Original Paper Unraveling centric diatoms from the Caatinga: Coscinodiscophyceae and Mediophyceae in northwestern Ceará, Brazil

Maria Gabrielle Rodrigues Maciel^{1,3,5}, Kaoli Pereira Cavalcante² & Thelma Alvim Veiga Ludwig^{1,4}

Abstract

The Caatinga is the largest tropical dry forest region in South America and harbors an impressive biological diversity. However, efforts in the studies of many groups of organisms, especially aquatic ones, are very small compared to other Brazilian regions. The state of Ceará stands out due to the major concentration of surface water in the semi-arid region, and the diatom flora is virtually unknown. We performed a pioneering and extensive taxonomic study on the centric diatoms from the Caatinga, documenting the morphological variation of the species found, expanding their geographic distribution, and reviewing taxonomic and nomenclatural aspects when relevant. The study was based on planktonic and periphytic samples collected in four hydrographic basins located in the northwestern region of Ceará, northeastern Brazil. Fifteen infrageneric diatom taxa were identified, described, and illustrated using light and scanning electron microscopy. *Discostella stelligera* was first recorded for northeastern Brazil and *D. woltereckii* is a new record to the country. Diminutive centric diatoms are well represented in the samples and their taxonomy is discussed. *Terpsinoë musica* occurred in a population with high phenotypic plasticity and we discussed the related taxonomic implications. **Key words**: Bacillariophyta, intermittent water bodies, semiarid, taxonomy.

Resumo

A Caatinga é a maior região de floresta tropicalmente seca da América do Sul e abriga uma diversidade biológica impressionante. Porém, os esforços no estudo de diversos grupos de organismos, principalmente aquáticos, são muito escassos se comparados a outras regiões brasileiras. O estado do Ceará destaca-se pela grande concentração de águas superficiais no semiárido e a flora de diatomáceas é praticamente desconhecida. Realizamos um estudo taxonômico pioneiro e extenso sobre as diatomáceas cêntricas da Caatinga, documentando a variação morfológica das espécies encontradas, ampliando sua distribuição geográfica e revisando aspectos taxonômicos e nomenclaturais quando relevantes. O estudo baseou-se em amostras planctônicas e perifíticas coletadas em quatro bacias hidrográficas localizadas na região noroeste do Ceará, nordeste do Brasil. Quinze táxons de diatomáceas infra-genéricos foram identificados, descritos e ilustrados usando microscopia óptica e eletrônica de varredura. *Discostella stelligera* foi registrada pela primeira vez para o nordeste do Brasil e D. woltereckii é um novo registro para o país. Diatomáceas cêntricas diminutas estão bem representadas nas amostras e sua taxonomia é discutida. *Terpsinoë musica* ocorreu em uma população com alta plasticidade fenotípica e se discutiram as implicações taxonômicas relacionadas. **Palavras-chave**: Bacillariophyta, corpos d'água intermitentes, semiárido, taxonomia.

See supplementary material at <https://doi.org/10.6084/m9.figshare.21339363.v1>

¹ Universidade Federal do Paraná, Setor de Ciências Biológicas, Depto. Botânica, Centro Politécnico, Curitiba, PR, Brasil.

² Universidade Estadual Vale do Acaraú, Centro de Ciências Agrárias e Biológicas, Campus Betânia, Sobral, CE, Brasil. ORCID: https://orcid.org/0000-0001-7843-4114>.

³ ORCID: <https://orcid.org/0000-0002-8594-2990>.

⁴ ORCID: < https://orcid.org/0000-0003-0576-3499>.

⁵ Author for correspondence: gabrielle.r.maciel@gmail.com

Introduction

The Caatinga is an important Brazilian ecological region, recognized as the largest seasonally dry tropical forest in South America (Silva *et al.* 2017). It is predominant in the semi-arid region of northeastern Brazil, but is interspersed with remnants of humid and sub-humid areas due to elevation and ocean proximity (Bastos & Cordeiro 2012). Studies have demonstrated the vast biodiversity of the Caatinga (Leal *et al.* 2005; Albuquerque *et al.* 2012). The fauna and flora are well adapted to water shortages (Santos *et al.* 2011; Silva *et al.* 2017), but significantly affected by extensive processes of environmental change and deterioration caused by unsustainable use of its resources (Leal *et al.* 2003).

The state of Ceará includes a major concentration of surface water in the Caatinga region (Andrade et al. 2017). A large part of the state has a tropical, semi-arid climate, with high annual average temperatures, high rates of evaporation, and scarce and irregular rainfall that is restricted to a short period of the year (IPECE 2016). Consequently, most water bodies are seasonally intermittent and many were made permanent by dam construction (IPECE 2016). Concerning factors are pollution from industry, lack of basic sanitation, siltation resulting from riparian deforestation, and the numerous dams built for water retention (Moro et al. 2015). Freshwater sources are threatened by anthropogenic pressures and biodiversity is declining (Virta et al. 2019).

Diatoms are ordinary and abundant components in freshwater systems. They play important ecological roles in aquatic environments as primary producers at the base of the trophic web, which can occur in different nutrient regimes, pH, salinity, and temperature (Julius & Theriot 2010). The rapid response time to environmental changes, make diatoms reliable aquatic bioindicators often employed to assess water quality (Kelly *et al.* 1998; Lobo *et al.* 2010, 2015; Álvarez-Blanco *et al.* 2013; Lai *et al.* 2014; Stevenson 2014; Dalu & Froneman 2016).

In Brazil, diatom research is mostly concentrated in the South and Southeast, due to the greater representation of specialized research centers in these regions (Menezes *et al.* 2015). Focusing on inventories describing the diversity of diatoms in poorly studied regions of the country is crucial. The earliest studies on diatoms in northeastern Brazil were carried out by Patrick (1940a, b), who recorded 30 taxa in Ceará. More recently, only a few studies involving microalgae have been conducted in the southern Ceará, and diatoms have generally been identified to class or genus level, rarely to species level (Aquino *et al.* 2011; Vieira *et al.* 2013; Amorim *et al.* 2015; Costa *et al.* 2015). There are approximately 50 taxa of centric diatoms registered in freshwaters from Brazil (Eskinazi-Leça *et al.* 2015; Ludwig & Tremarin 2017) but there are few records of the centric diatom in the Caatinga region (*e.g.*, Patrick *et al.* 1940a, b; Tremarin *et al.* 2013), highlighting actual regional biodiversity gap and the great need taxonomic studies in that area.

This study aims to expand the knowledge of diatom biodiversity in the state of Ceará reducing gaps in our understanding of the geographic distribution of centric diatoms in the semi-arid region of Brazil. We performed a taxonomic study including samples from four hydrographic basins in northwest Ceará. Herein, we focus on population analysis of the species, detailed descriptions, taxonomic comments, and illustrations using light and electron microscopy.

Material and Methods

Ceará state is divided into seven mesoregions. The study area is located in the northwest of the state (Fig. 1) and covers 34,560 km² with a population of 326,847 inhabitants distributed across 47 cities (IPECE 2008), 12 of which were included in this study (Tab. S1, available on supplementary material <https://doi.org/10.6084/ m9.figshare.21339363.v1>). Four hydrographic basins make up this mesoregion: Acaraú River, Coreaú River, Coastal rivers, and Parnaíba River (Nascimento 2011).

Sampling was conducted during 2016, 2018, and 2019 in different freshwater environments in the river basins (Tab. S1, available on supplementary material <https://doi.org/10.6084/ m9.figshare.21339363.v1>). Twenty-three samples were collected: 17 epiphytic, 3 epilithic, 1 epipsamic, and 2 phytoplanktonic. Plankton was obtained with a plankton net (20 μ m mesh) and periphyton, which are attached to natural substrates, were collected manually. We measured conductivity and pH, when possible (Tab. S1, available on supplementary material <https://doi. org/10.6084/m9.figshare.21339363.v1>), using conductivity meter CG1400 and pH-meter PG1400, respectively (Gehaka, Ltda).

Samples were preserved in 4% formaldehyde and cleaned according to Simonsen (1974), with modifications described by Moreira-Filho & Valente-Moreira (1981). Permanent slides were mounted with Naphrax® resin (refractive index = 1.74). Diatoms were analyzed and illustrated using an Olympus BX40 light microscope (Olympus, Tokyo, Japan) equipped with an Olympus DP71 image capture camera. Cleaned sub-samples were deposited in aluminum stubs, coated with gold using a Bal-Tec SCD050 Sputter Coater (Bal-Tec, Balzers, Liechtenstein). Preparations were analyzed in the JEOL JSM 6360-LV (Jeol, Japan) and TESCAN VEGA 3 LMU scanning electron microscopes (Tescan Analytics, Brno, Czech Republic), housed at the Electron Microscopy Center of the Federal University of Paraná (UFPR).

Classification follows Medlin & Kaczmarska (2004) for supra-ordinal taxa and Round *et al.* (1990) for subordinal ones. Striae density and marginal processes of centric

diatoms were calculated according to Hasle (1983) and modified by Syvertsen & Hasle (1984). Morphological terminology was based on Round *et al.* (1990), Houk (2003) and Houk *et al.* (2010). Samples and slides were registered and deposited in the herbaria of the Federal University of Paraná (UPCB), Curitiba, Paraná, and the State University of Vale do Acaraú (HUVA), Sobral, Ceará, Brazil (Tab. S1, available on supplementary material < https://doi.org/10.6084/ m9.figshare.21339363.v1>).

The frequency of occurrence was calculated according to Dajoz (2005), as follows: constant (C \geq 50%), common (C \geq 30% or \leq 50%), sporadic (C \geq 10% or \leq 30%) and rare (C \leq 10%).

Results and Discussion

We present 14 species and one non-typical variety of centric diatoms, distributed among one genera of Coscinodiscophyceae and six genera of Mediophyceae.

Descriptions and comments follow.



Figure 1 – Map of study area: hydrographic basins of northwestern region (in grey) of the state of Ceará, Brazil. Sampling locations (black circles) were numbered from 1 to 23. Information about the sampling points is shown in Table S1, available on supplementary material https://doi.org/10.6084/m9.figshare.21339363.vl.

4 de 22

Bacillariophyta Karsten

Coscinodiscophytina Medlin et Kaczmarska Coscinodiscophyceae Round et R.M. Crawford

Aulacoseirales Crawford

Aulacoseiraceae Thwaites

Aulacoseira Thwaites

Aulacoseira ambigua (Grunow) Simonsen, Bacill. 2:56. 1979. Fig. 2a-b

Frustules cylindrical; valve face flat with short rows of rounded areolae restricted to the margin (Fig. 2a); mantle ornamented with striae arranged obliquely in relation to the pervalvar axis in a dextrorse pattern; areolae rounded, delicate. Diameter $5.7-6.4 \mu m$; mantle height 9.9 μm ; 17 striae in 10 μm and 17 areolae in 10 μm .

Examined material: Graça, Belizário waterfall (UPCB: 78398, HUVA: 24522). Catunda, Celso weir (UPCB: 78411, HUVA: 24535).

Species found in epilithic and epiphytic samples. Literature consulted: Buczkó *et al.* (2010); Tremarin *et al.* (2013).

Aulacoseira granulata var. *granulata* (Ehrenberg) Simonsen, Bacill. 2:58. 1979. Fig. 2c-f

Frustules cylindrical, united in straight filaments; terminal valves with one or two long spines; mantle ornamented with striae arranged parallel to the pervalvar axis; areolae rounded to rectangular; coarse, v-shaped sulcus not very pronounced. Diameter $5.7-7.7 \mu$ m; mantle height $11.6-21.3 \mu$ m; 8-12 striae in 10 μ m and 8-10 areolae in 10 μ m.

Examined material: Varjota, Araras weir (UPCB: 78392, HUVA: 24516). Sobral, Jaibaras weir (UPCB: 78395, HUVA: 24519). Graça, Belizário waterfall (UPCB: 78398, HUVA: 24522). Sobral, Acaraú River (UPCB: 78407, HUVA: 24531). Meruoca, Sítio Cachoeira (UPCB: 78418, HUVA: 24542).

The species was found in epilithic, epiphytic and phytoplanktonic samples. Literature consulted: Krammer (1991); Houk (2003); Cavalcante *et al.* (2013).

Aulacoseira granulata var. *angustissima* (O. Müller) Simonsen, Bacill., 2:58. 1979. Fig. 2g-1

Frustules cylindrical, united in predominantly straight filaments by small connecting spines, terminal valves with a long spine; mantle ornamented by obliquely striae (dextrorse pattern) in the connecting valves and parallel in the separation valves; areolae rounded; sulcus not pronounced. Diameter 3–4 μ m; mantle height 10.6–13.3 μ m; 16–17 striae in 10 μ m and 18–20 areolae in 10 μ m. **Examined material**: Varjota, Araras weir (UPCB: 78392, HUVA: 24516). Sobral, Jaibaras weir (UPCB: 78395, HUVA: 24519). Sobral, Acaraú River (UPCB: 78404, 78407, HUVA: 24528, 24531). Catunda, Carmina weir and Celso weir (UPCB: 78409, 78410, HUVA: 24533, 24534).

Aulacoseira granulata var. angustissima was found mainly in epiphytic samples. Literature consulted: Krammer (1991); Houk (2003); Cavalcante *et al.* (2013).

Aulacoseira italica (Ehrenberg) Simonsen, Bacill. 2:60. 1979. Fig. 2m-q

Frustules cylindrical, united in straight filaments by conspicuous conneting spines; valve face flat with inconspicuous areolae (Fig. 2m); mantle ornamented with striae parallel to the pervalvar axis; areolae rounded, delicate. Diameter $8.5-10.6 \mu m$; mantle height $12.6-17.4 \mu m$; 22-24 striae in $10 \mu m$ and 18-22 areolae in $10 \mu m$. **Examined material**: Graça, Belizário waterfall (UPCB: 78398, HUVA: 24522). Catunda, Celso weir (UPCB: 78411, HUVA: 24535).

Species found in epiphytic and epilithic samples. Literature consulted: Crawford *et al.* (2003); Houk (2003).

Bacillariophytina Medlin *et* Kaczmarska Mediophyceae (Jousé *et* Proshkina-Lavrenko) Medlin *et* Kaczmarska

Stephanodiscales Nikolaev et Harwood

Stephanodiscaceae Makarova

Cyclotella (Kützing) Brébisson

Cyclotella atomus Hustedt, Arch. Hydrobiol. 15:143, pl. 9, figs 1-4. 1937. Fig. 3a-j

Valves circular, ornamented by marginal radiate striae separated by costae; marginal fultoportula ring, with fultoportulae distributed every 3 or 4 striae; one rimoportula located between two marginal fultoportulae; one subcentral fultoportula. Diameter 5–6.5 μ m; pervalvar axis 3 μ m; 8–14 striae in 10 μ m and 3.3–3.8 marginal fultoportulae in 10 μ m.

Examined material: Graça, Belizário waterfall (UPCB: 78398, HUVA: 24522). Massapê, temporary pond near to Acaraú River (UPCB: 78399, HUVA: 24523). Sobral, Acaraú River (UPCB: 78403, 78407, 78408, HUVA: 24527, 24531, 24532).

In SEM: valve surface is slightly undulated in the central area (Fig. 3h) and striae irregularly distributed from marginal valve face to mantle with delicate round poroids; marginal fultoportula ring located at the valve face/mantle junction, occurring at an interval of every three or four costae (Fig. 3i,j). Externally, fultoportulae and rimoportula openings are simple pores. Internally, striae are not alveolate (Fig. 3j); the subcentral fultoportula have three satellite pores and marginal fultoportulae have two satellite pores in radial position; one sessile marginal rimoportula with a slightly oblique labiate opening (Fig. 3j).

Populations of *Cyclotella atomus* in northwest Ceará follow the morphometric variation described in the literature (diameter $3.5-8.5 \mu m$), but the striae density showed lower values (12–20 in 10 μm ; Tanaka 2007; Houk *et al.* 2010). However, Cavalcante *et al.* (2013) have also registered lower striae density (9–16 in 10 μm) in specimens from Northeastern Brazil. *Cyclotella cryptica* Reimann, Lewin *et* Guillard mainly differs from *C. atomus* due to the marginal fultoportulae located at an interval of every one or two costae (Houk *et al.* 2010).



Figure 2 – a-q. *Aulacoseira* species – a-b. *Aulacoseira ambigua*, in valve and girdle views, respectively; c-f. *Aulacoseira granulata* var. *granulata*; g-l. *Aulacoseira granulata* var. *angustissima*; m-q. *Aulacoseira italica* – m. valvar view; n-q. girdle view. Scale bar: 10 µm.

Rodriguésia 73: e00222021. 2022

The species occurred in epiphytic, epilithic and phytoplanktonic samples. Literature consulted: Tanaka (2007); Cavalcante *et al.* (2013); Houk *et al.* (2010).

Cyclotella cryptica Reimann, Lewin *et* Guillard. Phycol. 3:82, figs. 4-11. 1963. Fig. 4a-k

Valves circular, ornamented by marginal radiate striae separated by costae; marginal fultoportulae ring, fultoportulae distributed in an interval of every one or two costae and always associated to the costa; one sessile rimoportula located between two marginal fultoportulae; one subcentral fultoportula. Diameter 6-12 µm; pervalvar axis 5.9 µm; 6-8 striae in 10 µm and 2–4.5 marginal fultoportulae in 10 µm. Examined material: Graça, Belizário waterfall (UPCB: 78398, HUVA: 24522). Massapê, temporary pond near the Acaraú River (UPCB: 78399, HUVA: 24523). Sobral, Acaraú River (UPCB: 78403, 78406, 78407, 78408, HUVA: 24527, 24530, 24531, 24532). Taperuaba, lake in Pedra da Andorinha (UPCB: 78402, HUVA: 24526). Catunda, Carmina weirs (UPCB: 78409, HUVA: 24533) and Celso weirs (UPCB: 78410, HUVA: 24534). Varjota, Araras weir (UPCB: 78392, HUVA: 24516).

In SEM: internally, semi-open alveolate striae (Fig. 4i-k); subcentral and marginal fultoportulae with three satellite pores around a long tube (Fig. 4i-j); one marginal rimoportula with small labiate

opening that is oriented obliquely lies on the costa (Fig. 4j).

Cyclotella cryptica and C. meneghiniana Kützing are similar in valve diameter and number of marginal processes, but C. meneghiniana differs mainly due to the internally closed alveoli, which makes the separation between the central and marginal areas quite evident (Houk *et al.* 2010). Moreover, it has already been observed that C. cryptica may resemble C. meneghiniana when found in low salinity (1.4) environments and show typical morphological characteristics of C. cryptica when salinity is > 4.3 (Schultz 1971).

The species occurred in epiphytic, epilithic, and phytoplanktonic samples. Literature consulted: Cavalcante *et al.* (2013); Houk *et al.* (2010).

Cyclotella marina (Tanimura, Nagumo *et* M. Kato) Aké-Castillo, Okolodkov. *et* Ector, in Aké-Castillo *et al*. Nova Hedwigia Beih. 141: 267, figs 2-9. 2012. Fig. 5a-h

Valves circular, delicate ornamentation, difficult to observe in MO; three to four marginal fultoportulae distant from each other; one rimoportula between two marginal fultoportulae; alveolate striae inconspicuous. Diameter 2.6–4.5 μ m; 2–4 marginal fultoportulae in 10 μ m.



Figure 3 – a-j. *Cyclotella atomus* – a-g. valves in LM; h-j. frustules and valves in SEM – h. frustule in girdle view showing marginal fultoportula external opening (arrow); i. external valve face view; j. internal view of the valve, marginal fultoportulae with two satellite pores (arrowhead), subcentral fultoportula with three satellite pores and marginal rimoportula with obliquely labiate opening (dark arrow). Scale bars: a-g = 10 μ m; h = 2 μ m; i-j = 1 μ m.

Examined material: Sobral, Acaraú River (UPCB: 78403, 78405, 78408, HUVA: 24527, 24529, 24532).

In SEM: internal valve surface flat; striae radiate, delicate, extending toward the central region; alveoli absent and marginal fultoportulae surrounded by two satellite pores, arranged at the face/mantle junction and one pedunculated marginal rimoportula (Fig. 5h).

Cyclotella marina differs from C. atomus due to less developed alveolate striae and the absence of central fultoportula (Tanimura et al. 2004). Also, the literature states the preference of C. marina for coastal, high-nutrient marine environments (Aké-Castillo et al. 2012; Hevia-Orube et al. 2015). However, the species has been registered in freshwater environments, which implies that it has a wide distribution (Cavalcante et al. 2013; Genkal & Yarmoshenko 2013; Genkal & Okhapkin 2013; Genkal & Bilous 2015). Cyclotella marina was registered in Brazil by Cavalcante et al. (2013) in riverine waters of Bahia state, Northeastern Brazil. According to Tanimura et al. (2004) and Chung et al. (2010), it is a metaphytic species occurring in both plankton and epiphyton. The present study is the second record of C. marina in freshwater systems in Brazil.

The species was registered exclusively in Acaraú River, influenced by domestic sewage, in epiphytic, epipsamic, and phytoplanktonic samples. Literature consulted: Aké-Castillo *et al.* (2012); Cavalcante *et al.* (2013).

Cyclotella meduanae Germain, Flore des Diatomées. p. 36, pl. 8, fig. 28, pl. 154, figs. 4, 4a. 1981.Fig. 5i

In SEM: internal view, circular valve ornamented by marginal radiate striae with delicate areolae, separated by costae; striae are not alveolate; subcentral fultoportulae absent; marginal fultoportulae ring surrounded by three satellite pores, located at the face/valve mantle junction, at every two or three striae; one marginal rimoportula located between two fultoportulae on the costae, obliquely oriented. Diameter 5.9 μ m; 9.5 striae in 10 μ m and 4.3 marginal fultoportulae in 10 μ m. **Examined material**: Sobral, Acaraú River (UPCB: 78408, HUVA: 24532). Catunda, Carmina weir (UPCB: 78409, HUVA: 24533).

The only specimen found during SEM preparations is consistent with descriptions by Houk *et al.* (2010) and Cavalcante *et al.* (2013). *Cyclotella katiana* Sala *et* Ramírez, which was proposed in Colombia (Sala & Ramírez 2008), was recently considered synonymous with *C. meduanae* based on



Figure 4 – a-k. *Cyclotella cryptica* – a-h. valves in LM; i-k. valves in SEM – i. internal valve view, detail of the subcentral fultoportula with three satellite pores (arrowhead); j. marginal fultoportula with three satellite pores (arrowhead), and detail of the sessile marginal rimoportula (dark arrow), and detail of the semi-open alveoli and ring of marginal fultoportulae; k. valve overview showing details of subcentral fultoportula and marginal rimoportula and fultoportula ring. Scale bars: $a-h = 10 \mu m$; $k = 2 \mu m$; $i-j = 1 \mu m$.



Figure 5 – a-i. *Cyclotella* species – a-g. *Cyclotella marina* – valve view in LM; h. internal view of the valve in SEM, detail of the sessile marginal rimoportula (arrow). i. *Cyclotella meduanae* – internal valve view in SEM, detail of the marginal rimoportula between a costa and a marginal fultoportula (arrow). Scale bars: $a-g = 10 \mu m$; h-i = 1 μm .

their overlapping diacritical characteristics (Genkal 2014). *Cyclotella meduanae* resembles *C. cryptica* but differs mainly in relation to the absence of the subcentral fultoportula in *C. meduanae* (Houk *et al.* 2010).

The species occurred only in plankton in epiphyton. Literature consulted: Tanaka (2007); Houk *et al.* (2010); Cavalcante *et al.* (2013).

Cyclotella meneghiniana Kützing, Die Kies. Bacill. oder Diat., p. 50, pl. 30, fig. 68. 1844.

Fig. 6a-k

Valves circular, with evident separation between central and marginal areas, central area with tangential undulation; marginal striae alveolate; marginal fultoportula ring, with one fultoportula in each stria, sometimes absent; one rimoportula inserted between two marginal fultoportulae; one to two subcentral fultoportula. Diameter 7.9–18.4 µm; 7–8 striae in 10 µm and 4.9 marginal fultoportulae in 10 µm.

Examined material: Varjota, Araras weir (UPCB: 78392, HUVA: 24516). Granja, Gangorra weir (UPCB: 78393, 78394, HUVA: 24517, 24518). Graça, Belizário waterfall (UPCB: 78398, HUVA: 24522). Massapê, temporary pond near the Acaraú River (UPCB: 78399, HUVA: 24523). Taperuaba, lake in Pedra da Andorinha

and Olho d'água do Pajé (UPCB: 78402, 78400, HUVA: 24526, 24524). Sobral, Acaraú River (UPCB: 78403, 78404, 78406, 78407, 78408, HUVA: 24527, 24528, 24530, 24531, 24532). Catunda, Carmina and Celso weirs (UPCB: 78409, 78410, HUVA: 24533, 24534). Viçosa do Ceará, Quatiguaba River (UPCB: 78413, HUVA 24537).

In SEM: the external valve surface is slightly undulated in the central region, ornamented by granules; subcentral fultoportulae; marginal single or double spines positioned in line with each costa (Fig. 6i). Internal view with closed alveoli, marginal and subcentral short tube fultoportulae surrounded by three satellite pores (Fig. 6j-k); one pedunculated marginal rimoportula between two marginal fultoportulae, with obliquely oriented labiate opening (Fig. 6k).

The species occurred in epiphytic, epilithic, and phytoplanktonic samples. Literature consulted: Houk *et al.* (2010); Cavalcante *et al.* (2013).

Discostella Houk et Klee

Discostella stelligera (Cleve *et* Grunow) Houk *et* Klee, Diat. Res. 19(2): 208. 2004. Fig. 7a-i

Valves circular, with convex central area, ornamented by short striae irregularly arranged in form of a rosette; marginal area occupies less than half of the valve surface; marginal alveolate Centric diatoms from Caatinga, Ceará



Figure 6 – a-k. *Cyclotella meneghiniana* (valve view in LM and SEM) – a-h. external view of valve surface in LM; i. external view of valve surface in SEM, detail of the valve surface, of the marginal spines; j. internal view, alveolate striae, closed alveolous (white arrow), subcentral fultoportula with three satellite pores (dark arrow); k. pedunculated marginal rimoportula (arrowhead) obliquely oriented, marginal fultoportula (dark arrow). Scale bars: a-h = 10 μ m; i, j = 5 μ m; k = 2 μ m.

striae, radial and regular in length; marginal ring of fultoportulae inconspicuous in LM. Diameter $5.9-12 \mu m$ and 7.5-11.5 striae in 10 μm .

Examined material: Graça, Belizário waterfall (UPCB: 78398, HUVA: 24522). Granja, Gangorra weir (UPCB: 78393, HUVA: 24517). Sobral, Acaraú River (UPCB: 78403, 78409, HUVA: 24527, 24533).

In SEM: internal view with marginal fultoportulae located in line with striae and between costae, in the valve face/mantle junction, surrounded by two satellite pores; one small marginal rimoportula present between marginal fultoportulae (Fig. 7i). The internal opening of the alveolate striae is shortened when it coincides with fultoportula or rimoportula. A hyaline area separates the marginal from the central striations.

Species found mainly in epiphytic samples. Literature consulted: Houk (2004); Houk *et al.* (2010); Tuji & Williams (2006); Guerrero & Echenique (2006).

Discostella woltereckii (Hustedt) Houk *et* Klee, Diat. Res. 19(2): 223. 2004. Fig. 7j-o

Valves circular, flat to a moderately convex central area, with two ornamentation patterns: elongated marginal striae, of irregular length, which extends to the valve center (Fig. 7j-m), or irregular marginal striae occupying more than one half of the valve, separated from the central region, which presents short radiated rosette-shaped striation, (Fig. 7n-o); marginal ring of fultoportulae inconspicuous in LM. Diameter 4.8–5 μ m; 8.5 striae in 10 μ m.

Examined material: Varjota, Araras weir (UPCB: 78392, HUVA: 24516).

Discostella woltereckii var. minor Öberg, Risberg *et* Stabell differs from the typical species due to the smaller valve diameter (1.9–4 μm) and the dichotomously arranged valve face (Öberg *et al.* 2009). *Discostella guslyakovyi* Genkal, Bondarenko *et* Popovskaya also differs in diameter (2.8–5.7 μm), valve contour, and non-tubular marginal fultoportulae (Genkal *et al.* 2007).

Similarities are notable between *D.* pseudostelligera (Hustedt) Houk et Klee and *D.* woltereckii. Both have irregular marginal striations, long tubular marginal fultoportulae, and may present a central area ornamented by short striae arranged in a rosette shape (Houk et al. 2010). However, according to Guerrero & Echenique (2006), *D. pseudostelligera* exhibits a broad hyaline ring occupying about half of the valve diameter, located between the central and the marginal area,

Maciel MGR, Cavalcante KP & Ludwig TAV



Figure 7 – a-o. *Discostella* species – a-i. *Discostella stelligera* – a-h. valves in LM; i valve in internal view, SEM; j-o. *Discostella wortereckii* – valves in LM. Scale bars: a-h, j-o = 10μ m; i = 2μ m.

while in *D. woltereckii* the central area is very small, sometimes reduced to an isolated stria.

The population in Ceará is similar to that presented by Houk *et al.* (2010) fig.19, pl.354, Hustedt (1942) fig.25, pl.324 for *D. woltereckii* type material, and also Huber-Pestalozzi (1942, fig. 488A, pl. CXVIII). When analyzing the type material of both taxa, Houk *et al.* (2010) stated that, although the morphology can sometimes overlap, making identification inaccurate, the separation of the taxa can be related to ecological differences; *D. pseudostelligera* is mainly a species of temperate regions, while *D. woltereckii* occurs preferentially in tropical zones. Morphological and ecological features led us to assume that the population in Ceará corresponds better with the characterization of *D. woltereckii*.

The studied population was recorded in epiphytic samples. Literature consulted: Houk *et al.* (2010); Guerrero & Echenique (2006).

Thalassiosirales Glezer et Makarova

Thalassiosiraceae M. Lebour

Conticribra Stachura-Suchoples et D.M. Williams Conticribra weissflogii (Grunow) Stachura-Suchoples et Williams, Eur. J. Phycol. 44(4): 482. 2009. Fig. 8a-m

Valves circular with a flat surface; striae delicate, irregularly oriented; marginal fultoportulae ring located in the face/mantle junction, with conspicuous external tubes; one pronounced rimoportula interrupting the ring of marginal fultoportulae. Diameter 19.8–32 μ m; marginal fultoportulae 5.5–7.6 in 10 μ m; central fultoportulae 5–6 in 10 μ m.

Examined material: Graça, Belizário waterfall (UPCB: 78398, HUVA: 24522). Sobral, Acaraú River (UPCB: 78403, 78406, 78408, HUVA: 24527, 24530, 24532).

In SEM: external valve surface ornamented with granules (Fig. 8h-j) and areolate striae with an irregular continuous radial pattern. Marginal ring of fultoportulae with long external tubes, central fultoportulae with moderately elongated tubes (Fig. 8i-j). Rimoportula with an elongated external tube, slightly longer than those of fultoportulae (Fig 8i). For internal view, marginal and central fultoportulae are present as small tubes with four satellite pores (Fig. 8k-m). Rimoportula with a large labial opening, short pedunculated, arranged radially (Fig. 8l).

The species occurred in epilithic, epiphytic, and phytoplanktonic samples. Literature consulted: Stachura-Suchoples & Williams DM (2009); Cavalcante *et al.* (2013). Eupodiscales Bessey Eupodiscaceae Ralfs *Pleurosira* (Meneghini) Trevisan *Pleurosira laevis* (Ehrenberg) Compère var. *laevis*, Bacill., 5: 177-178, fig. 1-17, 20, 39. 1982. Fig. 9a-d; 10a-f

Subcircular to elliptical valves; valve face flat, ornamented by radial striae with delicate round areolae; two large ocelli located at the valve margin, opposite to each other, ornamented by delicate poroids; two rimoportulae located near the center of the valve. Larger diameter $38.1-45.5 \mu m$; smaller diameter $30.9-47.2 \mu m$; 10-14 areolae in $10 \mu m$.

Examined material: Ipu, Bica do Ipu (UPCB: 78396, HUVA: 24520). Sobral, Acaraú River (UPCB: 78403, HUVA: 24527). Viçosa do Ceará, Quatiguaba River (UPCB: 78412, 78413, HUVA: 24536, 24537).

In SEM: valve surface is ornamented by irregular starry spines mostly concentrated in the central region and close to the ocelli (Fig. 10i-k); rimoportulae with an external opening as a simple slit (Fig. 10h) and internally as a sessile labiate opening (Fig. 10g).

Pleurosira laevis var. *paludosa* (Tempère *et* Peragallo *ex* Forti) Compère, differs from the typical variety as it shows rimoportulae closer to the central area (Compère 1982). *Pleurosira socotrensis* (Kitton) Compère differs due to its elliptical valves and irregularly arranged striae in the central region of the valve (Compère 1982; Ludwig *et al.* 2004; Karthick & Kociolek 2011).

Population recorded mainly in epilithic and epiphytic samples. Literature consulted: Compère (1982); Joh (2010); Cavalcante *et al.* (2013).

Orthoseirales Crawford

Orthoseiraceae Crawford

Orthoseira Thwaites

Orthoseira roeseana (Rabenhorst) Pfitzer, Bot. Abh. 1(2): 134. 1871. Fig. 11a-h

Cylindrical frustule in girdle view, united by inconspicuous spines; mantle ornamented by striae parallel to the pervalvar axis, little pronounced constriction (stricter region in the mantle) (Fig. 11a-c); valve surface slightly wavy, with scattered punctuations, striae radial, conspicuously areolate; central area with three carinoportulae (Fig. 11e). Diameter 8.7–26.4 µm; mantle height 25.7–35.6; 15–17 striae in 10 µm; 18–19 areolae in 10 µm.

Examined material: Ipu, Bica do Ipu (UPCB: 78396, HUVA: 24520). Ibiapina, Bica do Pajé (UPCB: 78397,



Figure 8 – a-m. *Conticribra weissflogii* (valve view in LM and SEM) – a-g. valve view in LM, flat surface and delicate stretch marks; h-j. external view of valve surface in SEM – h. external valve surface ornamented with granules, marginal ring of fultoportulae with long external tubes; i. details of marginal fultoportulae and rimoportulae openings (arrow); j. central fultoportulae openings; k-m. internal valve view in SEM – k. internal surface of the valve without pronounced ornamentation, internal view of the ring of marginal fultoportulae interrupted by a rimoportula; l. details of large sessile rimoportula; m. central fultoportulae with for satellite pores surrounding a short tube. Scale bars: $a-g = 10 \mu m$; $h-j = 5 \mu m$; k-m = 2 μm .

HUVA: 24521). Ubajara, Sítio São Luis (UPCB: 78414, HUVA: 24538).

In SEM: carinoportulae occluded internally (Fig. 11g) and externally, presence of spines (Fig. 11h).

In Brazilian studies, specimens of *Orthoseira roesena* are presented by Landucci & Ludwig (2005, fig. 1), Brassac *et al.* (1999, fig. 29), and Ferrari & Ludwig (2007, figs 7 and 8), while *Orthoseira dendroteres* (Ehrenberg) Genkal *et* Kulikovskiy is presented by Nardelli *et al.* (2014, fig. 13). When comparing the illustrations and descriptions of these studies, they likely correspond to the same taxon. The delimitation between *O. dendroteres* and *O.*

roeseana becomes difficult due to the vast morphological variation of both taxa (Houk 1993, 2003; Spaulding & Kociolek 1998). The populations in this study exhibited considerable morphological variation in terms of valve diameter, overlapping with the characteristics of both species. Therefore, we opted to adhere to the broad taxonomic concept of *O. roeseana* found in Houk (2003). Gargas *et al.* (2018) comment on the need for more studies to resolve the taxonomy and the typification of *O. dendroteress* and *O. roeseana*.

Populations found in periphyton in epilithic of humid subaerial samples. Literature consulted: Houk (1993, 2003). Centric diatoms from Caatinga, Ceará



Figure 9 – a-d. Pleurosira laevis var. laevis – valve view in LM. Scale bars: $a-d = 10 \mu m$.

Terpsinoaceae Ralfs in Pritchard Terpsinoë Ehrenberg

 Terpsinoë musica
 Ehrenberg, Abh. Akad. Wiss.

 Berl., p. 425, pl. 3, fig. IV.1, pl. 3, fig. VII. 30.
 1841 (1843).

 Figs. 12a-q; 13a-h
 Figs. 12a-q; 13a-h

Frustules rectangular in girdle view with transapical bars resembling musical notes and short pseudoseptum near the edge of valve mantle; bipolar, elongated valves, generally with three marginal undulations of nearly equal size, but smaller valves showed one (Fig. 12i-m) to three marginal undulations (Fig. 12a-g); valve ends rostrate to subcapitate with pseudocelli; transapical costae between each undulation and near to the valve ends (less developed); coarse areolae irregularly arranged on the surface of the valve; one or three (Fig. 12a) subcentral rimoportula located in the central undulation. Length 61.7–137.9 μ m; width 32.8–42.2 μ m; pervalvar axis 74.5–107.9 μ m and 8–10 areolae in 10 μ m.

Examined material: Ipu, Bica do Ipu (UPCB: 78396, HUVA: 24520).

In SEM: internal view shows a small rimoportula in form of a crack (Fig. 13c) or a closed lip (Fig. 13d), and the rimoportula external view shows a slit shape (Fig. 13e).

The wide morphological variation of *T. musica* populations was previously recorded in the literature (Schmidt 1812–1899; Luttenton *et al.* 1986; Jiménez *et al.* 2017; Metzeltin *et al.* 2005; Metzeltin & Lange-Bertalot 2007). However, documentation of specimens with only one central undulation is rare. Wu (2013) described valves with one undulation in *T. musica* specimens, stating that the number of undulations decreases in smaller valves. Metzeltin & Lange-Bertalot (2007) illustrated "*Terpsinöe* (? nov.) spec." with frustules containing a single undulation (pl. 296:5–12), demonstrating uncertainties in identification. In our material, all valves were found in the same

population (see Examined material), including intermediate forms between one and two marginal undulations. Our observations suggest that these forms correspond to the same taxon. Variability in morphology and symmetry may be the result of cell reduction or initial cell formation (Cox 2014), as in the interrupted projections of the bipolar diatom *Hydrosera* (Cox 2013). Functional aspects, such as nutrient availability and adaptation to the environment, also provoke significant morphological variability in populations (Jiménez *et al.* 2017).

Small specimens with a single central undulation from the study population are similar to Terpsinoë petitiana (Leuduger-Fortmorel) Hendey found in marine samples from West Africa (Leuduger-Fortmorel 1898) and the Galapagos (Hendey 1972). The possibility remains that T. musica and T. petitiana are conspecifics, not only because of their phenotypic plasticity, but also because T. musica presents a wide ecological distribution, occurring in fresh and brackish water, as well as marine environments (Round et al. 1990). In this study, specimens of T. musica were found on bryophytes growing on rocks in a humid subaerial environment, for which we documented valves with one to three central undulations (Fig. 11a-m).

Tuji (2018) describes *T. muninensis*, a species very similar to *T. musica*, as endemic to the freshwater of the North Pacific islands. The author differentiates *T. muninensis* as it presents less silicified apices and interrupted pseudosepta, which do not form musical notes, as is characteristic of *T. musica* (Ehrenberg 1843). However, this characteristic seems to vary within the same population. In the samples from Ceará, the pseudosepta present as well silicified (Fig. 12d-e), with a low level of silicification (Fig. 12a-c,f), or are not visible (Fig. 12n-q). In the



Figure 10 – a-f. *Pleurosira laevis* var. *laevis* (valve view in SEM) – a. internal view of the valve, two rimoportulae located near the center of the valve; b. detail of the rimoportula opening in internal view (arrow); c. external view of the rimoportula opening; d. external valve surface ornamented with small spines irregularly spaced; e. external view of ocellus; f. detail of the spines, SEM. Scale bars: a-b,d = 10 μ m; f = 5 μ m; c,e = 2 μ m.

Centric diatoms from Caatinga, Ceará

population described by Jiménez *et al.* (2017), Figs. 8 and 11 show well-developed pseudosepta, which is not seen in Fig. 10. The authors also state that *T. musica* would have a median marginal undulation greater than the others, differing from those of equal size in *T. muninensis*. However, Jiménez *et al.* (2017) illustrate (Fig. 8) *T. musica* with marginal undulation of the same size and apices with well-developed pseudosepta. Tuji (2018) states that differences in the molecular sequence support the existence of two taxa, but also recommends further studies on the morphological and molecular phylogenetic variability of the two species. Also, some more representatives of the genus *Terpsinoë* have sequences deposited at GenBank that should be used by the author for a better comparison and a closer representation of the genus phylogeny.

In light of the above discussion, we believe that the Ceará population fits the concept of *T. musica*, a taxon with significant morphological plasticity.

Population found in periphyton of humid subaerial samples, associated with bryophytes. Literature consulted: Metzeltin *et al.* (2005); Wu (2013); Jiménez *et al.* (2017).



Figure 11 – a-h. Orthoseira roeseana – a-f. valves in LM – a-c. girdle views, observe the valve constrictions (arrow); d-f. valve views; g-h. valves in SEM – g. detail of carinoportulae in internal view; h. external view. Scale bars: a-f = $10 \ \mu m$; g-h = $5 \ \mu m$.

g

Maciel MGR, Cavalcante KP & Ludwig TAV



Figure 12 - a-q. Terpsinoë musica (valves in LM) - a-m. valve view; n-q. girdle view. Scale bars: 10 µm.

Most taxa were rare (6) or sporadic (7). Only two species were frequent: *Cyclotella meneghiniana*, occurring in 16 of the 24 sampling points, and *Cyclotella cryptica* which occurred in 10 sampling points. Furthermore, only *C. meneghiniana* occurred in all hydrographic basins, showing its wide geographic distribution in the region. In general, *C. meneghiniana* is frequent and abundant in rivers and lakes, under different trophic conditions (Kiss *et al.* 2012), and is particularly common in shallow and nutrient-rich waters (Houk *et al.* 2010). The species has been classified as an eutrophic indicator for highly fertilized waters with high conductivity (Joh 2010). The taxa that occurred in at least three of the studied hydrographic basins were: *Cyclotella atomus*, *C. cryptica*, and *Discostella stelligera*. Furthermore, it was observed that there was no significant difference in richness among different substrates, but rather in different environments, being higher in rivers and lower in puddles and dams.

Fifteen taxa were identified, with 12 new occurrences for the northwest region of Ceará. *Aulacoseira ambigua* (cited as *Melosira ambigua* (Grunow) O.Müller), *Aulacoseira granulata*

var. granulata [cited as Melosira granulata (Ehrenberg) Ralfs], and Cyclotella meneghiniana were previously registered by Patrick (1940a) in the Jaibaras weir, in the municipality of Sobral. Discostella stelligera is registered for the first time in Northeastern Brazil, having been previously recorded in the South (Ferrari & Ludwig 2007; Nardelli et al. 2014; Silva-Lehmkuhl et al. 2019), Southeast (Morandi et al. 2006), and Central-west (Da Silva et al. 2011) of the country. Discostella woltereckii is cited for the first time in Brazil;



Figure 13 – a-h. *Terpsinoë musica* (valves in SEM) – a-b. internal valve view of the valve, observe the septa; c. internal view of the rimoportula, valve with less undulations; d. internal view of the rimoportula, valve with three undulations; e. external view of the rimoportula; f-g. valve apices of one or bi undulated valves; h. valve apice of triundulated valve. Scale bars: $a = 20 \mu m$; $b,h = 10 \mu m$; $d-g = 5 \mu m$; c. $2 \mu m$.

however, there are previous identifications of *D. pseudostelligera* for which conspecificity must be evaluated (Brassac *et al.* 1999; Morandi *et al.* 2006; Cavalcante *et al.* 2013; Faustino *et al.* 2016). The species complexes *Discostella pseudostelligera/D. woltereckii*, *Orthoseira roeseana/O. dendroteres* and *Terpsinoë musica/T. muninensis* require further attention and additional studies, including analyses of their ecology and lifecycle and assessments using molecular tools, to provide a better delimitation of each.

Cyclotella marina is registered for the second time in a Brazilian freshwater habitat. According to Aké-Castillo et al. (2012), this species is generally found in brackish environments with a high-nutrient content. The entry of the species into freshwater can reflect the intermittent conditions of the river systems in northwest Ceará, where evaporation and low-levels of rainfall result in continuous rivers being converted into isolated pools, or dry up completely, during the dry season. High levels of evapotranspiration in the dry seasons lead to ion concentration and an increase in nutrients, especially in streams with no canopy cover (Goméz et al. 2017; Olson 2019). In addition, the pollution caused by domestic sewage exacerbates the accumulation of nutrients. The environmental characteristics of the Acaraú River in our study are very similar to those reported in records of C. marina by Cavalcante et al. (2013) of a shallow urban river in Northeastern Brazil.

Finally, floristic studies are essential to understand the geographic distribution of taxa and to support future ecological studies. This study shows that the diatom diversity in Brazilian semi-arid region is underestimated, contributing to a more consistent understanding of diatom distribution in the country.

Acknowledgments

The authors thank the Center for Electron Microscopy of the Federal University of Paraná, for SEM availability; and to Eduardo Tusset, for operational assistance. Coordenação de Aperfeiçoamento Pessoal de Nível Superior (CAPES) provided a Master's degree scholarship for MGRM; and TAVL was supported by a productivity grant from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (process number: 311876/2019-6). Authors are also grateful to Evelyn R. Nimmo, for edited the English language of the manuscript. To Prof. Elnatan B. de Souza, Prof. Maria Luiza R. C. Ribeiro and Prof. Lúcia Betânia S. Andrade from State University Vale do Acaraú, for their contribution in the fieldwork and laboratory equipments.

References

- Aké-Castillo JA, Okolodkov YB, Espinosa-Matías S, Merino-Virgilio FC, Herrera-Silveira JA & Ector L (2012) Cyclotella marina (Tanimura, Nagumo et Kato) Aké-Castillo, Okolodkov et Ector comb. et stat. nov. (Thalassiosiraceae): a bloom-forming diatom in the southeastern Gulf of Mexico. Nova Hedwigia, Beiheft (Suppl.) 141: 263-274.
- Albuquerque UP, Araújo EL, El-Deir ACA, Lima ALA, Souto A, Bezerra BM, Ferraz EMN, Freire EMX, Sampaio EVSB, Las-Casas FMG, Moura GJB, Pereira GA, Melo JG, Ramos MA, Rodal MJN, Schiel N, Lyra-Neves RM, Alves RRN, Azevedo-Júnior SM, Telino-Júnior WR & Severi W (2012) Caatinga revisited: ecology and conservation of an important Seasonal dry Forest. The Scientific World Journal 2012: 1-18.
- Álvarez-Blanco I, Blanco S, Cejudo-Figueiras C & Bécares E (2013) The Duero Diatom Index (DDI) for river water quality assessment in NW Spain: design and validation. Environmental Monitoring and Assessment 185: 969-981.
- Amorim CA, Dias AS & Ferreira RJ (2015) Microalgas perifíticas associadas à *Nymphoides indica* (L.) O. Kuntze em um reservatório do semiárido cearense. Caderno de Cultura e Ciência 14: 43-54.
- Andrade EM, Aquino DN, Chaves LCG & Lopes FB (2017) Water as capital and its uses in the caatinga. *In*: Silva JMC, Leal IR & Tabarelli M (eds.) Caatinga: the largest tropical dry forest region in South America. Springer International Publishing AG, New York. Pp. 281-302.
- Aquino EP, Oliveira ECC, Fernandes UL & Lacerda SR (2011) Phytoplankton in stabilization ponds in northeast Brazil. Brazilian Journal of Aquatic Sciences and Technology 15: 71-77.
- Bastos FH & Cordeiro AMN (2012) Fatores naturais na evolução das paisagens no semiárido brasileiro: Uma abordagem geral. Revista Geonorte 3: 464-476.
- Brassac NM, Atab DR, Landucci M, Visinoni ND & Ludwig TAV (1999) Diatomáceas cêntricas de rios da região de abrangência da usina hidrelétrica de Salto Caxias, PR (Bacia do Rio Iguaçu) Acta Botanica Brasilica 13: 277-289.
- Buczkó K, Ognjanova-Rumenova N & Magyari E (2010) Taxonomy, morphology and distribution of some *Aulacoseira* taxa in Glacial Lakes in the south Carpathian region. Polish Botanical Journal 55: 149-163.
- Cavalcante KP, Tremarin PI & Ludwig TAV (2013) Taxonomic studies of centric diatoms (Diatomeae): unusual nanoplanktonic forms and new records for Brazil. Acta Botanica Brasilica 27: 237-251.

- Chung MH, Yoon WD & Lee JB (2010) Morphological description of *Cyclotella atomus* var. *marina* (Bacillariophyceae): newly reported in Korean waters Algae 25: 57-64.
- Compère P (1982) Taxonomic revision of the diatom genus *Pleurosira* (Eupodiscaceae). Bacillaria 5: 165-190.
- Costa ARS, Amorim CA, Nascimento KJ, Dias AS, Ferreira RJ & Lacerda SR (2015) Caracterization of microalgae periphytic community in a reservoir semiarid cearense. Caderno de Cultura e Ciência 14: 43-59.
- Cox EJ (2013) Recognising and defining taxonomic boundaries in 'well-known' freshwater diatoms and its relevance to water quality evaluation. Diatomededelingen 37: 17-26.
- Cox EJ (2014) Diatom identification in the face of changing species concepts and evidence of phenotypic plasticity. Journal of Micropalaeontology 33: 111-120.
- Crawford RM, Likhoshway YV & Jahn R (2003) Morphology and identity of *Aulacoseira Italica* and typification of *Aulacoseira* (Bacillariophyta). Diatom Research 18: 1-19.
- Dajoz R (2005) Princípios de ecologia. 7^a ed. Artmed, Porto Alegre. 520p.
- Da Silva WJ, Nogueira IS & Souza MGM (2011) Catálogo de diatomáceas da região Centro-Oeste brasileira. Iheringia Série Botânica 66: 61-86.
- Dalu T & Froneman PW (2016) Diatom-based water quality monitoring in southern Africa: challenges and future prospects. Water SA 42: 551-559.
- Ehrenberg CG (1843) Verbreitung und Einfluss des mikroskopischen Lebens in Süd- und Nord-Amerika. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin 1841: 291-445.
- Eskinazi-Leça E, Moura CWN, Cunha MGGS, Santiago MF, Borges GCP, Lima JC, Silva MH, Ferreira LC, Aquino E, Da Silva WJ & Menezes M (2015) Bacillariophyceae. *In*: Lista de espécies da flora do Brasil. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro. Available at http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB119495. Access on 28 November 2019.
- Faustino SB, Fontana L, Bartozek ECR, Bicudo CEM & Bicudo DC (2016) Composition and distribution of diatom assemblages from core and surface sediments of a water supply reservoir in Southeastern Brazil. Biota Neotropica 16: e20150129.
- Ferrari F & Ludwig TAV (2007) Coscinodiscophyceae, Fragilariophyceae e Bacillariophyceae (Achnanthales) dos rios Ivaí, São João e dos Patos, bacia hidrográfica do Rio Ivaí, município de Prudentópolis, PR, Brasil. Acta Botanica Brasilica 21: 421-441.
- Gargas CB, Theriot EC, Ashworthb MP & Johansen JR (2018) Phylogenetic analysis reveals that

the 'radial centric' diatom *Orthoseira* Thwaites (Orthoseiraceae, Bacillariophyta) is a member of a 'multipolar' diatom lineage. Protist 169: 803-825.

- Genkal SI & Bilous OP (2015) Centric Diatoms (Centrophyceae) of the lower portion of the Southern Bug river (Ukraine). International Journal on Algae 17: 339-350.
- Genkal SI & Yarmoshenko LP (2013) Centric Diatoms (Bacillariophyta) of the cooling pond of the Khmelnitskiy Nuclear Power Station (Ukraine). Hydrobiological Journal 49: 51-63.
- Genkal SI & Okhapkin AG (2013) Centric Diatoms (Centrophyceae) of the lower reaches of the Oka river (Russian Federation). Hydrobiological Journal 49: 41-57.
- Genkal SI (2014) Morphology, taxonomy, ecology and distribution of *Cyclotella meduanae* Germain (Bacillariophyta). Nova Hedwigia Beiheft 143: 127-140.
- Genkal SI, Bondarenko NA & Popovskaya GI (2007) New representative of the genus *Discostella* Houck *et* Klee (Bacillariophyta) from the Eastern Baikal area (Russia). International Journal on Algae 9: 359-364.
- Germain H (1981) Flore des diatomées Diatomophycées eaux douces et saumâtres du Massif Armoricain et des contrées voisines d'Europe occidentale. Collection "Faunes et Flores Actuelles". Société Nouvelle des Editions Boubée, Paris. 444p.
- Goméz R, Arce MI, Baldwin DS & Dahm CN (2017) Water physicochemistry in intermittent rivers and ephemeral streams. *In*: Datry T, Bonada N & Boulton A (eds.) Intermittent rivers and ephemeral streams ecology and management. Academic Press, Cambridge. Pp. 109-134.
- Guerrero JM & Echenique RO (2006) *Discostella* taxa (Bacillariophyta) from the Río Limay basin (northwestern Patagonia, Argentina). European Journal of Phycology 41: 83-96.
- Hasle GR (1983) The marine planktonic diatoms *Thalassiosira oceanica* sp. nov. and *T. partheneia*. Journal of Phycology 19: 220-229.
- Hendey NI (1972) Some marine diatoms from the Galapagos Islands. Nova Hedwigia 22: 371-422.
- Hevia-Orube J, Orive E, David H, Díez A, Laza-Martínez A, Miguel I & Seoane S (2015) Molecular and morphological analyses of solitary forms of brackish Thalassiosiroid diatoms (Coscinodiscophyceae), with emphasis on their phenotypic plasticity. European Journal of Phycology 51: 1-20.
- Houk V & Klee R (2004) The stelligeroid taxa of the genus *Cyclotella* (Kutz.) Brébisson (Bacillariophyceae) and their transfer to the new genus *Discostella* gen. nov. Diatom Research 19: 203-228.
- Houk V (1993) Some morphotypes in the *Orthoseira roeseana* complex. Diatom Research 8: 385-402.

Houk V (2003) Atlas of freshwater centric diatoms with a brief key and descriptions. Part I. Melosiraceae, Orthoseiraceae, Paraliaceae and Aulacoseiraceae. *In*: Poulícková A (ed.) Czech Phycology Supplement, Olomouc. 111p.

- Houk V, Klee R & Tanaka H (2010) Atlas of freshwater centric diatoms with a brief key and descriptions. Part III. Stephanodiscaceae A. *Cyclotella, Tertiarius, Discostella*. Fottea 10: 1-498.
- Huber-Pestalozzi G (1942) Diatomeen. *In*: Thienimann A (ed.) Das phytoplankton des susswassers, systematik und biologie. Stuttgart E. Schweizerbartsche Verlagsbuchhandlung 2: 367-549.
- Hustedt F (1937) Systematische und ökologische Untersuchungen über die Diatomeen-Flora von Java, Bali und Sumatra nach dem Material der Deutschen Limnologischen Sunda-Expedition. Archiv für Hydrobiologie (Supplement) 15: 131-177.
- Hustedt F (1942) Süßwasser-Diatomeen des indomalayischen Archipels und der Hawaii-Inseln. Nach dem Material der Wallacea-Expedition. Internationale Revue der gesamten Hydrobiologie und Hydrographie 42: 1-252.
- IPECE (2008) características geográficas, recursos naturais e meio ambiente. Ceará em números. Instituto de Pesquisa e Estratégia Econômica do Ceará. Pp. 30-31. Available at http://www2.ipece.ce.gov.br/publicacoes/ceara_em_numeros/2008/completa/. Access on 28 November 2019.
- IPECE (2016) Características geográficas, recursos naturais e meio ambiente. Ceará em números. Instituto de Pesquisa e Estratégia Econômica do Ceará. Pp. 21-44. Available at http://www2.ipece.ce.gov.br/publicacoes/ceara_em_numeros/2016/ completa/>. Access on 25 November 2019.
- Jiménez JA, Magos YB & Camarillo VHS (2017) Morphological and environmental characterization of *Terpsinoë musica* (Biddulphiaceae, Bacillariophyceae) in tropical streams from Mexico. Diatom Research 32: 185-193.
- Joh G (2010) Algal flora of Korea. Chrysophyta, Bacillariophyceae: centrales. Freshwater diatoms I. National Institute of Biological Resources 3: 1-161.
- Julius ML & Theriot EC (2010) The diatoms: a primer. *In*: Smol JP & Stoermer EF (eds.) The diatoms: applications for the environmental and earth sciences. 2nd ed. Cambridge University Press, Cambridge. Pp. 8-22.
- Karthick B & Kociolek JP (2011) Four new centric diatoms (Bacillariophyceae) from the Western Ghats, South India. Phytotaxa 22: 25-40.
- Kelly MG, Cazaubon A, Coring E, Dell'uomo A, Ector L, Goldsmith B, Guasch H, Hürlimann J, Jarlman A, Kawecka B, Kwandrans J, Laugaste R, Lindstrøm EA, Leitao M, Marvan P, Padisák J, Pipp E, Prygiel J, Rott E, Sabater S, Van-Dam H & Vizinet J (1998) Recommendations for the routine sampling of

diatoms for water quality assessments in Europe. Journal of Applied Phycology 10: 215-224.

- Kiss KT, Klee R, Ector L & Ács É (2012) Centric diatoms of large rivers and tributaries in Hungary: morphology and biogeographic distribution. Acta Botanica Croatica 71: 311-363.
- Krammer K (1991) Morphology and taxonomy in some taxa of the genus *Aulacoseira* Thwaites (Bacillariophyceae). II. Taxa in the *A. granulata-*, *italica-* and *lirata-*groups. Nova Hedwigia 53: 477-496.
- Kützing FT (1844) Die Kieselschaligen Bacillarien oder Diatomeen. Zu finden bei W. Köhne, Nordhausen. Pp. [i-vii], [1]-152, pls 1-30.
- Lai GG, Padedda BM, Virdis T, Sechi N & Lugliè A (2014) Benthic diatoms as indicators of biological quality and physical disturbance in Mediterranean watercourses: a case study of the Rio Mannu di Porto Torres basin, northwestern Sardinia, Italy. Diatom Research 29: 11-26.
- Landucci M & Ludwig TAV (2005) Diatomáceas de rios da Bacia Hidrográfica Litorânea, PR, Brasil: Coscinodiscophyceae e Fragilariophyceae. Acta Botanica Brasilica 19: 345-357.
- Leal IR, Silva JMC & Barros MLB (2003) Ecologia e conservação da caatinga. Editora Universitária da UFPE, Recife. 822p.
- Leal IR, Silva JMC, Tabarelli M & Lacher T (2005) Changing the course of biodiversity conservation in the Caatinga of Northeastern Brazil. Conservation Biology 19: 701-706.
- Leuduger-Fortmorel G (1898) Diatomées marines da costa ocidental de África. Saint-Brieuc Francisque Guyon, Saint-Brieuc. 41p.
- Lobo EA, Schuch M, Heinrich CG, Costa AB, Düpont A, Wetzel CE & Ector L (2015) Development of the Trophic Water Quality Index (TWQI) for subtropical temperate Brazilian lotic systems. Environmental Monitoring and Assessment 187: 1-13.
- Lobo EA, Wetzel CE, Ector L, Katoh K, Blanco S & Mayama S (2010) Response of epilithic diatom communities to environmental gradients in subtropical temperate Brazilian rivers. Limnetica 29: 10-20.
- Ludwig TAV & Tremarin PI (2017) Bacillariophyta. *In*: Bicudo CEM & Menezes M (eds.) Gênero de algas de águas continentais do Brasil: chave para identificação e descrição. 3^a ed. RiMa, Rio de Janeiro. Pp. 435-503.
- Ludwig TAV, Flores TL, Moreira-Filho H & Veiga LAS (2004) Inventário florístico das diatomáceas (Ochrophyta) de lagoas do Sistema Hidrológico do Taim, Rio Grande do Sul, Brasil: Coscinodiscophyceae. Iheringia, Série Botânica 59: 97-106.
- Luttenton MR, Pfiester LA & Timpano P (1986) Morphology and growth habitat of *Terpsinoe musica*

Ehr. (Bacillariophyceae). Castanea, Journal of the Southern Appalachian Botanical Club. Morgantown 51: 175-182.

- Medlin LK & Kaczmarska I (2004) Evolution of the diatoms: V. Morphological and cytological support for the major clades and a taxonomic revision. Journal Phycologia 43: 245-270.
- Menezes M, Bicudo CEM & Moura CWN (2015) Update of the Brazilian floristic list of algae and cyanobacteria. Rodriguésia 66: 1047-1062.
- Metzeltin D & Lange-Bertalot H (2007) Tropical Diatoms of South America II. Special remarks on biogeographic disjunction. Iconographia Diatomologica (H. Lange-Bertalot, ed.). Vol. 18. Koeltz Scientifc Books, Stuttgart. 877p.
- Metzeltin D, Lange-Bertalot H & García-Rodríguez F (2005) Diatoms of Uruguay, compared with other taxa from South America and elsewhere. Iconographia Diatomologica (H. Lange-Bertalot, ed.). Vol. 15. Koeltz Scientifc Books, Stuttgart. 736p.
- Morandi LL, Ritter LMO, Moro RS & Bicudo CEM (2006) Criptógamos do Parque Estadual do Ipiranga, São Paulo, SP. Algas, 20: Coscinodiscophyceae. Hoehnea 33: 115-122.
- Moreira-Filho H & Valente-Moreira IM (1981) Avaliação taxonômica e ecológica das diatomáceas (Bacillariophyceae) epífitas em algas pluricelulares obtidas nos litorais dos estados dos estados do Paraná, Santa Catarina e São Paulo. Boletim Museu Botânico Municipal de Curitiba 47: 1-17.
- Moro MF, Macedo MB, Moura-Fé MM, Castro ASF & Costa RC (2015) Vegetation, phytoecological regions and landscape diversity in Ceará state, northeastern Brazil. Rodriguésia 66: 717-743.
- Nardelli MS, Bueno NC, Ludwig TAV, Tremarin PI & Bartozek ECR (2014) Coscinodiscophyceae and Fragilariophyceae (Diatomeae) in the Iguaçu river, Paraná, Brazil. Acta Botanica Brasilica 28: 127-140.
- Nascimento F (2011) Categorização de usos múltiplos dos recursos hídricos e problemas ambientais. Revista da Associação Nacional de Pós-graduação e Pesquisa em Geografia 7: 81-97.
- Öberg H, Risberg J & Stabell B (2009) Morphology, valve ultrastructure and stratigraphical variability of *Discostella* taxa in a tropical crater lake, northern Tanzania. Diatom Research 24: 341-356.
- Olson JR (2019) Predicting combined effects of land use and climate change on river and stream salinity. Philosophical Transactions of the Royal Society, B: Biological Sciences 374: 20180005.
- Patrick R (1940a) Diatoms of Northeastern Brazil. Part I. Coscinodiscaceae, Fragilariaceae and Eunotiaceae. Proceedings of the Academy of Natural Sciences of Philadelphia 92: 191-226.
- Patrick R (1940b) Some new diatoms from Brazil. Notulae Naturae of the Academy of Natural Sciences of Philadelphia 59: 1-7.

- Pfitzer E (1871) Untersuchungen über bau und entwicklung der bacillariaceen (Diatomaceen). *In*: von Hanstein JLER (ed.) Botanische abhandlungen aus dem Gebiet der Morphologie und Physiologie. Vol. 1, A. Marcus, Bonn, 189p.
- Reimann BEF, Lewin JMC & Guillard RRL (1963) *Cyclotella cryptica*, a new brackish-water diatom species. Phycologia 3: 75-84.
- Round FE, Crawford RM & Mann DG (1990) The diatoms: biology and morphology of the genera. Cambridge University Press, Cambridge. 747p.
- Sala S & Ramírez JJ (2008) *Cyclotella katiana* sp. nov. from La Reina Swamp, Parque Nacional Natural los Katíos, Colombia. Diatom Research 23: 147-167.
- Santos JC, Leal IR, Almeida-Cortez JS, Fernandes GW & Tabarelli M (2011) Caatinga: the scientific negligence experienced by a dry tropical forest. Tropical Conservation Science 4: 276-286.
- Schmidt A (1812-1899) Verzeichniss der. *In*: A. Schmidt's Atlas der Diatomaceenkunde: Heft 1-36 (Serie I-III) abgebildeten Arten und benannten Varietäten nebst den mit angeführten Synonymen. Topics Diatoms. O.R. Reisland, Leipzig. Pp. 350.
- Schultz ME (1971) Salinity-related polymorphism in the brackish-water diatom *Cyclotella cryptica*. Canadian Journal of Botany 49: 1285-1289.
- Silva JMC, Barbosa LCF, Leal IR & Tabarelli M (2017) The Caatinga: understanding the challenges. *In*: Silva JMC, Leal IR & Tabarell M (eds.) Caatinga: The largest tropical dry forest region in South America. Springer International Publishing AG, Cham. Pp. 3-19.
- Silva-Lehmkuhl AM, Tremarin PI, Vercellino IS & Ludwig TAV (2019) Periphytic diatoms from an oligotrophic lentic system, Piraquara I reservoir, Paraná state, Brazil. Biota Neotropica 19: e20180568.
- Simonsen R (1974) The diatom plankton of the Indian Ocean Expedition of R/V "Meteor", 1964-65. "Meteor" Forschungsergbnisse, Reih D-Biol 19: 1-66.
- Simonsen R (1979) The diatom system: ideas on phylogeny. Bacillaria 2: 9-71.
- Spaulding SA & Kociolek JP (1998) The diatom genus *Orthoseira*: ultrastructure and morphological variation in two species from Madagascar with comments on nomenclature in the Genus. Diatom Research 13: 133-147.
- Stachura-Suchoples K & Williams DM (2009) Description of *Conticribra tricircularis*, a new genus and species of Thalassiosirales, with a discussion on its relationship to other continuous cribra species of *Thalassiosira* Cleve (Bacillariophyta) and its freshwater origin. European Journal of Phycology 44: 477-486.
- Stevenson J (2014) Ecological assessments with algae: a review and synthesis. Journal Phycology 50: 437-461.

Syvertsen EE & Hasle GR (1984) Thalassiosira bulbosa Syvertsen sp. nov., an Artic marine diatom. Polar Biology 3: 167-172.

Tanaka H (2007) Taxonomic studies of the genera Cvclotella (Kützing) Brébisson, Discostella Houk et Klee and Puncticulata Håkansson in the Family Stephanodiscaceae Glezer et Makarova (Bacillariophyta) in Japan. Bibliotheca Diatomologica, Band 53. J Cramer, Berlim. 204p.

- Tanimura Y. Nagumo T & Kato M (2004) A new variety of Cyclotella atomus from Tokyo Bay, Japan, C. atomus var. marina var. nov. Bulletin of the National Science Museum Series C (Geology and Paleontology) 30: 5-11.
- Tremarin PI, Ludwig TV & Torgan LC (2013) Morphological variation and distribution of the freshwater diatom Aulacoseira ambigua (Grunow) Simonsen in Brazilian continental environments. Iheringia Série Botânica 68: 139-157.
- Tuji A & Williams DM (2006) Type examination of

Cvclotella wortereckii Hust. (Bacillariophyceae) with special attention to the position of its rimoportula. Bulletin of the National Science Museum Series B (Botany) 32: 15-17.

- Tuji A (2018) A new freshwater diatom, Terpsinoë muninensis sp. nov., from the Ogasawara Islands, Japan. Memoirs of the National Science Museum (Tokyo) 52: 5-15.
- Vieira RDS, Lacerda SR, Oliveira ECC, Nascimento KJ & Dias AS (2013) Biodiversidade de microalgas perifíticas do Rio da Batateira (Sítio Fundão, Crato, CE). Cadernos de Cultura e Ciência 12: 7-15.
- Virta L, Gammal J, Järnström M, Bernard G, Soininen J. Norkko J & Norkko A (2019) The diversity of benthic diatoms affects ecosystem productivity in heterogeneous coastal environments. Ecology 100: 1-11.
- Wu S (2013) Terpsinoë musica. Diatoms of North America. Available at https://diatoms.org/species/ terpsinoe musica>. Access on 23 June 2020.