazilian northeastern semiarid basins.

This study documents the first record of *Ceratium* in South Brazil, including a preliminary analysis on dispersal patterns of *C. furcoides* and *C. hirundinella* in Brazilian environments.

Paraná (PR) samples are derived from phytoplankton monitoring program performed by Companhia Paranaense de Energia (COPEL) in hydroelectric power plants (HPP). Rio Grande do Sul (RS) samples are originated from phytoplankton monitoring in surface watersheds to water harvesting for human supplies, performed by Companhia Riograndense de Saneamento (CORSAN). Samplings were conducted weekly to quarterly (Table 1). Subsurface water samples (1L volume) were collected with Van Dorn bottle and preserved with acetic Lugol’s solution. *Ceratium* spp. cell densities were estimated by the monitoring teams and were granted for this study by the responsible companies. For qualitative analysis, subsamples were concentered by simple settling or centrifugation and mounted on slides analyzed using an Olympus BX-40 microscope with DP-71 digital camera coupled.

For scanning electron microscopy (SEM), subsamples were washed with distilled water, air-dried on stubs and covered with gold by Balser Sputtering/SDC 300

Table 1. Location of sampling sites, system types and periodicity of sampling.

Sampling sites	**Hydrographic basin**	**Location**	**Geographic coordinates**	**Sampling periodicity**
HPP Capivari	Capivari River Basin	Bocaiúva do Sul, PR	25˚08'25"S, 48˚52'19"W	quarterly
HPP Chopim	Chopim River Basin	Itapejara D'Oeste, PR	25˚59'18"S, 52˚44'45"W	quarterly
HPP São Jorge	Pitangui River Basin	Ponta Grossa, PR	25˚01'04"S, 50˚03'38"W	quarterly
Itá Dam	Apuaê-Inhandava Basin	Marcelino Ramos, RS	27˚27'53"S, 51˚54'06"W	monthly; weekly
Maia Filho Dam	Upper Jacuí Basin	Salto do Jacuí, RS	29˚04'46"S, 53˚13'31"W	monthly
Jacuí River	Lower Jacuí Basin	Dona Francisca, RS	29˚37'30"S, 53˚20'56"W	monthly
Jacuí River	Lower Jacuí Basin	Rio Pardo, RS	29˚59'43"S, 52˚22'38"W	quarterly
Jacuí River	Lower Jacuí Basin	Cachoeira do Sul, RS	30˚03'53"S, 52˚53'53"W	monthly
Uruguai River	Butuí-Icamaquã Basin	São Borja, RS	28˚37'26"S, 56˚02'13"W	monthly
Uruguai River	Ibicuí River Basin	Itaqui, RS	29˚06'59"S, 56˚32'35"W	monthly
Aceguá Stream Dam	Mirim-São Gonçalo Basin	Aceguá, RS	31˚52'07"S, 54˚08'53"W	bi-monthly

equipment. These samples were observed on Jeol JSM 6360LV electronic microscope (Centro de Microscopia Eletrônica, Universidade Federal do Paraná), at 15 kV and 8 mm work distance. Aliquots were housed in herbarium of Federal University of Paraná (UPCB 75101, 75105, 75118, 75124-75127).

Two *Ceratium* species were observed. *Ceratium furcoides* occurred in Paraná samples (HPP Chopim, HPP Capivari and HPP São Jorge) and in seven sampling sites from Rio Grande do Sul (Jacuí River, Uruguai River, Itá Dam and Maia Filho Dam). *Ceratium hirundinella* was found only in Aceguá Stream Dam, at Rio Grande do Sul. No co-occurrence of these species has been detected until now.

Despite the low densities in relation to total phytoplankton, *Ceratium* cells have continued to appear along the samplings (Table 2).

Ceratium spp. identification was based on classic studies for this genus (Huber-Pestalozzi 1950; Bourrelly 1970; Hickel 1988b; Popovský and Pfiester 1990; Calado and Larsen1997).

Ceratium hirundinella and *C. furcoides* are common and similar species in relation to outline and size, and may be confused. The main feature distinguishing them is regarding the shape and length of 4’ plate, which reaches the apical horn apex in *C. hirundinella* and is shortened in *C. furcoides* (Hickel 1988b; Popovský and Pfiester 1990; Calado and Larsen 1997). In this study, we were able to observe the short 4’ in all populations identified as *C. furcoides* (Figures 9–12).

In addition, Popovský and Pfiester (1990) and Hickel (1988b) noted that the epitheca of *C. hirundinella* is bell-shaped, forming an abrupt “shoulder” in apical horn base, whereas the epitheca of *C. furcoides* is conical, with attenuated apical horn, projected forward. This feature could be clearly observed here (compare Figures 1–14 to Figures 15–25). Samples with *C. furcoides* occurrence had no apical horns morphologically similar to *C. hirundinella*. This feature is an important information to practical monitoring purposes, since the epithecal plates shape are not usually noticeable using common cell count techniques.

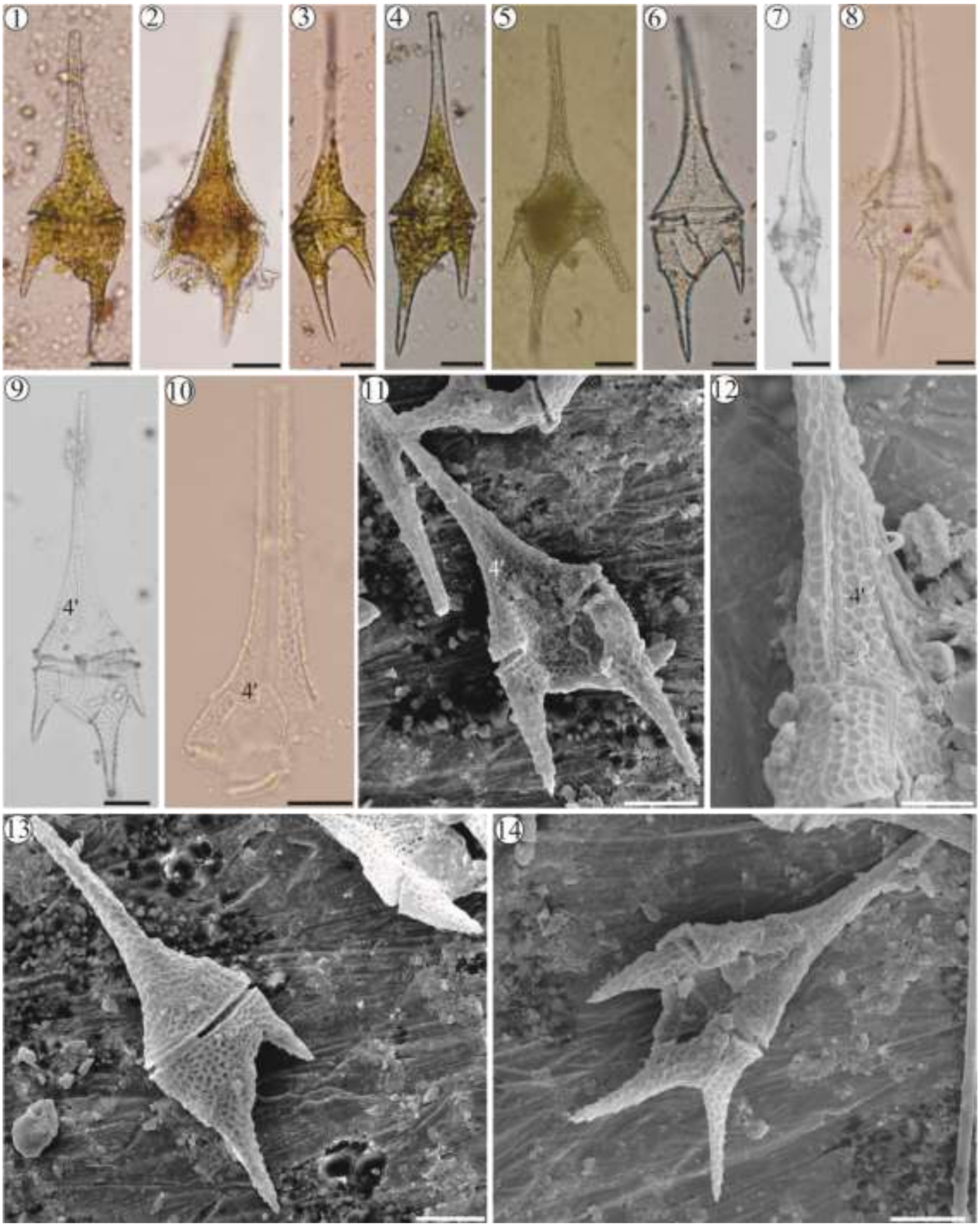
Table 2. Occurrence and relative density of *Ceratium* species in the sampling sites.

Sampling sites	**Occurrence in the samples**	**Density in relation to total phytoplankton**
HPP Capivari	Jan, Apr and Jul 2012	0.5 – 11.3%
HPP Chopim	Jun 2012	0.2%
HPP São Jorge	Apr 2012	not found in quantitative analysis
Itá Dam	May 2012	not found in quantitative analysis
Maia Filho Dam	Feb-Jul 2012	0.5 – 5.5%
Jacuí River, Cachoeira do Sul	Apr and Jul 2012	0.4 – 0.6%
Jacuí River, Dona Francisca	Mar-Jul 2012	0.4 – 0.9%
Jacuí River, Rio Pardo	Jul 2012	not found in quantitative analysis
Uruguai River, Itaqui	Dec 2011	not found in quantitative analysis
Uruguai River, São Borja	Jul 2012	not found in quantitative analysis
Aceguá Stream Dam	Jan, Mar and May 2012	0 – 7%

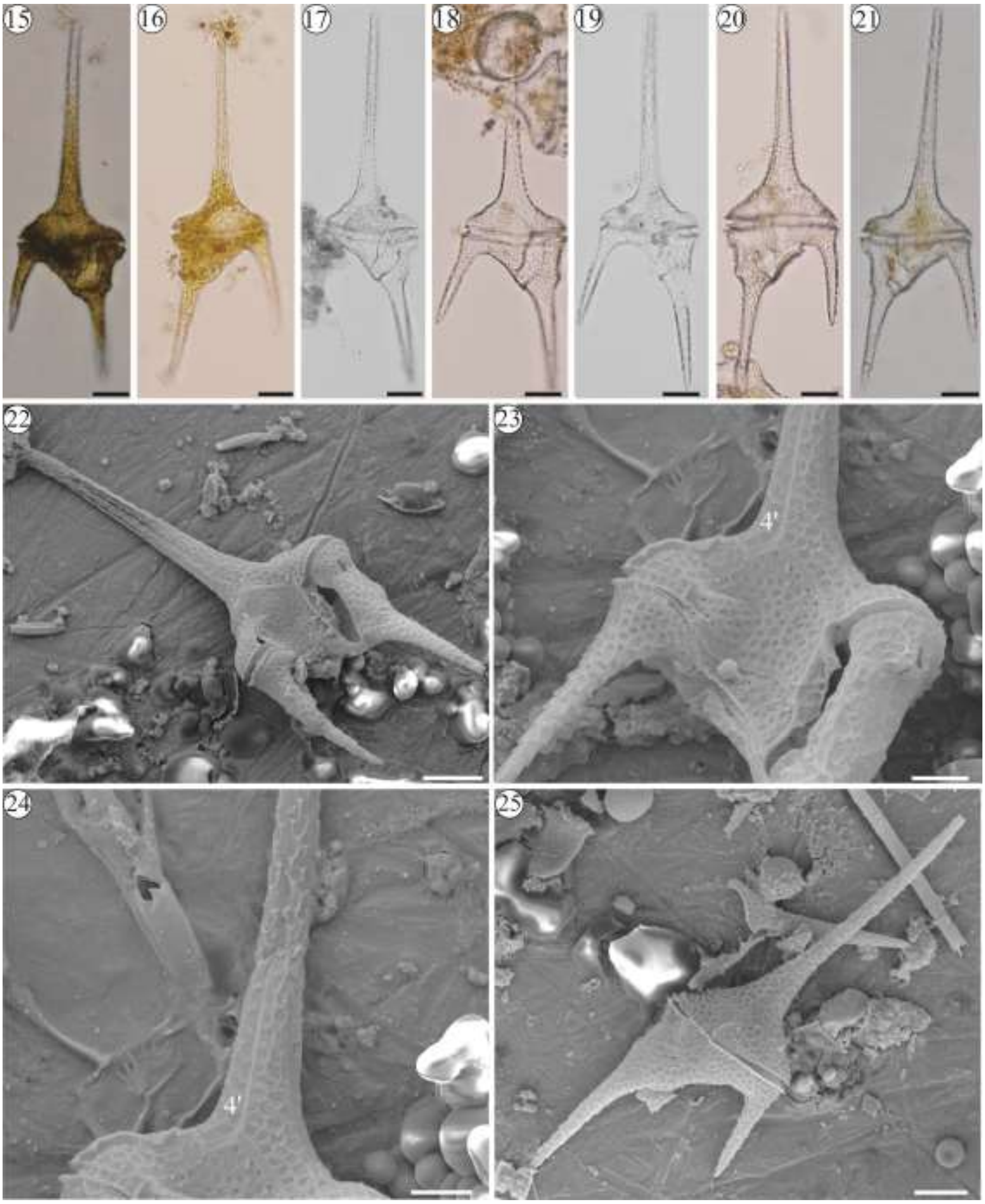
The hipotheca of both species is quite variable. Bourrelly (1970) pointed out that size and number of horns vary according to environmental changes, especially temperature. In our study, the single *C. hirundinella* population possesses two long antapical horns, being the right one always shorter than the left. In *C. furcoides* two antapical horns were often found: straight (Figure 4) or slightly directed to the right (Figures 1, 2 e 6). However three antapical horns were observed in some specimens, the third one (in the left) being formed by 1’” and 2’” plates (Figures 5, 8 and 14). These findings agree with the morphological variation documented by Hickel (1988b).

The invasive species in Brazilian environments

Ceratium spp., atypical in Brazilian freshwater systems, have been registered as invasive species in several recent limnological studies performed in Southeast and Northeast region of the country. *Ceratium furcoides* is the main recorded species, always accompanied by illustrations that allow corroborating the identification (Santos-Wisniewski *et al.* 2007; Matsumura-Tundisi *et al.* 2010; Oliveira *et al.* 2011). Conversely, *C. hirundinella* has few unconfirmed records. Ferrareze and Nogueira (2006), in an ecological survey, registered *C. hirundinella*, but no illustrations were added and the study area is located near to that where *C. furcoides* cells have been found. Oliveira *et al.* (2011) reported *Ceratium* cf. *hirundinella,* distinguished from *C. furcoides* specimens in that study only by presence of the third antapical horn. We believe that this taxon also corresponds to *C. furcoides,* considering the conical shape of apical horn from depicted specimen (Oliveira *et al.* 2011, Figure 2D) and the hipothecal variability of *Ceratium* spp. (compare, *e.g.*, with Figure 5 from this study). Based on the above remarks, it is possible that no *C. hirundinella* has so far been sampled in Brazilian environment. This is therefore the first confirmed record of this species to the country.



Figures 1–14. *Ceratium furcoides*. **1–2.** Cells in ventral view, LM. **3–6.** Cells in dorsal view, LM. **7.** Theca in lateral left view, LM. **8.** Cleaned theca in dorsolateral view, LM. **9–10.** Cleaned epithecal plates showing the shortened 4’ plate, LM. **11.** Cell in ventral view, SEM. **12.** Ventral epitheca detail showing the short plate 4’, SEM. **13.** Cell in dorsal view. **14.** Cell with three antapical horns, in ventral view, SEM. Scale bars: 10 µm (Figure 12) and 20 µm (Figures 1–11, 13, 14).



Figures 15–25. *Ceratium hirundinella.* **15.** Cell in ventral view, LM. **16.** Cell in dorsal view, LM. **17–19.** Cleaned thecae in ventral view, LM. **20–21.** Cleaned thecae in dorsal view, LM. **22.** Whole cell, in ventral view, SEM. **23.** Detail of ventral epitheca, showing the plate 4', SEM. **24.** Detail of apical horn, showing that 4' reaches the apex, SEM. **25.** Whole cell, in dorsal view, SEM. Scale bars: 10 µm (Figures 23, 24) and 20 µm (Figures 15–22, 25).

Ceratium hirundinella has often been reported to South America since 1990. First recorded in southernmost Argentine lakes, the species quickly established itself in northward Argentina, Chile and Bolivia, particularly in reservoirs (Guerrero and Echenique 1997; Mac Donagh *et al.* 2005; Fontúrbel *et al.* 2006; Silveiro *et al.* 2009). The single confirmed *Ceratium hirundinella* population in this study is from Aceguá, RS, located on the border between Brazil and Uruguay (Table 1), and it is certainly derived from populations that colonized the extreme South of America.

Ceratium furcoides establishment is more recent, and seems to have occurred as a radial dispersion (from southeastern to northwards and southwards). Being an episode in progress, little is known on the dispersal patterns of this flagellate in Brazilian environments. Silva *et al.* (2012) conducted an ecological study about *C. furcoides* in Furnas reservoir, Minas Gerais, and related species abundance with low temperatures and high nutrient concentrations (nitrate and nitrite), although it is considered a perennial dinoflagellate, occurring all the year, even at low densities. Another autecological study in South America involving *C. furcoides* was carried out in Colombia, in which *C. furcoides* abundance were positively related to high chlorophyll a concentration, ammonium, relative water stability column and wind direction, being considered a highly variable species in both temporal and spatial scales (Gil et al. 2012).

Understanding *Ceratium hirundinella* geographical dispersive patterns in Brazil, its co-occurrence with *C. furcoides,* and the controlling factors of distribution and abundance of both species are questions to be elucidated by monitoring of this systems. The tracked study of dispersive behavior of these species, to medium and long term, is a unique opportunity for unveiling the dispersive/establishment mechanisms of freshwater dinoflagellates in neotropical environments.

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Capítulo 2.

Rumo a uma compreensão sobre a invasão por *Ceratium* (Dinophyceae) em ambientes epicontinentais brasileiros: a autoecologia de *C. furcoides* em reservatórios subtropicais

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Towards a comprehension of *Ceratium* (Dinophyceae) invasion in Brazilian freshwaters: autecology of *C. furcoides* in subtropical reservoirs

Kaoli Pereira Cavalcante, Luciana de Souza Cardoso

Programa de Pós-Graduação em Botânica, Departamento de Botânica, Universidade Federal do Rio Grande do Sul. Instituto de Biociências, Av. Bento Gonçalves, 9500, Prédio 43433, Bairro Agronomia, CEP 91501-970, Porto Alegre, RS, Brasil.

Corresponding author e-mail: kaolicavalcante@gmail.com

Rovana Sussella

Serviço Autônomo Municipal de Água e Esgoto. Rua Nestor Moreira, 719, Parque da Imprensa, CEP 95052-500, Caxias do Sul, RS, Brasil.

Vanessa Becker

Programa de Pós-Graduação em Engenharia Sanitária, Universidade Federal do Rio Grande do Norte. Centro de Tecnologia, Av. Senador Salgado Filho, 3000, Campus Universitário, CEP 59078-970, Natal, RN, Brasil.

Ceratium species are not a common component of freshwater phytoplankton in South America. However, these dinoflagellates have often been observed in many water bodies over the past two and a half decades. We investigated *Ceratium furcoides'* abundance and morphological variation during its initial phase of colonization (2012–2013) in two subtropical reservoirs in southern Brazil in order to explore which environmental factors were related to the occurrence, persistence and bloom formation of this dinoflagellate in those environments. Biomass of *C. furcoides* showed a strong seasonal pattern, in which warm seasons led to an increase in population density, resulting in cell size reduction, while in the cold seasons cells increased in volume. Maximum densities over 2,500 cells mL^{-1} were observed in spring-summer periods in both reservoirs. *Ceratium furcoides*' abundance in the studied reservoirs was associated, primarily, with a combination of optimal conditions of temperature, organic matter, and pH, and secondarily, with nutrient availability. The possible factors for the successful colonization performed by *C. furcoides* across distinct Brazilian waterbodies include good swimming performance, low herbivory pressure and ability to form dense blooms, as strategies that allow maintenance of populations and effective dispersal.

Keywords bloom, cyclomorphosis, invasive species, southern Brazil

Introduction

Biological invasion is a central subject in management and conservation of natural landscapes. Well-established species can cause negative effects in the invaded ecosystems, such as loss of biological diversity, extinction of native species, changes in community dominance, and ecosystem alterations (Mooney & Cleland, 2001; Catford et al., 2012). Studies of macroscopic organisms are frequent, whereas the microbiological invasion is harder to detect and therefore much less documented (Elbrächter, 1999; Litchman, 2010; Lebret et al., 2013). Several microalgae species, in particular potentially harmful ones, are quickly expanding their geographic distribution (*e.g.* Elbrächter, 1999; Edwards et al., 2001; Hoppenrath et al., 2007; Lilly et al., 2007; Blanco & Ector, 2009; Sukenik et al., 2012). The dispersion of these species can be intensified by human activities (Nagai et al., 2007). Moreover, studies indicate that human-altered ecosystems, especially impoundments, favor the invasive species' spread (Johnson et al., 2008). Therefore, they are key-environments for understanding the processes governing colonization, establishment, and expansion of exotic species.

The dinoflagellate genus *Ceratium* Schrank is considered to be invasive in South American freshwaters (Boltovskoy et al., 2013). Species of this genus have rarely been reliably recorded in this region until the 1990s, when *C. hirundinella* (O. F. Müller) Dujardin started in southern Chile and spread 2,000 km northward in 10 years (Mac Donagh et al., 2005; Boltovskoy et al., 2013). In Brazil, the colonization by *Ceratium* was particularly distinct: it started in 2000s and the primary species was *C. furcoides* (Levander) Langhans, which was recorded in rivers and reservoirs from the southeastern (Matsumura-Tundisi et al., 2010; Santos-Wisniewski et al., 2007), northeastern (Oliveira et al., 2011), and southern regions (Cavalcante et al., 2013; Jati et al., 2014). Since Brazil, *C. furcoides* has been detected in other countries such as Colombia (Bustamante-Gil et al., 2012) and Argentina (Meichtry de Zaburlin et al., 2014), suggesting that this species has expanded in a radial pattern, first in Brazil, and then reaching areas not previously invaded by *C. hirundinella* (Boltovskoy et al., 2013; Cavalcante et al., 2013).

Ceratium species are not toxic, however high biomasses may be harmful to icthyofauna during bloom decay due to oxygen depletion from bacterial consumption (Smayda, 1997). Moreover, they can cause odor and taste in drinking water and clog filters during water purification, and are therefore considered prejudicial in monitoring programs of watersheds destined for public consumption (Ewerts et al., 2013).

Ecological studies were largely conducted in north temperate regions, especially of *Ceratium hirundinella* (eg. Dottne-Lindgren & Ekbohm, 1975; Moore, 1977; Heaney & Talling, 1980; Nicholls et al., 1980; Chapman et al., 1985; Padisák, 1985; Grigorszky et al., 2003). The autecology of *Ceratium furcoides* is poorly understood and probably much of the information related to *C. hirundinella* in the literature in fact corresponds to *C. furcoides*, due to the morphological similarity of these species (Calado & Larsen, 1997). *Ceratium furcoides* is often found co-occurring with other *Ceratium* species, at low abundance in temperate systems, but occasionally it was the representative or dominant species in relation to total *Ceratium* density, with blooms occurring during the summer in those regions (Canter & Heaney, 1984; Hickel, 1988; Lindström, 1992). According Heaney et al. (1988) and Bustamante-Gil et al. (2012), *C. furcoides*' ecology is also very similar to *C. hirundinella*: both organisms tolerate wide environmental variation, but prefer conditions of high nutrient availability, temperatures between 15°C and 25°C, thermal stratification, and pH higher than 8 (Heaney & Talling, 1980; Lindström, 1992). Laboratory experiments conducted with strains of *C. furcoides* have supported some of these environmental preferences, demonstrating optimal growth at temperatures of 14-25°C (Butterwick et al., 2005) and phototactic and chemosensory behavior of this species in response to photon irradiance and several chemical gradients (Clegg et al., 2003, 2004). However, some studies have shown a different seasonal pattern than that found in temperate systems for *C. hirundinella*, with winter dominance during water mixing (Pérez-Martínez & Sánchez-Castillo, 2001, 2002). Besides population fluctuations in terms of abundance, seasonal variation on morphometric characters (called "cyclomorphosis") is also reported in the literature for ceratioid dinoflagellates (Huber-Pestalozzi, 1950; Pollingher, 1988; Lindström, 1992; Gligora et al., 2003). High morphometric variation in *Ceratium* is considered to be an adaptive characteristic for environmental changes, especially temperature (Popovský & Pfiester, 1990; Lindström, 1992), but also seems to be related to biotic pressures, such as herbivory, and resistance to mechanical damage by filtering zooplankton (Hamlaoui et al., 1998; Bertolo et al., 2010).

With the fast expansion of *Ceratium* in South American systems, research investigating its ecological requirements and tolerance levels is necessary to understand its potential dispersal and possible impacts on those ecosystems. Some studies have already been published (on *C. hirundinella*: Mac Donagh et al., 2005; Parodi et al., 2007; Silverio et al., 2009; on *C. furcoides*: Bustamante-Gil et al., 2012; Silva et al., 2012), but the knowledge is still diffuse. In this study we investigated *Ceratium furcoides'* abundance and morphological variation during its initial phase of colonization (2012–2013) in two subtropical reservoirs in southern Brazil in order to explore which environmental factors were related to the occurrence, persistence and bloom formation of this dinoflagellate in those environments. These findings, together with other similar studies performed in the region, are a crucial first step toward understanding the invasive success of *Ceratium* in South American water systems.

Material and Methods

The present study was conducted in two subtropical reservoirs located in the city of Caxias do Sul, in southern Brazil. This region is characterized by a warm temperate climate without a dry season (Cfa, Kottek et al., 2006), annual mean temperature of 16°C, and total annual precipitation between 1,800 and 2,200 mm (Becker et al., 2009a). Faxinal and Maestra reservoirs (Fig. 1) are two unconnected systems included in the Taquari-Antas river basin and are used as a water supply by SAMAE (Serviço Autônomo Municipal de Água e Esgoto), the company responsible for limnological monitoring of these systems.

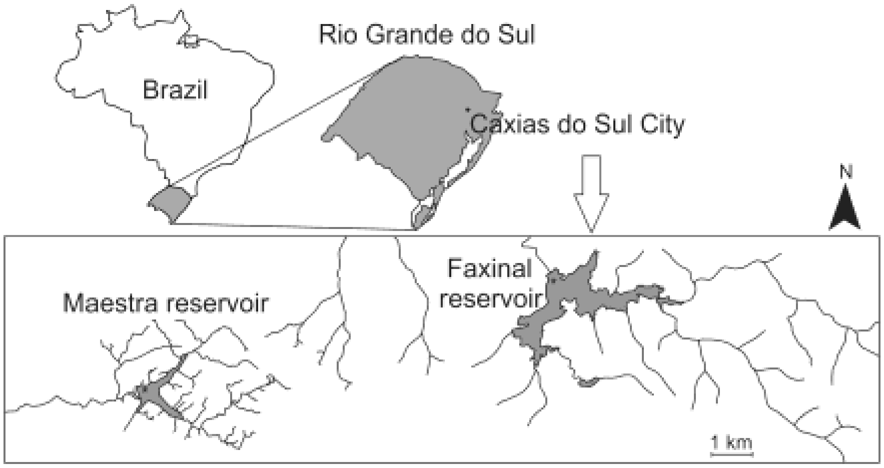

Fig. 1 Map of Faxinal and Maestra reservoirs and their main tributaries. Asterisks (*) indicate sampling stations.

Faxinal reservoir (29°05’00”S; 51°03’30”W) was constructed in 1992. It is a warm monomictic and meso-eutrophic system, with surface area of 3.1 km², z_{max} 30 m, and retention time of 191 days (Becker et al., 2009b). In contrast, Maestra reservoir (29°06’37”S; 51°09’51”W) is less studied than the former. The reservoir was built in 1968, has a surface area of 0.54 km², $z_{max} \approx 25$ m, and is regarded as a eutrophic system (SAMAE, unpublished data).

Samples derived from the phytoplankton monitoring program performed by SAMAE were preserved with Lugol’s iodine solution. Samples were gathered weekly near the water intake, from the surface layer (0–0.5 m), in both reservoirs, in 2012 and 2013. Simultaneously, physical and chemical parameters were measured; the analytical methods of APHA (1998) were followed. Temperature, dissolved oxygen, pH, and conductivity were measured by a Horiba U-10 multiparameter probe; turbidity was measured by a HACH 2100P turbidimeter. Organic matter was estimated by titration method. Nutrient (ammonium, nitrite, nitrate and phosphate) and metal (iron and manganese) concentration analyses were performed in a PHARO 300 UV/VIS spectrophotometer, using Merck’s colorimetric test kits. Precipitation data were obtained from Caxias do Sul meteorological station (OMM: 83942, at ca. 20 km from both reservoirs), available from the National Institute of Meteorology website (INMET, 2014).

Using analysis of the monitoring data previously provided by SAMAE, only subsamples containing *Ceratium* cells were selected for the present study, resulting in 91 sample units. To estimate abundance, 1–8 mL aliquots were concentrated by sedimentation, depending on the *Ceratium* concentration in the samples. At least 100 cells were counted at low magnification (100x) on the entire area of a Sedgewick-Rafter chamber, using an Olympus CH-2 light microscope. Two morphotypes were considered based on the number of antapical horns: two or three. Species identification was determined according to Cavalcante et al. (2013).

In this study, we arbitrarily assumed bloom cells densities above 1,000 cells mL^{-1} (Kawabata and Kagawa, 1988; Guerrero & Echenique, 1997; Mac Donagh et al., 2005; Hart & Wragg, 2009; Silverio et al., 2009), because densities above this threshold had a distinct ecological importance in the studied period.

Ten cells were measured per month from both reservoirs (n=240). The equation used to estimate the cell volume of *Ceratium furcoides* is the same as that employed in European monitoring programs (eg. INAG, 2011). Biomass was estimated from biovolume calculations, assuming a specific gravity of 1 $mm^3\ L^{-1}$ = 1 mg L^{-1} (Wetzel & Lichens, 2000). Cell volumes were also used to evaluate cyclomorphosis.

One-way analysis of variance (ANOVA) was carried out to test seasonal differences of cell densities and volumes, with post-hoc Tukey’s test to compare means. Pearson correlation was used to find relationships among cell biomass, cell volume, and environmental variables. The aforementioned univariate analyses were performed using the software Statistica 7.1©. Principal component analysis (PCA) was performed to determine spatial and temporal patterns in the physical and chemical data sets, using correlation to produce a cross product matrix (data not log transformed). This analysis was performed on PC-ORD 6.08©.

Results

Physical and chemical variables

Precipitation data showed that on a seasonal basis, winter and spring constituted the rainy seasons in 2012 and 2013 in this region, with monthly average of 200 mm and 193 mm respectively. The highest precipitation sampled was 68.3 mm on 12-Nov-13, whereas the accumulated precipitations during the weeks before sampling were 214.8 mm on 27-Aug-13 (winter), 197.3 mm on 12-Nov-13 (spring), and 189.2 mm on 2-Jan-13 (summer).

Both reservoirs were very distinct of each other in relation to the majority of the environmental variables (Table 1). The PCA ordination for 12 abiotic variables explained 55.21% of data variability in the first two axes (Fig. 2), only dissolved oxygen was not plotted. Manganese (r = -0.87), nitrite (r = -0.86), and phosphate (r = -0.83) were the principal variables in the composition of axis 1 (32.18%), while pH (r = 0.88), temperature (r = 0.84), and organic matter (r = 0.77) were the most important variables for axis 2 (23.02%). The PCA's diagram presented a clear seasonal pattern in the ordination of the units, but secondarily we can see the units grouped by reservoir into each season, highlighting the limnological distinction between these reservoirs, especially regarding to nutrient availability.

Ceratium furcoides **occurrence and abundance**

Cells of *Ceratium furcoides* were registered for the first time in Maestra in September 2012 and remained throughout the studied period. After detected introduction, it occurred in low densities, with the first growth peak in late October, followed by recurrent blooms throughout the summer with a maximum recorded density of 2,680 cells mL^{-1} (Figs 3 and 4). New blooms were observed in early fall and mid-November and December 2013.

Table 1 Range, mean values, and standard deviation of physical and chemicals variables of Faxinal and Maestra reservoirs, during *Ceratium* occurrence in 2012 and 2013

	Faxinal (n=35)				Maestra (n=56)			
	Min	Max	Mean	SD	Min	Max	Mean	SD
Temperature (°C)	11.8	25.8	17.6	3.7	11.4	26.9	19.6	4.2
Turbidity (NTU)	3.4	41.2	15.2	8.0	6.0	96.7	23.4	15.3
pH	6.0	9.4	7.6	0.9	6.3	10.5	8.5	1.2
Conductivity (µS cm^{-1})	31.2	50.2	39.1	5.2	54.3	79.6	64.2	6.2
Dissolved oxygen (mg L^{-1})	3.60	11.34	7.74	1.85	1.70	11.05	7.97	2.12
Organic matter (mg L^{-1})	2.20	15.90	6.37	3.21	2.00	19.80	9.02	5.49
NH_4 (mg L^{-1})	0.01	0.29	0.09	0.07	<0.01	0.80	0.15	0.16
NO_3 (mg L^{-1})	<0.2	0.35	0.05	0.09	<0.2	1.28	0.57	0.32
NO_2 (mg L^{-1})	0.02	0.05	0.03	0.008	0.01	0.10	0.04	0.02
PO_4 (mg L^{-1})	<0.01	0.09	0.02	0.02	<0.01	0.29	0.06	0.04
Fe (mg L^{-1})	0.12	1.43	0.54	0.30	0.12	1.83	0.48	0.24
Mn (mg L^{-1})	0.04	0.46	0.21	0.11	0.02	0.93	0.25	0.14

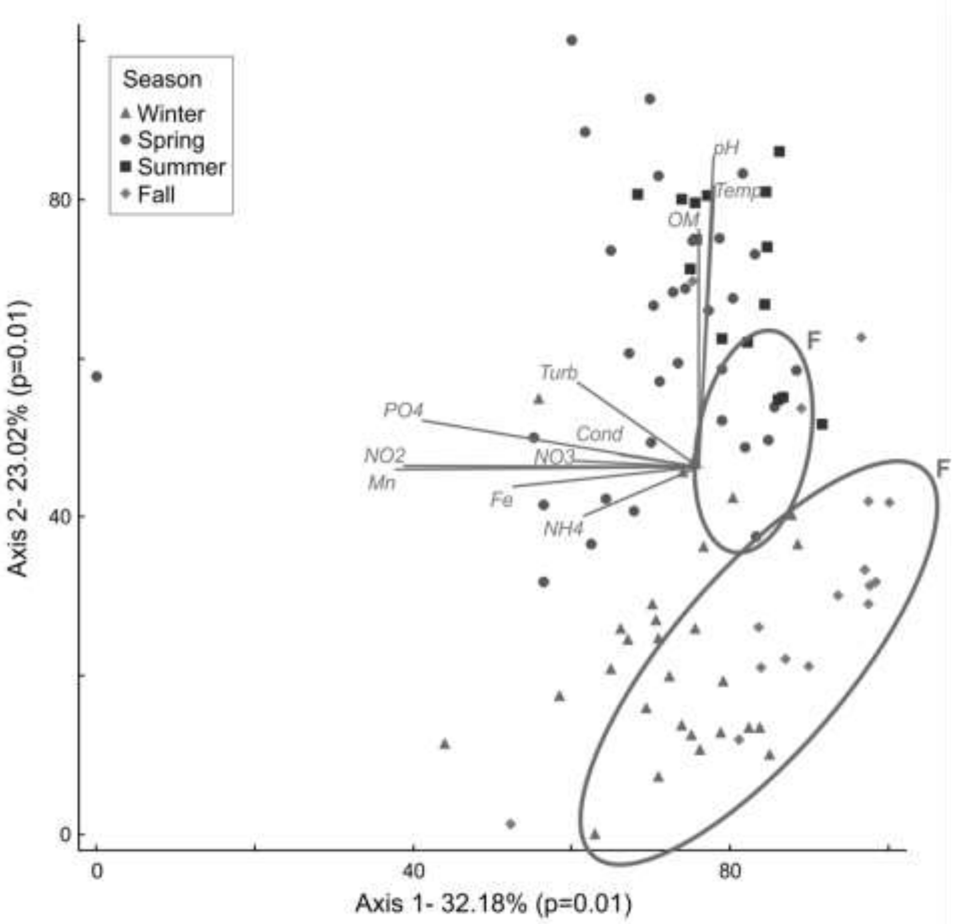

Fig. 2 PCA ordination diagram for the abiotic variables and sampling units of Faxinal and Maestra reservoirs during *Ceratium* occurrence. See Table 2 for variables abbreviations. Ellipsoids correspond to Faxinal (F) grouped samples

In Faxinal reservoir, *Ceratium furcoides* only was registered in phytoplankton counts in April 2013 (seven months after the colonization in Maestra), with low densities. The density rose sharply in early October and reached maximum density in mid-November (2,819 cells mL^{-1}) (Figs 3 and 4). No cysts were observed in the samples from either reservoir during the study period.

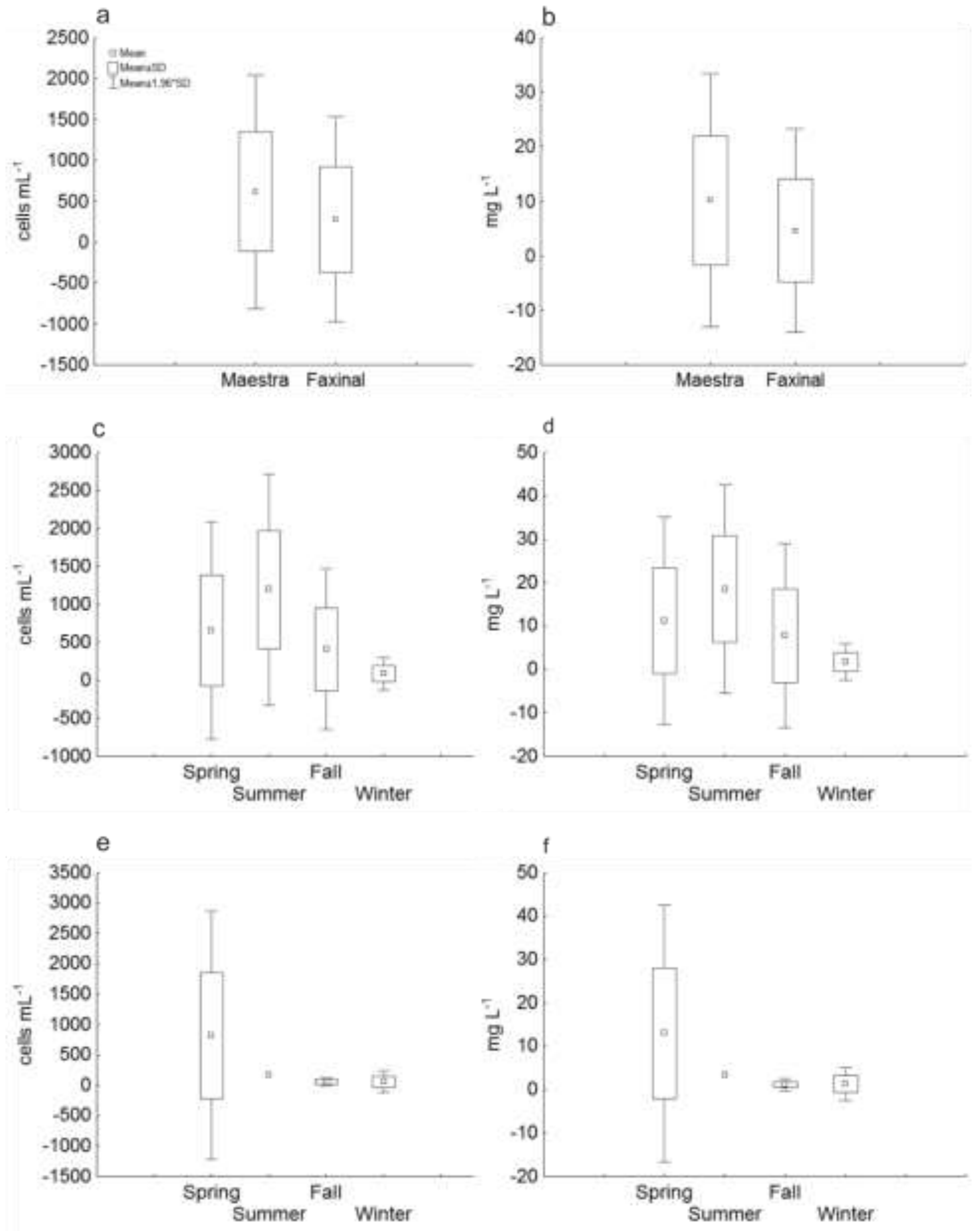

Fig. 3 Density and biomass variation of *Ceratium furcoides*. Total variation of density (a) and biomass (b) in both reservoirs; density and biomass by season at Maestra (c and d, respectively) and Faxinal (e and f)

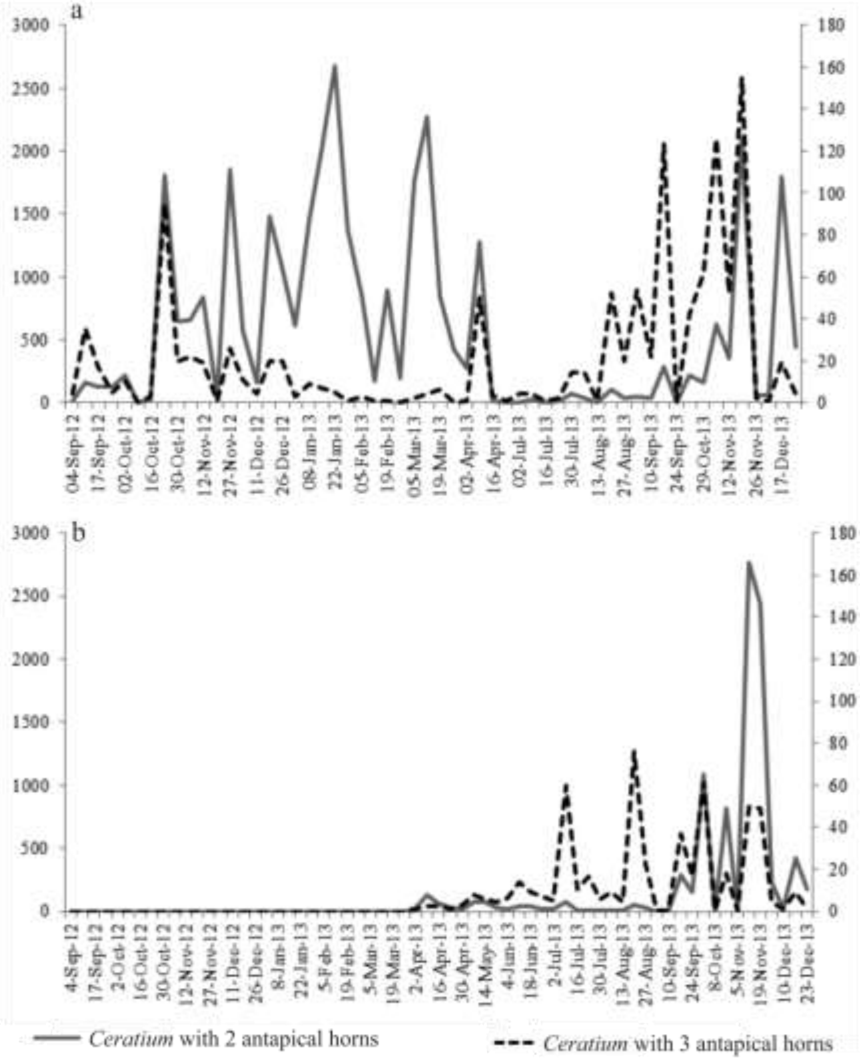

Fig. 4 Cell density (cells mL^{-1}) of *Ceratium furcoides* with two (solid line) and three (dashed line) antapical horns in Maestra (a) and Faxinal (b) reservoirs during 2012–13

Neither density nor biomass was significantly different between reservoirs (ANOVA, $p>0.05$). On the other hand, density was significantly different between seasons (ANOVA, F=18.05, $p<0.01$). Tukey test presented differences (mean log density in cells mL^{-1}) between spring (2.53)-summer (2.91) and fall (1.83)-winter (1.42).

Direct and inverse correlations among abiotic variables and biomass suggested some patterns (Table 2). Biomass peaks occurred in temperatures higher than 15°C; below 15°C, the biomass dropped. High organic matter values were also related to *Ceratium furcoides* biomass. Cell maxima were observed when organic matter was higher than 8 mg L^{-1}. The pH showed a similar pattern in promoting bloom: *Ceratium furcoides* bloomed at alkaline pH (8.5–10 in Maestra, 8–9 in Faxinal) except on 12-Nov-13 in Faxinal, when the biomass peak was recorded (40.39 mg L^{-1}), and when pH abruptly decreased to 6.1. *Ceratium furcoides* was abundant in periods of low conductivity in both reservoirs; however, biomass peaks occurred at 54 to 64 µS cm^{-1} in Maestra and approximately half of these values (33–37 µS cm^{-1}) in Faxinal. Turbidity was related more to biomass in Faxinal, and *Ceratium* peaks occurred with the highest values observed of that variable (25–41 NTU). Phosphate was an important factor for *Ceratium* growth in Faxinal, where blooms occurred when phosphate reached concentrations higher than 0.05 mg L^{-1}. Regarding nitrate concentrations, *C. furcoides* biomass showed a distinctive pattern between reservoirs. In Maestra, which had high nitrate availability, high biomass values were inversely related to nitrate concentrations; in Faxinal, which had lower nitrate availability, blooms were associated with higher nitrate concentrations. Precipitation on the sampling day and during the week prior had different interactions in the reservoirs, with no direct effects in Maestra but positive correlation in Faxinal. Heavy rainfalls occurred during the week of 2-Jan-13 (189.2 mm) interrupting the continuous summer bloom in Maestra; in Faxinal, the highest cumulative precipitation value (197.3 mm) coincided with the *Ceratium* peak on 12-Nov-13. Dissolved oxygen (DO) was

Table 2 Pearson correlation values ($p<0.05$) between *Ceratium furcoides* biomass and environmental variables (B2 = Biomass of two antapical horns cells, B3 = biomass of three antapical horns cells, TB = total biomass, Temp = temperature, Turb = turbidity, Cond = conductivity, OM = organic matter, Pday = precipitation on the sampling day; Pweek = precipitation accumulated over a week)

		Temp	Turb	pH	Cond	OM	NO_3	NO_2	PO_4	Fe	Mn	Pday	Pweek
Bloom periods (n=15)	B2			0.58		0.80	-0.60			-0.53			-0.52
	B3							0.52					
	TB			0.58		0.79	-0.57			-0.52			
Two reservoirs (n=91)	B2	0.51	0.34	0.50		0.79			0.24			0.22	
	B3						0.26	0.44	0.40		0.26		
	TB	0.49	0.34	0.49		0.79			0.25			0.23	
Maestra (n=56)	B2	0.56		0.56	-0.38	0.82	-0.34						
	B3						0.30	0.48	0.43				
	TB	0.54		0.55	-0.39	0.81	-0.32						
Faxinal (n=35)	B2		0.72		-0.38	0.68	0.65		0.65			0.51	0.34
	B3										0.38		
	TB		0.72		-0.37	0.68	0.64		0.65			0.50	0.34

not significantly correlated with *Ceratium furcoides* abundance; however, both reservoirs had presented a trend to well-oxygenated water column throughout the studied period (DO > 5 mg L^{-1}).

Ceratium morphometric variation

In both reservoirs, cells having two antapical horns were more common than those with three antapical horns during most of this study. The abundance of three-antapical-horned cells was higher in Maestra during the spring (maximum 155 cell mL^{-1} on November 2013) and in Faxinal, during the winter (Fig. 4). Biomass of this morphotype was significantly correlated with nitrate, nitrite, phosphate, and manganese (Table 2).

The mean cell volume showed seasonal variation during this study (Fig. 5; ANOVA, F = 8.309, $p<0.01$). In warm seasons (spring-summer) the cells were smaller than in cold seasons (fall-winter). However the abundance (Figs. 3 and 4) had the opposite pattern, showing inverse correlation between cell volume and cell density ($r = -0.70$, $p<0.05$). Regarding abiotic data, cell volume was negatively correlated with temperature ($r = -0.70$), pH ($r = -0.72$), organic matter ($r = -0.66$), and turbidity ($r = -0.47$).

Discussion

Ceratium furcoides cells are 123–322 µm long (Popovský & Pfiester, 1990) and, despite being a conspicuously large organism of the phytoplankton community, have never been found in Brazilian environments until 2003 (Cavalcante et al., 2013). From the southeastern region, where it was first detected, its distribution has expanded northwards and southwards.

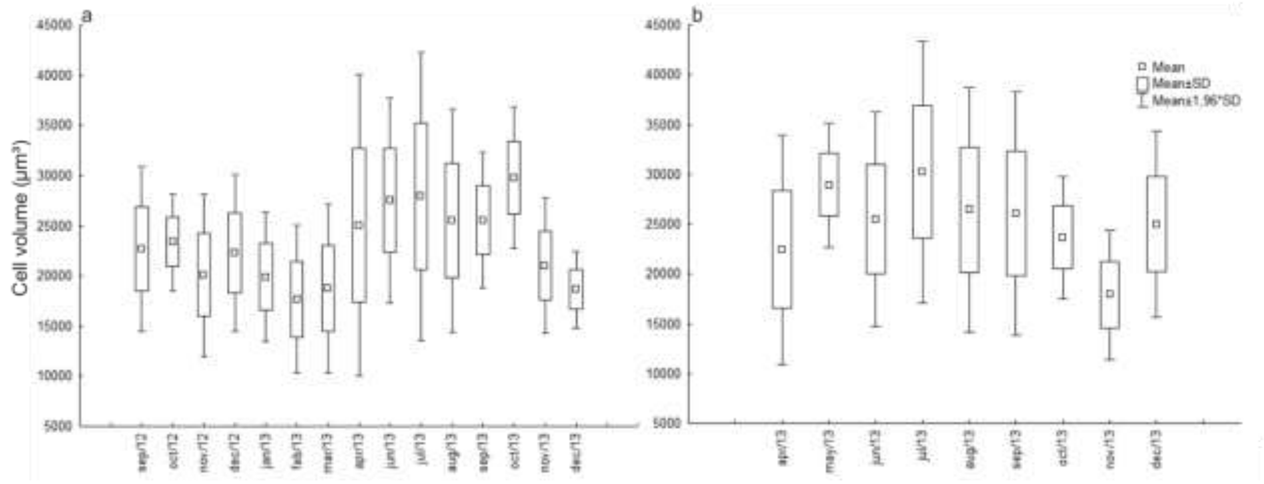

Fig. 5 Monthly variation of the cell volume of *Ceratium furcoides* in Maestra (a) and Faxinal (b) reservoirs

In state of Rio Grande do Sul (southern Brazil), *Ceratium furcoides* has been recorded in many reservoirs and rivers since 2011. In July 2012, it was detected in Jacuí River, ca. 150 km distant from Maestra reservoir (Cavalcante et al., 2013); these environments probably have been colonized from the same invading population (two months after registered in reservoir).

Faxinal and Maestra phytoplankton have been sampled since 2002, when a monitoring program was implemented (Frizzo et al., 2004) according to the standards of the Ministry of Health (BRASIL, 2004). In these reservoirs, there is a historical occurrence of cyanobacterial blooms of the genus *Dolichospermum* (Ralfs ex Bornet et Flahaut) Wacklin, Hoffman et Komárek and *Microcystis* Kützing ex Lemmermann (Frizzo et al., 2004; Yunes et al., 2005). Other studies were performed in those systems, for example: Becker et al. (2009a, b), revealing the important role of physical processes in the seasonal gradient in selecting for phytoplankton functional groups and Cardoso et al. (2010), which studied the dinoflagellate assemblages in reservoirs from Caxias do Sul City (including Faxinal and

Maestra) in 2002–2006. None of these studies found *Ceratium furcoides* in those environments. The absence of *Ceratium furcoides*, confirmed by extensive previous studies and monitoring program; its rapid expansion as soon as it was first reported; and the aggressive behavior of this dinoflagellate, quickly reaching high biomass in those systems, are strong evidence of the invasive nature of this microorganism.

High densities of *Ceratium* are usually recorded in literature as ordinary events in annual phytoplankton fluctuations of many temperate waterbodies (Table 3). The major bloom-forming species is *C. hirundinella*. Only a few papers described the bloom dynamics of *C. furcoides* (Canter and Heaney, 1984; Lindström, 1992). However, the majority of these density peaks were under 1,000 cells mL^{-1} (Padisák, 1985; Lindström, 1992; Pérez-Martínez & Sánchez-Castillo, 2002; Carty, 2003). In subtropical environments, *Ceratium* spp. tend toward higher population growth, as found for *Ceratium hirundinella* in Argentina (Silverio et al., 2009) and South Africa (Hart & Wragg, 2009), and for *C. monoceras* Temponeras in the boundary between Macedonia and Greece (Temponeras et al., 2000a). In South America, populations of *C. furcoides* were observed at a maximum of 41 cells mL^{-1} during the spring in Riogrande II reservoir (Bustamante-Gil et al., 2012), of 29 cells mL^{-1} during the winter in Furnas reservoir (Silva et al., 2012), and of 15 cells mL^{-1} during the fall in Yacyretá reservoir (Meichtry de Zaburlin et al., 2014). Matsumura-Tundisi et al. (2010: 828, table 2) found a maximum density of 21,455 cells mL^{-1} during the winter in Billings reservoir, but there is probably a typographical error since the same data (plotted in Fig. 1, p. 826 from

Table 3 The densest blooms of *Ceratium* spp. recorded in scientific literature

Environment	Bloom-forming species	Maximum density (cells mL^{-1})	Season	Reference
South America				
Faxinal and Maestra reservoirs, southern Brazil	*C. furcoides*	2,819	Spring-summer	Present study
Paso de las Piedras reservoir, east-central Argentina	*C. hirundinella*	2,000	mid-summer	Guerrero & Echenique (1997)
Río Tercero reservoir, central Argentina	*C. hirundinella*	1,244	late summer	Mac Donagh et al. (2005)
Sumampa and Las Pirquitas reservoirs, northwestern Argentina	*C. hirundinella*	5,634	winter	Silverio et al. (2009)
North America				
Heart Lake, southeastern Canada	*C. hirundinella*	1,300	summer	Nicholls et al. (1980)
Europe				
Lake Erken, southeastern Sweden	*C. hirundinella*	416	late summer	Dottne-Lindgren & Ekbohm (1975)
Esthwaite Water, northern England	*C. hirundinella*	370	late summer	Chapman et al. (1985)
Lake Sempach, central Switzerland	*C. hirundinella*	380	summer	Pollingher et al. (1993)
Blelham Tarn, northern England	*C. furcoides*	ca. 485	summer	Canter & Heaney (1984)
Lake Pluβsee, northern Germany	*C. furcoides*	670	summer	Hickel (1988)
Laje Doïrani, Macedonia, Greece	*C. monoceras*	3,339	spring	Temponeras et al. (2000a, b)
Asia				
Ishitegawa reservoir, Southern Japan	*C. hirundinella*	1,300	summer	Kawabata & Kagawa (1988)
Small pond in Tsukuba, east-central Japan	*C. hirundinella*	925.5	late spring	Xie et al. (1998)
Africa				
Albert Falls Dam, eastern South Africa	*C. hirundinella*	over 5,000	summer	Hart & Wragg (2009)
Oceania				
Chaffey Dam, eastern Australia	*C. hirundinella*	ca. 520	summer	Baldwin et al. (2003)

that paper) do not exceed 25 cells mL^{-1}. The densities that we observed, with peaks of 2,680 and 2,819 cells mL^{-1} during spring-summer in Maestra and Faxinal, respectively, represents the densest bloom ever reported for *C. furcoides* (Table 3).

Ceratium furcoides was a perennial form in the phytoplankton of Faxinal and Maestra during this study, with bloom formation at temperatures between 15 and 27°C just as *C. hirundinella* was in Río Tercero reservoir (Mac Donagh et al., 2005). In temperate systems, *Ceratium* spp. occurred during warm and stratified waters in a few summer months, completely disappearing from water column in cooler seasons (Heaney & Talling, 1980; Pollingher, 1988). In the subtropical lake Kinneret, *Ceratium hirundinella* reached maximum density during the spring but declined in summer, at temperatures higher than 25°C (Pollingher & Hickel, 1991). Despite the seasonality difference, the optimum range of temperature for *Ceratium* growth is similar, between 12 and 23°C (Heaney et al., 1988; Popovský & Pfiester, 1990). This seems to be a crucial factor for the distribution of these dinoflagellates throughout the year in subtropical reservoirs, such as Faxinal and Maestra. In these environments, the temperatures were moderate, seldom reaching the extreme temperatures assigned to *Ceratium* growth. On the other hand, in a Spanish reservoir, *C. hirundinella* occurred throughout the year with highest densities during mixing periods of fall-winter at temperatures of 7–14°C (Pérez-Martínez & Sanchez-Castillo, 2002), demonstrating a high tolerance of this species to temperature variation.

In this study, the occurrence and growth of *Ceratium furcoides* in the reservoirs of Caxias do Sul were controlled, primarily, by a combination of optimal conditions of temperature, organic matter, pH, and dissolved oxygen. Secondarily, although this species tolerates a wide range of conductivity and nutrient content, *Ceratium* abundance was associated with nutrient availability, especially phosphate and nitrate. Similar results were found by Grigorszky et al. (2003), for dinoflagellates in Hungarian water bodies, and Cardoso et al. (2010), in the same subtropical reservoirs of Caxias do Sul. The high biomass of *C. furcoides* was associated with high values of organic matter. Despite the potential autocorrelation between these variables, we didn't reject the contribution of other planktonic (phyto- and zoo-) organisms to organic matter, favoring a nutritional alternative by mixotrophy (Olrik, 1994). Mixotrophy has never been demonstrated in *Ceratium furcoides* and is a controversial topic concerning this genus (Gaines & Elbrächter, 1987; Hansen & Calado, 1999). However, it is a feature sometimes recorded for *C. hirundinella* (Dodge & Crawford, 1970) and well documented in marine relative species (Bockstahler & Coats, 1993; Jacobson & Anderson 1996, Jacobson 1999), and probably can occur in *C. furcoides*. Regarding pH, *Ceratium* peaks were registered in alkaline conditions, as in other recorded maxima (Lindström, 1992; Guerrero & Echenique, 1997; Temponeras et al., 2000b; Carty, 2003; Mac Donagh et al., 2005; Silverio et al., 2009; Matsumura-Tundisi et al., 2010). Only in an atypical event in Faxinal on 12-Nov-2013 did the highest cell abundance of *C. furcoides* occur at low pH, coinciding with highest accumulated precipitation and high values of turbidity and nutrients, especially nitrogen compounds. The heavy rainfall could have been responsible for pH reduction, as well as have provided input of nutrients from runoff or sediment to the water column. We postulate that in a mesotrophic system, nutrient availability can be an important factor for *Ceratium* growth, even at slightly acidic pH. Similar patterns were observed with *C. hirundinella* in Lake Biwa, suggesting that *Ceratium* abundance was controlled by nitrogen availability (Nakano et al., 1999). Well-oxygenated waters, such as those of Faxinal and Maestra reservoirs, are also an important factor for *Ceratium* development (Pollingher, 1988; Mac Donagh et al., 2005). Previous studies have showed that *C. furcoides* cells can swim toward high concentrations of O_2 in water column, filling their physiological requirements for oxygen during respiration and accelerating metabolic activity and growth (Clegg et al., 2004). In mesotrophic systems showing low phosphorus content, as in Faxinal reservoir, *Ceratium furcoides* abundance was associated with phosphorus peaks (Wu & Chou, 1998; Bustamante-Gil et al., 2012; Silva et al., 2012). Under eutrophic conditions, as in Maestra reservoir, phosphorus content was not a correlated factor for *Ceratium* growth (van Ginkel et al., 2001). However, Mac Donagh et al. (2005) showed high densities of *C. hirundinella* in a very low phosphorus context. It is stated that *Ceratium* spp. can obtain phosphorus from multiple sources when conditions of P-limitation exist in the epilimnion, by vertical migration (James et al., 1992; Olrik, 1994). Sexual reproduction (gamete fusion) of *C. furcoides* in Lake Pluβsee was linked to low nitrogen and phosphorus levels (Hickel, 1988). The contrasting behavior of *Ceratium* species in divergent lake types (with different climatic, morphometric, geological, hydrological, and trophic features) explains the existence of ecotypes of these species adapted to diverse environmental conditions and exhibiting high intra- and inter-population morphological variability (Salmaso, 2003).

Incidence of three-antapical-horned cells was higher in Faxinal during the winter and in Maestra during the following spring, correlating with the highest mean cell volume. Throughout the spring-summer blooms, *Ceratium furcoides* with two antapical horns was the dominant morphotype, in accordance with previous studies (Dottne-Lindgren & Ekbohm, 1975; Hickel, 1988; Lindström, 1992). Lindström (1992) pointed out that large cells, generally having three antapical horns, probably consist of forms adapted to low temperatures. However, it cannot be concluded that temperature directly affects the density of cells with different numbers of antapical horns (Dottne-Lindgren & Ekbohm, 1975). We found significant correlation between three-antapical-horned cell abundance and nutrient concentrations, in accordance with previous studies (Kimmel & Holt, 1988). Hamlaoui et al. (1998) have found that the proportion of three-horned cells tended to increase at high levels of nutrient content, but this effect was not statistically significant. No study has ever shown an association between three-antapical-horned cells and manganese like the positive correlation observed in Faxinal. However, experimental studies are necessary to verify the real influence of this micronutrient on the growth of the third antapical horn. Recent studies have also demonstrated that biotic pressure, especially protection against physical contact with the filtering apparatus of grazers, plays a strong role on morphological variability in *Ceratium* (Bertolo et al., 2010).

In the Faxinal and Maestra reservoirs, warm seasons promoted population increases, while in cooler seasons cells increased in volume. Similar seasonal cell-size variation was observed for different populations of *Ceratium* species (Dottne-Lindgren & Ekbohm, 1975; Lindström, 1992; Gligora et al., 2003). Temperature is a key factor in the cell-size dynamics for *Ceratium* spp. (Huber-Pestalozzi, 1950). *Ceratium furcoides* biomass peaks (smaller cells) were also inversely related to iron content. It is known that iron can bind with phosphorus and make it unavailable for phytoplankton consumption. Other studies have demonstrated increasing cell volume in dinoflagellates at P-depletion, probably due to cell-division inhibition resulting in large cells (Flaim et al., 2010). In the present study, *Ceratium* abundance and cell volume had similar temporal distribution in both reservoirs. In contrast, the reservoirs were typically different, especially regarding to nutrient availability. These findings can be explained by the high tolerance to various environmental conditions ascribed to this dinoflagellate (Pollingher, 1988).

The major *Ceratium* features that promote its wide environmental tolerance were summarized in Figure 6. *Ceratium* species are considered excellent competitors among freshwater phytoplankton due to intrinsic features, such as good swimming performance, enabling the cells to perform vertical migration in order to find optimal conditions of light and nutrients for their growth (Heaney & Talling, 1980); low herbivory pressure due to their size and shape (Xie et al., 1998); presumable mixotrophy, as an nutritional alternative for growing even under inorganic nutrient depletion (Olrik, 1998; Salmaso, 2003); and resting cyst production, which ensures the survival, bloom maintenance, and dispersal capacity of these species (Pollingher, 1988). We assume that these adaptive strategies are critical in understanding the invasive success demonstrated by *Ceratium* in Brazilian freshwaters (Fig. 6). Future studies should demonstrate the effects of each of these biological processes in the population dynamics of *Ceratium furcoides* in Brazilian reservoirs.

Previous studies on the dinoflagellate communities of reservoirs from Caxias do Sul suggested that the lack of dinoflagellate blooms in those reservoirs was related to nutrient limitation and consequent competition among phytoplankton (Cardoso et al., 2010). Now, it is possible to conclude that the initial lack of blooms was related to the absence of highly tolerant and excellent competitor populations, such *Ceratium* species. *Ceratium furcoides* performed a rapid colonization: it bloomed in Maestra just over a month after the first appearance and colonized Faxinal (ca. 10 km away) only seven months later. Dense blooms performed by *Ceratium furcoides* suggested that this species had found ideal conditions for growing in both subtropical reservoirs, with favorable limnological and climatic characteristics, probable low competition with native species, and absence of natural predators and parasites.

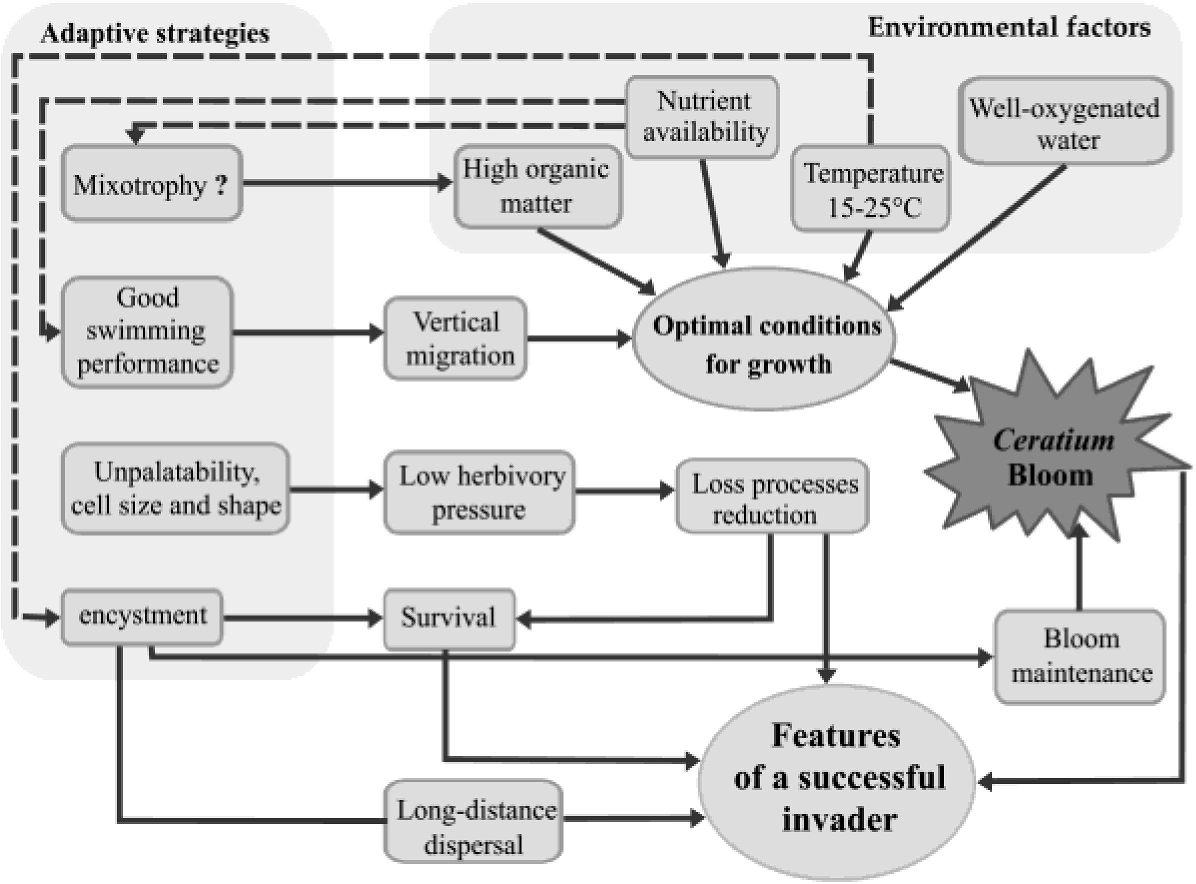

Fig. 6 A synthesis diagram showing relationships among environmental conditions, adaptive strategies and invasion success of *Ceratium furcoides*. Solid arrows represent direct relation while dashed arrows indicate inverse relation. A question mark (?) indicates a biological process that needs confirmation for this species.

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Capítulo 3.

Um método simples para o cálculo do volume celular de *Ceratium furcoides* (Dinophyceae): bases para o monitoramento em reservatórios subtropicais

Estruturado nas normas do periódico Journal of Applied Phycology

Finding an easy measure as a proxy of the cell volume of *Ceratium furcoides* (Dinophyceae): basis for monitoring in subtropical reservoirs

Kaoli Pereira Cavalcante[1]*, Rovana Sussella[2], Vanessa Becker[3] and Luciana de Souza Cardoso[1]

[1]Programa de Pós-Graduação em Botânica, Departamento de Botânica, Universidade Federal do Rio Grande do Sul, Porto Alegre–RS, Brasil. [2]Serviço Autônomo Municipal de Água e Esgoto, Caxias do Sul–RS, Brasil. [3] Programa de Pós-Graduação em Engenharia Sanitária, Universidade Federal do Rio Grande do Norte, Natal–RN, Brasil.

*Corresponding author e-mail: kaolicavalcante@gmail.com

Abstract *Ceratium furcoides,* a large bloom-forming dinoflagellate, is considered an invasive species in South American freshwaters. Since it can cause some ecological and economic problems, particularly in reservoirs, this phenomenon has been discussed among researchers and companies responsible for the monitoring of Brazilian aquatic systems. Biovolume estimatives are an important tool for ecological studies, however calculating it is an exhaustive work due to the high number of samples and measurements. The goal of this study was to provide an easy measured morphological trait as proxy of the cell volume in *C. furcoides*. Data were obtained from two subtropical reservoirs in southern Brazil with public supply purposes. Twelve dimensions were taken from 10 cells by month in each reservoir, accounting 240 measured cells. Cell volume showed seasonal variation, with significantly differences by months (ANOVA, $F=7.1$, $p<0.05$) and by seasons (ANOVA, $F=8.309$, $p<0.05$), but no between reservoirs or morphotypes with two or three antapical horns (ANOVA, $p>0.05$), then biovolume estimates should consider seasonal variations in dinoflagellate size. All measured dimensions were positively related to cell volume. Body width was significantly correlated to all other measured dimensions of the cell and highly correlated to cell volume (r-Pearson = 0.86, $p<0.05$), proving to be the most representative measure of the cell volume. Linear regressions were performed in order to estimate cell volume from cell body width and revealed strong positive trend when both full sampling and seasonally grouped samples were considered. These results are essential to facilitate the work routine in monitoring purposes.

Key words biovolume · cyclomorphosis · dinoflagellate · method · southern Brazil

Ceratium furcoides (Levander) Langhans is a large and ecologically variable species. It is considered as stress-tolerant, occurring in a wide range of environmental conditions (Olrik 1994; Bustamante-Gil et al. 2012). It is a common dinoflagellate in northern hemisphere, but had never been recorded in South America until 2003 (Cavalcante et al. 2013). Since then, brazilian phytoplanktologists have been surprised by the introduction and quick expansion of this dinoflagellate along freshwater environments from the country (Santos-Wisniewski et al. 2007; Matsumura-Tundisi et al. 2010; Oliveira et al. 2011; Silva et al. 2012; Cavalcante et al. 2013; Jati et al. 2014; Nishimura et al. 2015).

Some intrinsic ecological strategies ascribed for this dinoflagellate are determinant for its invasive success in South American waterbodies, namely good swimming performance, unpalatability, resting cysts production and presumable mixotrophy, which ensure survival, loss process reduction and long-distance dispersal (Cavalcante et al. 2016). The formation of dense blooms by *Ceratium* spp, which are considered non-toxic (Smayda 1997), may cause some ecological and economic impacts (Parodi et al. 2007; Hart and Wragg 2009; Ewerts et al. 2013) mainly in water bodies addressed to water supply.

Seasonal variation in morphology, called cyclomorphosis, is a common phenomenon in ceratioid dinoflagelates (Huber-Pestalozzi 1950; Pollingher 1988; Lindström 1992; Gligora et al. 2003) and seems to be related to abiotic (Popovský and Pfiester 1990; Lindström 1992) and biotic (Hamlaoui et al. 1998; Bertolo et al. 2010) pressures. Thus, cyclomorphosis can affect biomass estimation by cell volume. Biovolume estimatives are an important tool for ecological studies and monitoring purposes, since differences in size are intrinsically associated to how populations explore the available environmental resources (Reynolds 2006). Geometrical models of the cells are widely used to estimate algal biomass (Hillebrand et al. 1999; Sun and Liu 2003). However, calculating it is an exhaustive work due to the high number of samples and measurements, particularly in cells of complex shapes. The equation used to estimate the cell volume of *Ceratium* spp. requires the combination of 4–5 different geometric forms (Olenina et al. 2006).

This study aims to provide and easy measured morphological trait as proxy of the cell volume of *Ceratium furcoides*. Data were obtained from two subtropical reservoirs in southern Brazil with public supply purposes. The results are then essential to facilitate the work routine of the monitoring of these environments.

Samples containing *Ceratium furcoides*, derived from phytoplankton monitoring program performed by SAMAE (Serviço Autônomo Municipal de Água e Esgoto) in two subtropical reservoirs located in the city of Caxias do Sul, southern Brazil, were taken monthly in each reservoir from the surface layer (0–0.5 m) and preserved with Lugol's iodine solution. In Maestra reservoir (29°06'37"S; 51°09'51"W), *C. furcoides* was registered between September 2012 and December 2013 (except in May, when no *C. furcoides* cells were found), and in Faxinal reservoir (29°05'00"S; 51°03'30"W), between April and December 2013, totaling 24 samples. Limnological characterization of these environments as well as population dynamics of *C. furcoides* during the studied period can be found in Cavalcante et al. (2016).

The formula used to estimate cell volume is that employed in European monitoring programs (*e.g.* INAG 2011), that comprises the volumes of a truncated cone (apical horn), a flattened ellipsoid (cell body), and two or three cones (antapical horns). The formula is:

$$V = \left[\frac{\pi}{12} f_1(h_2^2 + h_2 g_1 + g_1^2) + \left(\frac{\pi}{6} l b h_1\right) + \frac{\pi}{12}(g_2^2 f_2 + g_3^2 f_3 + g_4^2 f_4)\right]$$

Where V= cell volume, l= body length, b = body width, h_1 = body depth (defined as $\frac{b}{2}$), f_1 = apical horn length, g_1 = apical horn base diameter, h_2 = apical horn apex diameter, f_2= left (bigger) antapical horn length, g_2= left (bigger) antapical horn base diameter, f_3= right antapical horn length, g_3 = right antapical horn base diameter, f_4= accessory (smaller) antapical horn length, g_4= accessory (smaller) antapical horn base diameter (Fig. 1). Ten cells were measured by month in each reservoir, accounting 240 measured cells. The dimensions above listed were used to characterize morphological variation of cells. The proposed formula performs a more accurate estimative of cell volume in *C. furcoides* than other ones often used in literature (Hillebrand et al. 1999; Sun and Liu 2003). The main difference between this formula and the others is to consider the apical horn shape as a truncated cone instead of a cylinder. Note in Fig. 1 that diameter of the apical horn is variable along its length. Sun and Liu (2003), in their formula for ceratioid cell, presupposed that diameters of the apical horn and antapical horn base are of equal value. We found that this is not precise in *C. furcoides*. In our material, the use of different formulas resulted in differences of 240–9600 μm^3 in each measured cell, which are larger than cell volume of several small phytoplanktonic species (Table 1).

One-way analysis of variance (ANOVA) was carried out to test temporal (month and seasonal scales) and spatial (between reservoirs) differences of cell volumes as well between morphotypes (two or three antapical horns). Pearson correlation was used to find relationships among cell dimensions and cell volume. To predict cell volume from cell dimensions was used simple linear regression analysis. These analyses were performed using the software Statistica 7.1©.

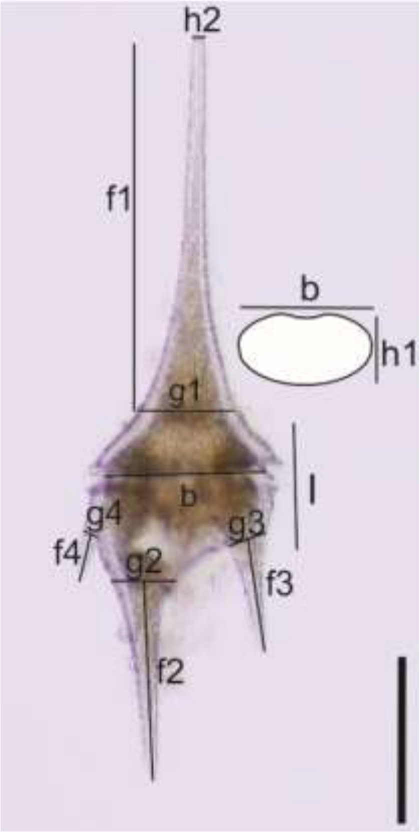


Fig. 1. Dimensions evaluated in each cell of *Ceratium furcoides*. The white oval form is a representation of a cross section of the middle cell in apical view, showing the body depth (h_1). Individual photographed from Faxinal reservoir. Scale bar = 50 µm (l= body length, b = body width, h_1 = body depth, f_1 = apical horn length, g_1 = apical horn base diameter, h_2 = apical horn apex diameter, f_2= left (bigger) antapical horn length, g_2= left (bigger) antapical horn base diameter, f_3= right antapical horn length, g_3 = right antapical horn base diameter, f_4= accessory (smaller) antapical horn length, g_4= accessory (smaller) antapical horn base diameter).

Table 1 Comparison among cell volume (µm³) of *Ceratium furcoides* calculated by different formulas from Faxinal and Maestra reservoirs (n=240 cells).

	Min–max	**Mean**	**SD**	**Mean difference in relation to formula used in this study**
This study	13143–39503	23833	5874	–
Hillebrand et al. (1999)	12066–37676	22211	5419	-1622
Sun and Liu (2003)	8040–33599	19164	5084	-4669

In both reservoirs, *C. furcoides*’ cell volume showed seasonal variation, with smaller cells registered in spring-summer periods, while larger cells occurred in fall and winter (Table 2). Analysis of variance presented significantly differences on cell volumes by months (ANOVA, $F = 7.1$, $p<0.0001$) and by seasons (ANOVA, $F = 8.309$, $p = 0.0004$), but no between reservoirs or morphotypes with two or three antapical horns (ANOVA, $p>0.05$). Dimensions of cell body contributed more in cell volume increasing that horns ones, although the latter were the most variable measurements in the cell (Table 2). For this reason, no significant difference on volume of different morphotypes was found.

All measured dimensions were positively related to cell volume (Table 3). The cell dimensions most related to cell volume were body width, apical horn base diameter and body length. Body width was significantly correlated to all other measured dimensions of the cell, proving to be the most representative measure to estimate the cell volume.

A linear regression between body width and cell volume for this study revealed strong positive trend (Fig. 2). Because of the clear difference in cell volume between spring-summer and fall-winter samples (mean 4660 μm^3, Table 2), we calculated separately the regression for these two periods, which also showed high correlation (Figs 3 and 4). Body width was also highly correlated to cell volume when calculated by formula proposed in Hillebrand et al. (1999) ($r=0.88$, $p<0.05$). For this reason, we also performed regression analysis considering cell volume calculated by the latter formula (Figs 5–7), since it is commonly used in phytoplankton researches. Nevertheless, we assume that the formula used in this study should be preferred, since it is more accurate as discussed above.

Table 2 Variation of cell dimensions and volume of *Ceratium furcoides* in Faxinal and Maestra reservoirs. For meanings of the codes see Fig. 1

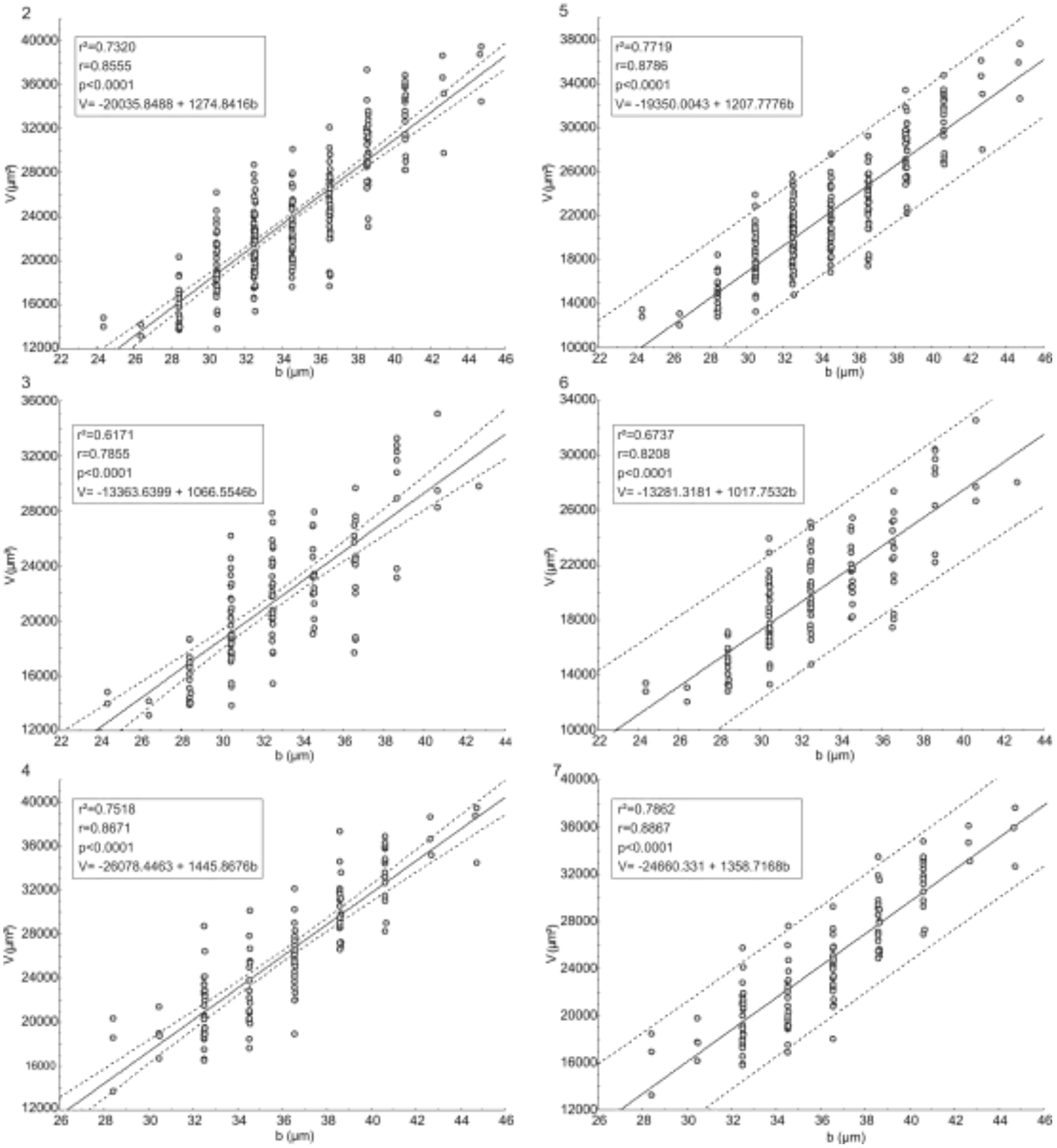
	Spring-summer (n=120)					**Fall-winter (n=120)**				
	Min.	**Max.**	**Mean**	**SD**	**Variance**	**Min.**	**Max.**	**Mean**	**SD**	**Variance**
l (µm)	28.42	44.73	35.32	3.38	11	26.39	48.72	37.32	3.88	15
b (µm)	24.36	42.69	32.69	3.55	13	28.42	44.73	36.13	3.55	13
f1 (µm)	58.87	107.76	78.44	9.93	99	58.87	103.53	81.56	10.02	100
g1 (µm)	10.15	26.43	19.97	2.80	8	12.18	30.45	21.11	3.19	10
h2 (µm)	2.03	4.06	3.12	0.29	0	2.03	5.69	3.36	0.54	0
f2 (µm)	18.27	81.20	33.78	8.96	80	20.30	60.90	37.50	8.10	66
g2 (µm)	6.09	16.26	10.63	1.86	3	8.12	16.24	10.49	1.65	3
f3 (µm)	10.15	34.56	21.05	4.86	24	10.15	40.60	24.56	5.48	30
g3 (µm)	6.09	12.19	8.73	1.48	2	6.09	12.18	9.14	1.34	2
V (µm^3)	13143.20	35074.98	21502.65	4825.76	23287970	13730.45	39503.20	26162.80	5921.41	35063047

Table 3 Correlation matrix (r-Pearson, $p<0.05$) between cell dimensions and volume of *Ceratium furcoides*. For meanings of the codes see Fig. 1.

	l (µm)	**b (µm)**	**f1 (µm)**	**g1 (µm)**	**h2 (µm)**	**f2 (µm)**	**g2 (µm)**	**f3 (µm)**	**g3 (µm)**	**V (µm^3)**
l		0.56		0.14	0.18				0.15	0.55
b			0.19	0.42	0.15	0.21	0.18	0.28	0.38	0.86
f1						0.43		0.38		0.38
g1					0.15		0.18		0.22	0.74
h2										0.23
f2							0.23	0.70	0.25	0.25
g2									0.42	0.27
f3									0.32	0.26
g3										0.40

No other study highlighted the relationship between cell dimensions and cell volume in ceratioid dinoflagellates. Morphometric analysis on *C. furcoides* and *C. hirundinella* (O.F. Müller) Dujardin showed that total length and horns length usually displayed strong seasonal variation (Hickel 1988; Lindström 1992; Gligora et al. 2003; Parodi et al. 2007; Varol 2015), like in this study. In a Turkish reservoir, body width was positively related to total length in *C. hirundinella* (Varol 2015), and probably it can be also related to cell volume. The mean cell volume of *C. furcoides* used as standard value by Portuguese monitoring agencies (25748 µm^3, INAG 2011) is close to the mean cell volume found in this study, for two limnologically distinct subtropical reservoirs in southern Brazil (Table 1). It is possible that high correlations between body width and cell volume found here are significant in other subtropical reservoirs.

Cell volume of *Ceratium* is difficult to estimate. Due to its complex shape, it is necessary to measure a large number of cell dimensions (12 in this study). This problem can be powered by monthly variation of cell volume found in this study: the mean of cell



Figs 2–4 Linear regression between body width (b) and cell volume (V) of *Ceratium furcoides* from Faxinal and Maestra by using the formula proposed by European monitoring. 2. Full sampling (n=240). 3. Only spring-summer periods (n=120). 4. Only fall-winter periods (n=120). **Figs 5–7** Linear regression between body width (b) and cell volume (V) of *Ceratium furcoides* from Faxinal and Maestra by using the formula proposed by Hillebrand et al. (1999). 5. Full sampling. 6. Only spring-summer periods. 7. Only fall-winter periods.

volumes measured by month should be performed to get a precise biomass estimative. The relevant correlations found between cell volume and body width (Figs 2–4) can be used to estimate biovolume from the measurement of a single cell dimension (body width) in those environments, and perhaps extrapolated to other subtropical environments. This is particularly important to monitoring teams that perform phytoplankton analysis (as in Faxinal and Maestra reservoirs), which need processing a large amount of samples in a short time. Finally, future studies in other environments (subtropical, tropical and temperate) should corroborate if the direct relationship between body width and cell volume is constant in *C. furcoides*.

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Capítulo 4.

Diversidade de dinoflagelados epicontinentais no Estado do Paraná, sul do Brasil, com comentários taxonômicos e de distribuição

Estruturado nas normas do periódico Fottea

Nota: as alterações nomenclaturais propostas neste capítulo ainda não foram efetivamente publicadas, conforme os Artigos 29 e 30 do *International Code of Nomenclature for algae, fungi and plants (Melbourne Code)*. Este capítulo, portanto, não deve ser utilizado como obra-fonte de tais alterações nomenclaturais.

Diversity of freshwater dinoflagellates in State of Paraná, southern Brazil, with taxonomic and distributional notes

Kaoli P. CAVALCANTE[1]*, Sandra C. CRAVEIRO[2], António J. CALADO[2], Thelma A. V. LUDWIG[3] & Luciana de S. CARDOSO[1]

[1]Postgraduate Program in Botany, Department of Botany, Federal University of Rio Grande do Sul, Porto Alegre-RS, Brazil.

[2]Department of Biology and GeoBioTec Research Unit, University of Aveiro, P-3810-193 Aveiro, Portugal.

[3]Department of Botany, Federal University of Paraná, Curitiba-PR, Brazil.

*Corresponding author: kaolicavalcante@gmail.com

Abstract: Dinoflagellates taxonomy is undergoing a comprehensive review in recent decades. The Brazilian dinoflagellate flora is still quite incomplete taking into account the huge area of the country. This study is the first taxonomic survey of freshwater dinoflagellates in State of Paraná, southern Brazil. Forty one freshwater environments were sampled in Paraná and two others on the border between Paraná and Santa Catarina during 2010-2015, and 21 dinoflagellate taxa assigned to 13 genera were identified and described based on light (LM) and scanning electron (SEM) microscopies. Two new combinations are proposed: *Parvodinium africanum* var. *javanicum* comb. nov. and *Parvodinium guildfordense* comb. nov. Four taxa are new records for Brazilian freshwaters: *Glenodiniopsis uliginosa*, *P. africanum* var. *javanicum*, *P. guildfordense* and *Tyrannodinium edax*. Taxonomic and nomenclatural comments about the recorded species as well as their known distribution in Brazil are also given.

Keywords: Dinophyceae, light microscopy, morphology, scanning electron microscopy, South America, taxonomy.

INTRODUCTION

Freshwater dinoflagellates have been extensively revised in recent decades (MOESTRUP & DAUGBJERG 2007). Modern integration of molecular, ultrastructural and life cycle studies, combined with the traditional morphological knowledge, has led to a number of nomenclatural changes, new generic propositions and a redefinition of the phylogenetic relationships among the taxa. Such revision was essentially based on populations sampled in Europe (e.g. CALADO et al. 2009; CRAVEIRO et al. 2010; MERTENS et al. 2015), Asia (TAKANO & HORIGUCHI 2004; ZHANG et al. 2011; TAKANO et al. 2014) or North America (FAWCETT & PARROW 2012). Few new informations were added about tropical/subtropical dinoflagellates from South Hemisphere.

The freshwater dinoflagellate species from Brazil are poorly known. The majority of the citations lack detailed morphological information. The first reference to a dinoflagellate collected in Brazil was from Rodrigo de Freitas Lagoon, State of Rio de Janeiro, made by MÖBIUS (1889), describing *Peridinium tabulatum* f. *brasilianum* ‘*brasiliana’* MÖBIUS (reinterpreted as *Bysmatrum subsalsum* (OSTENFELD) FAUST et STEIDINGER by POPOVSKÝ & PFIESTER 1990). In the first decades of the 20th century, studies on protozoofauna (dinoflagellates were then considered from a zoological viewpoint) identified some dinoflagellate species (DADAY 1905; PROWAZEK 1910; CUNHA 1913; 1916; 1918; KLEEREKOPER 1939). With a gap of almost 30 years, new records of this group were made in southeastern (BICUDO & BICUDO 1967; 1969; BICUDO & SKVORTZOV 1968; 1970; BICUDO & VENTRICE 1968) and northern Brazil (UHERKOVICH & SCHMIDT 1974; UHERKOVICH 1976; 1981; UHERKOVICH & RAI 1979; UHERKOVICH & FRANKEN 1980). More recent and important studies on dinoflagellate flora include MEYER et al. (1997), that described *Peridiniopsis amazonica* MEYER from Amazonian lakes; BORICS et al. (2005) that listed dinoflagellate species in tropical lakes from southeastern Brazil and proposed the new species *Peridinium brasiliense* BORICS et GRIGORSZKY; MENEZES & FERNANDES (1990), MENEZES (1995), MENEZES et al. (1995), ALBUQUERQUE & MENEZES (1997), CARDOSO & TORGAN (2007) and CARDOSO et al. (2010), that added new records to the dinoflagellates flora from northern to southern regions of Brazil; and finally the recent records of the invasive *Ceratium* SCHRANK spp. in Brazil (SANTOS-WISNIEWSKI et al. 2007; MATSUMURA-TUNDISI et al. 2010; OLIVEIRA et al. 2011; CAVALCANTE et al. 2013; JATI et al. 2014). Other punctuate dinoflagellate records can be found scattered in general lists of freshwater phytoplankton. As a result, the distribution dinoflagellates in Brazil is fairly diffuse, conditioned to few geographic regions and only focusing the more common species. Rio de Janeiro (20 spp. recorded), São Paulo (14 spp.) and Rio Grande do Sul (12 spp.) are states with the highest number of recorded species (ODEBRECHT et al. 2015), while only two species were registered in the State of Paraná, southern Brazil: *Peridinium gatunense* NYGAARD (ODEBRECHT et al. 2015) and *Ceratium furcoides* (LEVANDER) LANGHANS (CAVALCANTE et al. 2013; JATI et al. 2014).

In this study we performed an extensive dinoflagellate floristic survey considering 43 distinct freshwater environments of Paraná (two in Santa Catarina), including reservoirs, natural and urban artificial lakes, and lakes formed in disabled quarries. We also presented taxonomic and distributional notes that are relevant to the nomenclatural history of the dinoflagellate species found and consistent with the current systematics knowledge.

MATERIAL AND METHODS

Forty one water bodies from State of Paraná were sampled between 2010 and 2015 (Fig. 1, Table 1). The majority of the reservoirs (1–18, Table 1) were assembled quarterly between February 2011 and May 2013. Sampling in quarry lakes occurred in three periods (34–39, Table 1) and other environments were occasionally sampled, totaling 209 samples containing dinoflagellates. Two sample sites were in the State of Santa Catarina (42, 43, Table 1), close to the border with Paraná but were also included in this study due to the geographical record interest.

Plankton was collected using a 20-µm mesh plankton net. Periphyton from marginal macrophytes was also sampled when present. Not preserved samples were taken to the laboratory and observed as soon as possible and subsamples were preserved with Lugol’s solution, formalin 4% or glutaraldehyde 2–3%. Dinoflagellates were identified, measured and

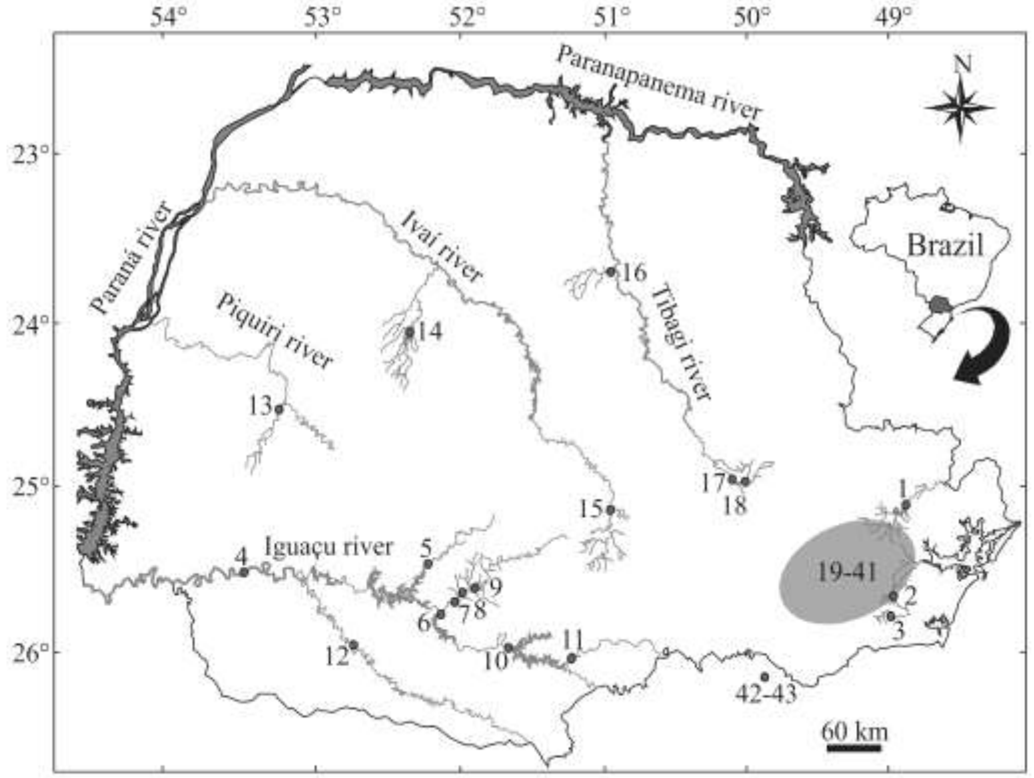


Fig. 1. Sampling localities in State of Paraná. Numbers are described in Table 1 as Code. Numbers 42 and 43 are located in State of Santa Catarina (see text).

photographed in light microscopes (LM) Olympus BX-40 equipped with Olympus DP71 digital camera and Zeiss Axioplan 2 equipped with DP70 and ColorView IIIu digital cameras. Epifluoresence observations were occasionally performed with CalcoFluor White stained cells according to FRITZ &TRIEMER (1985). For scanning electron microscopy (SEM), two treatments were used: preserved field samples (1) were settled in Poly-L-Lysine coated coverslips or (2) were filtered in Nuclepore polycarbonate membrane filters with 2–8 µm pore size; in both techniques, samples were subsequently washed in distilled water, dehydrated through ethanol series and critical point dried in BAL-TEC CPD 030. Filters and coverslips were sputter-coated with gold or gold-palladium and examined with Jeol JSM 6360LV or Hitachi S-4100 scanning electron microscopes, located at Electron Microscopy Center of the Federal University of Paraná, Brazil and Department of Materials and Ceramic Engineering of the University of Aveiro, Portugal (respectively). Vouchers of selected samples were stored in the herbarium of the Federal University of Paraná (UPCB, Table 1). Identification followed classical works, always confirmed by original publications and recent reviews. Descriptions of the taxa were only based on features that could be observed in our material; thecal plates tabulation that was not observed is indicated with question mark (?). No classification system was adopted, since a deep revision of this group at high levels is needed (MOESTRUP & DAUGBJERG 2007). However, the alphabetically arranged taxa were distinguished into three major morphological groups (naked and thin-walled, thecate and immobile taxa).

Table 1. List of sampling localities and dates. Vouchers of only selected samples were stored in the herbarium (UPCB).

Code	Locality, City	Coordinates	Dates	Herbarium Code (UPCB)
1	Capivari reservoir, Antonina	25°08'27"S, 48°52'21"W	Apr/11–Apr/13	68867, 72237, 78155
2	Guaricana reservoir, Guaratuba	25°42'39"S, 48°58'16"W	Feb/11–May/13	68875, 72245, 78163
3	Chaminé reservoir, São José dos Pinhais	25°49'19"S, 49°03'58"W	Feb/11–Feb/13	68869, 72239, 78157
4	Salto Caxias reservoir, Cap. Leônidas Marques	25°32'10"S, 53°29'31"W	Feb/11–May/13	68882, 72252, 78170
5	Cavernoso reservoir, Virmond	25°29'32"S, 52°12'53"W	Mar/11–Mar/13	68868, 72238, 78156
6	Segredo reservoir, Mangueirinha	25°47'37"S, 52°06'54"W	Mar/11–Mar/13	68886, 72256, 78174
7	Jordão reservoir, Reserva do Iguaçu	25°45'16"S, 52°04'56"W	Apr/11–Apr/13	68876, 72246, 78164
8	Santa Clara reservoir, Pinhão	25°38'59"S, 51°56'55"W	Apr/11–Mar/13	68887, 72257, 78176
9	Fundão reservoir, Pinhão	25°41'57"S, 51°59'58"W	Apr/11–Mar/13	68888, 72258, 78177

10	Foz do Areia reservoir, Pinhão	26°00'30"S, 51°39'48"W	Feb-11–Apr/13	68873, 72243, 78161
11	Salto do Vau reservoir, União da Vitória	26°02'05"S, 51°11'06"W	Mar/11–Mar/13	68883, 72253, 78171
12	Chopim reservoir, Itapejara d’Oeste	25°59'19"S, 52°44'47"W	Mar/11–Mar/13	68871, 72241, 78159
13	Melissa reservoir, Corbélia	24°32'14"S, 53°12'30"W	Mar/11–Mar/13	68877, 72247, 78165
14	Mourão reservoir, Campo Mourão	24°06'23"S, 52°19'44"W	Mar/11–Mar/13	68878, 72248, 78166
15	Rio dos Patos reservoir, Prudentópolis	25°10'11"S, 50°56'39"W	May/11–May/13	68880, 72250, 78168
16	Apucaraninha reservoir, Tamarana	23°45'01"S, 50°56'28"W	Jun/11–May/13	68866, 72236, 78154
17	Pitangui reservoir, Ponta Grossa	25°01'43"S, 50°06'10"W	Apr/11–Apr/13	68879, 72249, 78167
18	São Jorge reservoir, Ponta Grossa	25°01'06"S, 50°03'40"W	Apr/11–Apr/13	68884, 72254, 78172
19	Piraquara II reservoir, Piraquara	25°29'37”S, 49°05'13"W	May–Nov/13	78194
20	Irai reservoir, Pinhais	25°23'58"S, 49°05'52"W	Jan–Apr/13	78179
21	Smaller lake in São José dos Pinhais Urban Park, São José dos Pinhais	25°30'42"S, 49°12'12"W	Nov/11, Nov/12, Apr/13, Aug/14, Nov/14	78180-78185
22	Larger lake in São José dos Pinhais Urban Park, São José dos Pinhais	25°30'43"S, 49°12'11"W	Nov/11, Nov/12, Apr/13, Aug/14, Nov/14	78186-78190
23	Lake in Passeio Público Urban Park, Curitiba	25°25'32"S, 49°16'06"W	Sep/14	78191
24	Lake in Barigui Urban Park, Curitiba	25°25'45"S, 49°18'51"W	Sep/12	-
25	Lake in São Lourenço Urban Park, Curitiba	25°23'03"S, 49°15'56"W	Sep/15	-
26	Lake in Tanguá Urban Park, Curitiba	25°22'46"S, 49°17'05"W	Jan/14	-
27	Urban lake in Unilivre, Curitiba	25°23'48"S, 49°17'00"W	Mar/14	78239
28	Lake in Barreirinha Urban Park, Curitiba	25°21'42"S, 49°15'33"W	Mar/14	78238
29	Urban lake in Ópera de Arame, Curitiba	25°23'05"S, 49°16'33"W	Oct/10, Jan/13, Mar/14, Aug/14	78192, 78236

30	Urban lake in Paulo Leminski Quarry, Curitiba	25°23'05"S, 49°16'41"W	Sep/14, Mar/14, Dec/14	76054 78193, 78214
31	Azul lake, Paranaguá	25°32'17"S, 48°34'10"W	Dec/11	75223
32	Lake in Aníbal Khury Urban Park, Almirante Tamandaré	25°19'42"S, 49°17'35"W	Sep/14, Dec/14	78197, 78198
33	Luís Mussi Lake, in Aníbal Khury Urban Park, Almirante Tamandaré	25°19'09"S, 49°17'33"W	Sep/14, Dec/14	78199, 78200
34	Urban lake in Parque Ecológico da Lagoa Grande, Campo Largo	25°26'41"S, 49°31'55"W	Jan/12, Sep/14, Dec/14	76043, 78201, 78202
35	Lake in Cambuí Urban Park, Campo Largo	25°28'27"S, 49°31'46"W	Jan/12, Sep/14, Dec/14	76041, 78203, 78204
36	Quarry lake, Campo Magro	25°24'35"S, 49°22'48"W	Jan/12, Sep/14	76039, 78205
37	Lake in Sand mining region, Campo Largo	25°24'30"S, 49°33'50"W	Jan/12, Sep/14, Dec/14	76045, 78206, 78207
38	Quarry lake, Campo Magro	25°19'29"S, 49°27'17"W	Jan/12, Sep/14, Dec/14	76046, 78208, 78209
39	Quarry lake, Campo Magro	25°19'34"S, 49°27'36"W	Sep/14, Dec/14	78210, 78211
40	Lake in Pousada Recanto dos Lagos, Mandirituba	25°47'58"S, 49°16'38"W	May/15	-
41	Lake in Pousada Recanto dos Lagos, Mandirituba	25°47'59"S, 49°16'34"W	May/15	-
42	River in Recanto Pe. Francisco Hable Park, Mafra-SC	26°08'22"S, 49°53'30"W	Jan/12	78195
43	Small lake in Recanto Pe. Francisco Hable Park, Mafra-SC	26°08'07"S, 49°53'24"W	Jan/12	78196

RESULTS AND DISCUSSION

Naked and thin-walled planktonic taxa

Gymnodinium fuscum (Ehrenberg) Stein 1878, p. 95

Figs 2–4

Basionym: *Peridinium fuscum* Ehrenberg 1834, p. 270

Large cells, dorsoventrally flattened; epicone typically round, sometimes tapering to a narrow apex (Fig 3), hypocone apiculate, cingulum median; brown plastids, radially arranged;

nucleus in epicone; eyespot not observed. Spherical cysts with irregular external wall and large accumulation body positioned in the center. Length: 38–64 µm; width: 20–37.4 µm

Occurrence: 2, 3, 7, 8, 9, 10, 14, 16, 17, 19, 21, 22. It was observed in different times of the year.

Comments: we have found populations with smaller cells than commonly reported (*e.g.* POPOVSKÝ & PFIESTER 1990; HANSEN & FLAIM 2007; CARTY 2014). However, populations with similar size have been found by THOMPSON (1947), DODGE & CRAWFORD (1969) and SENZAKI & HORIGUCHI (1994). The smallest cells found in our populations could correspond to zoospore stages since, according to POPOVSKÝ & PFIESTER (1990), zoospores in this species are 35–45 µm long.

Distribution in Brazil: States of Rio de Janeiro (CUNHA 1913; 1916) and São Paulo (BICUDO & SKVORTZOV 1970). This is the first record for southern Brazil.

Gymnodinium mirabile **PENARD 1891, p. 56, pl. V, figs 1–7**

Figs 5–7

Large cells, dorsoventrally flattened; epicone round to bell shaped, hypocone flattened at the antapex, smaller than the epicone; cingulum slightly descending; sulcus narrow, extending into the epicone; brown plastids, radially arranged; sometimes with a hyaline area along the cell surface; large central nucleus; eyespot not observed; vegetative division was commonly observed (Fig. 7). Length: 30–65 µm; width: 22.5–57.5 µm.

Occurrence: 2, 6, 7, 8, 9, 10, 16, 19, 37. It was observed in different times of the year.

Comments: *Gymnodinium mirabile* was originally described as being 90 µm long and 65 µm wide (PENARD 1891) but such large measurements were seldom reported afterwards. The same author described *G. mirabile* var. *rufescens* PENARD, a smaller and more rounded variety.

Recent authors have used a broader concept for *G. mirabile*, including in this species smaller individuals, 40–70 µm long (HANSEN & FLAIM 2007; PANDEIRADA et al. 2013). *Gymnodinium mirabile* was regarded as synonym of *G. uberrimum* (ALLMAN) KOFOID et SWEZY in several floras (KOFOID & SWEZY 1921; POPOVSKÝ & PFIESTER 1990). However, the original description of *G. uberrimum*, without illustrations, is ambiguous, since its features fit more the current concept of woloszynskoid genera that, in fact, of a *Gymnodinium* species (ALLMAN 1854). Since both generic and specific circumscriptions of *G. uberrimum* is not accessible yet, we prefer to avoid this name.

Distribution in Brazil: there is only one record of *G. mirabile* in the coastal region of northern Brazil (WOOD 1968). BICUDO & BICUDO (1969) identified *G. uberrimum* in samples from Rio de Janeiro, which probably also corresponds to *G. mirabile*. This is the first record of the species in southern Brazil.

***Nusuttodinium aeruginosum* (STEIN) TAKANO et HORIGUCHI 2014, p. 773, figs 1(M–R) and 2 (H, I)**

Figs 8–10

Basionym: *Gymnodinium aeruginosum* STEIN 1883, pl. II, figs 19–22.

Ovoid cells, dorsoventrally flattened; epicone rounded or bell shaped, often smaller than the hypocone; hypocone rounded, antapex slightly flattened; cingulum slightly descending; sulcus narrow, extending into the epicone; numerous discoid green to blue-green plastids (kleptochloroplasts of cryptomonad origin) throughout the cell; nucleus in epicone; eyespot not observed. Length: 26.7–44.6 µm; width: 17.5–31.1 µm.

Occurrence: 19, 20, 21, 40, 41. It was observed in different times of the year.

Comments: *Nusuttodinium acidotum* (NYGAARD) TAKANO et HORIGUCHI and *Gymnodinium eucyaneum* HU are closely related to *N. aeruginosum*. Some authors have considered them as conspecific (POPOVSKÝ & PFIESTER 1990) while others have distinguished them mainly by the pointed antapex and by differences in relative size of epi- and hypocone (XIA et al. 2013). Based on molecular and morphological analysis, TAKANO et al. (2014) synonymized *G. eucyaneum* with *N. acidotum* but regarded *N. aeruginosum* as a separate species, pointing out that the number of longitudinal flagella and the typical form of a number of cells must be observed to identify with precision a population. Our populations fit *N. aeruginosum* morphospecies.

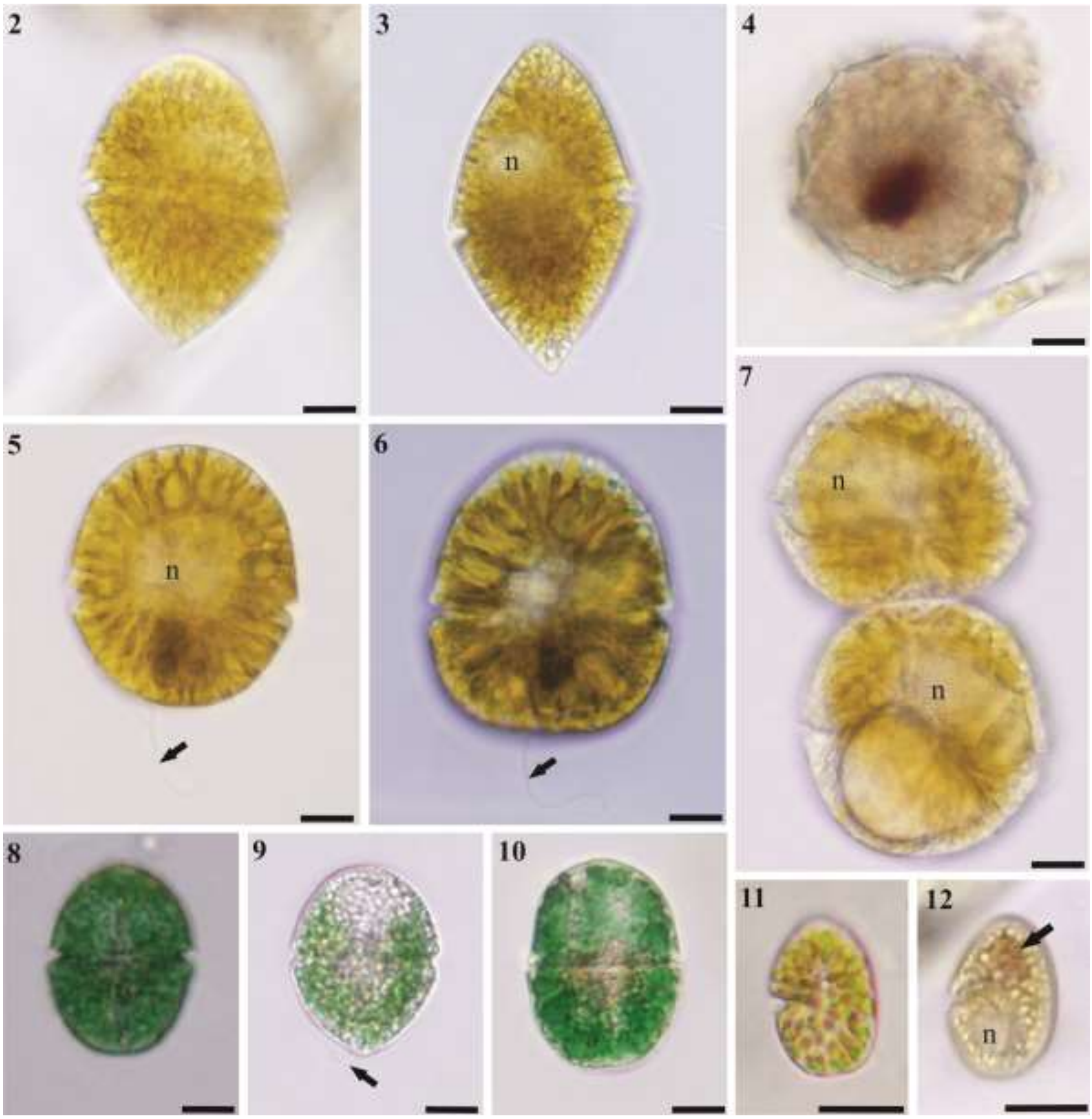
Distribution in Brazil: Rio de Janeiro (MENEZES & TEIXEIRA-JÚNIOR 2001) and Rio Grande do Sul (TORGAN et al. 2003). Early records of *G. viride* PENARD in Rio de Janeiro (CUNHA 1913) and Porto Alegre (CUNHA 1918), although it could not be confirmed due to lack of illustrations, may perhaps correspond to *N. aeruginosum*.

Hemidinium nasutum STEIN 1883, pl II, figs 23–26

Figs 11, 12

Elliptical cells, dorsoventrally flattened; epi- and hypocone ovoid; cingulum median, incomplete, present only in the left side of the cell; elongated yellow-brown plastids, radially arranged; nucleus in hypotheca; eyespot not observed; reddish accumulation bodies often seen in epitheca. The thin thecal tabulation commonly reported for this species was not detected. Length: 24.4–32.5 µm; width: 15.2–20 µm.

Occurrence: 22 and 43, in January and November 2012, respectively.



Figs 2–4. *Gymnodinium fuscum*, LM. Fig. 2. Typical form, dorsal view. Fig. 3. Specimen with a more conical epicone, ventral view. Fig. 4. Resting cyst. Figs 5–7. *Gymnodinium mirabile*, LM. Figs 5, 6. Typical cells with longitudinal flagellum (arrow), ventral view. Fig. 7. Cells in vegetative division, ventral view. Figs 8–10. *Nusuttodinium aeruginosum* in ventral view, LM. Longitudinal flagellum can be seen in Fig. 9 (arrow). Figs 11, 12. *Hemidinium nasutum*, dorsal views, LM. Fig. 12. Cell with red accumulation body in epicone (arrow). n = nucleus. Scale bars = 10 µm.

Comments: five different taxa of *Hemidinium* were reported in Brazilian waters (BICUDO & BICUDO 1967; BICUDO & VENTRICE 1968; BICUDO & SKVORTZOV 1970) but they were usually considered synonyms of *H. nasutum* or *H. ochraceum* LEVANDER (POPOVSKÝ & PFIESTER 1990). *Hemidinium brasiliense* BICUDO et SKVORTZOV reportedly differs from *H. nasutum* by cell shape, length and by having epicone larger than hypocone (BICUDO & SKVORTZOV 1970). There are also two non typical varieties described for that species: *H. nasutum* var. *tatricum* WOŁOSZYŃSKA, which differs by larger cells and distinct thecal tabulation (POPOVSKÝ & PFIESTER 1990) and *N. nasutum* var. *lapeanum* BICUDO et VENTRICE, with cells twice the size (60–70 µm long; 44–50 µm wide) than commonly found for *H. nasutum* (BICUDO & VENTRICE 1968). Our material fits perfectly the illustrations of typical *H. nasutum*.

Distribution in Brazil: recorded for Rio de Janeiro (CUNHA 1916); *H. nasutum* var. *tatricum* and *H. nasutum* var. *lapeanum* were observed in States of São Paulo and Minas Gerais, respectively (BICUDO & BICUDO 1967; BICUDO & VENTRICE 1968).

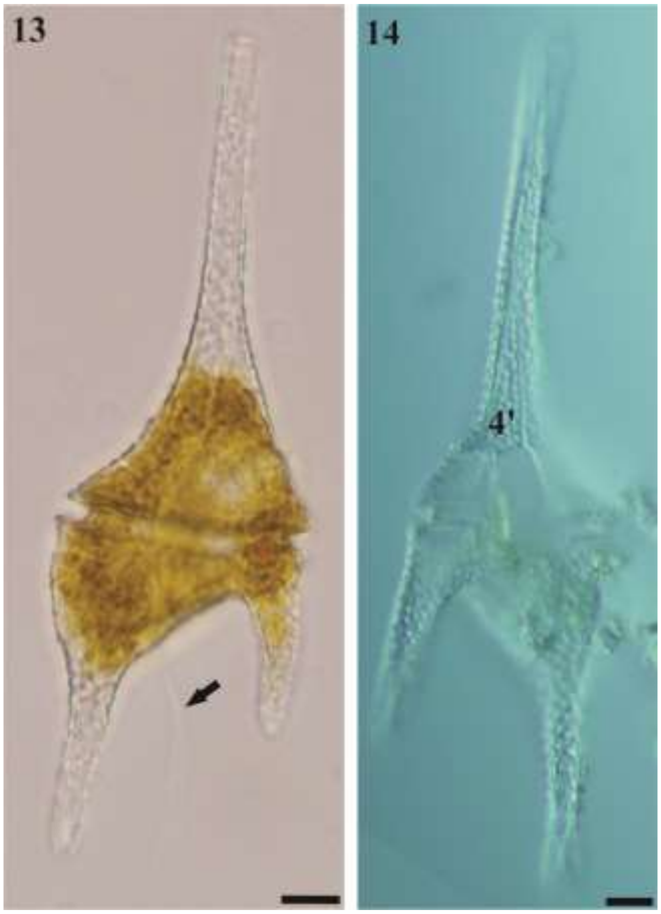
Thecate planktonic taxa

Ceratium furcoides (LEVANDER) LANGHANS 1925, p. 602

Figs 13–14

Basionym: *Ceratium hirundinella* var. *furcoides* Levander 1894, p. 53, pl. II, fig. 24.

Large cells, dorsoventrally flattened, with ventral area strongly concave; cingulum median, not displaced; one conical apical horn, ending in an apical pore; two or three conical antapical horns, distinct in size; brown-yellow plastids throughout the cell; oil and red bodies often present; thick theca, with reticulate ornamentation, plate formula: Po, 4’, 5”, 6c, ?s, 5’”, 2””; plate 4’ short, not reaching the apex. Length: 86–190 µm; width: 26–57.8 µm.



Figs 13–14. *Ceratium furcoides*, LM. Fig. 13. Living cell in dorsal view with longitudinal flagellum (arrow). Fig. 14. Empty theca in ventral view, showing 4' plate. Scale bars = 10 µm.

Occurrence: 1, 3, 4, 6, 10, 12, 20, 24, 26, 28, 29, 34, 35, 38. It was observed at all seasons.

Comments: shorter and rhomboidal cells found in this study could be interpreted as *C. rhomvoides* HICKEL, a species closely related to *C. furcoides* (HICKEL 1988). However, Brazilian populations studied here had a broad morphological variation. Moreover, preliminary molecular studies based on ITS and SSU sequences have indicated that Brazilian specimens are related to Portuguese populations clearly assigned to *C. furcoides* morphology (unpub. data). More studies are needed in order to clarify the boundary between these two species of *Ceratium* (PANDEIRADA et al. 2013).

Distribution in Brazil: *C. furcoides* is considered an invasive species in South America, recorded in southeastern (SANTOS-WISNIEWSKI et al. 2007; MATSUMURA-TUNDISI et al. 2010), northeastern (OLIVEIRA et al. 2011) and southern Brazil (CAVALCANTE et al. 2013; JATI et al. 2014).

Durinskia baltica **(LEVANDER) CARTY et COX 1986, p. 200, figs 11–14**

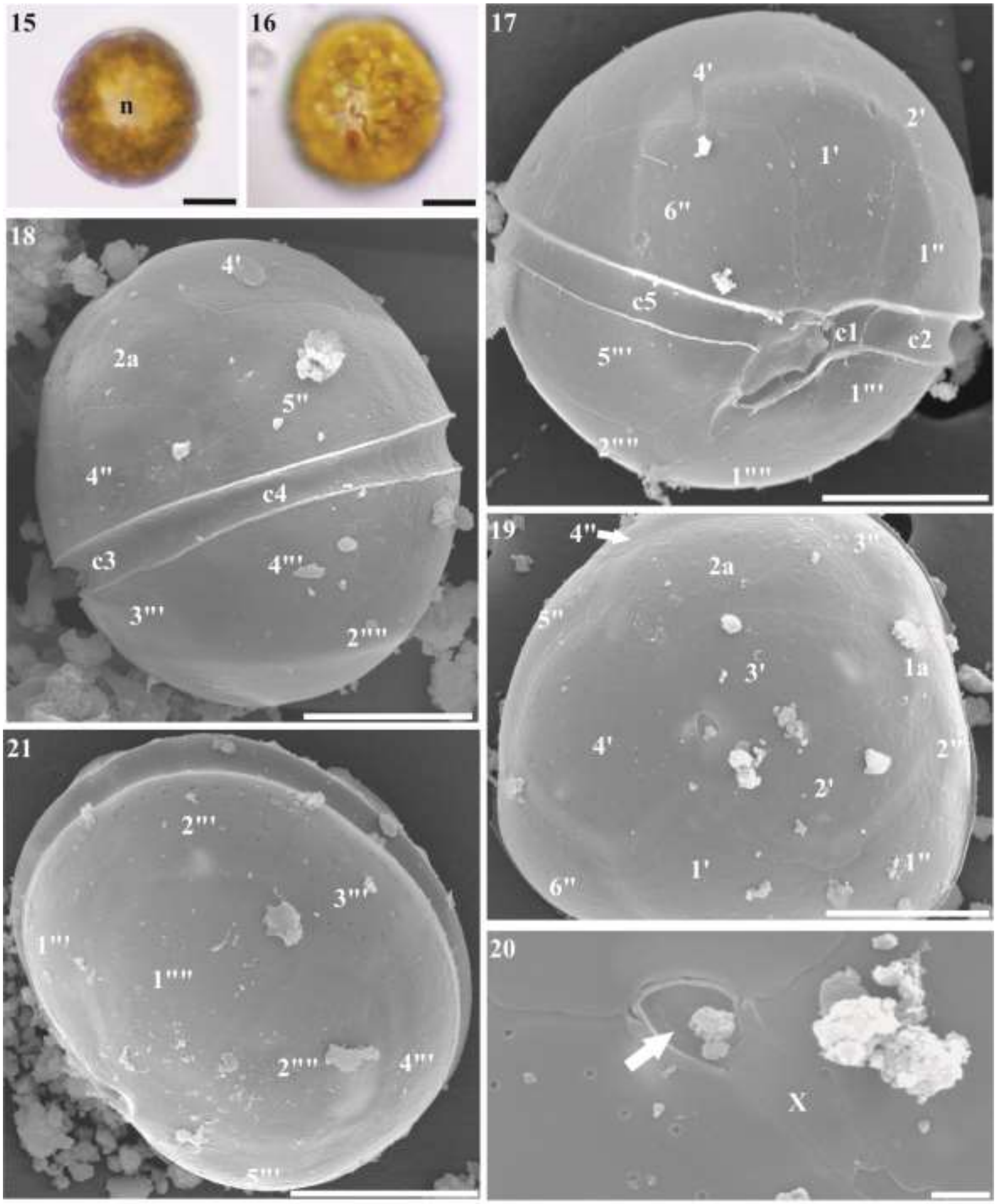
Figs 15–21

Basionym: *Glenodinium balticum* LEVANDER 1894, p. 52 (figures in LEVANDER 1892, p. 407, figs 1–4).

Round cells, spherical to slightly dorsoventrally flattened; epitheca larger than hypotheca, cingulum slightly descending; narrow and shallow sulcus, not reaching the antapex; apical pore not projected in the apex; numerous discoid brown-gold plastids; conspicuous eyespot, bright red, with an anterior comma-like projection (Fig. 16); thin theca, smooth, with scattered pores, sometimes forming rows; plate formula: Po, X, 4’, 2a, 6”, 5c, ?s, 5’”, 2’”’. Length: 23.7–36.7 µm; width: 21–35 µm.

Occurrence: 21, 25, 35, 40, 42. It was observed between September and January (spring-summer).

Comments: *Durinskia baltica*, the most usual name for this species complex, was originally described from brackish water (type locality: Gulf of Finland, near Helsinki, LEVANDER 1892). Thenceforth, it has been cited in marine (HALLEGRAEFF et al. 2010; HOPPENRATH et al. 2014), estuarine (COUTÉ et al. 2012), and freshwater environments (PANDEIRADA et al. 2013; ZHANG et al. 2011). The morphometry of individuals illustrated in different habitats overlaps. STEIN (1883) established the species *Glenodinium oculatum* STEIN, depicting no plates on the cell cover. However, the overall cell shape, the presence of a theca and the positions of nucleus and eyespot, as depicted by STEIN (1883), fit the current concept of *Durinskia* and were the basis for the species transfer (HANSEN & FLAIM 2007). However, the difference between individuals of *Durinskia oculata* (STEIN) HANSEN et FLAIM and *D. baltica*, as shown by HANSEN & FLAIM (2007), namely more dorsoventrally flattened cells in *D. baltica*, is not easily ascertained as both flat and globular cells can be seen in a population (eg. CARTY & COX 1986; ZHANG et al. 2011; COUTÉ et al. 2012). Moreover, it is unclear whether Stein's specimens were distinctly globular (STEIN 1883). The freshwater species *Peridinium dybowskii* was described by WOŁOSZYŃSKA (1916) with the same plate tabulation of *D. baltica*. In the same work, WOŁOSZYŃSKA (1916, p. 273, footnote) stated that the species was identical to that illustrated by LEVANDER (1892, as *Glenodinium cinctum* EHRENBERG). WOŁOSZYŃSKA was apparently unaware that LEVANDER published for that species the name *G. balticum* (LEVANDER 1894). The plate ornamentation of *P. dybowskii*, with pores arranged in parallel lines, was used by some authors as a distinctive feature between both species (HANSEN & FLAIM 2007). CARTY (2014) created the combination *Durinskia dybowskii* (WOŁOSZYŃSKA) CARTY, and proposed to refer all freshwater individuals to this species, while including marine and brackish populations in *D. baltica*. Apart from morphological limitation, ecological aspects need to be considered with caution, since the taxonomic markers traditionally used for differentiation of this species do not agree with habitat information. Considering them as separated entities requires modern analyzes of different populations and accurate taxonomic studies of the original material. For now, we prefer to maintain the name *Durinskia baltica*, since it is the most widely used name and has an unambiguous nomenclatural type associated.



Figs 15–21. *Durinskia baltica*. Figs. 15, 16. LM, showing nucleus (n) and eyespot with anterior comma-like projection. Figs 17–21. SEM. Fig. 17. Ventral view. Fig. 18. Dorsal view. Fig. 19. Apical view. Fig. 20. Detail of apical pore (arrow) and canal plate (X). Fig 21. Antapical view. Scale bars = Scale bars = 10 µm (Figs 15–19, 21), 1 µm (Fig. 20).

Distribution in Brazil: all three names have been reported in Brazilian environments. *D. dybowskii* was recorded in São Paulo (KLEEREKOPER 1939). *D. oculata* was reported in Rio Grande do Sul (FRANCESCHINI 1992; GARCIA-BAPTISTA 1993) and *D. baltica* in Rio de Janeiro (DOMINGOS & MENEZES 1998) and Rio Grande do Sul (CARDOSO & TORGAN 2007; CARDOSO et al. 2010). It is necessary to verify the conspecificity of those populations.

Glenodiniopsis uliginosa (A.J. SCHILLING) WOŁOSZYŃSKA in LINDEMANN 1928, p. 82

Figs 22–26

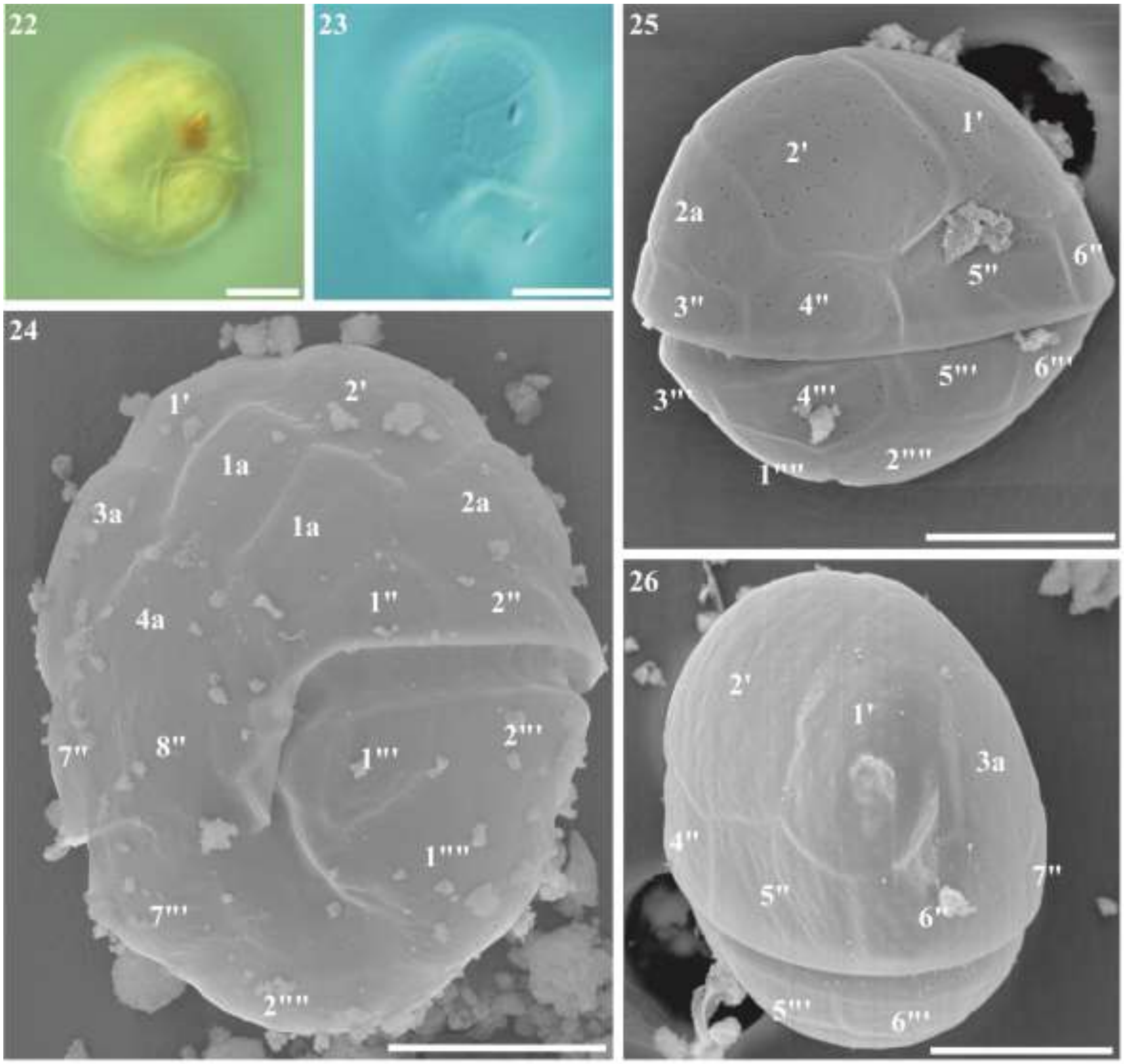
Basionym: *Glenodinium uliginosum* A.J. SCHILLING 1891, p. 283, pl. X, fig. 16.

Oval cells, dorsoventrally flattened; epitheca larger than hypotheca, cingulum slightly descending; narrow and shallow sulcus, not reaching the antapex; apical pore absent; brown-gold plastids; accumulation bodies often present; eyespot absent; thin theca, smooth, with scattered pores; two large apical plates along the apex; plate formula: 2’, 4(or 5)a, 8”, ?c, ?s, 7’”, 2””. Length: 26.3–36.8 µm; width: 18.9–30.5 µm.

Occurrence: 35. It was observed in September and December 2014.

Comments: plate tabulation is similar to that found in HANSEN & FLAIM (2007), with 1a divided in two plates (Fig. 24). This taxon was named *Glenodiniopsis steinii* WOŁOSZYŃSKA in several floras (POPOVSKÝ & PFIESTER 1990, CARTY 2014). However this name is a later synonym of *Glenodinium uliginosum* (SCHILLER 1937, HUBER-PESTALOZZI 1950, HANSEN & FLAIM 2007).

Distribution in Brazil: ODEBRECHT et al. (2015) referred to two previous records of *Glenodiniopsis* WOŁOSZYŃSKA to Rio de Janeiro and Mato Grosso, but they are linked to a species of *Sphaerodinium* WOŁOSZYŃSKA instead (PROWAZEK 1910, MENEZES & FERNANDES 1990). This is therefore the first confirmed record of this species for Brazil.



Figs. 22–26. *Glenodiniospsis uliginosa*. Fig. 22. Ventral view, LM. Fig. 23. Empty theca in LM, showing delicate plates. Fig. 24. Ventral view, SEM. Fig. 25. Dorsal view, SEM. Fig 26. Apical view of dorsal epitheca. Scale bars = 10 µm.

***Glochidinium penardiforme* (LINDEMANN) BOLTOVSKOY 1999, p. 99, figs 2–7, 14–23**

Figs 27–30

Basionym: *Peridinium penardiforme* LINDEMANN 1918, p. 126, figs 10–15.

Oval or pentagonal cells in ventral view, dorsoventrally flattened; epitheca variable, equal, larger or smaller than hypotheca; hypotheca bilobate in antapex; cingulum circular, excavated; narrow sulcus, reaching the antapex; apical pore slightly projected in the epicone; cells without plastids or with brown-gold plastid-like structures; accumulation bodies often present; eyespot absent; theca with irregular nodules and scattered pores; plate formula: Po, X, 4’ (or 3’+1a), 6”, 3c, ?s, 5’”, 2””. Length: 18.3–34 µm; width: 14.7–28 µm.

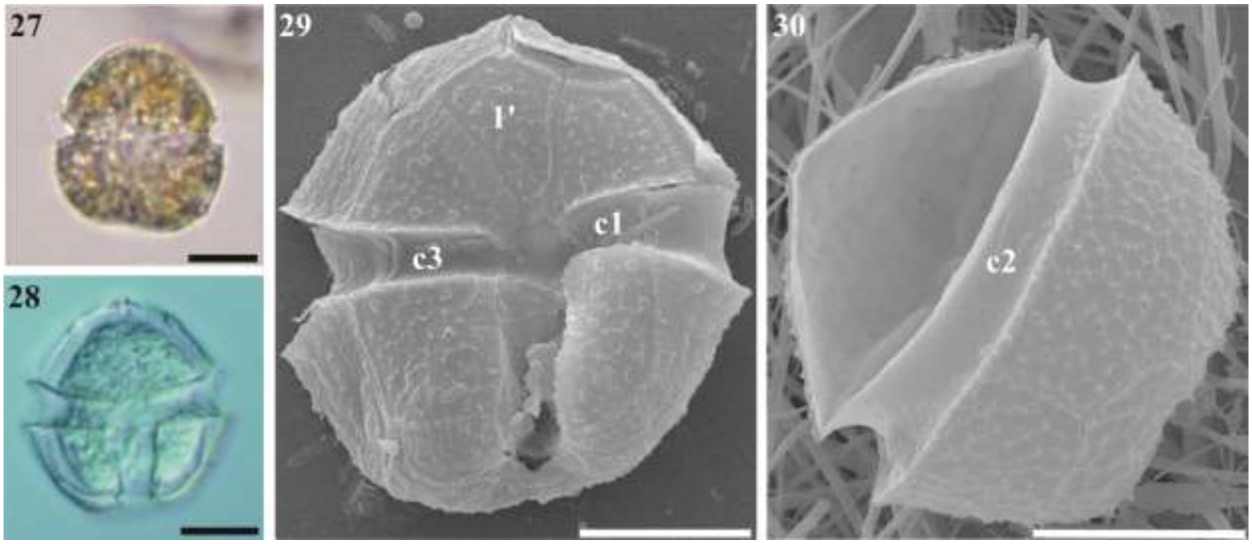
Occurrence: 1, 3, 5, 6, 7, 8, 9, 10, 12, 14, 16, 17, 18, 29. It was observed in different periods of the year.

Comments: this species has been found with or without plastids here and in several other works (HUBER-PESTALOZZI 1950; POPOVSKÝ & PFIESTER 1990; BOLTOVSKOY 1999; PANDEIRADA ET AL. 2013). This feature is unusual and intriguing and the nutritional strategy of this species needs to be elucidated.

Distribution in Brazil: Amazonas (UHERKOVICH 1976; UHERKOVICH & RAI 1979), Rio de Janeiro (MENEZES & TEIXEIRA-JÚNIOR 2001) and Rio Grande do Sul (CARDOSO et al. 2010).

***Parvodinium* CARTY 2008, p. 106**

This genus includes a group of small peridinioids with plate tabulation: Po, X, 4’, 2a, 7”, 6c, 4s, 5’”, 2”” (CARTY 2008). The wide morphological variability performed in this group resulted in the description of many species over time (CARTY 2008). In contrast, some authors considered such variations as phenotypic plasticity within the few species, and then synonymized the majority of those names (POPOVSKÝ & PFIESTER 1990). Preliminary molecular studies indicated that there is distinct species within this complex (Y. TAKANO, unpubl. data, see HANSEN & FLAIM 2007), but the phylogenetic relationships among *Parvodinium* spp. have not been resolved yet. In this study, in order to highlight morphological variation, we decided to consider morphospecies strictly based on the original publication concept, as follows:



Figs. 27–30. *Glochidinium penardiforme.* Fig. 27. Living cell, LM. Fig. 28. Fixed cell in ventral view, LM. Fig. 29. Ventral view, SEM. Fig. 30. Dorsal view, SEM, showing ecdysis opening formed by detachment of plates 1a (or 3’ for some authors) 3” and 4”. Scale bars = 10 µm.

***Parvodinium africanum* var. *africanum* (LEMMERMANN) CARTY 2008, p. 106**

Figs 31–33

Basionym: *Peridinium africanum* LEMMERMANN in WEST 1907, p. 188, pl. 9, fig. 1 a–e.

Pentagonal cells in ventral view, dorsoventrally flattened; angular outline, formed by elevations in the plates junctions; epitheca conical, larger than hypotheca; hypotheca trapezoidal, with many spines of variable length; cingulum circular, excavated; wide sulcus, slightly extending onto the epitheca and reaching the antapex; apical pore protruded; large intercalary plates. Length: 21.9–40 µm; width: 18.8–36 µm.

Occurrence: 2, 5, 6, 8, 9, 14, 17, 18, 35. It occurred predominantly in summer samples.

Comments: four infraspecific taxa have been formally proposed for *P. africanum* (LEFÈVRE 1932), but considered as synonyms in some floras (POPOVSKÝ & PFIESTER 1990). The typical variety of *P. africanum* has shorter pentagonal cells, with shorter spines and its sulcus slightly extends onto the epitheca (WEST 1907).

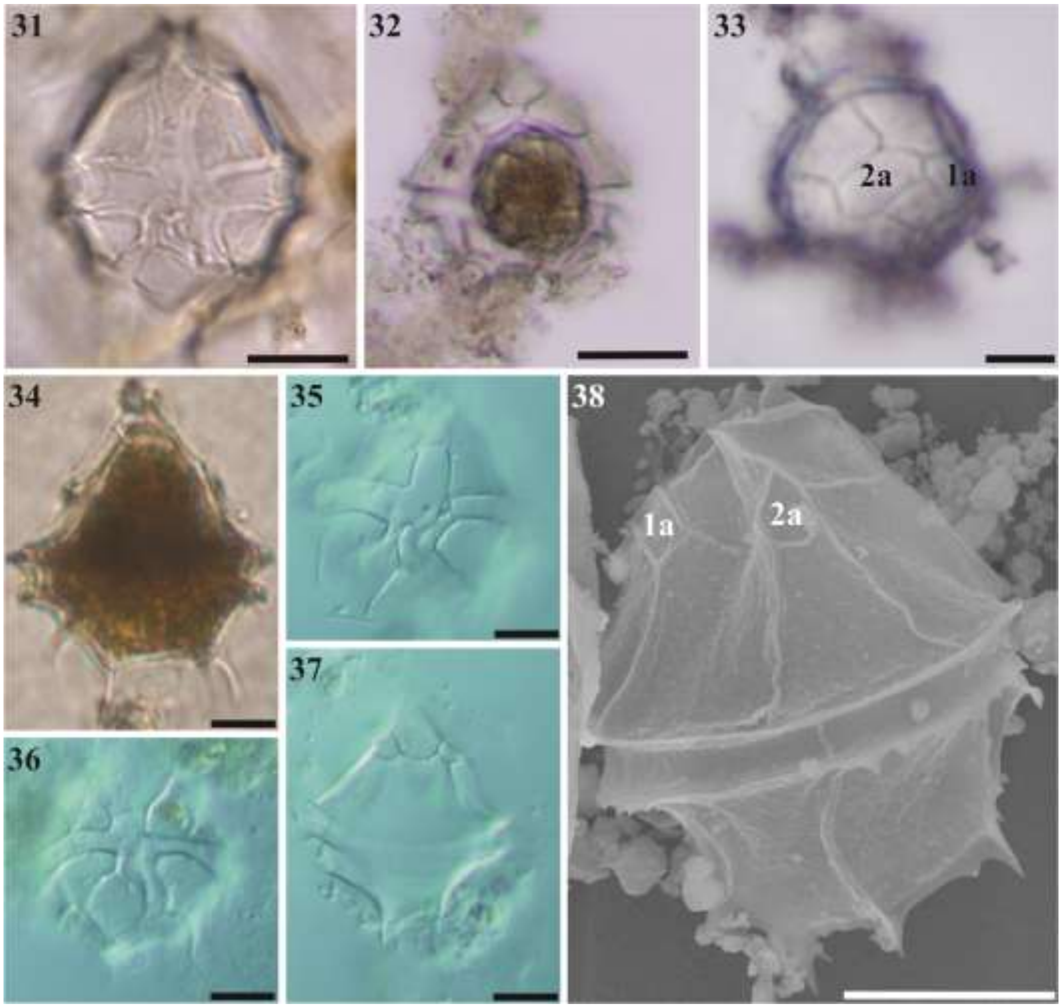
Distribution in Brazil: *Parvodinium africanum* has been recorded in Mato Grosso (MENEZES & FERNANDES 1990), Amazonas (MENEZES et al. 1995), Minas Gerais (BORICS et al. 2005) and Rio Grande do Sul (CARDOSO et al. 2010) without identification at infraspecific level. Records in São Paulo by SANT'ANNA et al. (1988, as *Peridinium quadricens* STEIN) and in Espírito Santo by DELAZARI-BARROSO et al. 2007 (as *Peridinium umbonatum*) may correspond to *P. africanum* as shown by their illustrations.

***Parvodinium africanum* var. *javanicum* (WOŁOSZYŃSKA) CAVALCANTE, CRAVEIRO, CALADO et CARDOSO comb. nov.**

Figs 34–38

Basionym: *Peridinium marchicum* var. *javanicum* WOŁOSZYŃSKA 1912, Bull. Int. Acad. Sci. Cracovie B: Sci. Nat., p. 703, fig. 25 A–D.

Pentagonal cells in ventral view, dorsoventrally flattened; angular outline, formed by elevations in the plates junctions; epitheca conical, larger than hypotheca; hypotheca trapezoidal, with many long spines; cingulum circular, excavated; wide sulcus, extending onto the epitheca and reaching the antapex; apical pore protruded; small intercalary plates. Length: 30.8–36.6 µm; width: 26.2–32.3 µm.



Figs. 31–33. *Parvodinium africanum* var. *africanum*, LM. Fig. 31. Ventral view. Fig. 32. Dorsal view. Fig. 33. Apical view. Figs. 34–38. *P. africanum* var. *javanicum* comb. nov. Fig. 34. Fixed cell, LM. Fig. 35. Ventral view, LM. Fig. 36. Ventral view of the hypotheca, LM. Fig. 37. Dorsal view, LM. Fig 38. Dorsal view, SEM. Scale bars = 10 µm.

Occurrence: only in 7. This population occurred during fall 2012.

Comments: this population had larger cells, many long spines, sulcus broadly extended into epitheca and reduced intercalary plates. These features correspond to the circumscription of

Peridinium marchicum var. *javanicum* (WOŁOSZYŃSKA, 1912). This taxon was never transferred to *Parvodinium*, and the new combination is proposed here.

Distribution in Brazil: first record of this variety in Brazilian freshwaters, but see comments on distribution of *P. africanum* var. *africanum*.

Parvodinium guildfordense **(PLAYFAIR) CAVALCANTE, CRAVEIRO, CALADO et CARDOSO comb. nov.**

Figs 39–44

Basionym: *Peridinium caudatum* var. *guildfordense* PLAYFAIR 1919, Proc. Linn. Soc. N. South Wales 44, p. 800, text-fig. 5 a–f.

Elliptical cells; epitheca widely round, markedly larger than hypotheca; hypotheca round, no spines; cingulum slightly descending; round shallow sulcus, obliquely extending onto the epitheca and not reaching the antapex; apical pore not projected, slightly shifted to the left; brown-golden plastids; nucleus located in hypocone, and a large inclusion body (maybe a pyrenoid) in the epitheca; diminute eyespot sometimes observed; plates smooth, with scattered pores. Length: 20–33.6 µm; width: 13.3–24.2 µm.

Occurrence: only in 21. It occurred in different periods of the year.

Comments: some authors have considered *P. caudatum* var. *guildfordense* as synonym of *Peridinium umbonatum* var. *inaequale* LEMMERMANN (LEVEFRE 1932, HUBER-PESTALOZZI 1950). However, they can be distinguished by an apical pore not displaced and a sulcus reaching to antapex in *P. umbonatum* var. *inaequale* (LEMMERMANN 1910). Our specimens are identical to those showed in HANSEN & FLAIM (2007) as *Parvodinium centenniale* (PLAYFAIR) CARTY. Indeed these species, described in PLAYFAIR (1919), are very similar. However, some important differences can be highlighted by the analysis of original description and illustrations. *P.*

centenialle is a round form, 30–44 µm long, 32 µm wide, with clearly descending cingulum, apical pore typically displaced to the left, sulcus reaching the antapex and unequal antapical plates; in contrast, *P. guildfordense* is an elliptical cell, 19–31.5 µm long, 17–28.5 µm wide, with slightly descending cingulum, less displaced apical pore, sulcus does not reach the antapex and antapical plates are equal in size (PLAYFAIR 1919). Our specimens thus have features closer to the original description of the later species.

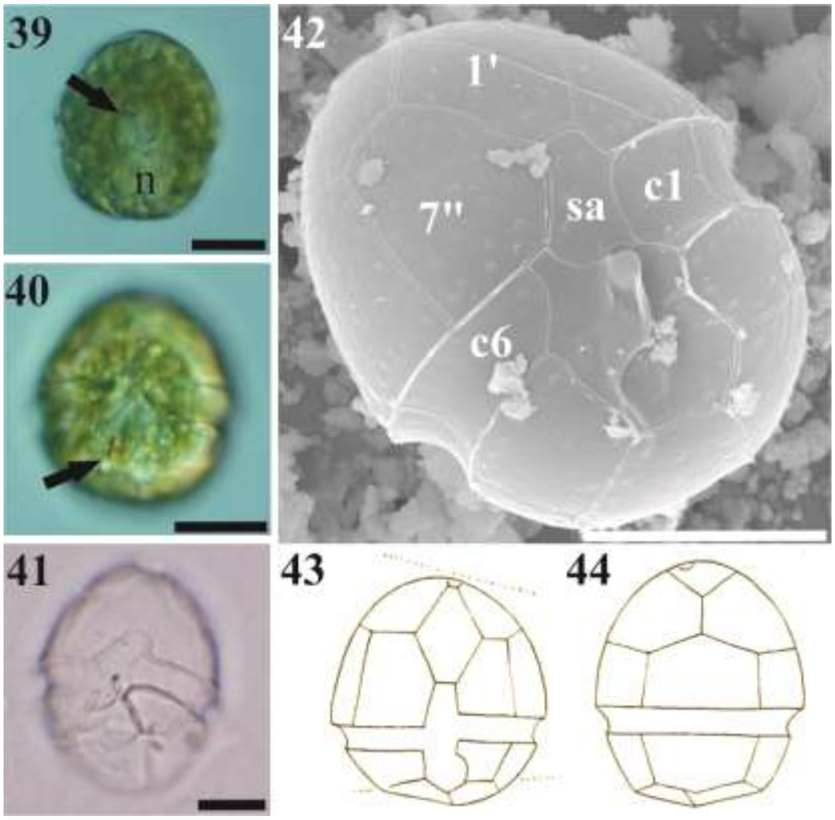
Distribution in Brazil: this is the first record of *P. guildfordense* in Brazilian freshwaters. There are records of *P. centenniale* in States of São Paulo (KLEEREKOPER 1939) and Minas Gerais (BORICS et al. 2005), both lacking illustrations, which makes impossible the comparison with our taxon. The specimen identified and illustrated as "*Peridinium centenialle* forma ?" in UHERKOVICH (1981) for Amazonas does not correspond to *P. centenniale* or *P.guildfordense* stricto sensu.

Parvodinium inconspicuum (LEMMERMANN) CARTY 2008, p. 106

Figs 45–51

Basionym: *Peridinium inconspicuum* LEMMERMANN 1899, p. 350.

Pentagonal cells in ventral view, dorsoventrally flattened; epitheca conical, larger than hypotheca; hypotheca angular, no spines; cingulum slightly descending; wide sulcus, extending onto the epitheca and reaching the antapex; apical pore not or slightly projected; brown-golden plastids; plates densely ornated with diminute warts and scattered pores. Length: 24–29.7 µm; width: 19.4–24.6 µm.



Figs 39–44. *Parvodinium guildfordense* comb. nov. Fig. 39. Living cell, LM, showing nucleus (n) and a large inclusion body in epitheca (arrow). Fig. 40. Living cell, LM, showing eyespot (arrow). Fig. 41. Empty theca in ventral view, LM. Fig. 42. Cell in ventral view, SEM. Figs 43, 44. Original illustrations of *Peridinium caudatum* var. *guildfordense*, reproduced from PLAYFAIR (1919, p. 801, text-fig 5 b and a respectively), scale not available. Scale bars = 10 µm.

Occurrence: only in 31. It was found in high numbers in an acidic lake in December 2011.

Comments: distinction between *P. inconspicuum* and *P. umbonatum* is quite inaccurate (HANSEN & FLAIM 2007, PANDEIRADA et al. 2013). We have considered as *P. inconspicuum* more pentagonal cells, with more angular epi- and hypotheca. The spines represented in the illustrations by LEMMERMANN (1910, pl. 663, figs 28 and 29, reproduced here as figs 46 and 47) are consistent with angular sutures in the antapical plates, as seen in our material, but without spines (Figs 45, 48).

Distribution in Brazil: Minas Gerais (BICUDO & VENTRICE 1968), Rio de Janeiro (BICUDO & BICUDO 1969; DOMINGOS & MENEZES 1998, as *Peridinium umbonatum*), Amazonas (UHERKOVICH 1976; 1981; UHERKOVICH & RAI 1979; UHERKOVICH & FRANKEN 1980) and Pará (HUSZAR 1996, as "*Peridinium umbonatum* var. 2"). Much of its occurrence can be hidden in the *P. umbonatum* distribution, as these species were commonly considered as synonyms.

***Parvodinium umbonatum* (STEIN) CARTY 2008, p. 106**

Figs 52–60

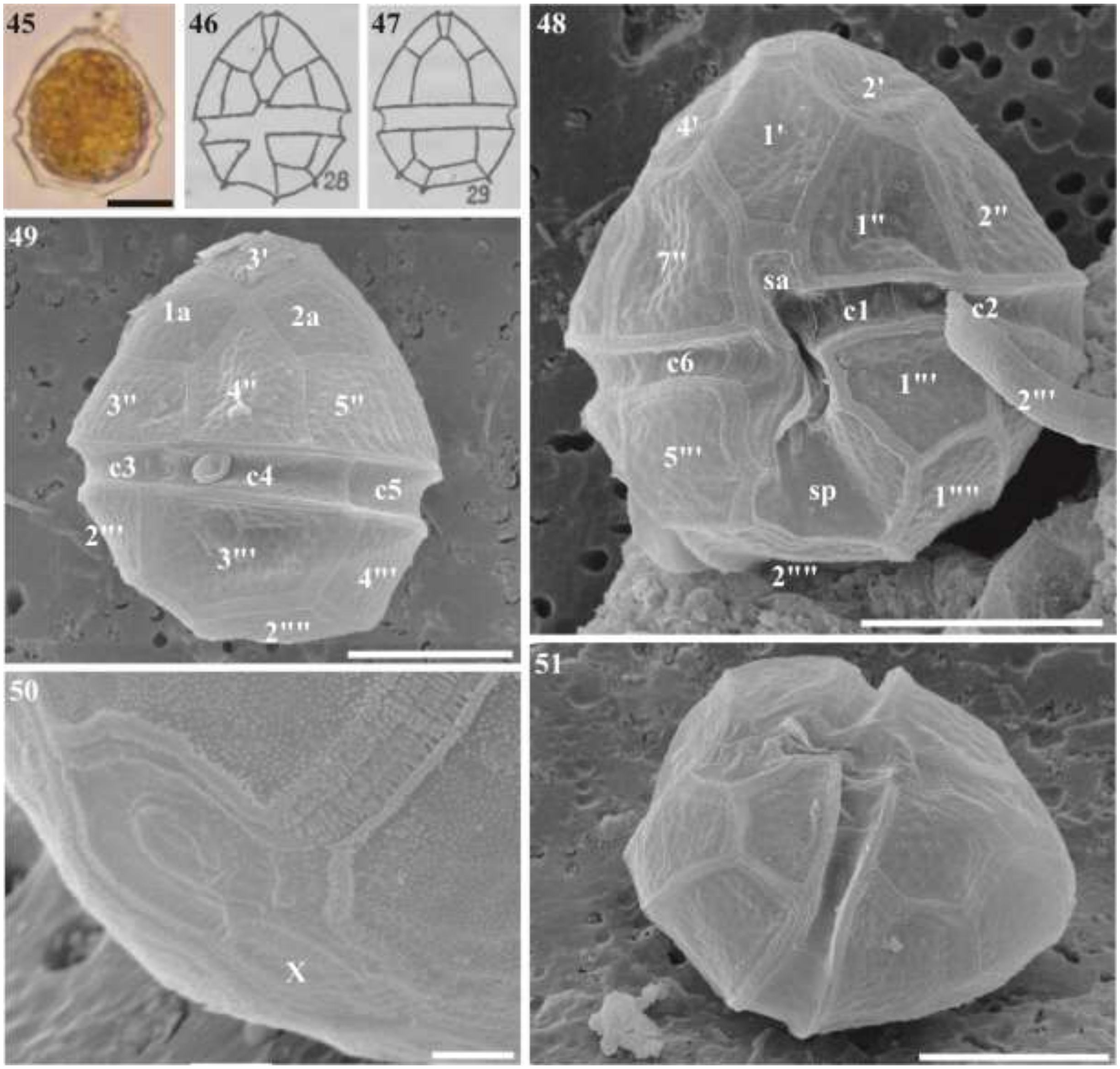
Basionym: *Peridinium umbonatum* STEIN 1883, pl. XII, figs 1–8.

Elliptical cells, slightly flat in the ventral side; epitheca conical, markedly larger than hypotheca; hypotheca angular with spines; cingulum slightly descending; wide sulcus, extending into the epitheca and reaching the antapex; apical pore large and projected; brown-golden plastids; plates smooth with scattered pores. Length: 14–23.3 µm; width: 10–20 µm.

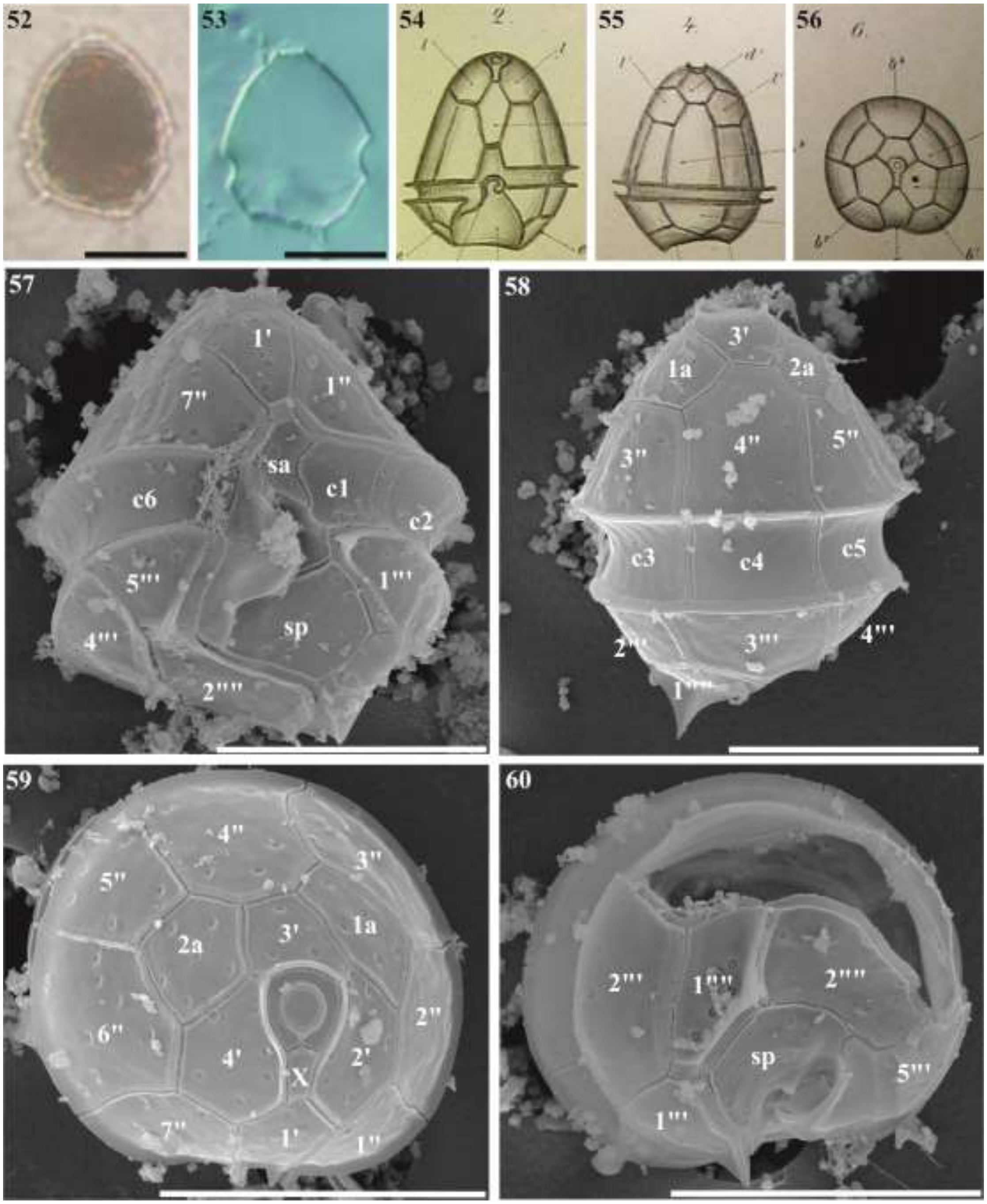
Occurrence: 2, 3, 6, 7, 14, 16, 19, 35, 37, 41. It was observed at all seasons.

Comments: only typical forms, consistent with the original illustrations (Figs 54–56, reprinted from STEIN 1883, pl. 12, figs 2, 4 and 6), were considered here.

Distribution in Brazil: species with broad distribution in Brazilian freshwaters, recorded in Pará, Amazonas, Rondônia, Mato Grosso, Goiás, Distrito Federal, Minas Gerais, Rio de Janeiro, São Paulo and Rio Grande do Sul (ODEBRECHT et al. 2015). The record of *P. umbonatum* in the State of Espírito Santo based on illustrations provided by DELAZARI-BARROSO et al. (2007) corresponds to *P. africanum*.



Figs 45–51. *Parvodinium inconspicuum.* Fig. 45. Fixed cell in ventral view, LM. Figs 46, 47. Original illustrations of *Peridinium inconspicuum*, reproduced from LEMMERMANN (1910, p. 663, figs 28 and 29 respectively), scale not available. Fig. 48. Ventral view, SEM. Fig. 49. Dorsal view, SEM. Fig. 50. Detail of the apical pore complex, SEM. Fig. 51. Left lateral view. Scale bars = 10 µm (Figs 45, 48, 49, 51), 1 µm (Fig. 50).



Figs 52–60. *Parvodinium umbonatum.* Fig. 52. Fixed cell in ventral view, LM. Fig. 53. Empty theca in ventral view, LM. Figs 54–56. Original illustrations of *Peridinium umbonatum,* reproduced from STEIN (1883, pl. 12, figs 2, 4 and 6 respectively), scale not available. Fig. 57. Ventral view, SEM. Fig. 58. Dorsal view, SEM. Fig. 59. Apical view, SEM. Fig. 60. Antapical view, SEM. Scale bars = 10 µm.

Peridiniopsis cunningtonii LEMMERMANN in WEST 1907, p. 189, fig. 2 a–e

Figs 61–64

Piriform cells, dorsoventrally flattened; epitheca conical, larger than hypotheca; hypotheca round, with 4-6 spines, one in each posterior plate; cingulum slightly descending; wide sulcus, extending onto the epitheca and reaching the antapex; apical pore projected; brown-golden plastids; nucleus located in hypotheca; eyespot present; plates with small warts; plate formula: Po, X, 4’, 1a, 6”, ?c, 5s, 5’”, 2””. Length: 22–28µm; width: 15–25 µm.

Occurrence: 17, 18, 30, 32, 33, 36. It was observed in different periods of the year.

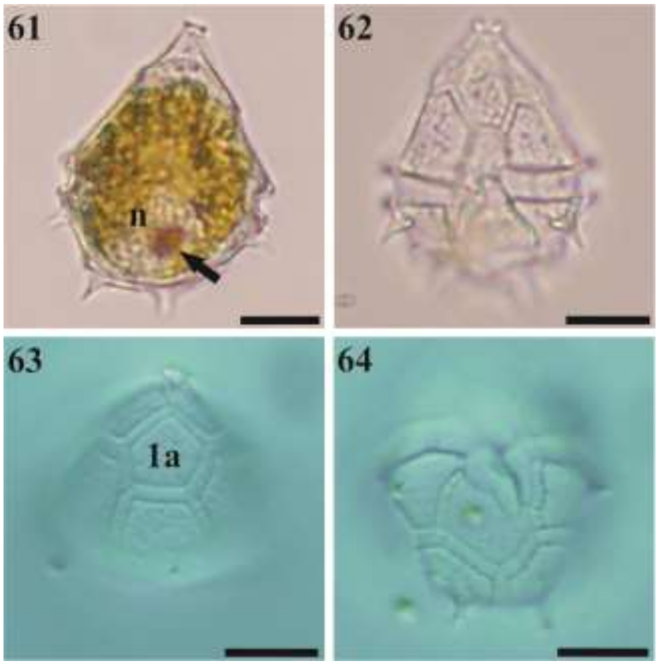
Distribution in Brazil: São Paulo (SANT’ANNA et al. 1989), Mato Grosso (MENEZES & FERNANDES 1990) and Minas Gerais (BORICS et al. 2005). Previous records of *P. cunningtonii* in Amazonian region (UHERKOVICH 1976; 1981; UHERKOVICH & RAI 1979) corresponds to *Peridiniopsis amazonica* instead (MEYER et al. 1997).

Peridiniopsis elpatiewskyi (OSTENFELD) BOURRELY 1968, p. 9

Figs 65–73

Basionym: *Peridinium umbonatum* var. *elpatiewskyi* OSTENFELD 1907, p. 391, pl. 9, figs 9–12 (*typus conservandus*, see MEYER & ELBRÄCHTER 1996)

Pentagonal cells in ventral view; epitheca conical, larger than hypotheca; hypotheca angular, with numerous spines along sutures of posterior plates; cingulum almost circular; wide sulcus, extending into the epitheca and reaching the antapex; apical pore protruded; brown-golden plastids; plates reticulated, with small warts and scattered pores; plate formula: Po, X, 4’, 7”, 6c, 4s, 5’”, 2””. Length: 20–36 µm; width: 16–27 µm.



Figs 61–64. *Peridiniopsis cunningtonii*, LM. Fig. 61. Living cell in ventral view, showing nucleus (n) and eyespot (arrow). Fig. 62. Empty theca in ventral view. Fig. 63. Epithecal tabulation in dorsal view. Fig. 64. Ventral view of hypotheca. Scale bars = 10 µm.

Occurrence: 30, 32, 33, 35, 36, 42. It was observed in several periods of the year, especially in quarry lakes.

Comments: *Peridinium pygmaeum* LINDEMANN was proposed as being a *P. elpatiewskyi* “in miniature”, 22 µm long (LINDEMANN 1918), while *P. elpatiewskyi* is 30–45 µm long (LEFÈVRE 1932). The measures of the population found in this study include the measurements given for both species. Some authors have considered these species as conspecific (POPOVSKÝ & PFIESTER 1990; ASCENCIO et al. 2015). Differences in size are common among different populations of the same dinoflagellate species. Moreover, we didn't find morphological evidence for discrimination between the specimens described in this study and larger *P. elpatiewskyi* cells from literature (compare Figs 65–73 with those illustrated in SENZAKI & HORIGUCHI 1994; HANSEN & FLAIM 2007; CARTY 2014 or ASCENCIO et al. 2015).

Distribution in Brazil: the only record of this species in Brazilian waters is from Amazonas (UHERKOVICH & RAI 1979) as '*P. elpatiewskyi* forma ("*minor*")'. *P. pygmaeum* was also reported for the same region (UHERKOVICH 1976; 1981; UHERKOVICH & RAI 1979).

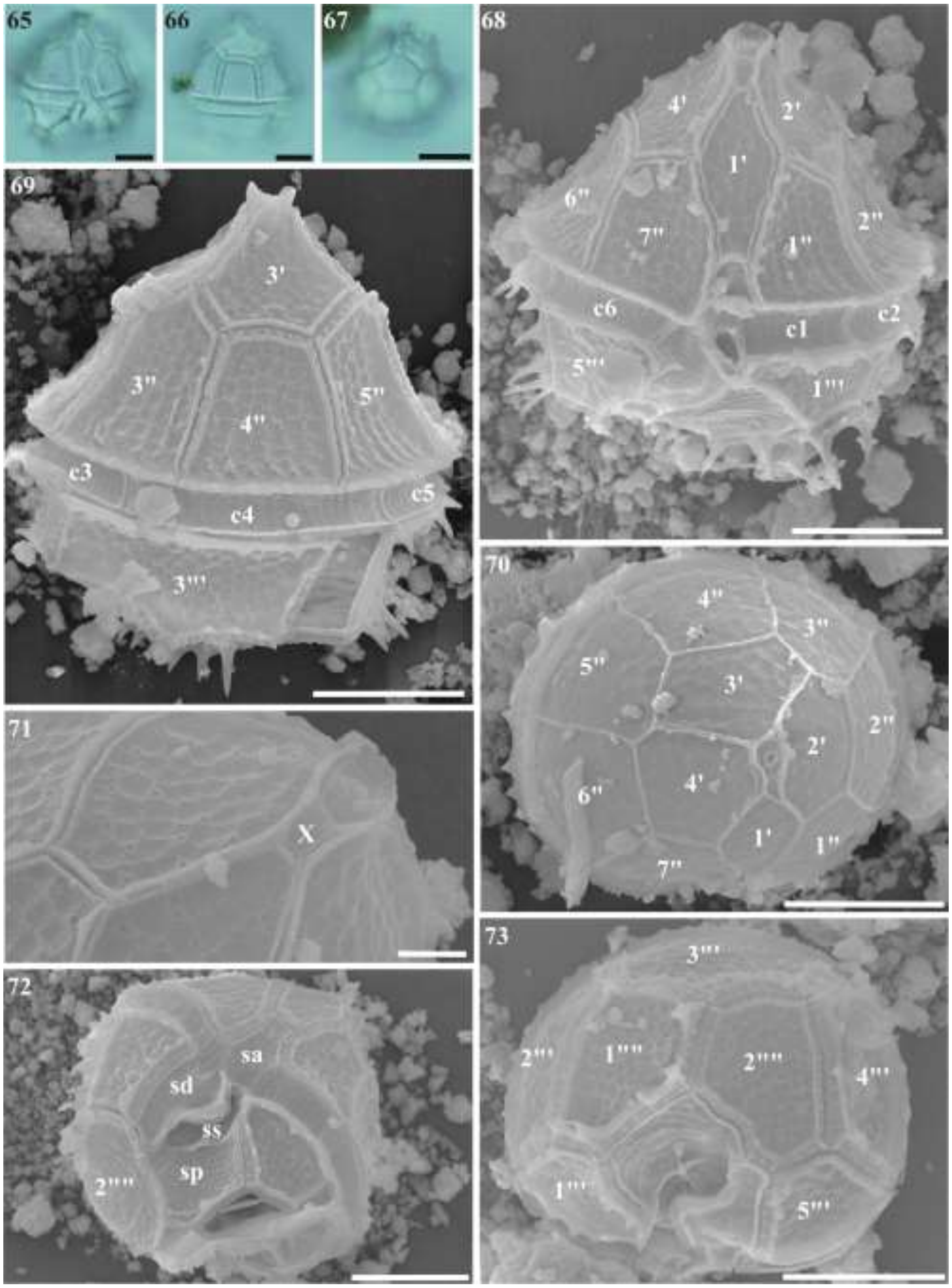
***Peridiniopsis* cf. *kevei* GRIGORSZKY et VASAS in GRIGORSZKY 1999, p. 31, figs 23, 24, SEM plates: figs 3–10**

Figs 74–82

Bi-conical cells; epi- and hypotheca equal in size; hypotheca with a horn-like projection of variable length, formed by the antapical plates; cingulum almost circular, with short and indented lists; narrow and shallow sulcus, not reaching the antapex; apical pore projected; numerous brown-golden plastids; plates smooth, with scattered pores; plate formula: Po, X, 3', 1a, 6'', ?c, ?s, 5''', 2''''. Length: 26–45.7 µm; width: 23.5–38 µm.

Occurrence: 7, 9, 17, 18. It was observed in different periods of the year.

Comments: *Peridiniopsis kevei* has priority in relation to *P. corillionii* LEITÃO, TEN-HAGE, MASCARELL et COUTÉ and *P. rhomboides* KRAKHMALNY, with basis in the valid publication of this name in GRIGORSZKY's thesis according to ICN (GRYGORSZKY 1999, see also discussion in HANSEN & FLAIM 2007). The populations observed here had some important differences from the *P. kevei* recorded in Europe (GRIGORSZKY et al. 2001; LEITÃO et al. 2001; KRAKHMALNY 2002; HANSEN & FLAIM et al. 2007). In *P. kevei*, cells are dorsoventrally flattened, plates ornamentation is reticulate and the plate 1a is four-sided (GRIGORSZKY et al. 2001), while *P.* cf. *kevei* observed here was almost circular in the cingulum, it had smooth plates and plate 1a was five- or six-sided, never quadrangular (Figs 76, 77, 80). Moreover, the apical



Figs 65–73. *Peridiniopsis elpatiewskyi*. Fig. 65. Empty theca in ventral view, LM. Figs 66, 67. Epitheca in dorsal and almost apical view, LM. Fig. 68. Ventral view, SEM. Fig. 69. Dorsal view, SEM. Fig. 70. Apical view, SEM. Fig. 71. Detail of apical pore complex, SEM. Fig. 72. Hypotheca in ventral view, showing sulcal plates, SEM. Fig. 73. Antapical view. Scale bars = 10 μm (Figs 65–70, 72, 73), 2 μm (Fig. 71).

pore in *P. kevei* is usually hidden by elevated apical plates edges, with 3’ margin often higher than 2’ one, giving the impression that the pore is oriented to the left (GRIGORSZKY et al. 2001; LEITÃO et al. 2001; KRAKHMALNY 2002). In *P.* cf. *kevei*, the apical plates borders formed a collar around of the apical pore complex (Figs 76, 80). Finally, the hypothecal extension observed in *P. kevei* is excentrical and formed by plate 1””. In *P.* cf. *kevei* this prolongation is formed by the two antapical plates (Figs 78, 79). Such differences lead to uncertainties about the true relationship between these taxa. More detailed studies are need for an accurate identification of *P.* cf. *kevei*.

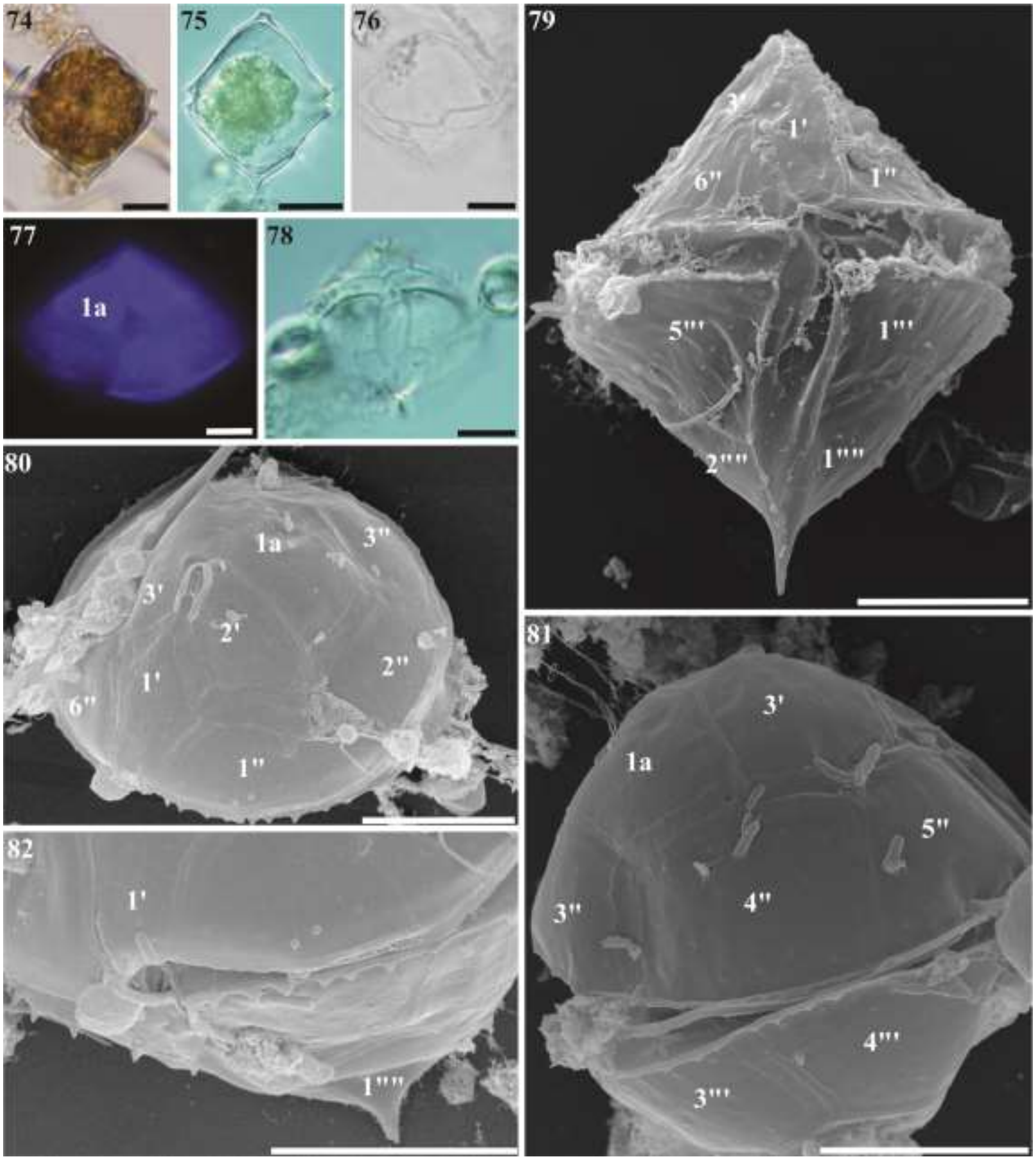
Distribution in Brazil: *P. corillioni* was cited for State of Goiás, but without figures or description (NABOUT & NOGUEIRA 2007). In South America, ILTIS & COUTÉ (1984) recorded in Bolivia one taxon very similar in shape to our material, which they identify as “*P. wisconsinense* ?”. No other record of *P. kevei* has been found. A more extensive survey of these forms is needed.

***Peridinium gatunense* NYGAARD in OSTENFELD & NYGAARD 1925, p. 10, figs 5–10**

Figs 83–87

Cells spherical, epi- and hypotheca equal in size; cingulum median, descending, often with wide lists; sulcus shallow, not extending into the epitheca; numerous golden- brown plastids throughout the cell; nucleus central; eyespot not observed; thick plates surface reticulated, each reticule containing a pore; plate formula: 4’, 3a, 7”, ?c, ?s, 5’”, 2””. Length: 30–46.7 µm; width: 36–51 µm.

Occurrence: 1, 2, 3, 6, 7, 8, 9, 10, 11, 14, 16, 18, 19, 20, 26, 27, 28, 29, 32, 35, 39. This widely distributed species occurred during all seasons.



Figs 74–82. *Peridiniopsis* cf. *kevei*. Fig. 74. Living cell, LM. Fig. 75. Fixed cell, LM. Fig. 76. Empty epitheca in ventral view, LM. Fig. 77. Epitheca in dorsal view, showing plate 1a, epifluorescence LM. Fig. 78. Hypotheca in ventral view, showing narrow sulcus and antapical plates, LM. Fig. 79. Ventral view, SEM. Fig. 80. Apical view, SEM. Fig. 81. Dorso-lateral view, SEM. Fig. 82. Detail of ventral cingular area, showing serrated lists. Scale bars = 10 μm.

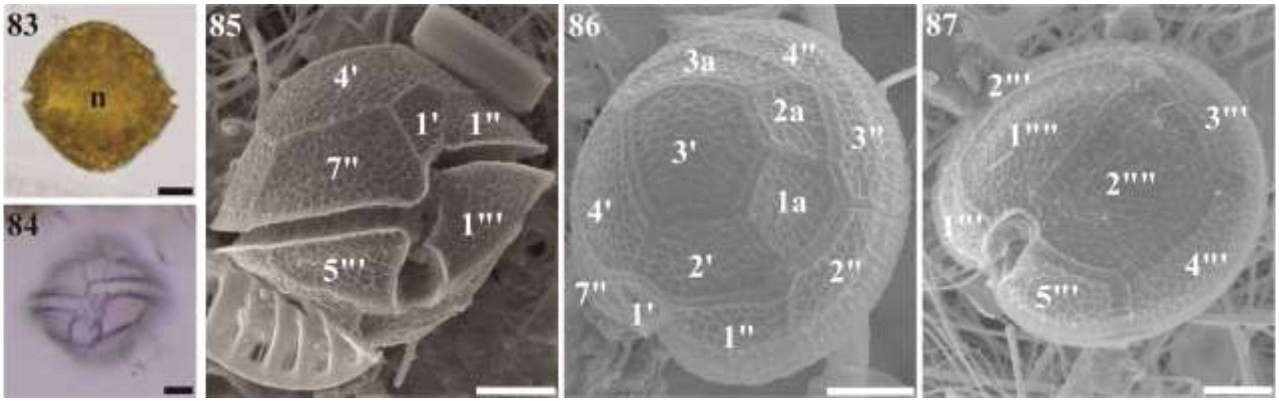
Comments: the taxonomy of this known worldwide species has been very stable (POPOVSKÝ & PFIESTER 1990). Along its taxonomic history, six non-typical infraspecific taxa were related to *P. gatunense*, primarily differentiated by general shape, size and plate ornamentation (LEFÈVRE 1932, KRAKHMALNY et al. 2014). However, "*P. gatunense* var. *zonatum* (PLAYFAIR) LEFÈVRE", a variety attributed to this species (LEFÈVRE 1932), is an improper combination, since *P. zonatum* (PLAYFAIR) PLAYFAIR 1919 is earlier legitimate name in the same rank than *P. gatunense* (Art. 11.4, MCNEILL et al. 2012). *P. zonatum* can be distinguished of *P. gatunense* by having more rounded cell, narrower 1a plate and plates ornamented by irregular ribs arranged side by side on each plate (PLAYFAIR 1912). Although the thecal ornamentation is not considered enough conservative character to distinguish species (POPOVSKÝ & PFIESTER 1990), it is not appropriate at this moment to make any nomenclatural change without studying the relationship of both taxa based on molecular data. To preserve stability in this name, for now we consider *P. zonatum* a separate species of *P. gatunense*.

Distribution in Brazil: *P. gatunense* is the most recorded freshwater dinoflagellate in Brazil, found in all regions of the country (ODEBRECHT et al. 2015).

***Peridinium volzii* var. *cinctiforme* LÈFEVRE, 1927, p .122**

Figs 88–92

Round cells, dorsoventrally flattened; epi- and hypotheca equal in size; cingulum median, descending, often with wide lists; wide sulcus, extending into the epitheca; numerous golden-brown plastids throughout the cell (not shown); nucleus and eyespot not observed; thick plates with surface reticulated, each reticule containing 1–2 pores; plate formula: 4', 3a, 7'', ?c, ?s, 5''', 2''''. Length: 36–54.8 µm; width: 30.6–52 µm.

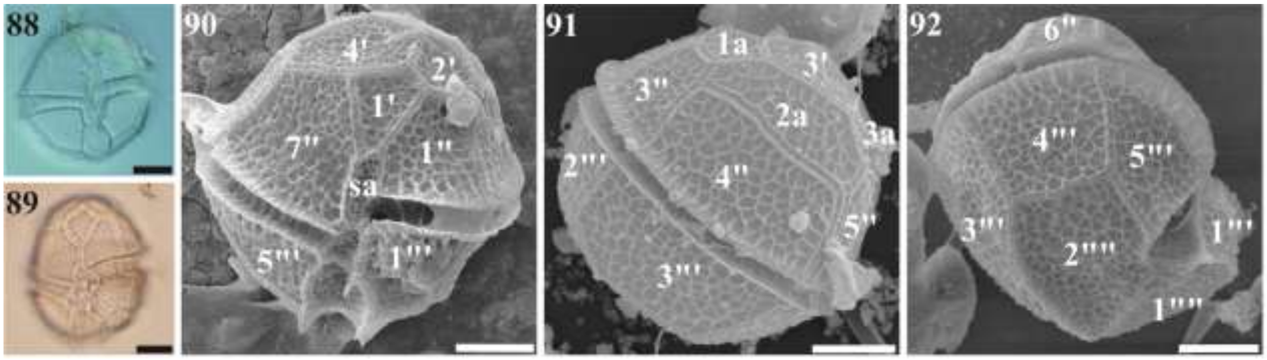


Figs 83–87. *Peridinium gatunense.* Fig. 83. Living cell, n = nucleus, LM. Fig. 84. Empty theca in ventral view, LM. Fig. 85. Ventral view, SEM. Fig. 86. Apical view, SEM. Fig. 87. Antapical view, SEM. Scale bars = 10 µm.

Occurrence: 2, 7, 14, 17, 18, 25, 29, 35, 38. Observed in different periods of the year.

Comments: there are two varieties and five forms, besides the typical one, formally proposed to *P. volzii* LEMMERMANN. They are distinguished by the different symmetry in plate 1’, presence or not of spines in hypotheca, plate ornamentation and general shape of the cell (LEFÈVRE 1932, HUBER-PESTALOZZI 1950). A revision of these group is needed using modern tools in order to establish the phylogenetic relationships among them. For now, only morphological features are used in the infraspecific differentiation, especially on a way of describing as accurate as possible the morphological variation found in populations. In material from Paraná, *P. volzii* was identified at infraspecific level, as *P. volzii* var. *cinctiforme*, distinguished from typical variety especially by the asymmetric shape of the upper margins of the plate 1’, due to difference in size of adjacent plates 2’ and 3’ (LÈFEVRE 1932). This feature showed little variation in the studied populations. *P. volzii* has also been often confused with *P. willei* HUITFELD-KAAS, however these species are morphologically, ecologically (OLRIK 1992) and genetically (LOGARES et al. 2007) distinct.

Distribution in Brazil: the majority of works that cite *P. volzii* don't use infraspecific level. The distribution of *P. volzii* varieties is therefore underestimated. *P. volzii* var. *cinctiforme* was confirmed in Minas Gerais (Borics et al. 2005) and in Rio de Janeiro (Huszar et al. 1988), São Paulo (Sant'Anna et al. 1989) and Rio Grande do Sul (Franceschini 1992) taking into account the illustrations provided. Some records of *P. willei* in Brazilian freshwaters may correspond to *P. volzii* instead.



Figs 88–92. *Peridinium volzii* var. *cinctiforme.* Fig. 88. Empty theca in ventral view, LM. Fig. 89. Theca with atypical variation in tabulation, showing 1" linked to 7", LM. Fig. 90. Ventral view, SEM. Fig. 91. Dorsal view, SEM. Fig. 92. Antapical view, SEM. Scale bars = 10 µm.

***Tyrannodinium edax* (A.J. Schilling) Calado 2011, p. 643, figs 1–3**

Figs 93–99

Basionym: *Glenodinium edax* A.J. Schilling 1891, p. 206, pl. X, figs 23–24.

Elliptical cells; epitheca conical, with similar size as the hypotheca; hypotheca round to conical, no spines observed; cingulum slightly descending; narrow sulcus, not extending onto the epitheca nor reaching the antapex; apical pore not protruded; plastids and eyespot absent; large nucleus located in hypocone and food items in epicone; plates smooth, with scattered pores; plate formula: Po, X, 4’, 6”, ?c, ?s, 5’”, 2””. Length: 18.7–29.1 µm; width: 15.3–25.1 µm.

Occurrence: 2, 4, 6, 8, 14, 17, 18, 23, 27, 34, 41. It was observed at different times.

Comments: *Tyrannodinium berolinense* (LEMMERMANN) CALADO, CRAVEIRO, DAUGBJERG et MOESTRUP, type species of the pfiesteracean freshwater genus *Tyrannodinium* CALADO, CRAVEIRO, DAUGBJERG et MOESTRUP, should be regarded as later synonym of *T. edax* according to CALADO (2011).

Distribution in Brazil: this characteristic species is recorded for first time in Brazilian freshwaters.

Immobile taxa

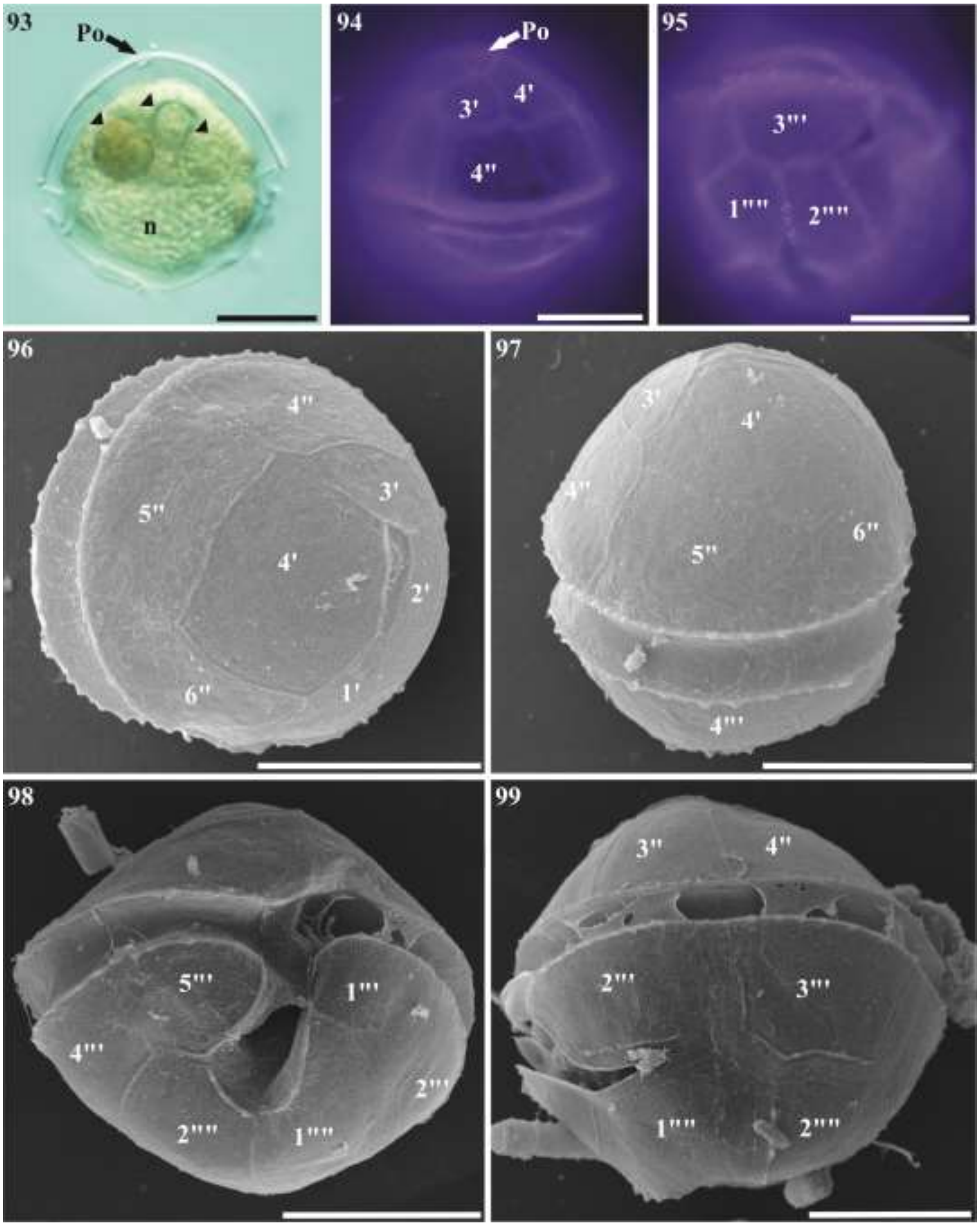
Tetradinium javanicum KLEBS 1912, p. 408, 444, figs 11, pl. X, fig. 3.

Figs 100–102

Tetrahedral cells, with 2 spine-like projections at each angle; one angle prolonged into a stalk ending in an adhesive disk, by which the cell attaches to filamentous green algae; numerous discoid green plastids throughout the cell. Length: 40.8–61.7 µm; width: 20–34.2 µm; stalk: 9.2–12.5 µm.

Occurrence: only in 21. This species has been found once in November 2011.

Comments: five species are validly published in *Tetradinium* KLEBS: *T. javanicum*, *T. minus* PASCHER, *T. intermedium* GEITLER, *T. chiastosporum* HARRIS and *T. simplex* PRESCOTT. Recognition of these species as distinct entities or as taxonomic synonyms varies with authors (POPOVSKÝ & PFIESTER 1990, CARTY 2014). In original publications, *T. javanicum* was characterized by having cells with two spines in each angle and attached by stalk (KLEBS 1912). *T. minus* was depicted with one spine in each angle (POPOVSKÝ & PFIESTER 1990).



Figs 93–99. *Tyrannodinium edax*. Fig. 93. Fixed cell, showing large nucleus (n), food vacuoles (arrowheads) and apical pore (Po, arrow), LM. Figs 94, 95. Tabulation of epi- and hypotheca, respectively, in epifluorescence LM. Fig. 96. Apical view, SEM. Fig. 97. Dorso-lateral view of epitheca, SEM. Fig. 98. Hypotheca in ventral view, SEM. Fig. 99. Hypotheca in lateral view, SEM. Scale bars = 10 µm.

Tetradinium intermedium was distinguished from *T. javanicum* in POPOVSKÝ & PFIESTER (1990) by having more concave sides, but this feature is not readily recognized in the illustrations. *T. chiatosporum* was characterized by having no stalk (HARRIS 1940), but it also seems to be variable in the same species. Finally, *T. simplex* is a small form, with one spine in each angle and only two plastids (POPOVSKÝ & PFIESTER 1990). The phylogenetic relationships among them need to be revised. Our specimens fit *T. javanicum* circumscription, which is also the oldest name and the type species of the genus.

Distribution in Brazil: records of this alga were done in São Paulo (BICUDO & SKVORTZOV 1968), Rio de Janeiro (MENEZES 1995) and Rondônia (ALBUQUERQUE & MENEZES 1997). This is its first record in southern Brazil.

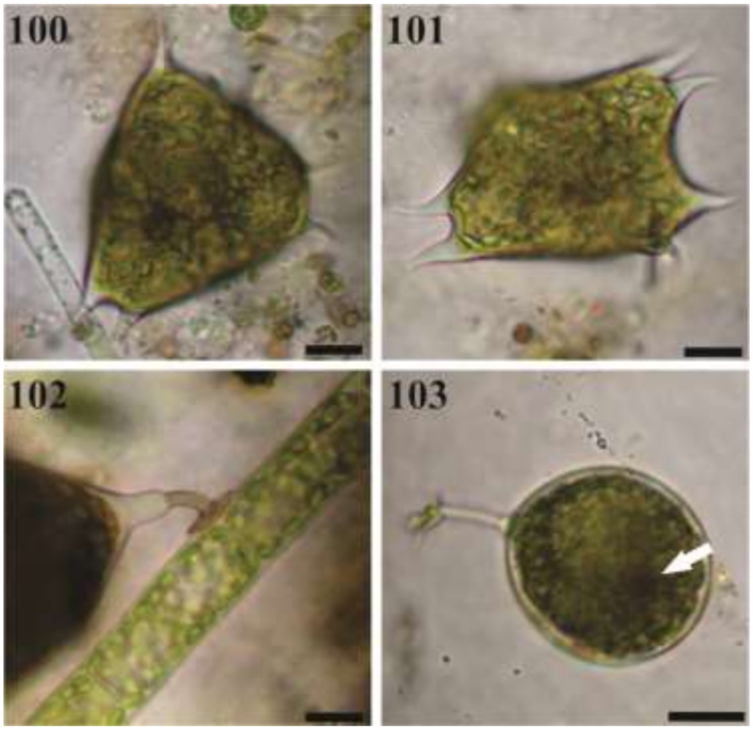
***Stylodinium globosum* KLEBS 1912, p. 410, 445, fig. 12 A–C**

Fig. 103

Roundish cells, with one stalk ending in an adhesive disk by which the cell attaches to filamentous green algae; numerous yellowish-brown plastids throughout the cell. A large red body present in the region opposite to the stalk insertion. Length: 28.3 µm; width: 25.8 µm; stalk: 10.8 µm.

Occurrence: only in 21. This species was found once in November 2011.

Comments: a number of species and genera related to *Stylodinium* KLEBS were proposed, but, as in *Tetradinium*, there is no consensus on their relationships. According to BOURRELY (1970), species can be distinguished by cell shape, stalk length and plastids and pyrenoids. However, POPOVSKÝ & PFIESTER (1990) considered all to be a broad morphological variation of the species *S. globosum*. Our taxon fits the original concept of *S. globosum* (KLEBS 1912).



Figs 100–102. *Tetradinium javanicum*, LM. Fig. 100, 101. Living cells. Fig. 102. Detail of the stalk attached to filamentous algae. Fig. 103. *Stylodinium globosum*, LM. Note a large red body (arrow). Scale bars = 10 µm.

Distribution in Brazil: four species of *Stylodinium* were identified in States of Rio de Janeiro and São Paulo: *S. cerasiforme* Pascher, *S. lindemannii* Baumeister, *S. tarnum* Baumeister (Bicudo & Skvortzov 1968) and *Stylodinium globosum* (Menezes 1995). A new species of *Dinopodiella* Pascher, *D. baumeisteri* Bicudo et Skvortzov, was described from São Paulo (Bicudo & Skvortzov 1968). The illustrations of these taxa in Bicudo & Skvortzov (1968) apparently show morphological variants of *S. globosum*. This is the first record in southern Brazil.

This study presented new data about freshwater dinoflagellate diversity in southern Brazil. The Paraná flora, still unknown, revealed high species richness when compared to other Brazilian states with the highest number of dinoflagellate records, including Rio de Janeiro, São Paulo, Minas Gerais and Rio Grande do Sul (ODEBRECHT et al. 2015). We believe that the dinoflagellate flora of the Paraná is still far of being completed, since a number of environments were not collected.Twelve taxa were cited for the first time in southern Brazil, and four of them are new records for Brazilian freshwaters. Dinoflagellates were particularly commom in quarry lakes (especially *Peridiniopsis* spp.) and urban lakes, where taxa with more restricted occurrence (*H. nasutum*, *G. uliginosa*, *P. guildfordense* and immobile taxa) were found. Finally, one taxon found in this study could not be precisely identified, namely *Peridiniopsis* cf. *kevei*, and more detailed studies are needed to understand the relationship among this species and those already described, with high potential of being new for science.

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Capítulo 5.

Caracterização ambiental e espacial de populações de dinoflagelados em reservatórios subtropicais do sul do Brasil

Estruturado nas normas do periódico Hydrobiologia

Environmental and spatial characterization of dinoflagellate populations in subtropical reservoirs from southern Brazil

Kaoli Pereira Cavalcante

Programa de Pós-Graduação em Botânica, Departamento de Botânica, Universidade Federal do Rio Grande do Sul. Instituto de Biociências, Av. Bento Gonçalves, 9500, Prédio 43433, Bairro Agronomia, CEP 91501-970, Porto Alegre, RS, Brazil.

Corresponding author e-mail: kaolicavalcante@gmail.com

Vanessa Majewski Algarte, Thelma Alvim Veiga Ludwig

Departamento de Botânica, Universidade Federal do Paraná. Setor de Ciências Biológicas, Caixa Postal 19031, Jardim das Américas, CEP 81531-980, Curitiba, PR, Brazil.

Luciana de Souza Cardoso

Departamento de Botânica, Universidade Federal do Rio Grande do Sul. Instituto de Biociências, Av. Bento Gonçalves, 9500, Prédio 43433, Bairro Agronomia, CEP 91501-970, Porto Alegre, RS, Brazil.

Dinoflagellates are a minor component in plankton of the majority of Brazilian subtropical reservoirs and their ecology is virtually unexplored. Here we assess environmental requirements and spatial patterns that shape dinoflagellate populations in 18 reservoirs from 19 sampled in State of Paraná, southern Brazil. We tested the hypothesis that the influence of environmental conditions in structuring dinoflagellate populations is higher than influence of spatial factors (*e.g.*, dispersion). Samples were conducted quarterly between February 2011 and May 2013 in a pelagic station near to dam in each reservoir. Higher biomasses were found in reservoirs with high retention time, thermal stratification in warm months and complete mixing periods. Turbulence, water transparency, pH, conductivity and phytoplankton density were the environmental factors more related to dinoflagellate biomass variation. Variation partitioning (pRDA) showed that environmental and spatial components significantly explained the dinoflagellate biomass variation. The environmental component had stronger signal than spatial one on dinoflagellates communities, showing that niche conditions are strongly shapping dinoflagellate populations than dispersal. Twelve taxa were observed in this study, and autecological data were presented by means of environmental correlations, species associations and indicator species analysis. This study is pioneer in considering the spatial structure as a driver of dinoflagellate population dynamics among basins. Furthermore, these findings provide substantial ecological information about dinoflagellate taxa occurring in subtropical reservoirs.

Keywords Dinophyceae, freshwater, Paraná, Partial Redundancy Analysis, plankton.

Introduction

The ecological knowledge about freshwater dinoflagellates is underestimated (Grigorszky et al., 2003). An important compilation of data was conducted at the beginning of the last century (Höll, 1928) and is still the main source of autecological information for many species. Some bloom-forming species have been widely studied, such as *Peridinium gatunense* Nygaard, an important component of phytoplankton during winter-spring from subtropical Lake Kinneret, Israel (Berman-Frank & Erez, 1996; Zohary et al., 1998, 2012), *Tovellia sanguinea* Moestrup, Hansen, Daugbjerg, Flaim et D'Andrea a summer form in the alpine oligotrophic Lake Tovel, Italy (Cantonati et al., 2003; Flaim et al., 2003; Calliari et al., 2004a; b) and species of *Ceratium* Schrank, a conspicuous, widely distributed and highly variable dinoflagellate genus (Dottne-Lindgren & Ekbohm, 1975; Heaney et al., 1988; Hickel, 1988; Lindström, 1992). Ecological information on the majority of other species is scattered or virtually unexplored.

In Brazil, despite the extensive studies on phytoplankton ecology in a number of ecosystems (Nabout et al., 2015), dinoflagellate occurrence and distribution usually are not covered. In general, dinoflagellates dot not represent more than 10% of the freshwater phytoplankton density in Brazilian water bodies (*e.g.*, Calijuri et al., 2002; Cardoso & Motta-Marques, 2004; Crossetti & Bicudo, 2005; Chellappa et al., 2008). Moreover, they are difficult to identify when compared to marine members (Carty, 2014), and there are few specialists in this subject, making ecological studies on freshwater dinoflagellates a hard task (Tolotti et al., 2003). Some studies were performed about spatial and temporal patterns of dinoflagellates in Brazilian environments: Oda & Bicudo (2006) and Gomes et al. (2010) have studied the autecology of *Peridinium gatunense* and *Parvodinium umbonatum* (Stein) Carty in oligotrophic shallow systems from southeastern and Central Brazil, respectively.

Cardoso & Torgan (2005; 2007) have analyzed the diversity, density and distribution of dinoflagellates in lakes from southern Brazil. Cardoso et al. (2010) have investigated the biomass variation of Dinophyceae in relation to environmental factors in three subtropical reservoirs from southern Brazil. Finally, some autecological studies have been performed on the invasive species *Ceratium furcoides* (Levander) Langhans in reservoirs from southeastern and southern regions (Silva et al., 2012; Nishimura et al., 2015; Cavalcante et al., 2016). However, there is still a gap in the knowledge of dinoflagellates in Brazilian subtropical reservoirs, in particular about which factors are related to their occurrence and abundance. For example, can general patterns of planktonic dinoflagellates in freshwater ecosystems be influenced by spatial factors since they have high possibility of dispersion?

That way, we performed an exploratory study on the dinoflagellate communities in 19 subtropical reservoirs from southern Brazil, in order to identify seasonal and spatial patterns of those populations and to relate their biomass and occurrence with environmental and geographic attributes of those systems. We tested the hypothesis that the influence of environmental conditions in structuring dinoflagellate populations is higher than the influence of spatial factors (*e.g.*, dispersion). Moreover, we have added autecological information about the taxa found.

Material and Methods

Study area

This study was performed in 19 reservoirs from State of Paraná, southern Brazil, which are mainly used for energy production purpose (Hydroelectric Power Plants: HPP). These reservoirs are distributed in six watersheds (Fig. 1) and have distinct hydrological and trophic features (Table 1). HPP Capivari (Cap) is included in Ribeira River Basin and is diverted to Coastal Basin across the Cachoeira River. The HPPs Marumbi (Mar), Guaricana (Gua) and Chaminé (Cha) are in Coastal Basin of Paraná. These reservoirs, located in Serra do Mar, are characterized by high altitudes (>740 m above sea level), high temperature fluctuations along the year and thermal and chemical stratification in warmer months. HPPs Foz do Areia (Foz), Segredo (Seg) and Salto Caxias (SCx) are deep reservoirs comprising a cascading system on Iguaçu River Basin. Jordão (Jor), Santa Clara (SCl) and Fundão (Fun) are also deep dams in cascade located on Jordão River, a tributary of Iguaçu River. Salto do Vau (SVa), Chopim (Cho) and Cavernoso (Cav) are shallower reservoirs located on other tributaries of this Basin. The deepest reservoirs constructed on Iguaçu River watershed (Foz and Seg) seem to have geomorphological meromixis, with marked stability in thermic stratification, while less deep systems in the same basin (SCx, Jor, SCl and Fun) are considered holomictic. In SVa, Cav and Cho, shallow depths and short retention times are determinant in the absence of stratification. There are still the Melissa (Mel) reservoir, on Piquiri River Basin; Mourão (Mou) and Rio dos Patos (RiP), distant reservoirs located in Ivaí River Basin, and Apucaraninha (Apu) and the Pitangui (Pit)-São Jorge (SJo) cascade system, included in Tibagi River Basin. The reservoirs located in Piquiri, Ivaí and Tibagi river Basins are typically shallow and have low retention time, showing polymictic patterns (Júlio-Júnior et al., 2005; Pagioro et al. 2005).

Sampling data

The samples used here are derived from phytoplankton monitoring program performed by the State Power Company (Companhia Paranaense de Energia: COPEL). Samples were conducted quarterly between February 2011 and May 2013 in a pelagic station near to dam in each reservoir. Abiotic (depth of sampling station, temperature, secchi, total solids, turbidity, dissolved oxygen, pH, conductivity, total phosphorus, total nitrogen, organic nitrogen, nitrate, molar N:P ratio, chemical oxygen demand) and biotic (chlorophyll a, phytoplankton density and richness) data were provided by the Lactec Institute, responsible for these analysis. Analytical methods were according to APHA (1998). Precipitation data were obtained from the nearest meteorological station of each reservoir (OMM: 83766, 83783, 83813, 83836, 83844), available from the National Institute of Meteorology website (INMET, 2015). Phytoplankton was sampled simultaneously to environmental variables with a Van Dorn bottle in a subsurface water layer (54% Secchi, according IAP, 2009) and preserved with Lugol's solution.

Data analysis

Aliquots of 10 mL were used to quantify dinoflagellates using an inverted light microscope by counting the whole surface of Utermöhl's chambers. Only samples containing dinoflagellates were considered in this study, accounting 119 samples (69%). Cell density was converted into biomass by biovolume estimatives, from geometrical approximations (Olenina et al., 2006) and assuming a specific gravity of 1 $mm^3 L^{-1}$ = 1 mg L^{-1} (Wetzel & Likens, 2000).

Dinoflagellates were identified according to Cavalcante et al. (in press) at specific level whenever possible. Small species within *Parvodinium umbonatum* species complex could not be accurately identified in the counting analysis, thus they were referred as *P. umbonatum* group.

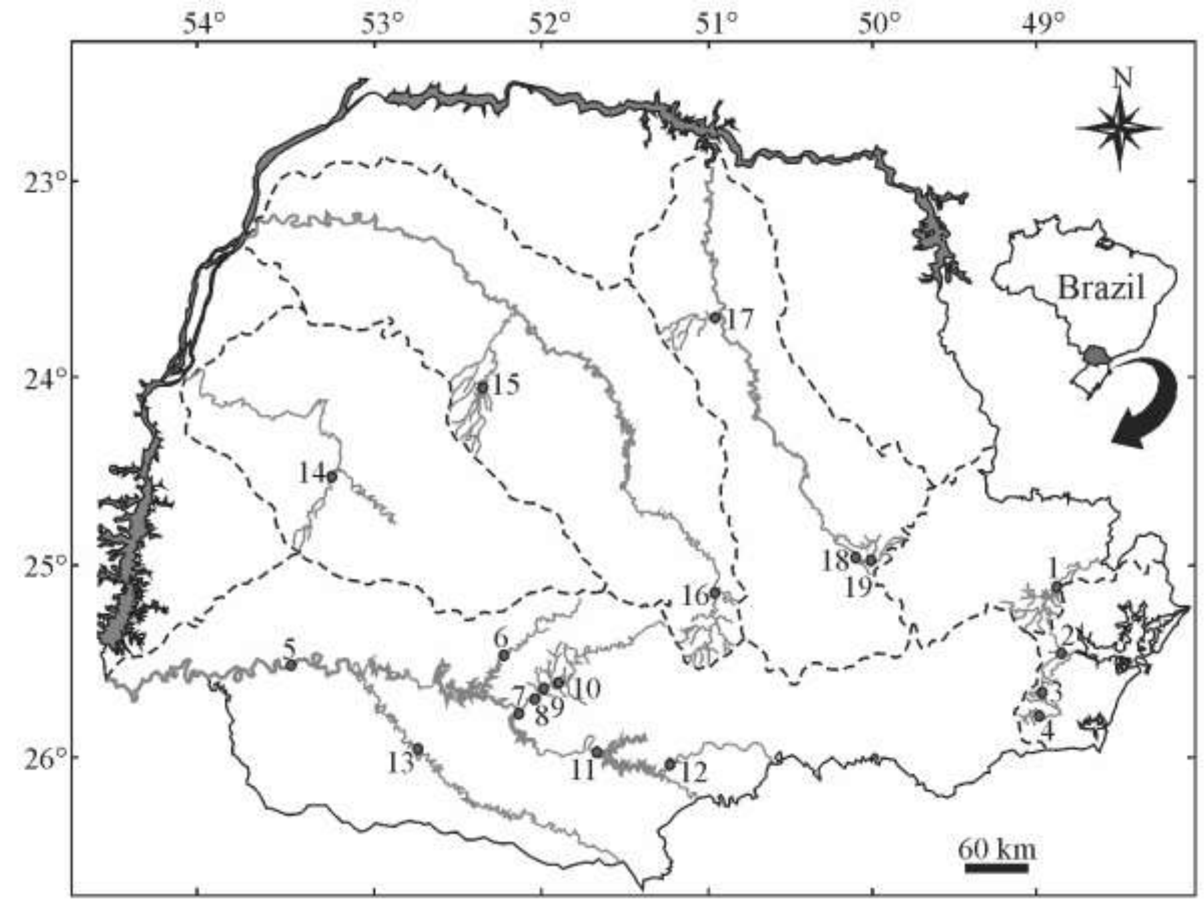

Fig. 1 Nineteen hydroelectric power plants sampled in the State of Paraná. 1. Capivari; 2. Marumbi; 3. Guaricana; 4. Chaminé; 5. Salto Caxias; 6. Cavernoso; 7. Segredo; 8. Jordão; 9. Santa Clara; 10. Fundão; 11. Foz do Areia; 12. Salto do Vau; 13. Chopim; 14. Melissa; 15. Mourão; 16. Rio dos Patos; 17. Apucaraninha; 18. Pitangui; 19. São Jorge. Dashed lines indicate micro-basin boundaries, according SUDERHSA (1998).

Table 1 Morphological, hydrological and trophic characterization of the reservoirs studied.*Classified according Nürnberg (1996).

HPP	Coordinates	Water body classification	Mean retention time (days)	Maximum depth (Zmax, m)	Mean depth (Zmed, m)	Trophic State*
Apucaraninha (Apu)	23°45'01"S, 50°56'28"W	Intermediate	14	14	6.3	mesotrophic
Capivari (Cap)	25°08'27"S, 48°52'21"W	Lentic	107	30	13.6	mesotrophic
Cavernoso (Cav)	25°29'32"S, 52°12'53"W	Lotic	<2	7	6.3	mesotrophic
Chaminé (Cha)	25°49'19"S, 49°03'58"W	Lentic	121	16	7.1	meso- to eutrophic
Chopim (Cho)	25°59'19"S, 52°44'47"W	Lotic	<2	12	10.8	mesotrophic
Foz do Areia (Foz)	26°00'30"S, 51°39'48"W	Lentic	102	121	41.6	mesotrophic
Fundão (Fun)	25°41'57"S, 51°59'58"W	Lotic	4	41.5	16.2	oligo- to mesotrophic
Guaricana (Gua)	25°42'39"S, 48°58'16"W	Intermediate	12	13	7.9	meso- to eutrophic
Jordão (Jor)	25°45'16"S, 52°04'56"W	Intermediate	10	65	32.8	mesotrophic
Marumbi (Mar)	25°25'46"S, 48°56'52"W	Lotic	1	3	3.0	oligotrophic
Melissa (Mel)	24°32'14"S, 53°12'30"W	Lotic	<2	5	4.5	oligo- to mesotrophic
Mourão (Mou)	24°06'23"S, 52°19'44"W	Lentic	53	13	5.8	mesotrophic
Pitangui (Pit)	25°01'43"S, 50°06'10"W	Lotic	<2	4	3.6	eutrophic

Rio dos Patos (RiP)	25°10'11"S, 50°56'39"W	Lotic	<2	5	4.5	eutrophic
Salto Caxias (SCx)	25°32'10"S, 53°29'31"W	Intermediate	31	60	25.3	oligotrophic
Salto do Vau (SVa)	26°02'05"S, 51°11'06"W	Lotic	<2	3	2.7	oligo- to mesotrophic
Santa Clara (SCl)	25°38'59"S, 51°56'55"W	Lentic	49	60	21.4	oligo- to mesotrophic
São Jorge (SJo)	25°01'06"S, 50°03'40"W	Lentic	43	9	3.8	eutrophic
Segredo (Seg)	25°47'37"S, 52°06'54"W	Lentic	45	130	36.6	mesotrophic

Principal Component Analysis (PCA) was used to establish relationships among environmental factors (17 variables, excluding phytoplankton density and richness) and sampling units using correlation to produce a cross product matrix (data not log transformed). Only significant axes ($p<0.05$) were interpreted. Pearson's r correlation analyzes were carried out to find relationships between dinoflagellates biomass and environmental variables. Partial Redundancy Analysis (pRDA) was performed to partition the effects of environmental and spatial components on dinoflagellate biomass. Biotic data (biomass) was Hellinger transformed (Legendre & Gallagher, 2001), while environmental data was log-transformed and standardized. Spatial matrix was obtained from geographic coordinates by Principal Coordinates of Neighborhood Matrix (Borcard & Legendre, 2002). Variables were selected by forward selection function. The best environmental and spatial overall models were chosen by Akaike Information Criterion (AIC, Burnham & Anderson, 2002). pRDA fractions were tested by 999 permutations test using 999 randomizations (Peres-Neto et al., 2006). Indicator Species Analysis was performed in order to show taxa with high seasonal or habitat specificity. PCA and Indicator Species Analysis were performed on PC-ORD 6.08©. Pearson correlations were performed using the software Statistica 7.1©. pRDA was carried out in R program using vegan package (Oksanen et al., 2016).

Results

In HPP Marumbi, dinoflagellates have never been found, and therefore this reservoir was excluded from results of this study.

Environmental characterization (Supplementary data, Appendix I)

The reservoirs from Paraná were characterized by low values of turbidity (1–74, mean 5.3 NTU) and total solids (4–217, mean 44 mg L^{-1}) and consequently by high water transparency (Secchi up to 75% of the depth of sampling point) during this study. Higher turbidity values was found in Melissa (74 NTU); in other reservoirs the turbidity was often less than 20 NTU. The pH ranged between 6.2 and 9.6. The HPPs Apucaraninha, Fundão and Jordão had the lowest average values of pH (6.2–7), while HPPs Chopim, Guaricana, Melissa, Rio dos Patos, Salto Caxias, Salto do Vau and Foz do Areia showed neutral pH (around 7.0) and the HPPs Capivari, Cavernoso, Chaminé, Pitangui and São Jorge were slightly alkaline in average (7.5–9.6). The HPPs Mourão, Santa Clara and Segredo showed wide pH range (6–9).

The conductivity ranged between 14 and 79 µS cm^{-1}, with narrow range in the most of the reservoirs, except by Foz do Areia (43–73, mean 55 µS cm^{-1}). The HPPs Apucaraninha, Chaminé, Chopim, Fundão, Guaricana, Jordão, Mourão, Santa Clara and Salto do Vau showed lower mean values of conductivity (14–40 µS cm^{-1}), while Cavernoso, Melissa, Pitangui, Salto Caxias and Segredo had intermediate values (40–50 µS cm^{-1}) and Capivari, Rio dos Patos, São Jorge and Foz do Areia had higher conductivity (50–79 µS cm^{-1}). Dissolved oxygen was higher than 5 mg L^{-1} in almost all sampling units, showing that these reservoirs are usually well oxygenated.

In the most of reservoirs, low concentrations of total P was found (<0.01–0.05 mg L^{-1}), except by Pitangui (0.03–0.06 mg L^{-1}), Rio dos Patos (0.05–0.08 mg L^{-1}) and Melissa (0.04–0.29 mg L^{-1}). Regarding nitrate content, it ranged between <0.03 and 0.99 mg L^{-1}, with lowest concentrations recorded in Apucaraninha, Cavernoso, Chaminé, Guaricana, Mourão, Pitangui and São Jorge, mainly during summer but occasionally during spring and fall; highest values were found in Melissa, Rio dos Patos, Segredo and Foz do Areia during summer and spring periods.

The chlorophyll a content was also a disparate variable among these environments. The HPPs Pitangui and São Jorge had mean values of chlorophyll a above 20 µg L^{-1}, showing summer maxima. Capivari, Chaminé, Foz do Areia, Guaricana and Segredo showed mean values of chlorophyll a between 5 and 11 µg L^{-1}, with peaks occurring during summer (Cap, Cha), spring (Gua, Seg), or fall (Foz). The HPPs Chopim, Fundão, Jordão and Salto Caxias had low chlorophyll a content (always < 5 µg L^{-1}) during the studied period.

The first two axis of the PCA ordination for 17 environmental variables explained 36.78% of data variability (Fig. 2). Total solids (r=0.44), total phosphorus (r=0.43) and turbidity (r=0.37) were the principal variables in the composition of axis 1 (20.44%), while molar N:P ratio (r=-0.80), depth (r=-0.53) and nitrogen compounds were the most important variables for axis 2 (16.35%). In general, the sampling units have been distributed in the first axis based on suspended material content and P availability, with the most of transparent-water reservoirs in an extreme and the turbid Melissa in the other one. With respect to second axis, the units were plotted based on depth and nitrogen availability, with the deep and N-rich reservoirs Foz do Areia and Segredo in an extreme, and the shallow and low N-content reservoirs São Jorge and Pitangui in the other one.

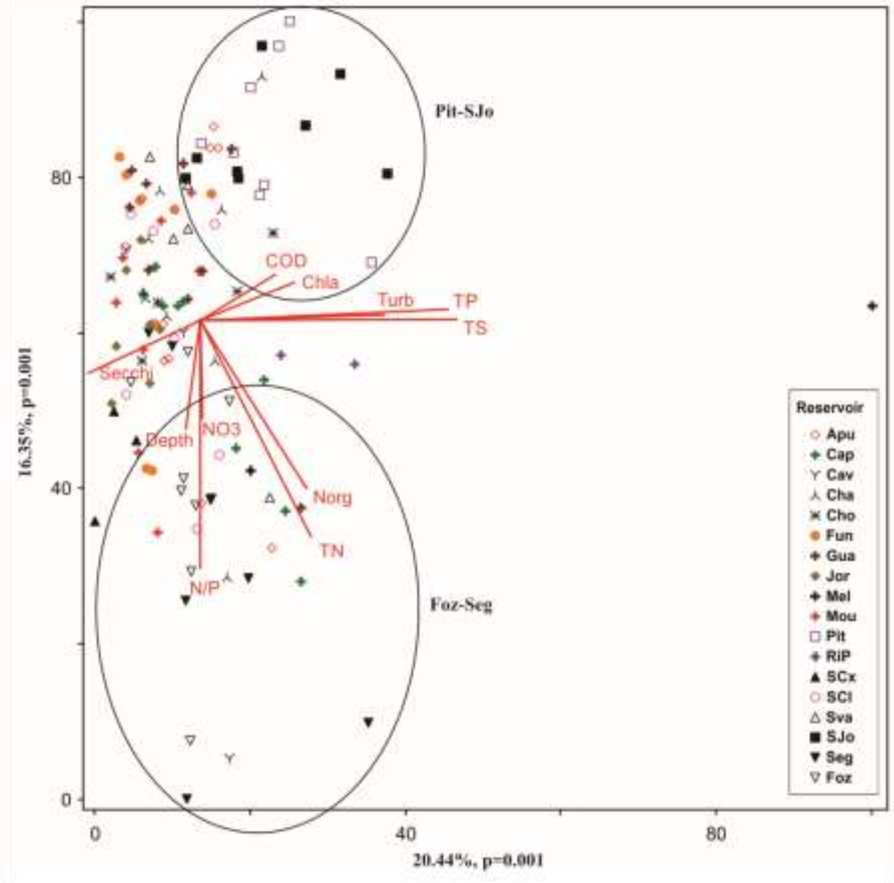

Fig. 2 PCA ordination diagram of the environmental variables and sampling units of the reservoirs from Paraná, during dinoflagellate occurrence. Chla= chlorophyll a, COD= chemical oxygen demand, Depth= depth of the sampling station, NO3= nitrate, Norg= inorganic nitrogen, N/P= molar N:P ratio, TN= total nitrogen, TP= total phosphorus, TS= total solids, Turb=turbidity. See Table 1 for reservoirs code.

Dinoflagellates occurrence and abundance

Dinoflagellates were a minority but a present component of phytoplankton community in the most of reservoirs. They occurred in all samples from HPPs Apucaraninha, Capivari, Chaminé, Fundão, Guaricana and Mourão. The lower frequencies were observed in Cavernoso (38% of the samples), Salto Caxias (30%), Melissa and Rio dos Patos (both 22%).

The dinoflagellate biomass ranged from 0.2 to 11903.6 µg L^{-1} (mean 284.6 µg L^{-1}, SD 1278.3 µg L^{-1}). The higher biomasses were recorded in two reservoirs having more retention time, namely Chaminé (mean 1601.4 µg L^{-1}) and Capivari (mean 1544.9 µg L^{-1}), while the lower ones were observed in lotic environments (HPPs Rio dos Patos, Cavernoso, Salto do Vau, Chopim and Melissa). Higher mean values of biomass (130–1600 µg L^{-1}) was found in reservoirs with intermediate depth (10–30 m), moderate mean biomasses (25–45 µg L^{-1}) occurred in the deepest reservoirs (60–130 m), and lower biomasses (up 14 µg L^{-1}) were observed in the shallow ones (<10 m). Dinoflagellates were also more abundant in meso- to eutrophic systems, when compared to oligotrophic ones (Fig. 3).

Dinoflagellate biomass had weak correlations to environmental variables when all reservoirs were considered together. The only significantly correlations ($p<0.05$) was with pH ($r= 0.27$) and chlorophyll a ($r= 0.26$). In order to explore specific relationships in each environment, we performed correlation analysis by reservoir (Table 2). Positive correlation between dinoflagellate biomass and chlorophyll a has been found in HPPS Capivari, Chaminé, Foz do Areia and Fundão. Nitrogen compound had also significant correlations. In Foz do Areia, the deepest reservoir, fluctuations in the water level were inversely correlated to dinoflagellate abundance.

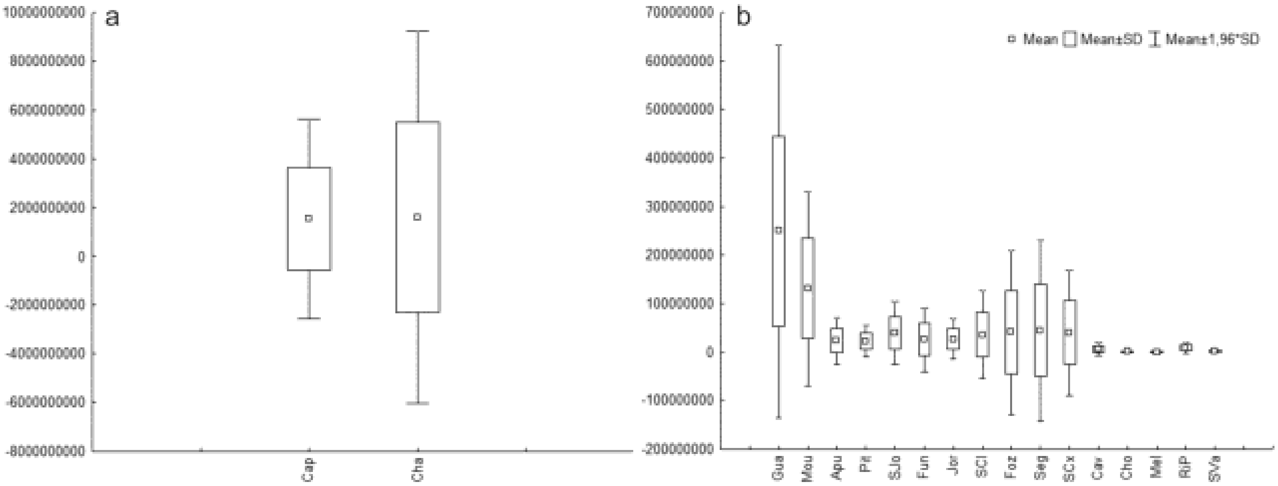

Fig. 3 Variation of dinoflagellate biomass in reservoirs from Paraná. **a**. HPPs Capivari and Chaminé. **b**. Other reservoirs. Codes were given in Material and Methods and Table 1.

The selected environmental model indicated phytoplankton density, water transparency (Secchi) and conductivity as the most explanatory variables on the dinoflagellate biomass variability ($p=0.005$). The spatial model selected included six spatial vectors (1, 3, 5, 6, 9 and 11). Partial RDA showed that pure environmental (17%, $p=0.001$) and pure spatial (9%, $p=0.001$) components explained 26% of the dinoflagellate biomass variation (Fig. 4). High spatially structured environmental fraction was observed (32%).

Twelve dinoflagellate taxa were found in this study: *Ceratium furcoides*, *Glochidinium penardiforme* (Lindemann) Boltovskoy, *Gymnodinium fuscum* (Ehrenberg) Stein, *G. mirabile* Penard, *Parvodinium africanum* (Lemmermann) Carty, *P. umbonatum* group, *Peridiniopsis cunningtonii* Lemmermann, *P.* cf. *kevei* Grigorszky et Vasas, *Peridinium gatunense*, *P. volzii* Lemmermann, *Tyrannodinium edax* (Schilling) Calado and one unidentified dinoflagellate. The richness was from nine taxa on the HPPs Jordão, Pitangui and São Jorge until one taxon on the HPPs Melissa. Significant ($p<0.05$)

correlations between species biomass and environmental variables considering all data set were summarized in Table 3.

Table 2 Pearson correlation values ($p<0.05$) between dinoflagellate biomass (DINO) and environmental variables (Norg= inorganic nitrogen, DO= dissolved oxygen, TN= total nitrogen, N:P= molar N:P ratio, Chla= chlorophyll a, Depth= depth of the sampling station, Temp= temperature, Phyto_dens= denstity of phytoplankton, Pweek= accumulated precipitation in a week, Cond=conductivity, NO_3= nitrate).

Reservoirs	Variables	DINO
Apucaraninha (n=9)	Norg	0.68
Capivari (n=9)	DO	0.75
	TN	0.81
	Norg	0.79
	N;P	0.79
	Chla	0.94
Chaminé (n=9)	pH	0.69
	Chla	0.98
Foz do Areia (n=8)	Depth	-0.99
	Chla	0.96
Fundão (n=8)	Chla	0.72
Guaricana (n=9)	Temp	0.68
	Phyto_dens	0.68
Pitangui (n=8)	DO	0.78
Santa Clara (n=8)	Pweek	-0.73
São Jorge (n=8)	N:P	0.85
Segredo (n=8)	Cond	-0.91
	NO_3	0.77

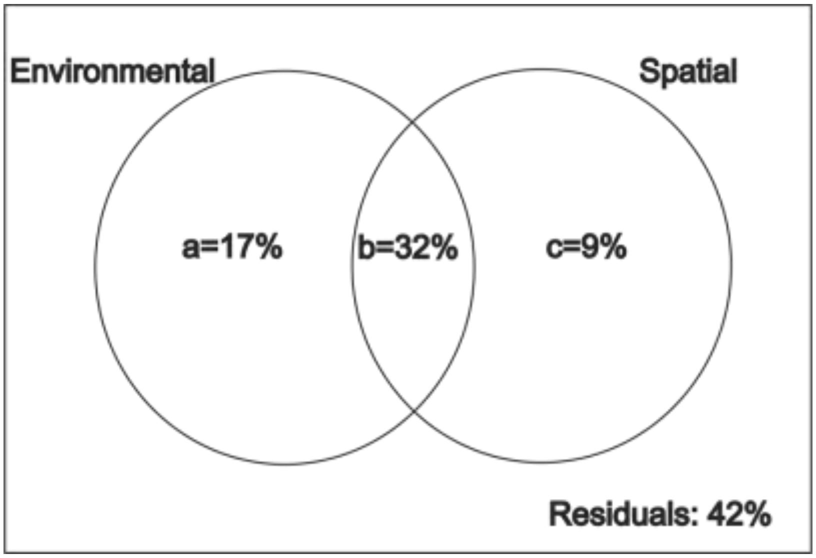

Fig. 4 Adjusted coefficients of determination (R^2_{adj}) of environmental and spatial fractions that explain the dinoflagellate biomass. [a] and [c] were significant (p=0.001) by Monte Carlo test.

Parvodinium umbonatum group was the widest distributed taxon, present in all reservoirs and all seasons. It occurred throughout the range of environmental variation sampled (Table 4). The highest biomasses were recorded in Guaricana (summer 2012, 133 µg L^{-1}), Mourão (summer 2011, 99 µg L^{-1}), Santa Clara (summer 2012, 95 µg L^{-1}) and Apucaraninha (fall 2012, 74 µg L^{-1}, Fig. 5a). Biomass of *P. umbonatum* group were specifically related to organic nitrogen in Apucaraninha (r= 0.69); total solids (r= -0.97), total P (r= -0.95), nitrate (r= -0.88), COD (-90) and phytoplankton density (r= 0.99) in Chopim; pH in Fundão (r= -0.92); dissolved oxygen in Jordão (r=-0.76) and weekly precipitation in Santa Clara (r= -0.87). *P. africanum* occurred in nine environments (Fig. 5b), with higher abundance recorded during summer 2013 in São Jorge (41 µg L^{-1}) and Pitangui (31 µg L^{-1}). Indicator Species Analysis showed *P. africanum* as a typical summer

Table 3 Pearson correlation matrix ($p<0.05$) between environmental variables and dinoflagellate taxa considering all data set (Depth= depth of the sampling station, Secchi= water transparency, TS= total solids, Pday= precipitation in the sampling day, Pweek= accumulated precipitation in a week of sampling, Temp= temperature, Cond=conductivity, NO_3= nitrate, TN= total nitrogen, Norg= organic nitrogen, COD= chemical oxygen demand, Chla= chlorophyll a, Phyto_dens= phytoplankton density, Phyto_rich= phytoplankton richness, Cfurc= *C. furcoides*, Gpena= *G. penardiforme*, Gfusc= *G. fuscum*, Gmira= *G. mirabile*, Pafri= *P. africanum*, Pumbo= *P. umbonatum* group, Pcunn= *P. cunningtonii*, Pkeve=*P.* cf. *kevei*, Pvolz= *P. volzii*, Tedax= *T. edax*, Undino= unidentified dinoflagellate).

	Cfurc	Gpena	Gfusc	Gmira	Pafri	Pumbo	Pcunn	Pkeve	Pvolz	Tedax	Undino
Depth				0.18							
Secchi								-0.21			
TS						-0.24					
Pday							0.46			0.65	
Pweek			0.20				0.19			0.26	
Temp		0.27						-0.19			
pH	0.27			-0.20	0.20						
Cond	0.19		-0.23			-0.32					
NO_3		-0.19	-0.23								0.19
TN			-0.18						0.25		
Norg									0.31		
COD					0.27				0.19		
Chla	0.25				0.53		0.34			0.38	
Phyto_dens					0.50		0.48			0.56	
Phyto_rich		0.33					0.30	0.25		0.32	0.29
Pumbo		0.18									
Pkeve											0.22
Tedax							0.77				

taxon (IV= 19.6, p= 0.001). *P. africanum* and *P. umbonatum* group biomasses were strongly related in almost all reservoirs where both species co-occurred.

Peridinium species found in this study had somewhat distinct ecological preferences. *P. gatunense* was widely distributed, occurring in 12 reservoirs (Fig. 5c). Maxima biomasses were observed in Guaricana (fall 2013, 295 µg L^{-1}) and Chaminé (winter 2011, 73 µg L^{-1}; fall 2011, 53 µg L^{-1}). Indicator Species Analysis showed *P. gatunense* as a typical taxon in Chaminé reservoir (IV= 20.8, p= 0.001). Biomass of *P. gatunese* was related to weekly precipitation in Apucaraninha (r= 0.74); turbidity (r= 0.67), dissolved oxygen (r= 0.71), nitrate (r= 0.86) and COD (r= 0.68) in Capivari; turbidity in Chaminé (r= 0.81); total N (r= -0.83) and chlorophyll a (r= 0.85) in Mourão; and total P in Segredo (r= 0.84). It was associated to biomass of *C. furcoides* in Capivari (r= 0.74), *G. mirabile* in Fundão (r= 0.90), Guaricana (r= 1.0), Jordão (r= 0.96) and Segredo (r= 0.87) and to *G. penardiforme* in Santa Clara (r= 0.98). *P. volzii* had a more restrict distribution, found in five reservoirs (Fig. 5d), sometimes co-occurring with *P. gatunense*. The highest biomasses were recorded in Guaricana (spring 2012, 307 µg L^{-1}; fall 2012, 104 µg L^{-1}) and Mourão (summer 2012, 115 µg L^{-1}). In Guaricana, *P. volzii* was related to organic N (r=0.98) and COD (r=0.70), while in São Jorge positive correlations with daily (r=0.92) and weekly (r=0.74) precipitation, molar N:P ratio (r=0.83), organic N (r=0.73) and phytoplankton density (r=0.72). It was associated to *G. penardiforme* (r=0.94) and unidentified dinoflagellate (r=0.94) in Jordão; and *T. edax* (r=0.93) and *P. cunningtonni* (r=0.88) in São Jorge. Both *Peridinium* species typically occurred in samples with low turbidity (Table 4).

Ceratium furcoides had been first detected in HPP Capivari during spring 2011 and it was recurrent since then. Thereafter it colonized Chaminé (since winter 2012), Foz do Areia, Segredo and Salto Caxias (summer-fall 2013). In Chopim, it was detected only during winter 2012, without persistence in this reservoir. The highest biomasses were recorded in Chaminé (11,869 µg L^{-1}) and Capivari (3,719 µg L^{-1}) during summer 2013 (Fig. 5e). Initial populations often had higher proportion of large three-antapical horns cells, which were reduced in subsequent samples. In Capivari, *C. furcoides* abundance was related to chlorophyll a (r=0.94), total N (r=0.81), molar N:P ratio (r=0.79) and dissolved oxygen (r=0.74), while in Chaminé, correlated to chlorophyll a (r=0.98) and pH (r=0.70). The presence of *C. furcoides* was often associated to *P. gatunense* co-occurrence in the invaded reservoirs.

Gymnodinium fuscum occurred in nine reservoirs (Fig. 5f), at low conductivity and high organic N content (Table 4). Maxima biomasses were observed during summer 2011 in Chaminé (618 µg L^{-1}), Guaricana (509 µg L^{-1}) and Mourão (211 µg L^{-1}). Specific relationships were found with dissolved oxygen in Guaricana (r= 0.71), COD in Jordão (r= 0.78), organic N in Mourão (r= -0.77) and phytoplankton richness in Foz do Areia (r= 0.71). This species was associated to biomass of *G. penardiforme* in Pitangui (r= 0.82) and Foz do Areia (r= 0.74) and to *P. africanum* in Guaricana (r= 0.69). *G. mirabile* was found in seven reservoirs (Fig. 6a), at slightly acidic pH and narrower range of conductivity than *G. fuscum* (Table 4). Higher biomasses were observed in Jordão (fall 2011, 30 µg L^{-1}; winter 2011, 28 µg L^{-1}) and Santa Clara (spring 2011, 28 µg L^{-1}). Biomass of *G. mirabile* was related to turbidity in Apucaraninha (r= 0.87); COD (r= 0.87) and total N (r= -0.73) in Foz do Areia; molar N:P ratio in Santa Clara (r= 0.89) and total P in Segredo (r= 0.73).

Glochidinium penardiforme was broadly distributed but occurred in low abundances, always at low turbidity (Table 4, Fig. 6b) and during summers the higher values. Indicator Species Analysis has showed *G. penardiforme* as a typical summer taxon (IV= 30.3, p= 0.001). Biomass of this species was related to dissolved oxygen (r= -0.70) and total solids (r= -0.69) in Apucaraninha; COD in Pitangui (r= 0.73) and weekly precipitation in Mourão (r= 0.71) and Santa Clara (r= -0.74). *Tyrannodinium edax* was found occasionally in seven reservoirs, during periods of low turbidity, neutral to alkaline pH and high organic N content (Table 4, Fig. 6c). Biomass of *T. edax* was related to molar

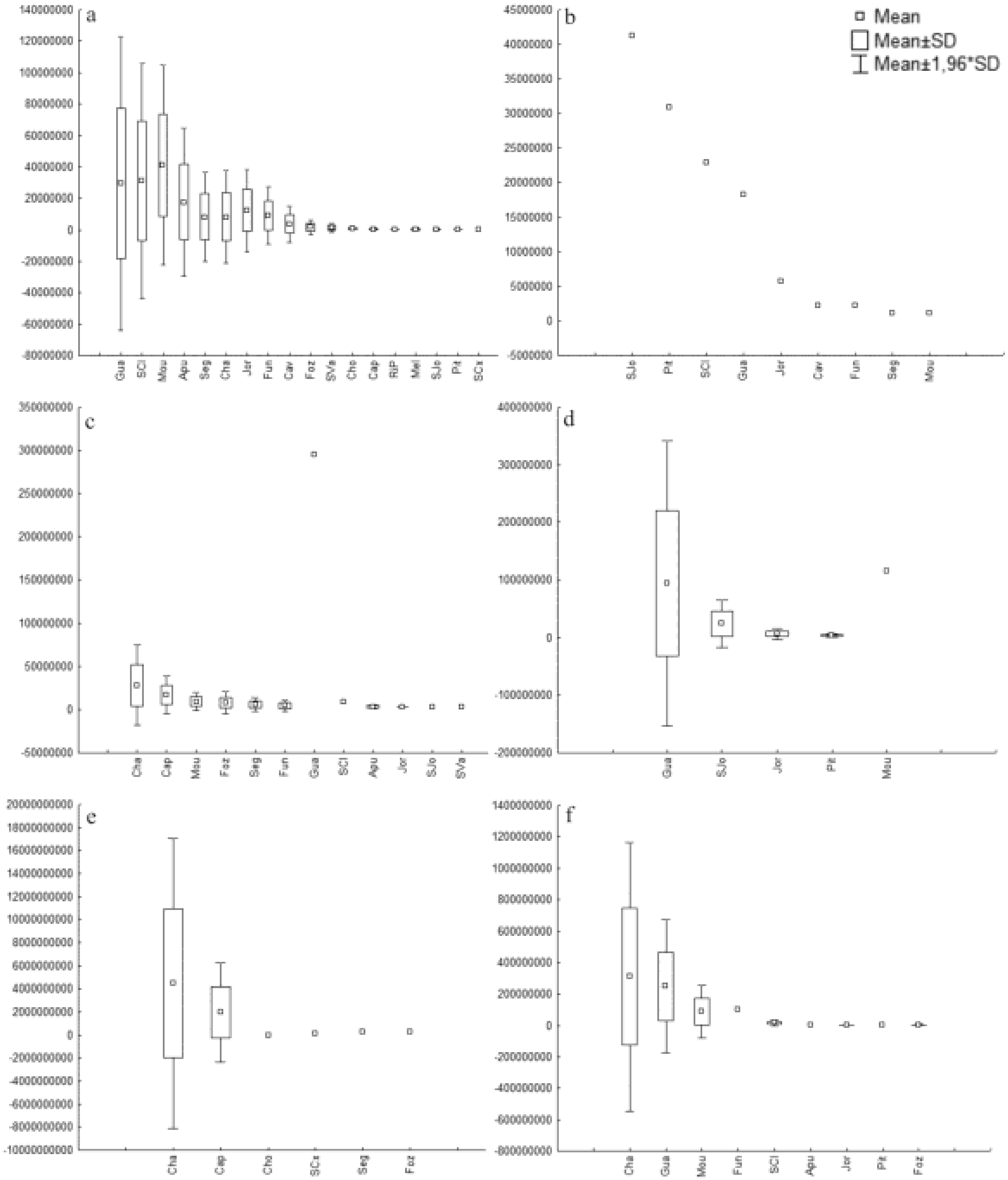

Fig. 5 Biomass variation of each dinoflagellate taxa by reservoir. **a** *Parvodinium umbonatum* group. **b** *P. africanum*. **c** *Peridinium gatunense*. **d** *P. volzii*. **e** *Ceratium furcoides*. **f** *Gymnodinium fuscum*. Codes of reservoirs are indicated in Table 1.

N:P ratio (r= 0.98) and organic N (r= 0.94) in Pitangui; organic N (r= 0.71) in São Jorge and turbidity (r= 0.74) in Segredo. It was associated to *P. cunningtonii* (r= 0.98) and *P. volzii* (r= 0.93) in São Jorge and to unidentified dinoflagellate (r= 0.98) in Pitangui.

Peridiniopsis cf. *kevei* was a common dinoflagellate species in Pitangui and São Jorge reservoirs. It occurred once in Fundão and Jordão reservoirs, in spring of 2011 (Fig. 6d). Its higher biomasses was recorded during winter 2012 in São Jorge (47 µg L^{-1}) and spring 2011 in Pitangui (44 µg L^{-1}). In Pitangui, *P.* cf. *kevei* was related to turbidity (r= 0.84) and temperature (r= -0.76), while in São Jorge it was related to pH (r= -0.82), temperature (r= -0.73), and associated to *P. umbonatum* (r= 0.79) and unidentified dinoflagellate (r= 0.74). *P. cunningtonii* was a rare species, found only in three samples from São Jorge and Pitangui reservoirs in summer and fall of 2012 (Fig. 6e). It was found during high density and richness of the phytoplankton in those environments (Table 3). Finally, one species could not be identified in light microscopy and then it was referred as “unidentified dinoflagellate”. It occurred sporadically in 14 reservoirs (Fig. 6f), with higher biomasses recorded in São Jorge (winter 2012, 13 µg L^{-1}), Foz do Areia (winter 2012, 12 µg L^{-1}), Rio dos Patos (spring 2012, 12 µg L^{-1}) and Chaminé (winter 2012, 12 µg L^{-1}). Its biomass was correlated to temperature in São Jorge (r= -0.80); total solids in Fundão (r= 0.85) and Santa Clara (r= 0.80); daily and weekly precipitation in Mourão (r= 1.0 and 0.86, respectively) and Pitangui (r= 0.97 and 0.78); chlorophyll a in Mourão (r= 0.72); organic N (r= 0.91), molar N:P ratio (0.96) in Pitangui; conductivity (r= -0.88) and water transparency (secchi, r= -0.85) and Santa Clara. It was associated to *G. penardiforme* (r= 1.0) and *P. volzii* (r= 0.94) in Jordão, *G. penardiforme* in Mourão (r= 0.72), *T. edax* in Pitangui (r= 0.98), *P.* cf. *kevei* (r= 0.74) and *P. umbonatum* (r= 0.73) in São Jorge.

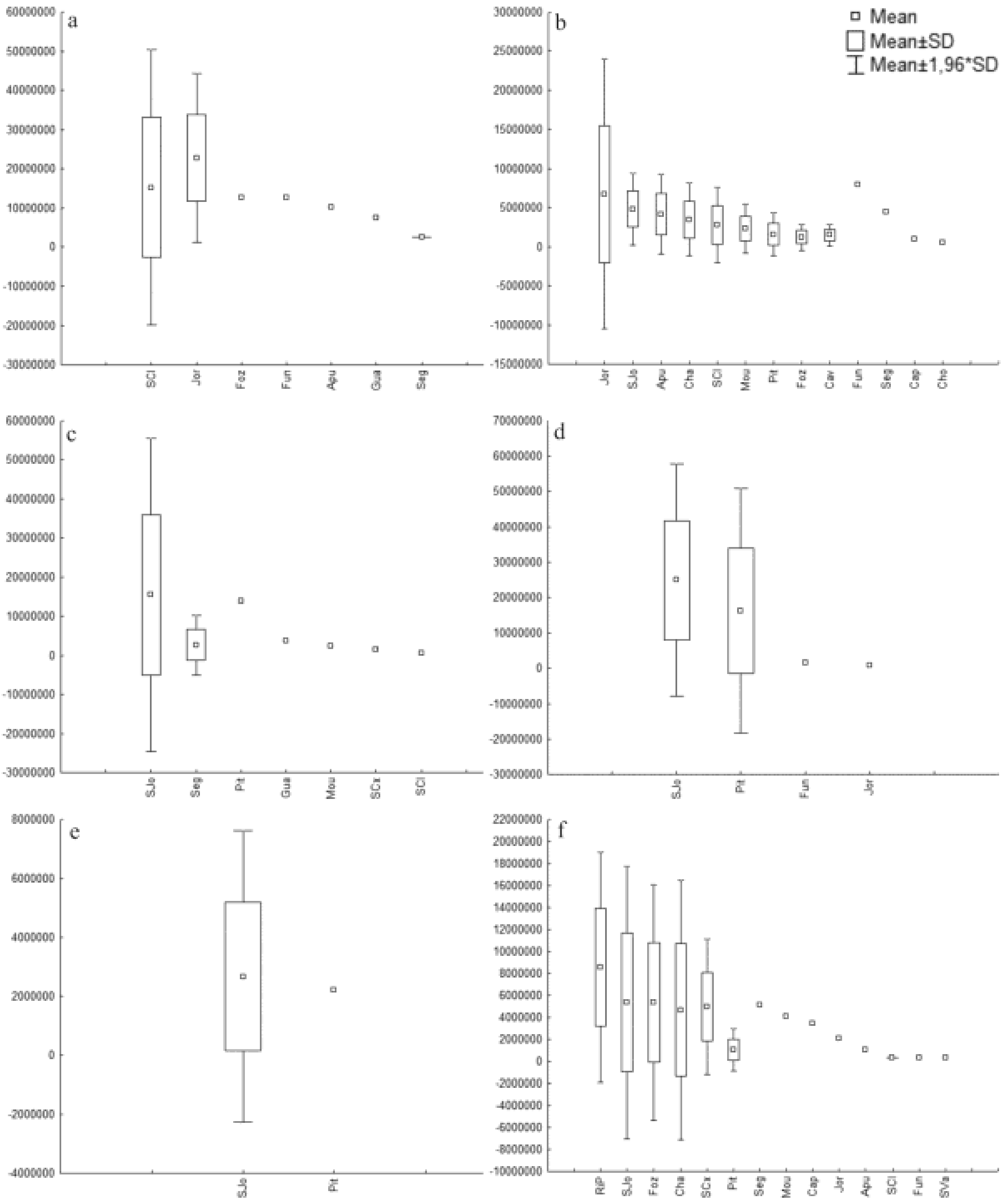

Fig. 6 Biomass variation of each dinoflagellate taxa by reservoir. **a** *Gymnodinium mirabile*. **b** *Glochidinium penardiforme*. **c** *Tyrannodinium edax*. **d** *Peridiniospsis* cf. *kevei*. **e** *P. cunningtonii*. **f** unidentified dinoflagellate. Codes of reservoirs are indicated in Table 1.

Table 4 Range of environmental variables for each dinoflagellate taxon. n = samples. Codes environmental variables are indicated in Table 3.

Taxa	n	Secchi (m)	Temp (°C)	Turb (NTU)	DO (mg L^{-1})	pH	Cond (µS cm^{-1})	TP (mg L^{-1})	NO_3 (mg L^{-1})	Norg (mg L^{-1})	COD (mgO_2 L^{-1})
C. furcoides	14	0.55–3.15	16.2–28.3	1–9	5.5–9.1	6.9–8.6	29–79	<0.01–0.05	0.03–0.78	0.01–2.79	<2.0–15.6
G. penardiforme	36	0.50–3.00	17.2–29.2	1–16	5.0–9.0	6.6–8.8	21–65	<0.01–0.06	<0.03–0.71	0.03–3.46	2.0–28.9
G. fuscum	23	0.35–3.00	15.3–29.2	1–27	4.6–10.0	6.3–8.6	14–55	<0.01–0.05	<0.03–0.65	0.21–1.90	2.0–27.4
G. mirabile	11	0.80–3.00	15.8–25.2	1–18	6.4–9.4	6.2–7.6	26–51	0.01–0.05	0.06–0.60	0.11–2.18	<2.0–14.1
P. africanum	9	0.35–2.70	22.6–27.6	1–15	4.6–9.3	6.8–8.8	19–58	0.01–0.03	<0.03–0.65	0.35–2.04	<2.0–23.1
P. umbonatum group	85	0.05–3.00	13.0–29.2	1–74	3.5–13.5	6.2–8.6	15–79	<0.01–0.29	<0.03–0.99	0.01–3.46	<2.0–27.4
P. cunningtonii	3	0.60–1.00	21.8–24.5	2–4	6.4–7.0	7.5–8.2	55–63	0.03–0.05	<0.03–0.10	0.03–1.38	11.9–14.9
P. cf. *kevei*	12	0.50–1.25	15.6–24.5	2–17	5.7–9.3	7.1–8.2	25–63	<0.01–0.06	<0.03–0.37	0.03–1.19	<2.0–27.4
P. gatunense	42	0.60–3.00	13.0–29.2	1–10	4.7–13.5	6.2–9.6	14–79	<0.01–0.05	<0.03–0.65	0.03–3.46	<2.0–19.1
P. volzii	16	0.35–2.50	15.6–28.4	1–15	4.6–9.3	6.8–8.8	19–58	0.01–0.05	<0.03–0.39	0.35–3.43	4.5–23.1
T. edax	10	0.55–3.70	17.3–29.2	1.0–9.6	5.4–9.3	7.0–8.8	21–58	<0.01–0.05	<0.03–0.60	0.49–1.78	4.5–22.6
Unidentified dinoflagellate	24	0.30–3.15	13.0–25.6	1–12	5.2–10.5	6.7–8.1	14–68	<0.01–0.08	<0.03–0.72	0.04–3.12	2.5–26.4

Discussion

Turbulence was an important factor influencing dinoflagellate distribution in Paraná hydroelectric power plants. Dinoflagellate biomass was more relevant in plankton from environments with high retention time and thermal stratification during warmer months, with complete mixing periods, when compared to deep and meromictic reservoirs from Iguaçu River Basin or typically lotic and turbulent ones. According to Pollingher & Hickel (1991), turbulence is necessary for population growth of dinoflagellates, since it resuspend resting cysts from sediment. Then, holomictic reservoirs ensure the annual dynamics of populations of cyst-producing species. However, high turbulence has negative effects on division rate in this group (Pollingher & Zemel, 1981). Thus, intensity and duration of mixing periods, followed by stability in the water column, determine the success and temporal dynamics of dinoflagellates in different water bodies.

Habitat preferences and environmental controlling factors for freshwater dinoflagellates occurrence are still controversial. In this study, fluctuations on dinoflagellate biomass were mainly associated to turbulence, water transparency, pH, conductivity and phytoplankton density. Grigorszky et al. (2003) identified temperature and organic matter as the most related factors to distribution of dinoflagellates in 86 water bodies from Hungary. In high mountain alpine lakes, the dinoflagellate distribution was driven by a combination of thermal stratification, altitude, alkalinity, dissolved P and, in a lesser extent, by lake depth and nitrate (Tolotti et al., 2003). In the subtropical Feitsui reservoir (Taiwan), the dinoflagellate abundance was associated to increase of phosphorus, total organic carbon, biochemical and chemical oxygen demand (Wu & Chou, 1998). Many authors highlighted the importance of temperature (Pollingher & Hickel, 1991; Calliari et al., 2004b; Canion & Ochs, 2005; Cardoso & Torgan, 2007) and dissolved oxygen (Pollingher, 1988; Canion & Ochs, 2005) for the dinoflagellate growth, indicating the seasonality to be important to abundance of them. According to Pollingher & Hickel (1991), dinoflagellates find unfavorable conditions for reproduction during summer in subtropical Lake Kinneret and during winter in temperate lakes. This pattern was not observed in reservoirs from Paraná, since peaks of biomass was found in different seasons, depending on the species. Distinct relationships among dinoflagellates and environmental variables in different regions of the world reflect their occurrence as minor component of the phytoplankton. It is expected that rare species have a more restrict range of environmental preferences than common ones (Heino & Soininen, 2006). Higher densities of rare species are related to optimal conditions (with narrow range) of many environmental factors (climatic, abiotic and biotic ones) interacting with each other. These optimal conditions are dependent of intrinsic limnological interactions that occur in each water body. For this reason, it is difficult to predict a clear pattern of occurrence of minor groups, such as dinoflagellates. By analyzing 18 reservoirs different in morphology, hydrology and trophy, we could note that specific relationships in each environment are stronger that general patterns among dinoflagellates occurrence and limnological variables.

Regarding nutrient availability, dinoflagellates showed positive association with N compounds in HPPs Apucaraninha, Capivari, São Jorge and Segredo. Organic nitrogen sources can be facilitators of dinoflagellates growth, especially under nutrient stress conditions (Cardoso et al., 2010; Flaim et al., 2010). We have detected weak associations between dinoflagellate biomass and total phosphorus; however, highest biomasses usually have occurred at low P content, as reported in other studies (Canion & Ochs, 2005; Oda & Bicudo, 2006; Niesel et al., 2007; Cardoso et al., 2010). Some strategies attributed to dinoflagellates as high motility, mixotrophic nutrition and ability to store P are related to the success of this group at low P levels (Niesel et al., 2007; Cardoso et al., 2010).

In this study, we showed that both environmental and spatial factors were significant in structuring dinoflagellate communities in Paraná reservoirs. Indeed, the effects of environmental conditions were predominant, supporting our prediction. This pattern is often found in some works about freshwater phytoplankton structure, by using similar approaches (Soininen et al., 2007; 2011). There are also studies showing that only environmental component explained the phytoplankton structure (Vanormelingen et al., 2008; Mazaris et al., 2010; Padial et al., 2014; Huszar et al., 2015) or showing no spatial or environmental structure for the phytoplankton (Nabout et al., 2009). Spatial structure of the planktonic communities is particularly explained by landscape connectivity and dispersal mechanisms (Padial et al., 2014). In reservoirs from Paraná, the most abundant dinoflagellate taxa were also widely distributed, suggesting their high potential for dispersal, which justifies the greater influence of the environmental effects on the dinoflagellate populations. In addition, broader geographic scales tend to have stronger spatial signals, since they involve historical and evolutionary processes occurring in those communities (Soininen, 2007). Significant spatial signal and high percentage of fraction *b* (showed in Fig. 4) indicates that dinoflagellate biomass was not randomly distributed, but spatially structured by environmental factors.

Autecology of the species

Parvodinium umbonatum group was the widest distributed taxon in this study, suggesting broad environmental tolerance. This result agrees with the ecological requirements of *Parvodinium* spp. found in the literature (Grigorszky et al., 2003; Calliari et al., 2004a; Cardoso et al., 2010). It was tolerant to high turbidity values, the only dinoflagellate recorded in the turbid HPP Melissa. This affinity to high turbidity has been recorded in other Brazilian subtropical reservoirs (Cardoso et al., 2010). Seasonal variation of this species complex has been evaluated in distinct tropical and subtropical Brazilian water bodies. *Parvodinium umbonatum* has often reached maximum abundance in the end of dry season and early rainy season (Gomes et al., 2010;

Cardoso & Torgan, 2005). However, biomass peak of *P. umbonatum* has been found during dry season, at cold temperature and low nutrient content, in an oligotrophic tropical reservoir (Oda & Bicudo, 2006). In the present study, higher densities were observed during summer and fall, at low precipitation. Negative correlations with nutrient content were found as a trend in the majority of studied reservoirs, but it was significant only in HPP Chopim. It suggests that *P. umbonatum* group, although occurs in wide environmental variation, prefers condition of low nutrient availability. The tolerance displayed by this group could be an effect of its taxonomic problematic. This is a complex of morphologically similar species whose diacritic features are still under review (Cavalcante et al., in press). Molecular data have revealed that there are cryptic species included in this group (Hansen & Flaim, 2007), but morphological characterization of these species is a challenging task, especially in counting analyses for ecological purposes. In this way, ecological information of closely related species, which may have more restrict niches, are hidden in a concept of high environmental tolerance, when they are considered together.

Peridinium gatunense was a generalist taxon in Paraná reservoirs. It had wide range of environmental variation and showed weak relationships with the limnological variables analyzed. In well-studied Lake Kinneret, historical data of *P. gatunense* blooms indicated few significant relationships among dinoflagellate abundance and environmental factors sampled (Roelke et al., 2007; Zohary et al., 2012). High biomass was observed in meso-eutrophic reservoirs with low conductivity in our study, unlike Lindström (1991), which identified high growth rate of *P. gatunense* under high conductivity (140 µS cm^{-1}). Preference for moderate temperature and neutral to alkaline pH, as observed here, seems to be common for this species in subtropical water bodies from southern Brazil (Cardoso & Torgan, 2005; 2007; Cardoso et al., 2010). *Peridinium volzii* was more restricted in distribution and environmental preference than *P. gatunense*, with evident affinity to nitrogen compounds. It is known that nitrogen content induces sexual reproduction in *P. volzii* (Pfiester & Skvarla, 1979). Ecological characterization provided by Höll (1928) and Olrik (1992) agrees with our findings for this species. Typical of transparent waters and sensitive to high organic matter content, *P. volzii* prefers to grow under oligo-mesotrophic conditions. Despite of it is not a stenothermic species, higher biomasses of *P. volzii* occurred in warm seasons and alkaline pH.

Ceratium furcoides has been a successful invader in water bodies from Paraná since late 2011 (Cavalcante et al., 2013). Recent studies have showed that optimal conditions for growth and bloom formation of this species include temperature between 15 and 25°C, high organic matter content, alkaline pH and well-oxygenated waters. South American subtropical reservoirs offer these conditions throughout the year, thus favoring colonization and dispersion of *Ceratium* spp. in that region (Mac Donagh et al., 2005; Cavalcante et al., 2016). In the present study, we have observed that the occurrence of *C. furcoides* confirmed the environmental preferences before mentioned. It is a large species in phytoplankton and has greatly increased the chlorophyll content in the invaded systems of Paraná. Harmful effects of *Ceratium* invasion have not been evaluated yet. However, when *C. furcoides* is established, we noticed the reduction of other dinoflagellates species occurrence in the environments. *P. gatunense* was usually found co-occurring with *C. furcoides*. Interspecific competition among dinoflagellates can determine the dominance of one species in the community (Canion & Ochs, 2005). Some physiological strategies such as mixotrophy, encysting or P storage may be beneficial for some species against others.

Glochidinium penardiforme and *Parvodinium africanum* were typically related to summer periods, as in subtropical reservoirs studied by Cardoso et al. (2010). *P. africanum* is usually recorded to tropical and subtropical region (Couté & Iltis, 1984; Popovský & Pfiester, 1990; Carty, 2008; Alfinito, 2011; Alfinito & Iberite, 2013), with some reports to temperate environments (Harris, 1940; Huber-Pestalozzi, 1950). Ecological knowledge about this species is restricted (Cardoso et al., 2010). In this study we observed affinity with high temperature, positive correlation with pH, COD and phytoplankton density, showing a considerable preference of *P. africanum* for high productivity conditions. The common association between *P. africanum* and *P. umbonatum* group suggests that related species in this genus have similar ecological requirements. *Glochidinium penardiforme* is a widely distributed taxon, but often occurs in low abundance (Pollingher & Hickel, 1991; Boltovskoy, 1999; Hansen & Flaim, 2007), indicating a generalist behavior (Grigorszky et al., 2003). Preference for clear waters and high temperatures for this species has been also demonstrated by Cardoso et al. (2010). *G. penardiforme* is often reported with and without plastids (Boltovskoy, 1999; Hansen & Flaim, 2007; Cavalcante et al., in press.). Plastid origin, nutritional strategies or ultrastructural apparatus for possible predation in *G. penardiforme* are unknown, limiting the understanding on the role of the species in food web interactions.

Tyrannodinium edax is the only exclusively heterotrophic species reported in this study. Their nutritional behavior was extensively studied. It is a voracious planktonic predator that feeds on injured or dying algae, protists (including own cells) and small metazoans through a feeding tube (Calado & Moestrup, 1997). According Höll (1928), this species tolerates high organic matter content and occurs from neutral to slightly acidic pH. Calado & Moestrup (1997) pointed out that higher densities of this species occurred during autotrophic algae blooms. In reservoirs of Paraná, the species showed strong correlation with N compounds, precipitation, phytoplankton density and richness. Rainy periods can be a significant disturbance for high phytoplankton biomass, causing death of part of these organisms. We thereby postulate that the occurrence of *T. edax* in these environments was mainly related to their predatory behavior.

Gymnodinium fuscum and *G. mirabile* were the only naked species found here. Autecology of athecate species is hardly assessed, since common fixation techniques do not maintain their delicate cell structure, which becomes indistinguishable or even collapsed (Calliari et al., 2004a). The identification of both species was possible by analyzing live material and comparing with preserved samples. *G. fuscum* is considered typical in oligotrophic, low calcium content and acidic environments (Höll, 1928; Hansen & Flaim, 2007). Our results presented a larger environmental variation for this taxon. *G. mirabile* is rarely cited in recent literature due to the taxonomic confusion between this taxon and *G. uberrimum* (Allman) Kofoid et Swezy (Hanse & Flaim, 2007). Recent studies have proposed the use of the name *G. mirabile* instead of *G. uberrimum* for this taxon (Pandeirada et al., 2013; Cavalcante et al., in press). Ecological characterization of *G. uberrimum* confirms the results found in this study for *G. mirabile* (Höll, 1928; Tolotti et al., 2003; Calliari et al., 2004a; b; Niesel et al., 2007). It is an opportunistic species, with biomass peaks at different periods in the year. Although it showed wide tolerance to trophic state, preferred oligo- to mesotrophic, deep, stratified and slightly acidic environments (Tolotti et al., 2003; Niesel et al., 2007).

Peridiniopsis cf. *kevei* and *P. cunningtonii* were typically found in the eutrophic cascading system Pitangui-São Jorge. In these reservois, phytoplankton reached the highest mean richness during the studied period. It is known that more productive regions have higher biodiversity levels as resulted of the stochastic processes (Chase, 2010). Alternatively, some dinoflagellates species require concentrations of some specific micronutrients for growth (Lindström, 1991; Zohary et al., 2012). Although we have not sampled micronutrient data, we did not reject the possibility of these reservoirs have sources of particular micronutrients necessary for growth of species with more specific requirements. *P.* cf. *kevei* could not be morphologically assigned to typical *P. kevei* form in accuracy (Cavalcante et al., in press). Here we have showed additional distinct ecological relationships among these taxa. In Paraná reservoirs, *P.* cf. *kevei* had restrict occurrence and marked preference to low temperatures and water transparency, while European *P. kevei* is considered invasive bloom-forming species in geographical expansion in the last 5 years, with preference to warm waters (15–26°C), tolerant to trophic levels, nutrient content and turbulence (Grigorszky et al., 2001; Leitão et al., 2001; Kaštovský et al., 2010). Ecological preferences of *P. cunningtonii*, reported in other tropical and subtropical systems, are confirmed in our analysis. It is considered a sporadic species in those environments, occurring in low densities, especially in meso-eutrophic systems during summer (Pollingher & Hickel, 1991; Borics et al., 2005; Hansen & Flaim, 2007).

Dinoflagellates exhibit a wide variety of strategies that ensure survival, advantages under low nutrient concentrations and predation defense (Pollingher, 1988). Furthermore, they display a wide range of trophic roles in aquatic foodweb, as primary producers, grazers, predators, endossimbionts or parasites (Schnepf & Elbrächter, 1992). However, these strategies are not fully understood in the vast majority of species. In this way, more life cycle studies, linked to ultrastructural and molecular analysis are necessary in order to recognize evolutionary biological mechanisms that support the ecological strategies performed by dinoflagellate species.

This study provides an important contribution to the ecological knowledge on dinoflagellate species occurring in subtropical reservoirs. Papers about freshwater phytoplankton generally include all dinoflagellates into a single generic group, then assuming they have the same environmental requirements. Studies focusing on freshwater dinoflagellate ecology are scarce and usually limited in spatial or temporal scales, making the ecological information about this group diffuse and inconsistent. This is the first study that considers geographical distances when investigating dinoflagellate community dynamics as far we know. By covering a large-scale area in southern Brazil (ca. 360 km^2), considering hydrological and limnological distinct environments, we were able to observe seasonal, spatial and environmental factors that design dinoflagellates communities.

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Suplementary data

Appendix I. Range and mean values (in parenthesis) of physical, chemical and biotic variables of 18 reservoirs from Paraná during the studied period.

Codes of reservoirs and environmental variables are indicated in Table 1 and Table 3 respectively.

	Depth (m)	Secchi (m)	TS (mg L^{-1})	Turb (NTU)	Pday (mm)	Pweek (mm)	Temp (°C)	DO (mg L^{-1})	pH	Cond (µS cm^{-1})	TP (mg L^{-1})	NO_3 (mg L^{-1})	TN (mg L^{-1})	Norg (mg L^{-1})	COD (mg L^{-1})	N:P	Chla (µg L^{-1})
Apu	7–10 (9)	0.7–1.8 (1.1)	34–50 (40)	2–18 (7)	0–29.6 (4.1)	0–123.6 (39.0)	17.7–26.9 (21.6)	5.0–7.7 (6.7)	6.4–7.4 (7.2)	30–47(36)	<0.01–0.05 (0.03)	<0.03–0.26 (0.11)	<0.5–3.6 (1.3)	0.23–3.46 (1.13)	2.0–11.9 (5.9)	22–441 (167)	1.6–8.1 (4.8)
Cap	11–23 (16)	0.7–2.8 (1.8)	42–85 (56)	1–5 (3)	0–10.4 (3)	13.8–107.7 (55.5)	16.2–28.3 (22.0)	4.7–9.1 (6.9)	7.4–8.6 (7.7)	65–79 (71)	<0.01–0.03 (0.02)	0.19–0.44 (0.31)	<0.5–3.2 (1.4)	0.05–2.79 (0.97)	1.9–15.0 (7.1)	55–311 (156)	1.8–19.5 (7.0)
Cav	3–4 (4)	1.2–2.0 (1.5)	4–50 (30)	2–4 (3)	0–14.2 (4.7)	0–16.1 (5.6)	18.6–26.6 (23.5)	6.1–8.0 (7.0)	7.4–8.6 (7.9)	40–50 (45)	<0.01–0.02 (0.01)	0.10–0.27 (0.19)	0.8–3.5 (1.7)	0.49–3.12 (1.38)	5.0–13.1 (7.9)	110–772 (353)	1.0–5.7 (4.1)
Cha	11–15 (14)	0.6–2.7 (1.8)	33–51 (42)	1–6 (2)	0–38.7 (9.2)	0–83.2 (36.8)	15.2–25.3 (20.3)	5.2–8.8 (7.2)	6.7–8.6 (7.6)	37–46 (42)	0.01–0.03 (0.02)	<0.03–0.20 (0.10)	<0.5–2.8 (1.2)	0.23–2.70 (0.94)	5.0–19.1 (10.8)	32–441 (159)	3.6–41.6 (11.3)
Cho	3–8 (7)	0.6–3.0 (1.5)	2755 (40)	2–9 (4)	0–30 (6)	2.2-112.9 (49.9)	16.8–26.9 (22.3)	4.8–8.7 (6.6)	6.9–7.6 (7.3)	15–37 (31)	0.02–0.06 (0.04)	0.38–0.64 (0.52)	0.6–1.7 (1.2)	0.05–1.00 (0.55)	2.0–14.1 (7.7)	49–121 (73)	0.7–2.8 (1.5)
Fun	34–68 (41)	0.3–2.1 (1.2)	26–47 (34)	2–12 (6)	0–26.1 (9.3)	0–61.3 (35.7)	15.8–24.7 (20.8)	6.2–13.5 (8.7)	6.2–7.2 (6.9)	14–35 (27)	<0.01–0.04 (0.02)	0.17–0.59 (0.36)	<0.5–1.8 (1.0)	0.04–1.19 (0.55)	1.9–11.1 (5.9)	2–255 (95)	0.3–4.5 (2.4)
Gua	5–11 (8)	0.4–2.1 (1.3)	30–44 (36)	1–15 (4)	0–16.9 (3.6)	0–83.2 (44.1)	15.3–23.9 (19.4)	6.4–10.0 (8.0)	6.7–8.0 (7.4)	19–29 (25)	0.01–0.03 (0.02)	<0.03–0.20 (0.11)	0.5–3.7 (1.3)	0.32–3.43 (1.07)	3.5–18.6 (10.4)	58–287 (146)	3.4–20.8 (11.2)
Jor	54–61 (59)	0.9–2.5 (1.4)	26–38 (33)	1–10 (5)	0–26.2 (5.0)	0–76.3 (38.9)	15.8–25.1 (21.5)	4.6–9.4 (7.4)	6.2–7.1 (6.9)	24–33 (27)	<0.01–0.02 (0.01)	0.28–0.50 (0.40)	0.5–1.4 (0.9)	0.11–0.81 (0.45)	3.0–8.6 (5.7)	55–309 (159)	1.7–4.7 (3.0)

Mel	5 (5)	0.1–0.6 (0.3)	53–217 (135)	7–74 (41)	0–36.5 (18.3)	0–65.2 (32.6)	23.7–24.2 (24.0)	5.0–5.9 (5.5)	7.2 (7.2)	40–46 (43)	0.04–0.29 (0.17)	0.61–0.99 (0.80)	2.3–4.0 (3.2)	1.19–3.08 (2.14)	6.1–14.1 (10.1)	30–127 (79)	1.4–13.3 (7.4)
Mou	12–15 (14)	1.3–2.8 (2.0)	25–33 (29)	1–27 (6)	0–46.2 (6.1)	0–189.1 (53.4)	17.9–29.2 (24.7)	5.4–7.5 (6.6)	6.3–8.3 (7.5)	21–32 (26)	<0.01–0.05 (0.02)	<0.03–0.17 (0.10)	<0.5–1.8 (1.0)	0.28–1.66 (0.86)	2.0–13.1 (6.9)	22–397 (186)	1.9–7.6 (3.6)
Pit	1–4 (3)	0.5–1.0 (0.8)	41–65 (54)	2–16 (5)	0–91.2 (13.2)	0–117.9 (40.7)	15.6–23.3 (20.7)	5.7–8.1 (7.1)	7.1–8.1 (7.6)	43–58 (50)	0.03–0.06 (0.04)	<0.03–0.37 (0.16)	<0.5–2.1 (0.9)	0.19–1.78 (0.62)	7.0–27.4 (18.1)	28–116 (48)	5.6–62.8 (24.5)
RiP	3–4 (4)	0.30.6 (0.4)	64–84 (74)	7–11 (9)	0–4.8 (2.4)	10.8–13.6 (12.2)	24.6–25.0 (24.8)	5.2–5.9 (5.6)	6.7–7.2 (7.0)	63–68 (66)	0.05–0.08 (0.07)	0.62–0.72 (0.67)	1.8–2.3 (2.1)	0.88–1.41 (1.15)	9.0–14.1 (11.5)	63–79 (71)	9.1–9.7 (9.4)
SCx	62–63 (62)	2.2–3.7 (3.0)	37–53 (44)	1–6 (3)	0–0.10 (0.03)	0.2–33.3 (16.1)	20.5–23.3 (22.4)	6.8–9.0 (7.6)	7.1–7.7 (7.3)	46–48 (47)	<0.01–0.01 (0.01)	0.60–0.62 (0.61)	0.7–1.2 (1.0)	0.04–0.49 (0.30)	3.0–7.5 (5.5)	154–265 (221)	2.3–3.5 (3.0)
SCl	48–62 (56)	0.4–2.0 (1.3)	25–49 (34)	1–12 (5)	0–23.8 (4.9)	0–57 (34)	16–27.2 (21.9)	6.4–10.7 (8.0)	6.8–8.2 (7.2)	14–33 (28)	<0.01–0.06 (0.03)	0.21–0.45 (0.33)	<0.5–2.6 (1.3)	0.01–2.18 (0.88)	2.0–12.0 (7.4)	36.8–287 (109)	0.4–5.9 (3.3)
Seg	93–105 (102)	1.1–2.3 (1.6)	37–55 (46)	2–9 (5)	0–42.5 (13.2)	1.9–112.9 (49.9)	18.3–26.7 (23.4)	6.6–8.6 (7.6)	6.6–9.6 (7.5)	29–53 (46)	0.01–0.05 (0.02)	0.40–0.78 (0.56)	0.9–3.6 (2.1)	0.01–3.05 (1.44)	5.0–12.5 (8.4)	68–618 (272)	1.2–40.0 (8.8)
SJo	7–8 (8)	0.6–1.1 (0.8)	28–65 (49)	2–17 (6)	0–91.2 (13.2)	0–117.9 (40.7)	16.0–24.5 (21.6)	6.0–8.2 (7.2)	7.3–8.8 (8.0)	44–63 (52)	0.02–0.04 (0.03)	<0.03–0.26 (0.08)	0.4–1.6 (0.8)	0.03–1.38 (0.62)	6.0–28.9 (17.4)	28–95 (58)	7.6–69.4 (31.6)
SVa	1–3 (2)	0.8–1.1 (0.9)	33–48 (39)	2–11 (5)	0–42.5 (9.5)	5.8–61.3 (40.5)	13.0–23.7 (18.7)	5.5–10.5 (7.4)	6.9–7.2 (7.0)	22–33 (27)	0.02–0.03 (0.02)	0.22–0.31 (0.25)	<0.5–2.8 (1.4)	0.04–2.44 (1.04)	4.0–12.9 (8.9)	39–257 (135)	0.2–8.2 (2.5)
Foz	103–105 (105)	1.2–3.0 (2.0)	33–63 (49)	2–5 (4)	0–5.4 (2.2)	0–64.5 (36.6)	17.4–27.2 (22.0)	3.5–9.0 (6.6)	7.0–7.8 (7.5)	46–73 (55)	0.01–0.05 (0.02)	0.29–0.90 (0.61)	0.5–2.3 (1.5)	0.28–1.90 (0.89)	7.0–14.1 (9.2)	48–441 (170)	1.0–20.7 (4.9)

Considerações finais

Os dinoflagelados epicontinentais foram analisados através de estudos taxonômicos e ecológicos realizados em 53 corpos d’água localizados no sul do Brasil. Os resultados obtidos, em conjunto, expressam a mais extensa contribuição para o conhecimento deste grupo de organismos naquela região. A julgar pela carência de pesquisas sobre este grupo nas demais regiões do país, salienta-se a relevância nacional dos estudos desenvolvidos.

Certamente, o aspecto mais interessante nas pesquisas recentes sobre dinoflagelados no Brasil é o processo de invasão estabelecido por *Ceratium furcoides*. A partir das primeiras detecções, um alto interesse pelo estudo desta espécie tem sido observado, considerando o crescente número de artigos científicos publicados, e as discussões cada vez mais comuns em sessões orais e mesas redondas de congressos especializados. De fato, este fenômeno é uma preocupação nacional, tanto entre os fitoplanctólogos, quanto entre as empresas de monitoramento de mananciais e reservatórios. Trata-se de uma espécie de alta variabilidade morfológica e ambiental, adaptando-se a ambientes distintos, competindo bem com espécies nativas e expandindo a sua distribuição rapidamente. Por este motivo, mais estudos devem ser encorajados, do ponto de vista morfológico, ambiental, ecofisiológico, biogeográfico ou genético, com o intuito de tentar compreender o processo de invasão em andamento e as possíveis consequências ambientais. Os resultados obtidos aqui são um importante avanço no entendimento da colonização destas espécies na região sul do Brasil.

No **capítulo 1**, o detalhamento morfológico empregado permitiu a confirmação precisa das populações de *Ceratium* que colonizam a região, bem como a distribuição das duas espécies ocorrentes e possíveis rotas de dispersão. Este foi o primeiro estudo, baseado em microscopia de luz e eletrônica de varredura, que apresenta com segurança a ocorrência das duas espécies em território brasilero, e confirma que *Ceratium furcoides* é, de fato, a principal espécie invasora de sistemas aquáticos neste país até o momento.

No **capítulo 2**, foram indicados alguns fatores ambientais relacionados ao sucesso invasor de *Ceratium furcoides* em reservatórios subtropicais. A análise de amostras coletadas semanalmente, em dois reservatórios limnologicamente distintos, permitiu a constatação de um forte padrão sazonal na ocorrência e abundância de *C. furcoides*, junto à alta tolerância ambiental, especialmente em relação à disponibilidade de nutrientes. Várias estratégias adaptativas atribuidas a esta alga foram discutidas, então, com o objetivo de se desenhar um modelo que justifique o sucesso biológico desta espécie como invasora de ambientes subtropicais brasileiros.

O **capítulo 3** contribuiu com uma facilitação metodológica em análises de biovolume de *Ceratium*, descrevendo a variação morfológica encontrada para a espécie e padronizando a metodologia de cálculo do volume celular. São resultados relevantes tanto para atividades de rotina em monitoramentos, que queiram usar o biovolume como atributo de avaliação populacional de forma rápida e precisa, quanto para fins científicos.

No **capítulo 4**, vinte e um táxons de dinoflagelados foram descritos para o Estado do Paraná. Dezenove deles são citações novas para o Estado, treze foram citados pela primeira vez no sul do Brasil e quatro são novas citações para todo o país. Estes registros fazem do Paraná o estado brasileiro com maior número de espécies de dinoflagelados citadas até o momento. Entretanto, ainda há lacunas na dinoflora do Paraná, haja vista a quatidade de ambientes ainda inexplorados e as prováveis espécies raras que, por questões metodológicas, não foram amostradas neste estudo. Além dos aspectos florísticos mencionados, esta investigação revelou a morfologia de populações de dinoflagelados em ambientes subtropicais brasileiros, permitindo um maior conhecimento sobre a variação intraespecífica e a distribuição geográfica de táxons pouco citados, além de divulgar as atualizações nomenclaturais decorrentes de recentes revisões ocorridas. Tais informações, muitas vezes, restringem-se a artigos científicos muito especializados e à comunidade científica especializada nestes estudos.

A escassez de estudos ecológicos envolvendo grupos minoritários do fitoplâncton acarretam no desconhecimento sobre os gatilhos ambientais que determinam a ocorrência e abundância destes. Prognósticos ecológicos sobre dinoflagelados de água doce no Brasil é uma tarefa desafiadora, pois não se conhece a composição nem a distribuição das espécies para a maioria dos ambientes. Muitos estudos ecológicos realizados com dinoflagelados possui limitada escala temporal ou espacial, o que, muitas vezes, dificulta a observação de padrões de ocorrência. O **capítulo 5** apresentou um estudo em 18 reservatórios do Estado do Paraná, e registrou a ocorrência de 12 espécies de dinoflagelados e suas relações com parâmetros físicos, químicos, biológicos. Ademais, este estudo foi pioneiro em considerar fatores espaciais (distância geográfica) como estruturador das comunidades de dinoflagelados de água doce.

Em suma, os estudos realizados aqui fornecem um arcabouço consistente de informações sobre morfologia, distribuição, ocorrência, sazonalidade e fatores ambientais relacionados aos dinoflagelados, as quais servem de base para futuros estudos (sistemáticos, ultraestruturais, moleculares, biogeográficos, testes de hipóteses...), com análises mais refinadas e, consequentemente, o desenvolvimento desta área do conhecimento no país.

Finalmente, pesquisas envolvendo extensas áreas e/ou coletas com periodicidade curta são uma das questões-chave quando se faz um projeto de pesquisa.

Nós, aqui, advogamos o uso de amostras coletadas durante programas de monitoramento ambiental, geralmente de longo prazo, também para fins científicos, como um importante meio de se estudar padrões gerais de distribuição e ocorrência de espécies. Por três motivos: a) primeiro, apesar da limitação amostral (coletas para fins de monitoramento não foram realizadas em função das perguntas às quais a pesquisa se propõe a responder e, muitas vezes, a hipótese precisa ser readequada pela amostragem), o pesquisador tem acesso a um conjunto de dados abrangente, logisticamente difícil de se obter atráves de outras vias de financiamento de pesquisa, o que torna estudos em grande escala (espacial ou temporal) viáveis e com baixo custo; b) segundo, a pesquisa acadêmica em parceria com o monitoramento de ambientes permite o enriquecimento teórico para ambos os lados e atualiza as atividades rotineiras de monitoramento, estendendo-se além dos muros acadêmicos; c) por fim, grande parte das atividades de monitoramento de sistemas aquáticos no Brasil é financiada por recursos públicos, e a maioria das amostras/informações coletadas são usadas apenas em relatórios de avaliação dos ambientes. O uso destes dados para outros fins, sobretudo científicos, podem ser vistos como uma utilização consciente de recursos.