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Morphological and environmental characterization of *Terpsinoë musica* (Biddulphiaceae, Bacillariophyceae) in tropical streams from Mexico

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The morphological and environmental characteristics of the genus *Terpsinoë* were assessed from five populations from tropical streams in central Mexico. Four populations of *Terpsinoë musica* were characterized by one eccentric rimoportula with a short stalk. Only one population was characterized by one to three eccentric rimoportulae. For the first time the external process known as a rota is described for this genus, a taxonomic character employed to differentiate genera and species in other members of the Biddulphiaceae. Populations of *T. musica* occurred in warm freshwater habitats (20–29°C), neutral to slightly alkaline waters (pH 7–8), with medium to high ionic content (specific conductance 268–2640 μ S cm⁻¹) and dominance of sulphate/bicarbonate and calcium/magnesium. Highest abundances occurred in microhabitats at shallow depths, with variable water flux, low to medium irradiance on the bedrock, suggesting that *T. musica* is an abundant fresh hard-water species, even though it could be found over a wide range of conditions. The morphological analysis identified all the studied populations as *T. musica*. However, the morphological and morphometric variation found in these populations suggests ecophenotypic variation, broadening the taxonomic characteristics of this species.

Keywords: Biddulphiaceae, morphology, ecology, Mexico, streams, Terpsinoë musica

Introduction

The freshwater and marine members of the family Biddulphiaceae are distinguished by: pseudocellate elevations, vertical valve mantles (turned outwards to the valve margin in some species), internal ribs (when present) and labiate processes (when present) in an irregular group in the central part of the valve or on the mantle (Ross et al. 1979, Hoban 1983). The genus Terpsinoë Ehrenberg was first described from Mexico (Ehrenberg 1843), based on the type species Terpsinoë musica Ehrenberg, with the following morphological characters: quadrangular cells in girdle view, with deep mantles and several straight or curved septa (resembling musical notes), elliptical valves with strongly undulate margins, transverse ribs extending across the shorter axis, pore fields (pseudocelli) at the apices, flat valve faces without spines, with one or no eccentric rimoportulae in the middle, reticulated or punctate areolation, living cells solitary or in zig-zag colonies, linked together by mucilage secreted through the pseudocelli (Boyer 1900, Round et al. 1990).

There are five currently recognized species of *Terpsinoë* in America: *T. brebissonii* (Kützing) Van Heurck, *T. brasiliensis* Ehrenberg, *T. americana* Bailey, *T. intermedia* Grunow and *T. musica*. The characteristics used

to differentiate these species include habit, valve structure (shape, size and ornamentation), presence of transverse ribs and the presence of rimoportulae (number and disposition). Three species of *Terpsinoë* have been reported from Mexico: T. intermedia from the Gulf of Mexico (Krayesky et al. 2009), T. americana from the Gulf of Mexico and Baja California Sur (Krayesky et al. 2009, Fuerte et al. 2010) and T. musica, which is the most common species of this genus in the country, occurring over a wide spectrum of habitats, from marine (Krayesky et al. 2009), coastal (Moreno et al. 1996, Nava-Ruiz & Valadez 2012) and continental waters, such as cenotes, karstic wetlands (Sánchez-Molina et al. 1994, Tavera et al. 1994, Sánchez et al. 2002, Schmitter-Soto et al. 2002, Siqueiros-Beltrones 2002, Novelo et al. 2007, Nava-Ruíz & Valadez 2012) and streams (Ehrenberg 1843, Valadez-Cruz et al. 1996, Montejano et al. 2004, Beltrán-Magos et al. 2005, López-Adrián & Barrientos Medina 2005, Novelo et al. 2007, Metzeltin & Lange Bertalot 2007, Novelo 2012).

In order to characterize the degree of morphological variability and their ecological requirements, this study analysed the morphology of *Terpsinoë* populations from five sites along the central region of Mexico to determine their taxonomic status.

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Materials and methods

Populations of *Terpsinoë* were sampled from five sites, shaded by overhead vegetation in humid to sub-humid tropical climates, at altitudes of 120 to 2,121 m a.s.l., between 18° -22° N and 96° -100°W (Fig. 1). Epilithic diatoms were collected by brushing pebbles located within the laminar flow layer of the stream bed. Samples were observed alive and subsequently preserved in 3% formalin and deposited in the FCME herbarium (Holmgren et al. 1990). Frustules were cleaned following the method of Rushforth et al. (1984) and permanent slides were mounted in Naphrax resin (Brunel Microscopes, Chippenham, UK). A staining procedure for possible extracellular sulphated polysaccharides (0.3% alcian blue in 3% acetic acid at pH 2.5) was applied to live individuals (Sheath & Cole 1990).

The following physical and chemical parameters were measured *in situ* at each site: water temperature, pH, specific conductance (standardized to 25° C, K₂₅) with a Conductronic PC-18 conductivity meter (Puebla, México), dissolved oxygen using an YSI-85 oxygen meter (YSI, Ohio, USA), current velocity (cm s⁻¹) using a Swoffer 2100 current velocity meter (Swoffer Instruments 3000, WA, USA) and irradiance with a LI-COR LI-1000 quantum meter with a flat subaquatic sensor of photosynthetically active radiation (LI-COR Corporate, Lincoln, NE).

Samples for measuring nutrient concentrations in water were collected in duplicate; each sample (30 mL of stream water) was filtered *in situ* through 0.45 and 0.22 μ m pore size membranes (Millipore, MA, USA), preserved with a few drops of chloroform, and frozen for subsequent analysis in the laboratory with a SAN Plus Segmented Flow



Fig. 1. Location of the study sites (•) and previous records (o) of *Terpsinoë* populations in Mexico. 6 – Oaxaca (Tavera et al. 1994), 7 – Morelos (Valadez-Cruz et al. 1996), 8 – Huasteca (Cantoral-Uriza et al. 1997), 9 – Puebla (Novelo et al. 2007), 10 – Quintana Roo (Sánchez et al. 2002), 11 – Yucatán (Sánchez–Molina et al. 1994, Schmitter-Soto et al. 2002, López-Adrián & Barrientos Medina 2005), 12 – Baja California (Siqueiros-Beltrones 2002).

Analyzer (Skalar, GA, USA) following standard titration protocols. Soluble reactive phosphorus (in theory mostly in the form of orthophosphate, PO₄-P), nitrite nitrogen (NO₂-N), nitrate nitrogen (NO₃-N), ammonium nitrogen (NH₄-N), dissolved inorganic nitrogen (DIN) and silicon dioxide (SiO₂) were analysed following APHA (1989). Water samples for the determination of anions and pH were preserved frozen in the dark, while samples for cations were preserved with 40% nitric acid (pH 2–3). Determination of carbonates was performed using the titration method, chlorides by the selective electrode method, hardness by the titration method with ethylenediamine tetraacetic acid, and Na + and K + by the spectrophotometric atomic absorption method (APHA 1989).

All characteristics previously considered to have taxonomic importance in *Terpsinoë* were examined (Hustedt 1930, Luttenton et al. 1986, Round et al. 1990, Sterrenburg 1994). Specimens were observed and measured with an Olympus BX51 contrast interference microscope and a scanning electron microscope (Jeol JSM-5310LV, MA, USA). At least 100 specimens were measured (length of apical axis, breadth of pervalvar axis and mantle depth) from each population, and the significance of differences was assessed using a Mann–Whitney *t*-test.

Results

Morphological analysis (Figs 2–23)

Chains of cells (4-5 cm length) were observed at three sites (Itzamatitlán, Santa Anita and Manantiales). Each cell had numerous, uniformly scattered, discoid plastids (Figs 2, 5) and was joined to other cells at one or both extremes by pads of mucilage with sulphated polysaccharides, resulting in the typical zig-zag colonies (Figs 3, 6). The valves were narrowly lanceolate and triundulate in valve view, with strongly undulate margins (Figs 8-11). In smaller valves, undulations were asymmetrical (Fig. 9) or head poles were sharply rounded. The three inflations were nearly equal in width. Lengths of apical axis ($80.2-135.6 \,\mu m$), breaths of pervalvar axis (33.6–50 μ m) and mantle depths (64.4– $125 \,\mu\text{m}$) did not differ significantly between populations (p 0.05). The number of transverse ribs varied from two to six. Cells are rectangular in girdle view with a pseudoseptum at each valve apex and several septa that are thickened towards the interior, resembling 'musical notes', and sometimes less developed near the valves (Figs 4, 7). No auxospores were observed.

Pseudocelli were present at the valve apices, composed of randomly arranged, closely packed, fine areolae, while the rest of the valve surface and mantle were coarsely areolate (Figs 12, 13, 18, 19). Rotae, vela with a thin perforate layer of silica across an areola (Ross et al. 1979), were exclusively observed at the pseudocellus margins in external valve views. In all populations, rotae comprised six radial bars fusing with a circular area in the centre (Fig. 16).



Figures 2–11. Morphological and cytological characteristics of *Terpsinoë musica* in LM. Figs 2, 5. Living cells with abundant discoid plastids. Figs 3, 6. Extracellular mucilage pads of sulphated polysaccharides (arrow) join cells to form chains. Figs 4, 7. Septa visible in girdle view; rimoportulae indicated by arrows. Figs 8–11. Valvar views showing eccentric rimoportulae. (Figs 2–4, 8, Samples from sites 2–5. Figs 5–7, 9–11. Samples from site 1). Scale bars = $20 \,\mu m$ (Figs 2–7), $10 \,\mu m$ (Figs 8–11).

Their frequency varied between populations and between individuals of the same population.

A variable number of eccentric rimoportulae were observed in all populations, occasionally of different sizes.

Populations from site 1 had one or two, rarely three, rimoportulae (Figs 9–11), while populations from the other sites (2–5) had a single eccentric rimoportula (Fig. 17). Internal valvar views showed rimoportulae with a sig-



Figures 12–23. Morphological characteristics of *Terpsinoë musica* under SEM. Figs 12, 18. Whole frustules showing presence of spines around the outer rim of the valves. Figs 13, 19. Pseudocelli with fine areolae and small spines (blunt in Fig. 13). Rotae located exclusively in the pseudocelli (arrow). Fig. 14. Internal view of pseudocelli without any sign of rotae in internal valvar view. Fig. 15. External view of the rimoportula with a large slit (arrow). Fig. 16. Detail of the rota in Fig. 13, consisting of a central circular region connected to the margin by six radial bars (arrow). Figs 17, 22, 23. Internal views of different sized, sigmoid and stalked rimoportulae. Fig. 20. Detail of the marginal spines on valve surface. Fig. 21. Internal view of valve with two eccentric rimoportulae. (Figs 12–17. Samples from sites 2–5. Figs 18–23. Samples from site 1.) Scale bars = $10 \mu m$ (Figs 12, 18, 21), $5 \mu m$ (Figs 13–14, 19) 1 μm (Figs 15–17, 20, 22–23).

moid slit and a slight stalk (Figs 7, 17, 21–23). These opened to the exterior by a straight slit (Fig. 15), similar to other populations from Mexico and the rest of the world. Small, sometimes blunt, spines were observed around the outer valve margin in populations from every site (Figs 18–20).

Ecology

Terpsinoë populations were found in first- and secondorder streams (Table 1) with $100-164 \text{ mg L}^{-1}$ total dissolved solids, moderate to high mineralization (22–75 meq L⁻¹), warm temperatures (20–29°C), neutral to slightly alkaline pH (7.2–7.7), medium to high specific conductance (K₂₅) (268–2,640 μ S cm⁻¹), high concentrations of silica (Si-SiO₂ = 8–58 mg L⁻¹) and low reactive soluble phosphorus (0.001–0.03 mg L⁻¹, theoretically, primarily P - PO₄³⁻⁻). In general, sites had high DIN (2–239 mg L⁻¹) with high sulphate, bicarbonate, calcium and magnesium.

In terms of microhabitat characteristics (Table 2), all populations were characterized by the presence of moderate to high dissolved oxygen concentrations (5– 8 mg L^{-1}), shallow depth (5–10 cm), null to high current velocity (0–110 cm s⁻¹), variable irradiance (5– 419 µmol photons m⁻² s⁻¹) and substratum (bedrock, clay, roots and lime). They could also grow entangled with macroscopic cyanobacteria (*Blennothrix ganeshii* Watanabe et Komárek). Numerous freshwater species were also present: *Amphipleura lindheimeri* Grunow, *A. pellucida* Kützing, *Gomphonema parvulum* Kützing, *Nitzschia clausii* Hantzsch, *Pinnularia maior* (Kütz.) Cleve, *Pleurosira laevis* (Ehrenberg) Compere, *Rhopalodia gibba* (Ehrenberg) O. Müller and *Synedra ulna* (Nitzsch) Ehrenberg var. *contracta* Østrup.

Discussion

The presence of extracellular mucilage composed of sulphated carbohydrates explains how this species is anchored and forms long chains of cells in environments with a constant flux of water, similar to that of *Diatoma hiemale* var. *mesodon* (Ehrenberg) Grunow, *Diatoma vulgare* Bory, *Tabellaria flocculosa* Roth (Luttenton et al. 1986), *Hydrosera triquetra* Wallich (Round et al. 1990) and *Pleurosira laevis* (Ehrenberg) Compère (Cantoral-Uriza et al. 1997, Necchi et al. 1997). According to Luttenton et al. (1986), this type of growth habit may allow a greater

Table 1. Morphometric characters (range, mean \pm standard deviation) of studied specimens and previous reports of *Terpsinoë musica* populations from Mexico and the rest of the world.

				Breadth in			
	Type of	Apical	Breadth	girdle view	~		
Populations	growth	length (μ m)	(µm)	(µm)	Septa	Rimoportulae	
Examined populations							
Site 1. Itzamatitlán	Visible	98-119	41-45	65-113	4-6	1–3	
BA3178		111 ± 6	44 ± 1	89 ± 12			
BA3179	Visible	90-130	37–50	70-125	4-6	1-2	
		113 ± 11	43 ± 4	97 ± 17			
Site 2. Micos	Non-visible	95-136	39–47	64-122	4-6	1	
PA4262		114.7 ± 11	44 ± 3	76 ± 14			
Site 3. Santa Anita	Visible	80-121	37-40	74–104	4	1	
PA4263	(4 cm)	110 ± 9	38 ± 2	91 ± 8			
Site 4. Manantiales	Visible	99–125	34-48	65-110	2-6	1	
BA3182	(5 cm)	112 ± 8	41 ± 4	90 ± 13			
Site 5. Pedregal	Non-visible	102-121	37-40	74–104	4	1	
LM6		110 ± 9	8 ± 2	91 ± 8			
Previous reports							
Puebla, Mexico	Visible	110-130	39–50	—	_	_	
(Ehrenberg 1843)							
Oaxaca, Mexico	Non-visible	122-126	38–39	—	—	_	
(Tavera et al. 1994)							
Morelos, Mexico	Visible	114-119	_	112-116	4-6	1	
(Valadez-Cruz et al. 1996)							
La Huasteca, Mexico	Visible	100-130	44–53	100-125	—	_	
(Cantoral-Uriza et al. 1997)							
Baja California, Mexico	_	-	_	-	-	1–2	
(Metzeltin & Lange-Bertalot 2007)							
Puebla, Mexico	Visible	128-142	48–52	110-118	4-6	1	
Novelo 2012)							
Europe	_	35-250	25-50	—	> 4	1	
(Hustedt 1930)							
Argentina	_	137–140	_	108–113	—	1	
(Maidana 1985)							
U.S.A.	Visible	49–116	37–43	—	2–6	_	
(Luttenton et al. 1986)	(2.5 cm)						
Western Pacific Islands	_	100-110	85–95	—	—	_	
(Navarro & Lobban 2009)							

Populations and locations	Temperature (°C)	pH	K_{25} (μ S cm ⁻¹)	Dissolved oxygen (mg L ⁻¹)	Current velocity $(cm s^{-1})^a$	Irradiance (μ mol photons m ⁻² s ⁻¹) ^a	Substratum	Ionic con- centration (meq l ⁻¹)	Ionic dominance	$\begin{array}{l} \text{Si-SiO}_2 = \\ (\text{mg } \text{L}^{-1}) \end{array}$	$DIN (mg L^{-1})$	RSP (mg L ⁻¹)
Site 1. Itzamatitlán, Morelos	24	7.5	2640	6	1	419	В	75	$SO_4^- > HCO_3^- > Cl^- > CO_3^- $ $> Cl^- > CO_3^- $ $Ca^{++} > Mg^{++} $ $> Na^+ > K^+ $	47	ND	ND
Site 2. Micos, San Luis Potosí	20	7.2	948	8.4	20	12	В	22	$SO_4^- > HCO_3^- > CO_3^- > Cl^- Ca^{++} > Mg^{++} > Na^+ > K^+$	9	184	0.005
Site 3. Santa Anita, San Luis Potosí	25	6.9	1032	6.2	110	67	В, С	28	$SO_4^- > HCO_3^- > CO_3^- > Cl^- Ca^{++} > Mg^{++} > Na^+ > K^+$	8	239	0.018
Site 4. Manantiales, Morelos	29	7.4	1703	7.9	14	23	R	48	$SO_4^- > HCO_3^- > CO_3^- > CI^- Ca^{++} > Mg^{++} > Na^+ > K^+$	47	203	0.031
Site 5. Pedregal, Michoacán	23	7.7	268	4.8	0	5	B, L	ND	$HCO_{3}^{-} > Cl^{-}$ > SO_{4}^{-} $Mg^{++} > Ca^{++}$ > $Na^{+} > K^{+}$	58	2	0.001

Table 2. Physical and chemical characteristics of the study sites (K_{25} = Specific conductivity (standardized to 25°C), DIN = Dissolved Inorganic Nitrogen [N - NO₃⁻, N - NO₂⁻, N-NH⁴], RSP = Reactive Soluble Phosphorus [P - PO₄³⁻]).

Note: Substratum: B: bedrock; C: clay; R: roots; L: lime.

 $a_n = 10.$

degree of rotation along the filament, allowing greater flexibility and thus reducing breakage.

All populations corresponded to descriptions of *T. musica*, based on the type species and previous reports from Mexico and the rest of the world (Table 1). The detailed morphological study of several populations in the central region of Mexico allowed the characterization of the rota, which apparently show wide variation in the Biddulphiacae (Ross & Sims 1972, Ross et al. 1979, Hoban 1983, Round et al. 1990). Morphological variation in the rota and its disposition on the valve surface were described for a population of *T. musica* in Guam (Navarro & Lobban 2009). This variation may allow taxon separation.

A variable number of rimoportulae has been recorded for some species in the Biddulphiaceae, for example, Biddulphia biddulphiana (J.E. Smith) Boyer and Trigonium arcticum (Brightwell) Cleve (Hoban 1983), Pseudotriceratium sp. and Biddulphiopsis sp. (Round et al. 1990), but this study is the first report of up to three rimoportulae for T. musica and Terpsinoë as a whole. The presence of spines has already been recorded for this genus (Franco 2003). Both the arrangement and shape of the spines (sometimes blunt) agree with descriptions of its relative, Hydrosera triquetra Wallich (Round et al. 1990); however, our populations showed a greater abundance of spines. Despite the morphological differences in our populations compared to the type (number of rimoportulae and presence of spines) (Hoban 1983), position and number of rimoportulae are not reliable taxonomic characters on which to base new species within the Biddulphiaceae, as in some other centric genera. Both characteristics could be related to functional aspects, such as the availability of nutrients, or be a morphological response to high current velocity.

Published environmental information suggests that T. musica is a halophilic species that can penetrate upstream in rivers and into other freshwater sites (Wujek & Welling 1981). Nevertheless our results suggest that T. musica is an abundant freshwater species, supported by previous reports for Mexico and the rest of the world (Ehrenberg 1843, Peckham & Clarence 1953, Whitford 1956, Cholnoky 1968, Wallace et al. 1976, St. Clair & Rushforth 1977, Alvarez & Estévez 1982, Luttenton et al. 1986, Round et al. 1990, Sterrenburg 1994, Sánchez-Molina et al. 1994, Valadez-Cruz et al. 1996, Stoermer et al. 1999, Schmitter-Soto et al. 2002, Siqueiros-Beltrones 2002, Montejano et al. 2004, Sherwood 2004, Aysel 2005, Beltrán-Magos et al. 2005, López-Adrián & Barrientos Medina 2005, Kociolek 2005, Sherwood 2006, Novelo et al. 2007, Metzeltin & Lange-Bertalot 2007, Adesalu & Nwankwo 2009, Bahls 2009, Navarro & Lobban 2009, Novelo 2012, Maulood et al. 2013). Moreover, studies confirming the presence of T. musica in coastal areas commonly lack information on whether the cells were alive, or on their abundance. Freshwater distribution is also supported by the presence and abundance of several associated species, which also occur in freshwater environments (Montejano et al. 2004, Beltrán-Magos et al. 2005, Bojorge-García & Cantoral-Uriza 2007, Bojorge-García et al. 2014).

Our results suggest that the following combination of microhabitat characteristics is favourable for the development of this species in the sampled streams: low depth, low to moderate current velocities and irradiance, and a bedrock substratum. Similar conditions have been recorded for this species in major rivers of the central region of Mexico (Montejano et al. 2004). Preferences for low irradiance sites could indicate a shade-adapted species, which agrees with the low, net photosynthetic values recorded for this species in Brazil (Necchi 2004).

Based on shared morphological characters and similar environmental conditions, all the studied populations were considered the same species. The morphological variation suggests ecophenotypic plasticity, broadening the concept of this species. Understanding the function of the variable morphological characters and the implementation of molecular analyses could indicate their phylogeographic origin.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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