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On the geographical distribution and ecology of *Pseudostaurosira cataractarum* (Bacillariophyceae): new findings in the Palearctic and Neotropic ecozones

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Abstract The aim of this paper is to expand the current knowledge on the distribution, ecology and morphology of *Pseudostaurosira cataractarum* (Hustedt) C.E. Wetzel, E. Morales et Ector. We analysed several freshwater diatom assemblages within the Palearctic (Czech Republic, Europe) and Neotropic ecozones (Argentina and Bolivia, South America). In all localities, small araphids were the dominant or co-dominant group. Inside this group, *P. cataractarum* was only dominant in the samples from Argentina and Czech Republic, while the Bolivian samples had only a few individuals. RDA and PCA analyses show that the relative abundance of *P. cataractarum* was positively correlated with water conductivity. The following measurements resulted from the morphometric analysis, apical axis: 2.8–8.2 µm, transapical axis: 2.7–7.2 µm and stria density: 15–29 in 10 µm. In conclusion, the present is the first report of *P. cataractarum* for continental Europe (from fossil material) and the Neotropic ecozone (from extant populations). Besides having a preference for subaerial habitats, this taxon could be locally conditioned by water conductivity, although in each of the analysed samples this species was associated with cosmopolitan diatoms

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that are tolerant to a wide range of environmental conditions. Based on the morphometric analyses in studied populations, we propose that the size range for the apical and transapical axes of *P. cataractarum* should be expanded at the lower end of the range. Likewise, the range of stria density should be expanded since it is wider than that presented for the type population from Indonesia (Java). Consequently, an emended description is presented based on our study and on published data on type and fossil populations.

Keywords Araphid diatoms · Bacillariophyta · Europe · Palearctic · Neotropic · *Pseudostaurosira cataractarum* · South America

Introduction

Small araphid diatoms, traditionally placed in the genus *Fragilaria* sensu lato, include several geographically widespread genera such as *Pseudostaurosira* D.M. Williams et Round, *Punctastriata* D.M. Williams et Round, *Staurosira* Ehrenberg, and *Staurosirella* D.M. Williams et Round. They are important components of benthic and periphytic communities in a wide range of freshwater ecosystems in the world. Several researchers have considered that these taxa are generalists with an *r*-strategy and their rapid substrate colonization and high reproduction rate confer them resilience to short-term environmental fluctuations, making them very competitive species under unstable limnological conditions (Lotter and Bigler 2000; Weckström and Juggins 2006; Lotter et al. 2010). The presence of a given genus and species of this group has been used as an indication of changes in prolonged ice cover, water temperature, nutrient status, salinity, pH and climate-driven environmental variables (Smol 1988; Dixit et al. 1992; Wilson et al. 1997; Douglas and Smol 1999; Lotter and Bigler 2000; Karst-Riddoch et al. 2009). Thus, they are regarded as good environmental indicators in research projects focused on paleo- and neolimnological conditions.

However, investigations on these small araphid diatoms are still problematic and sometimes produce conflicting results (Morales et al. 2010, 2014). Some diagnostic characters have similar appearance when analysed only under light microscopy (LM), and this generates taxonomic uncertainties and mistakes regarding distributional and ecological ranges for many taxa identified based on current literature reports. This is the case of *Staurosira venter* (Ehrenberg) Cleve et Möller and *Staurosirella pinnata* (Ehrenberg) D.M. Williams et Round (Paull et al. 2008; Morales et al. 2010), among others. For this reason, it became necessary to review and re-examine type material of several taxa using detailed analyses encompassing LM and scanning electron microscopy (SEM) in order to discriminate diagnostic ultrastructural features. The results have generated significant taxonomic changes and a better understanding of the ecology and biogeography of some species (Williams and Round 1987; Round et al. 1990; Flower et al. 1996; Morales 2001; Morales et al. 2001, 2010, 2014; Schmidt et al. 2004; Williams and Morales 2010).

Recently, Wetzel et al. (2013) proposed the transfer of *Melosira cataractarum* Hustedt, a species formerly ascribed to the centric diatoms by Hustedt (1938), to *Pseudostaurosira cataractarum* (Hustedt) C.E. Wetzel, E. Morales et Ector, based on detailed LM and SEM observations of the type material from Indonesia. The authors pointed out that characteristics of the striae, spines and the overall construction of the valves are similar to small-sized species of *Pseudostaurosira*. They reported that this species had been found, until then, only in the Indomalaya, Palearctic and Nearctic ecozones.

The aim of this paper is to expand the current knowledge on the distribution, ecology and morphology of *P. cataractarum* and also to evaluate its association with other species, mainly *Fragilaria* sensu lato, in different regions of the world with different environmental conditions. For that purpose, we analysed several freshwater diatom assemblages within the Palearctic and Neotropic ecozones, taking into account that studies of distribution of diatoms in relation to environmental conditions could also provide important ecological information for paleolimnological studies.

Methods

Sampling design

Palearctic ecozone (50°N)

Samples were gathered from sediment profiles collected from the Soos National Nature Reserve situated in the northwestern part of the Czech Republic (50°08′55.28″N 12°24′13″E, 450 m a.s.l.) (Fig. 1). Samples containing *P. cataractarum* (320, 280 and 80 cm of the profile "Soos C") originated, according to the results of pollen analysis (Suda 2012), in the Boreal and Atlantic period (~8200–3800 cal yr BC) (Walanus and Nalepka 2010). More precise dating was not possible due to strong hard water effect at the locality, preventing the use of ^{14}C radiocarbon dating.

The recent conditions at the sampled locality in Soos are typified by high content of salts caused by the occurrence of numerous mineral springs. For example, Císařský Spring, situated in the vicinity of the location where the profile was sampled, contains 5269.4 mg/L of salts (HCO_3^- 1257 mg/L; Cl^- 587.9 mg/L; SO_4^{2-} 1754.1 mg/

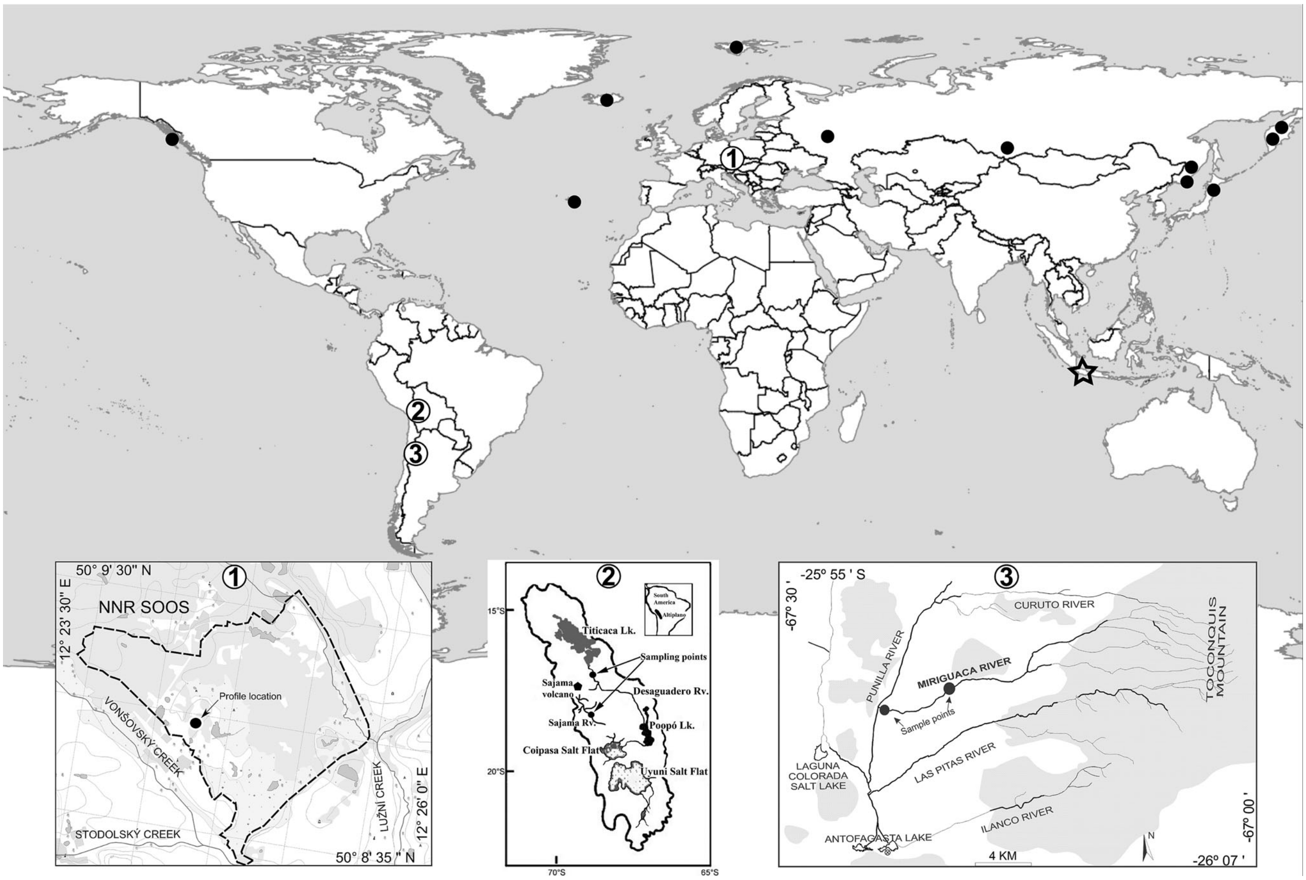


Fig. 1 World distribution of *Pseudostaurosira cataractarum*, based on new studied localities. *1* Soos National Nature Reserve (Czech Republic). *2* Desaguadero and Sajama Rivers (Bolivia). *3* Miriguaca River (Argentina). *Black dots* are occurrences mentioned in Wetzel et al. (2013) and Keller and Straub (2014). Type locality in Indonesia (Java) represented by a *star*

L; Ca^{2+} 72.7 mg/L; Mg^{2+} 25.1 mg/L; Fe^{2+} 47.5 mg/L; Na^+/K^+ 1525.1 mg/L), and stagnant waters found on the diatomite shield where the profile was extracted contain 3111.4 mg/L of salts (Cl^- 86.3 mg/L; SO_4^{2-} 2565.4 mg/L; Ca^{2+} 91.4 mg/L; Fe^{2+} 368.5 mg/L) (Brožek and Dvořák 1971). The salinity in the water body during sediment deposition was probably lower due to rainfall and surface water supply, but it still had to be affected considerably by mineral inputs, since tectonic activity linked with mineral water seepage started most probably in the preboreal period (~9500 cal yr BC) (Keilhack and Rudolph 1929).

Neotropic ecozone (25°–17°S)

In Argentina, the samples came from Miriguaca River (25°59′59.4″S 67°23′51.1″W, 3400 m a.s.l., Antofagasta de la Sierra, Catamarca Province) (Fig. 1). Miriguaca River is located in the Altiplano Puna, an extremely dry and unstable environment (Cabrera 1957). It is one of the main tributaries of the Punilla basin, the most important hydrographic network in the area. Miriguaca River is a permanent shallow river and the area of its drainage basin is 131 km^2. The springs where the river originates are in the western slope (Galán caldera) of the Toconquis mountain (5250 m a.s.l.). During summer 2009, eight surface sediment samples and seven periphytic samples were collected. The samples were stored in 250 ml plastic bottles and fixed in situ with 40 % formaldehyde. Water chemical and physical parameters were measured on site using a portable metre (HI 98107 and Dist3, Hanna Instruments) (Table 1).

In Bolivia, the samples came from the Desaguadero and Sajama rivers (17°23′51″S 68°14′33″W and 17°30′33″S 68°20′35″W, respectively) in Curahuara de Carangas, Sajama Province, Department of Oruro (Fig. 1). The site sampled from the Sajama River has an altitude of 4000 m a.s.l., lies within the Altiplano biogeographic province and it is fed by snow melting water and springs originating near the Sajama peak (6542 m a.s.l.). The sampled site is in an area with dwarf vegetation mixed with the tall grass *Festuca* sp. The river in this area meanders and flows throughout the entire year, although it is deeper during the time of highest snow melt (September through April).

The sample from the Desaguadero River was collected at 3928 m a.s.l. The river carries water from Lake Titicaca

Table 1 Samples and associated data for the localities studied herein

Sites	Name	Sample	Chron.	pH	Vel. (cm/s)	Cond. (µS/cm)	Temp. (°C)
Former lake, Soos National Nature Reserve, Czech Republic	Soos C 320 cm	Sediment-profile	Boreal period	n.d.	n.d.	n.d.	n.d.
	Soos C 280 cm	Sediment-profile	Atlantic-Boreal period	n.d.	n.d.	n.d.	n.d.
	Soos C 80 cm	Sediment-profile	Atlantic period	n.d.	n.d.	n.d.	n.d.
Miriguaca River (mid-basin), Argentina	MR-1	Periphyton	Modern	7.9	0.50	361	28.2
	MR-2	Periphyton	Modern	8.9	6.98	344	39.7
	MR-3	Benthos-surface sediment	Modern	9.2	50.25	272	25.9
	MR-4	Benthos-surface sediment	Modern	9.4	116.28	265	26.4
	MR-5	Periphyton	Modern	8.6	0.50	414	33
	MR-6	Periphyton	Modern	9.2	0.50	262	23
	MR-7	Periphyton	Modern	9.3	54.35	332	21.6
	MR-8	Benthos-surface sediment	Modern	9.1	54.35	266	22
	MR-9	Benthos-surface sediment	Modern	9.8	0	261	22.7
	MR-10	Benthos-surface sediment	Modern	9.9	0	263	20.5
	MR-11	Benthos-surface sediment	Modern	10	0	263	20.1
	MR-12	Benthos-surface sediment	Modern	8.7	0	169	18.5
Miriguaca River (low-basin), Argentina	MR-13	Periphyton	Modern	8.2	0.5	1707	18.2
	MR-14	Periphyton	Modern	7.7	0.5	782	20.3
	MR-15	Benthos-surface sediment	Modern	9.2	39.53	451	20.2
Desaguadero River, Bolivia	HCUCB D-00246	Benthos-epipsammon	Modern	8.3	n.d.	241	21.9
Sajama River, Bolivia	HCUCB D-00249	Benthos-epipsammon	Modern	7.6	n.d.	546	9.9

Chron. chronology, *Vel.* water velocity, *Cond.* electric conductivity, *Temp.* water temperature, *n.d.* no available data. MR 1–15 = samples from Miriguaca River

to Lake Poopó throughout the entire year, but is deeper during the rainy season (September–April). The river has formed an extensive sandy alluvial valley through which it meanders and continuously erodes the landscape dominated by nearly the same vegetation present near Sajama.

The high conductivity in both of these Bolivian rivers (Table 1) is due to inputs of organic matter from animals such as llamas (*Lama glama* Linnaeus 1758) and the agricultural activities in the region. Sediments were collected in May 07, 2009 from the river banks at a depth of 10–15 cm using a turkey baster (large plastic pipette) and then poured into 250 ml plastic bottles and fixed with 20 drops of 40 % formaldehyde. Water chemical and physical parameters were measured on site using a portable metre (HI 99300, Hanna Instruments S.L., Eibar, Spain).

Laboratory methods, data treatment and statistical analysis

Processing of samples for LM analysis of the Czech Republic material followed Battarbee et al. (2001). Dry sediment (0.01–0.05 g) was placed into 50 ml beaker and treated repeatedly with hydrogen peroxide (30 %) until the oxidation process (bubbling) stopped. Then, 10 % hydrochloric acid was added to dissolve precipitated salts and metal oxides. The samples were rinsed with distilled water and after the last rinsing, 10 % ammonium hydroxide was used to eliminate clay particles. Permanent slides were mounted using Naphrax® (refraction index = 1.74) and observed under an Olympus BX 51 light microscope equipped with Nomarski interference contrast at a magnification ×1000. At least 400 valves were counted to obtain relative proportions of taxa in the diatom community. For the morphometric analysis, diatom valves were photographed with an Olympus DP72 digital camera and measured using QuickPhoto Micro 2.3 software. The apical and transapical axis lengths and striae were measured on at least 30 valves per sample (total 96 valves). Areola density was measured on 7 SEM images taken with a JEOL JSM-7401F electron microscope operated at 4 kV and 8 mm distance, housed in the Laboratory of Electron Microscopy, Institute of Parasitology, Academy of Science of the Czech Republic, České Budějovice. For SEM analysis, clean material was mounted on metal blocks and coated with gold using a Bal-Tec SCD 050.

For LM analysis of Argentinian samples, subsamples of 10–20 ml were processed following the standard protocol of Battarbee (1986), the organic matter was removed by adding hydrogen peroxide (30 %) and heating at 80 °C for 2 h. Then, the samples were repeatedly washed with distilled water until neutralization. A subsample of the resulting slurry (0.5 ml) was poured onto coverslips and allowed to dry at room temperature. Permanent slides were mounted with Naphrax®. Slides were examined under a Leica Reichert–Jung Polyvar equipped with Nomarski interference contrast optics at a magnification of ×1000. Relative abundances of taxa were obtained counting 400–500 valves on each slide. For SEM analysis, subsamples of clean material were mounted and dried at room temperature on small metal plates, and then, coating with platinum was accomplished using a Thermo VG Scientific SC 7620 sputter coater. The images were captured using a SUPRA 40, CARL ZEISS, electron microscope operated at 15 kV and from 4.0 to 5.0 mm distance, housed at the Centro de Microscopías Avanzadas (CMA), University of Buenos Aires, Argentina. For the morphometric analysis, diatom valves were photographed with a Sony Cybershot 5.1 MPx digital camera mounted on the mentioned microscope and individual valves were measured using SigmaScan Pro 5.0 software. The apical and transapical axis lengths were measured on 30 valves per sample (total 450 valves). Striae and areolae densities were measured on 31 SEM images. Slides and samples are stored in the collection of Laboratorio de Diatomeas Continentales, Facultad de Ciencias Exactas y Naturales, University of Buenos Aires.

To choose which ordination methods to apply, the length of the gradient (1.2 SD units) was calculated using detrended correspondence analysis (DCA) and a linear distribution for species data was proved (ter Braak and Prentice 1988; Lepš and Šmilauer 2003). Therefore, we proceeded with principal component analysis (PCA) and redundancy analysis (RDA), both ordination methods assuming a linear response. RDA was performed in order to analyse the influence of environmental variables (specific conductance, pH, temperature and current velocity) on studied species data, mainly *Pseudostaurosira cataractarum*. Each of the explanatory variables in the RDA model were tested for significance using Monte Carlo test with permutations 999 to determine variables that explained significance ($P < 0.05$). Percentage diatom data, including taxa reaching >3 % abundance, were square root transformed and environmental variables were standardized prior to numerical analyses (Legendre and Birks 2012) in order to balance variances. The species–environment relationships were expressed as environmental variables plotted passively on the principal component analysis (PCA), since such visualization keeps accurate distances in species space. All analyses were performed in CANOCO for Windows, version 4.5 (ter Braak and Šmilauer 2002).

For LM analysis of the Bolivian samples, subsamples of 20–30 ml were oxidized with a similar volume of 70 % nitric acid. The mixture was boiled on a hot plate for 45 min and rinsed in distilled water until neutrality. A few drops of the resulting slurry were poured onto coverslips, allowed to dry at room temperature, and mounted onto glass slides using Naphrax®. Slides were analysed using a Zeiss Universal microscope suited with DIC and a Jenoptik ProgRes CF colour digital camera. Microphotographs were taken at ×2500 with the aid of the ProgRes CapturePro version 2.8 software. The apical and transapical axis lengths were measured on 50 valves from Sajama River material, which was better preserved and easier to inspect than material from the Desaguadero River. For SEM analysis, 2 ml aliquots of clean material were further digested with 100 ml of hydrogen peroxide (35 %), placing test tubes containing the mixture in hot sand for 36 h, reaching a temperature 210 °C for at least 24 h during the process. Preparations were then allowed to settle and the peroxide was eliminated by vacuum aspiration. One ml of hydrochloric acid (37 %) was then added to the samples and allowed to rest for 2–4 h. Samples were rinsed at least three times with distilled water. The material was filtered and rinsed with deionized water through glass fibre filters with a 3-µm pore diameter. Coating with platinum was accomplished using a BAL-TEC MED 020 Modular High Vacuum Coating System for 30 s at 100 mA. A Hitachi SU-70 electron microscope operated at 5 kV and 10 mm distance and housed at the Luxembourg Institute of Science and Technology, Environmental Research and Innovation Department was used for the analysis. Slides and samples are stored in the collection of the Cryptogams Herbarium of the Bolivian Catholic University, Cochabamba (HCUCB).

For morphometric analysis, the minimum and maximum values, median and interquartile ranges for each morphometric parameter mentioned were calculated and plotted in boxplots to compare the variation in different populations, and the average and standard deviation to show the variability within each studied site.

Morphological terminology follows Barber and Haworth (1981) for valve shape and stria pattern, Cox and Ross (1981) and Cox (2012) for lateral extensions and cross bars, Williams and Round (1987) and Round et al. (1990), Hasle et al. (1983) and Rivera et al. (2010) for areolar substructures, apical pore fields and girdle bands.

Results and discussion

Distribution, associated taxa, and ecology

The geographical distribution of *Pseudostaurosira cataractarum* extends to the Palearctic ecozone (now

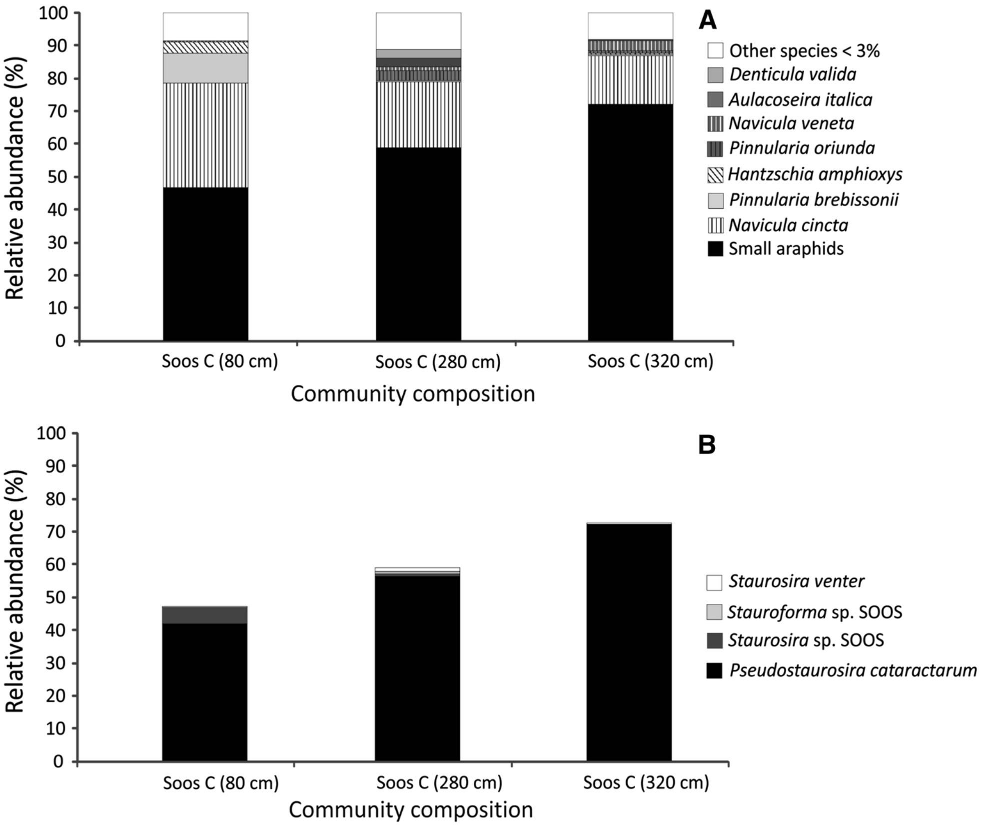


Fig. 2 Diatom community composition in the Soos National Nature Reserve, Czech Republic. **a** Most abundant species in the fossil diatom assemblages at different depths. **b** Percent composition of the small araphids

including the Czech Republic) and, by this report, in the Neotropic ecozone (Argentina and Bolivia) (Fig. 1). As far as we know, our citations for Argentina and Bolivia are the first in the literature for the Neotropic ecozone. Also, our record for the Czech Republic is the first for continental Europe from fossil material.

From the review of Wetzel et al. (2013), the taxon can be said to occur in rivers and lakes, but seems to be more common in cold and hot springs (see also Keller and Straub 2014, not reviewed by Wetzel et al. 2013), and spray zones of waterfalls and dripping walls. In the same review it is shown that the taxon has also been found on wet rocks and mosses, as well as in deep volcanic sediments in swamp peat.

This distribution is also applicable to the populations studied herein, which were found in or near cold and hot springs (9–33 °C) from the modern material (Table 1). However, as can be seen below, each studied site exposed a particular diatom assemblage.

Soos National Nature Reserve (Czech Republic): a total of 39 infrageneric diatom taxa were identified. Additionally, two taxa were set apart as unknowns assigning them provisional names (e.g. *Staurosira* sp. SOOS and *Stauroforma* sp. SOOS). *Pseudostaurosira cataractarum* was found in 3 of 16 sediment samples analysed. The relative abundances of the latter oscillated between 42 and 72 %, with *Navicula cincta* (Ehrenberg) Ralfs as subdominant (14–32 %). Other small araphids were relatively rare (*Staurosira* sp. SOOS < 5 %, *Staurosira venter* <1 %, *Stauroforma* sp. SOOS <1 %) (Fig. 2).

Miriguaca River (Argentina): a total of 88 infrageneric diatom taxa were identified and one additional taxon was set apart as unknown (i.e. *Pseudostaurosira* sp. MIRIGUACA). In all samples, the group of the small araphids (*Pseudostaurosira cataractarum*, *P. pseudoconstruens* (Marciniak) D.M. Williams et Round, *Pseudostaurosira* sp. MIRIGUACA, *Staurosirella pinnata* and *Staurosira venter*) was dominant (50–80 %). Species with more than 3 % of relative abundance were *Fragilaria capucina* Desmazières, *Frankophila similioides* Lange-Bertalot et M. Rumrich, *Cocconeis placentula* Ehrenberg, *Gomphonema parvulum* Kützing, *Nitzschia palea* (Kützing) W. Smith and *Ulnaria ulna* (Nitzsch) Compère (Fig. 3).

In the middle basin, *P. cataractarum* was dominant (25–45 %), and *Pseudostaurosira* sp. MIRIGUACA was subdominant (37–16 %), while in the low-basin *P. cataractarum* was clearly dominant (>48 %).

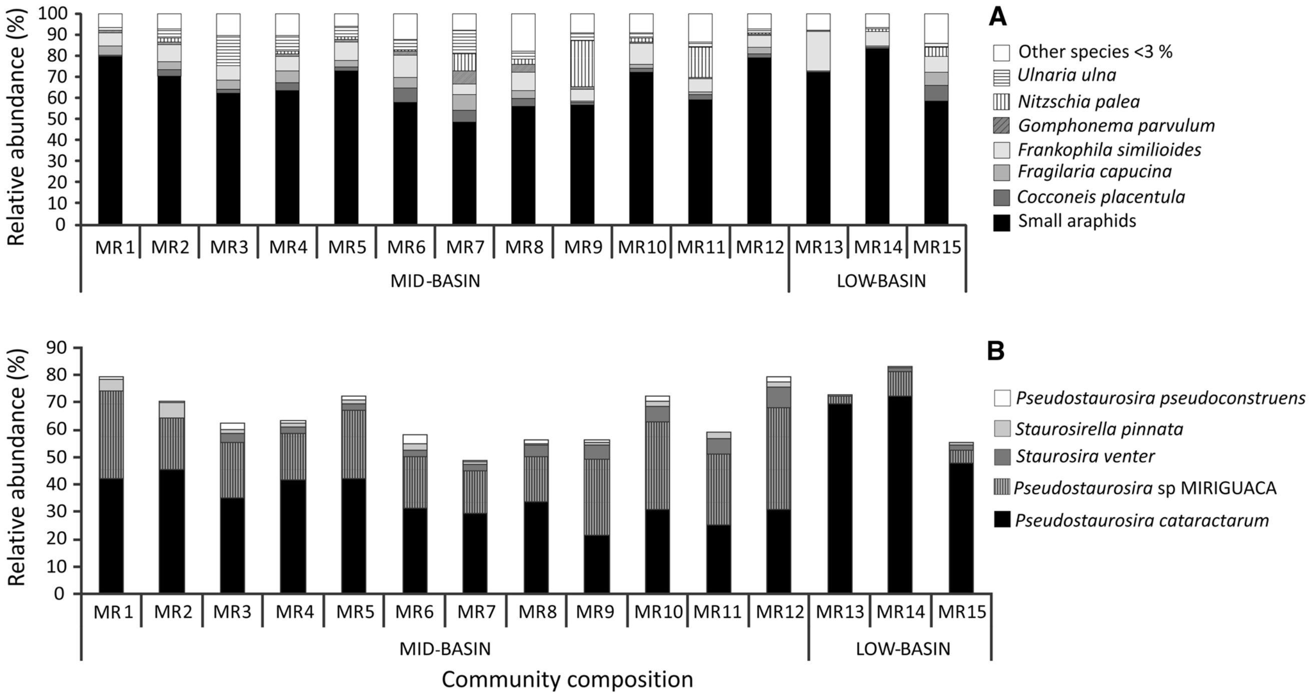


Fig. 3 Diatom community composition at Miriguaca River, Argentina. **a** Diatom assemblages of the most abundant species; **b** percent composition of the small araphids. The reference of the sample point names are described in Table 1

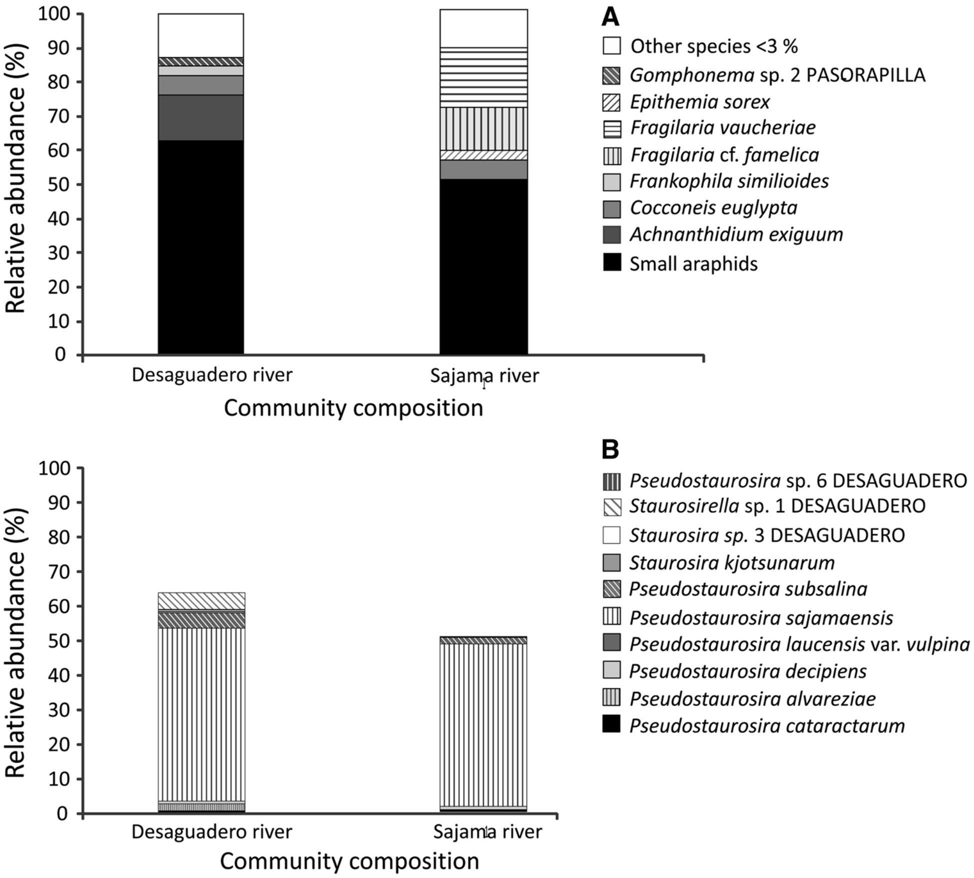
Desaguadero and Sajama rivers (Bolivia): in the Desaguadero River sample, a total of 25 infrageneric taxa were identified and additional 9 taxa were set apart as unknowns, assigning them provisional names (e.g. *Staurosira* sp. 3 DESAGUADERO, *Staurosirella* sp. 1 DESAGUADERO). *Pseudostaurosira cataractarum* was rare, reaching a relative abundance of only 0.17 %. The dominant taxon in the sample was *Pseudostaurosira sajamaensis* E. Morales et Ector (50 %), followed by *Achnanthidium exiguum* (Grunow) Czarnecki (13.7 %), *Cocconeis euglypta* Ehrenberg (5 %), *Staurosirella* sp. 1 DESAGUADERO (5 %) and *Pseudostaurosira subsalina* (Hustedt) E. Morales (4 %). Other small araphids were also present in the sample, but reached abundances of <2 %, among them were *Pseudostaurosira alvareziae* Cejudo-Figueiras, E. Morales et Ector, *Pseudostaurosira decipiens* E. Morales, G. Chávez et Ector, *Staurosira kjotsunarum* E. Morales, Novais et Ector, *Staurosira* sp. 3 DESAGUADERO and *Pseudostaurosira laucensis* var. *vulpina* (Lange-Bertalot et Rumrich) E. Morales (Fig. 4).

For the Sajama River, 26 species and varieties were recorded with an additional 8 unknowns, designated with provisional names. In this case, *P. cataractarum* was also rare reaching only 0.67 % of the total diatom community in the preparation. The dominant taxa in decreasing order were *P. sajamaensis* (46.7 %), *Fragilaria vaucheriae* (Kützing) J.B. Petersen (17.3 %), *Fragilaria* cf. *famelica* (Kützing) Lange-Bertalot (12.5 %), *C. euglypta* (5.7 %), *Epithemia sorex* Kützing (2.5 %) and *P. subsalina* (2 %). Other small araphids were relatively rare with less than 1 % of relative abundance; among them are *P. decipiens*, *P. subsalina* and *Pseudostaurosira* sp. 6 DESAGUADERO (Fig. 4).

Because of the amount of data collected, only the samples from Miriguaca River were suitable to explore the ecological preferences of *P. cataractarum*. These samples come from different microhabitats with slightly different environmental conditions, i.e. moderate to strong alkaline waters (pH: 7.6–9.8), low to high conductivities (169–1.707 µS/cm) and stagnant to strong water current velocity (Table 1). *Pseudostaurosira cataractarum* was dominant in all of these samples, regardless of the observed environmental differences, although it presented the highest relative abundances in environments with high conductivities, associated to periphyton (MR13 and MR14) (Table 1; Fig. 3).

According to the results of RDA analysis, environmental variables explained 58 % of the total variability in species data. Therefore, conductivity (34.4 %; $P = 0.002$) and pH (12.5 %; $P = 0.014$) were significant whereas velocity (7.6 %; $P = 0.12$) and temperature (4.4 %; $P = 0.426$) were found insignificant on $\alpha = 0.05$. It demonstrates that conductivity was the most important factor driving the studied diatom community. The first two PCA axes

Fig. 4 Diatom community composition at the Desaguadero and Sajama rivers, Bolivia. **a** Diatom assemblages of the most abundant species. **b** Composition of small araphids



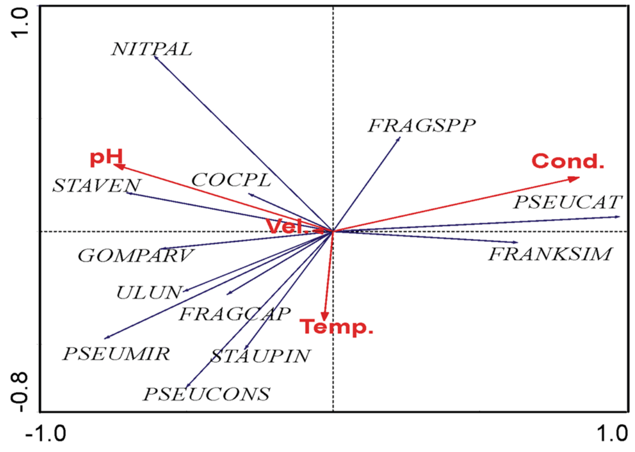


Fig. 5 Principal component analysis of relationships of diatom assemblages and environmental parameters in the Miriguaca River. *Vel.* current velocity, *Cond.* specific conductance, *Temp.* water temperature. *COCPL Cocconeis placentula; FRAGCAP Fragilaria capucina; FRAGSPP Fragilaria* spp.; *FRANKSIM Frankophila similioides; GOMPARV Gomphonema parvulum; NITPAL Nitzschia palea; PSEUCAT Pseudostaurosira cataractarum*; *PSEUCONS Pseudostaurosira pseudoconstruens; PSEUMIR Pseudostaurosira* sp. MIRIGUACA; *STAUPIN Staurosirella pinnata*; *STAVEN Staurosira venter; ULUN Ulnaria ulna*

explained 65.5 % ($\lambda_1 = 0.435$; $\lambda_2 = 0.220$) of variability in species data (Fig. 5). PCA biplot shows that abundances of *P. cataractarum* rise with rising conductivity values, whereas it is negatively correlated with pH (Fig. 5). The influence of current velocity and temperature was negligible.

Regarding life-form strategy, Hustedt (1938) placed *P. cataractarum* among the aerophile forms. In the Miriguaca River, the highest percentages were associated with periphyton samples (MR1, MR2, MR5 and mainly MR13 and MR14) which were samples collected near the shoreline with fluctuations in water level. In the Soos National Nature Reserve (Czech Republic), *P. cataractarum* was dominant together with *Navicula cincta*. The latter has been documented as an aerophilous species in several water bodies from the Netherlands (Van Dam et al. 1994; Vos and de Wolf 1988), and the Bolivian Altiplano (Servant-Vildary et al. 2001). In Bolivia, epipsammon samples were also collected near shore in places that were periodically exposed to air due to fluctuations in water level and current. In the Sajama River, where *P. cataractarum* reached its highest abundance, the most abundant accompanying taxa were the

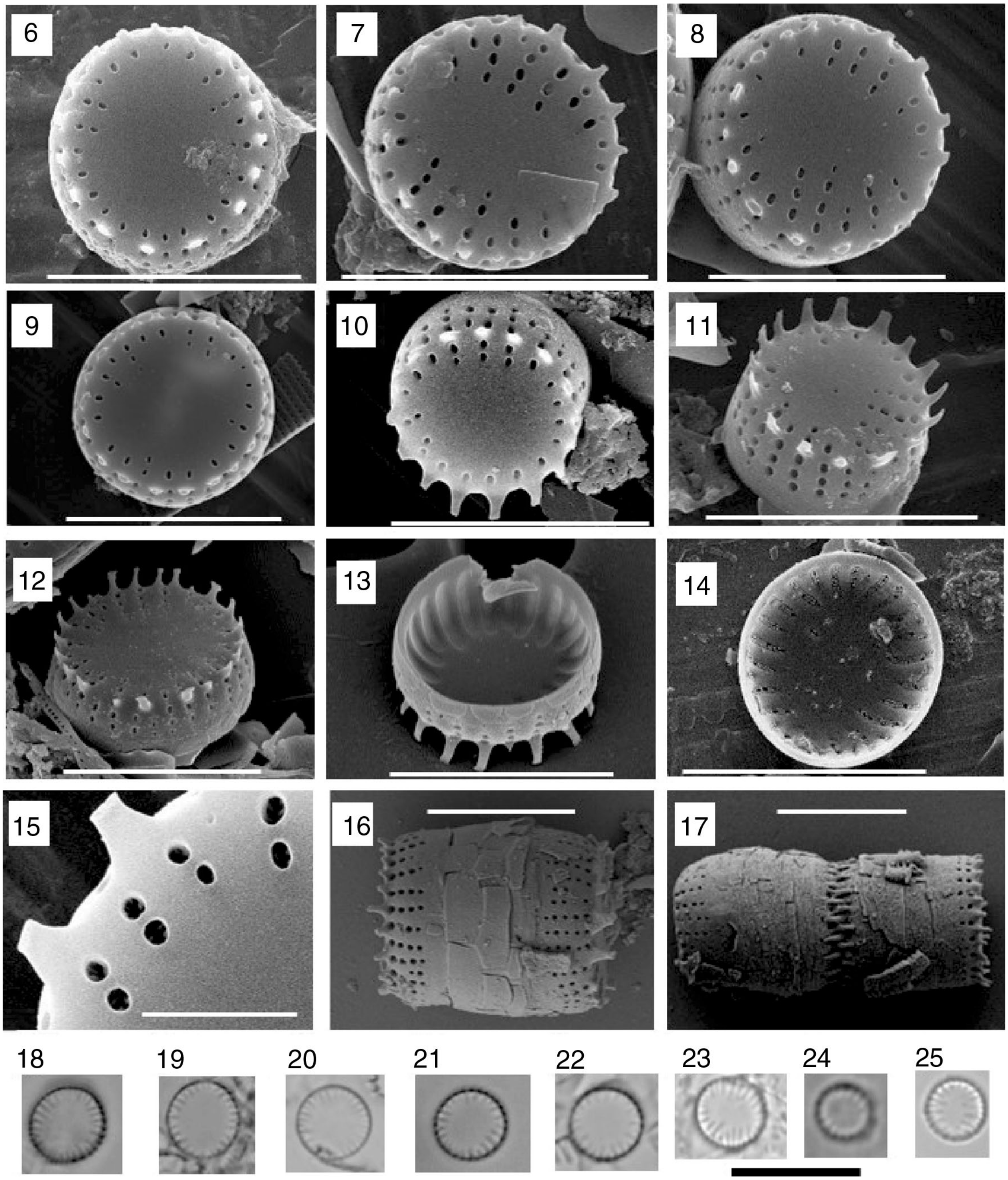


Fig. 6–25 SEM and LM images showing key characteristics of *Pseudostaurosira cataractarum* in all studied sites. **6**, **9** Valve exterior. **10**, **12** Valve mantle. **13**, **14** Valve inner side. **15** Details of the areolae. **16**, **17** Girdle view showing two contiguous cells. *Bar* 5 µm (**6–14**, **16**, **17**—SEM). 1 µm (**15**—SEM); 10 µm (**18–25**—LM). **16–22** from Soos National Nature Reserve (Czech Republic). **6–11**, **14**, **15**, and **24** from Miriguaca River (Argentina). **12**, **13**, **19**, **23** and **25** from Sajama River (Bolivia)

widely distributed monoraphid diatoms *Achnanthidium exiguum* (Taylor et al. 2014) and *Cocconeis euglypta* (Romero and Jahn 2013), cited by Van Dam et al. (1994) as taxa that can be found in wet and moist sites.

Based on our observations and those of type material by Wetzel et al. (2013), and additional populations from Spitsbergen, Norway by Keller and Straub (2014), we present the following emended description of *P. cataractarum.*

***Pseudostaurosira cataractarum* (Hustedt) C.E. Wetzel, E. Morales et Ector emend. E. Morales et Grana**

Frustules barrel-like in girdle view (Fig. 16), joined into chains with the aid of linking spines (Fig. 17). Valves flat (Fig. 6–12), round to slightly elliptical in outline, were 2.8–8.2 µm long and 2.7–7.2 µm wide. Valve apices

Table 2 Minimum, maximum, average and standard deviation for each morphometric parameter of studied *P. cataractarum* populations, the analysis was done measuring at least 30 valves in each point sample (30 measures for the 15 sample points from Argentina, at least 30 for the 3 samples from Czech Republic, and 50 for the one sample from Bolivia)

	Apical axis (µm)	Transapical axis (µm)	Apical/transapical axes ratio	Striae/10 µm	Areolae/1 µm
Wetzel et al. (2013)	5.8–8.2[a]	5.4–7.2[a]	–	15–18[a]	1–4[a]
Soos National Nature Reserve (Czech Republic)	3.3–5.9 (4.42 ± 0.36)	3.1–5.7 (4.34 ± 0.33)	1.02 ± 0.03	19–29	2–4
Miriguaca River (Argentina)	2.8–5.2 (3.97 ± 0.39)	2.7–6.5 (3.75 ± 0.41)	1.06 ± 0.06	16–23	1–4
Sajama River (Bolivia)	4.5–5 (4.60 ± 0.18)	4.5–5 (4.59 ± 0.18)	1 ± 0.03	18–20	–

[a] Calculated from published photos in Wetzel et al. (2013)

distinguished by differences in striation pattern (Fig. 7–9), but many times undistinguishable (Fig. 10–12). Axial area wide, irregular to elliptical (Fig. 6–10, 18–25). Transition between valve face and mantle abrupt and limited by conical linking spines, approximately 0.8 µm long (Fig. 6–12). Abvalvar edge of mantle parallel to valve face/mantle junction (Fig. 11–13). Striae radiate, distinct, 15–29 in 10 µm, sometimes restricted to valve mantle and, in all cases, stopping shortly before valve mantle abvalvar edge (Fig. 8, 10–12). Striae composed of 1–5 round to oval areolae on valve face and 2–5 on valve mantle, decreasing in size from the valve face/mantle edge towards the central sternum and the valve mantle (Fig. 6–12, 14, 18–25). Volae growing profusely from areolae inner periphery (Fig. 14–15). Costae broad, wider than striae (Fig. 6–12, 14). Spines spatulate, solid and located along valve face edge, including apices (Figs. 6–15). Spines interrupt striae, but sometimes displaced towards costae due to size reduction (Figs. 6–15). Spicules, flaps, apical pore fields and rimoportula absent. Well-developed blister-like accumulations on abvalvar edge of mantle (Fig. 12, 13). Cingulum composed of numerous open, imperforated bands, quasifract-like and similar to that of Cymatosiraceae (Fig. 16, 17). Plastids not observed.

The morphometrics determined from populations studied for the present manuscript are as follows:

Soos National Nature Reserve (Czech Republic): Apical axis 3.3–5.9 µm; transapical axis 3.1–5.7 µm; 19–29 striae in 10 µm; areolae 2–4 in 1 µm.

Miriguaca River (Argentina): Apical axis 2.8–5.2 µm; transapical axis 2.70–6.5 µm; 16–23 striae in 10 µm; areolae 1–4 in 1 µm.

Sajama River (Bolivia): Apical axis 4.5–5 µm; transapical axis 4.5–5 µm; 18–20 striae in 10 µm; areolae densities not determined.

The morphometric analysis highlights that measured specimens are smaller (2.8–5.9 µm apical axis) than those registered by Wetzel et al. (2013, 5.4–8.2 µm apical axis) (Table 2). Comparing the samples from Soos National Nature Reserve (Palearctic ecozone) and Sajama and Miriguaca rivers (Neotropic ecozone), *P. cataractarum* in the Miriguaca River is slightly smaller; however, the variation ranges overlap among these three populations (Fig. 26). The Sajama River population is composed of valves that are more elliptical and have smaller apical/transapical ratio (Fig. 26). Some specimens showed a much higher stria density, so the ranges are wider (16–29 in 10 µm) than for the type population (Table 2).

Conclusion

The distribution of *P. cataractarum*, originally described from Indonesia and then reported from several Indomalaya, Palearctic and Nearctic environments is hereby extended to the Neotropic ecozone, with the report of Argentinian and Bolivian populations. The record for the Soos National Nature Reserve (Czech Republic) constitutes the first report of this diatom from fossil material for continental Europe in the Palearctic ecozone. No reports of extant populations exist for this diatom for Europe.

In all localities studied herein, small araphids were the dominant or co-dominant group. Inside this group *P. cataractarum* was dominant in samples from Argentina and Czech Republic, but not in samples from Bolivia, where the taxon had low frequencies. The assemblages of diatoms were different in each of the studied localities.

The distribution of *P. cataractarum* could be conditioned by conductivity and have an aerophilous life-form strategy, though it was associated with cosmopolitan diatoms, tolerant of a wide range of conditions.

Our morphometric analyses show that the size range for the apical and transapical axes of *P. cataractarum* should be expanded at the lower end of the range, since valves found in continental European and South American populations were consistently smaller than the type population. Likewise, the stria density range is wider than originally mentioned for the type and should be expanded at the

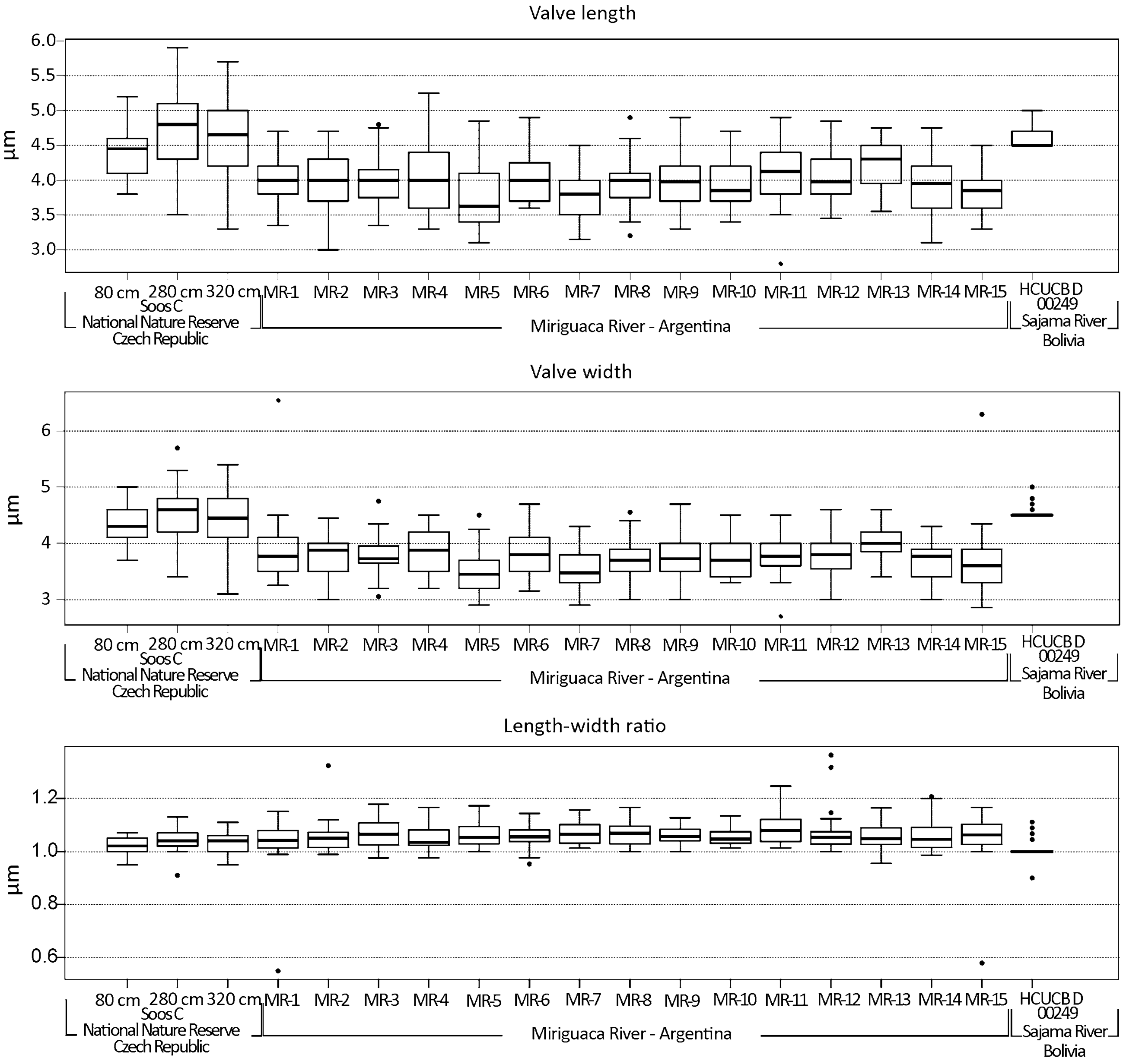


Fig. 26 Boxplots of morphometric parameters for the populations of *Pseudostaurosira cataractarum* presented herein. The reference of the sample point names are described in Table 1

higher end of the range. Therefore, *P. cataractarum* has the following morphometric features: apical axis: 2.8–8.2 µm, transapical axis: 2.7–7.2 µm and stria density: 15–29 in 10 µm.

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