

Cyanobacterium *Petalonema alatum* BERK. ex KIRCHN. – species variability and diversity

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Abstract: *Petalonema alatum* is an interesting cyanobacterial species of subaerial calcareous habitats in gorges of the National Park Slovenský raj, Slovakia. Observation of different morphological forms in natural and culture materials is demonstrated and discussed. Cultures of *P. alatum* differed from natural populations mainly in the width of the filament apex, massiveness of mucilage sheaths, and degree of heteropolarity. This means that these features are more likely controlled by environmental variables. Other characteristics (heteropolarity, false branching, sheath structure) were found to be stable and consequently can have taxonomical importance.

Key words: cyanobacterium, *Petalonema alatum*, Microchaetaceae, subaerial habitat, morphometric analysis, National Park Slovenský raj, Slovakia

Introduction

Petalonema alatum was described as *Oscillatoria alata* for the first time and also illustrated later by CARMICHAEL (in GREVILLE 1823, fig. 1–60; 1826, fig. 181–240) from wet rocks from Scotland (Argyll, Appin) as “stratum rufo–fuscum, filis brunneis, minutis, late alatis, alis albidis.” However, BERKELEY (1833, p. 23, tab.7, fig. 2) synonymized it to a new established name *Petalonema alatum* and BORZI (1879) combined it with *Scytonema densum* (A.BRAUN) BORNET under a new name *Scytonema alatum*. ITZIGSOHN (1855, p. 165) even combined *Petalonema alatum* with *Scytonema myochrous*. Although this species has long been known (Tables 1 and 2), its taxonomy has still not been clarified and the range of its morphological variability under different conditions is unknown. The present study focuses on morphological variation of natural population of *Petalonema alatum* in comparison to clones growing under laboratory conditions and to published data (Tables 1 and 2).

Material and methods

Samples were taken from a wet calcareous wall of the Piecky Gorge (Veľký vodopád waterfall) in the National

Park Slovenský raj (Slovakia). The substrate hosting an algal biofilm was limestone (90% of calcite, and 4% of quartz, from Powder Diffraction data). The samples were collected by random scraping of rock surface (2–4 mm) into sterile tubes during summer seasons (June 24th 1998, August 1st 1999, September 27th 2000, July 9th 2002, August 7th 2005 and on September 16th 2007). Environmental variables (relative humidity and temperature) were measured (1 meter above the soil surface) using a thermo–hygrometer (Mütec Instruments GmbH, Germany). Irradiance values were measured using a radiometer equipped with a quantum sensor (Excellent Technology Co., Italy). Both natural samples and isolates maintained in cultures were observed and documented using an Olympus BX 50 light microscope equipped with Lucia Image Analysis and stereomicroscope Olympus SZH. Cultures were kept in Petri dishes and tubes containing culture medium BBM (SMITH & BOLD, 1966) under controlled conditions (temperature 21°C, humidity 60%, irradiance 10.3 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$, light 660 lx, (PhAR) 2.14 $\text{W}\cdot\text{m}^{-2}$ and in a photoperiod 12:12h light:dark). The initial sample incubation in Petri dishes (7–21 days) was followed by isolation of clones. The following morphometric data were measured from natural populations (60 specimens) and from cultures (60 specimens): Apical zones – width of filament apex; heterocyte zones – width of the part with the first heterocyte; terminal zones – width of terminal part (with many heterocytes). Afterwards these data were statistically visualised using the program STATISTICA (StatSoft®). Dimensions of cells, trichomes, and filaments of cyanobacteria

from the wild sample and the cultivation sample were compared using the Wilcoxon Signed Ranks Test (© Microsoft Excel).

Results

Morphology and taxonomy

Natural samples were dominated by *P. alatum*. The dominant cyanobacterium was accompanied by other coccal and trichal cyanobacteria. Crusts with *Petalonema* were caespitose, mucilaginous, from yellowish green or greyish green to blackish brown in colour. *Petalonema alatum* is classified as an euendolithic species, which actively penetrates the calcareous substrate. The major part of filaments was inside the limestone rock, except for the wide apical parts. Filaments of *P. alatum* were flexuous, loosely entangled, single or branching, procumbent, and about 2500 μm long, (25)30–115(130) μm broad; heteropolarity was obvious. False branching was observed at heterocytes (Figs 1d, e); sheaths were very thick, with distinct funnel-shaped mucilage sheaths consisting of divergent layers (Fig. 1b). Inner layers were from yellowish, yellow, orange to brown (in old filaments), outer layers were colourless or yellowish (in old filaments). Trichomes were typically constricted at the cross walls, heteropolar, with apical meristematic zones, with rounded or globular apical cells (Figs 1b–d, f; 2 a, b, k–n). Cells at the apical growing region were short and barrel shaped, in older parts long and cylindrical, up to twice as long as broad (5)6–15(18) \times (4)5–8(9) μm . Heterocytes were basal or intercalary, (12.5)15–17.5 \times (5)7.5–10.5 μm . Hormogonia occurred rarely in the apical part of the filaments (Figs 2d, n).

Cultures of *P. alatum* were not axenic. Mucilaginous cyanobacteria are usually accompanied by microorganisms such as bacteria, fungi, small coccal green algae or cyanobacteria, and diatoms. *Petalonema* grown on an agar plate forms mucilaginous, compact, dark-green colonies; filaments were horizontal or erect, mostly unbranched, rarely with single lateral false branching at the heterocytes. Heteropolarity of the filament was reduced (30)35–70(80) μm , but still visible. It had scytonematoid character and lost the majority of mucilage layers. Reduced sheaths were still lamellated, both layers being colourless (Figs 1g, h); only old filaments were yellowish. Trichomes were generally constricted at the

cross walls, heteropolar, with apical to subapical meristematic zones, with rounded or globular apical cells. Shapes of cells are the same such as in a wild sample, only the size range differs (2.5)5–15 \times 7.5–15(16) μm . Heterocytes were rare, basal or intercalary, 7.5–10 \times 7.5–10 μm in diameter; hormogonia were present often in apical parts of the filaments. Heteropolar development of hormogonia begins from one pole, where cells are intensively divided, the other pole ending cell often becomes a heterocyte. Hormogonia germinated typically within lamellated sheath.

P. alatum from cultures differed significantly in morphological characters (Figs 1–3). They were significantly narrower than that from natural populations (Wilcoxon Signed Ranks Tests, significant value 0.05; Apical zones: $Z = -5,62$, $p < 0.0001$; Heterocyte zones: $Z = -3,16$, $p = 0.0016$; Terminal zones: $Z = -2,09$, $p = 0.0370$) The following features were found to be relatively stable: the heteropolarity of trichomes with basal heterocytes, lateral false branching starting at the heterocytes, heteropolar germination; presence of apical or subapical meristematic zones and rounded apical cells.

Discussion

The taxonomic position of *Petalonema* and *Scytonema* species has been based on different morphological features since the beginning of 19th century. The old descriptions (CARMICHAEL in GREVILLE 1823, 1826; BERKELEY 1833; LEMMERMANN 1910; MIGULA 1915; GEITLER 1932) mentioned only the structure type of the trichome sheaths and filament envelopes including the colour. Additional important information (the presence of heterocytes, meristematic zones on trichomes, filament growth and branching) recorded later by TILDEN (1910), KOSSINSKAJA (1926), GEITLER (1942) and SKUJA (1929, 1964) have been found to be crucial. The first more comprehensive set of data on the false branching and sheath structure was recorded by BHARADWAYA (1933). Phycologists interested in these genera, could be separated into groups depending on their interpretation of the morphological data, in particular whether the definition of the main diacritical taxonomic features was validated or shuffled (Table 1). Interestingly, the article published by ZEHNDER (1985) caused taxonomic discussion between phycologists. Based on comparative studies he explained it



Fig. 1. *Petalonema alatum*: (a–e) natural sample; (f–h) culture; (a) filament arising from substrate, (b, c, f) apices with apical rounded cell, (d) tolypotrichoid fragment of filament; (e) false branching; (g, h) well established sheath stratification. Scale bars 30 μ m.

as follows: “*Petalonema alatum* and *Scytonema myochrous* are not, as has been suggested on the basis of observation in situ, ecomorphoses (status) of the same taxon, but two different taxa. Cultured side by side in the laboratory under the same conditions, width and structure of the sheaths are different and thus, these differences are genetically rather than environmentally controlled.” In particular, the development of the preferred main diacritical taxonomic features is

interesting to observe (Table 1), BERKELEY (1833) stressed the branching, filament lined by lamella, and structure of the envelopes (*Petalonema alatum*). KOMÁREK & ANAGNOSTIDIS (1989) stressed the type of heterocytes, type of branching (asymmetric), wide apex of filament and structured sheath and consequently the genus *Petalonema* became an independent taxon in the subfamily Tolypotrichoideae of the Microchaetaceae. This relatively complicated history of the taxonomy

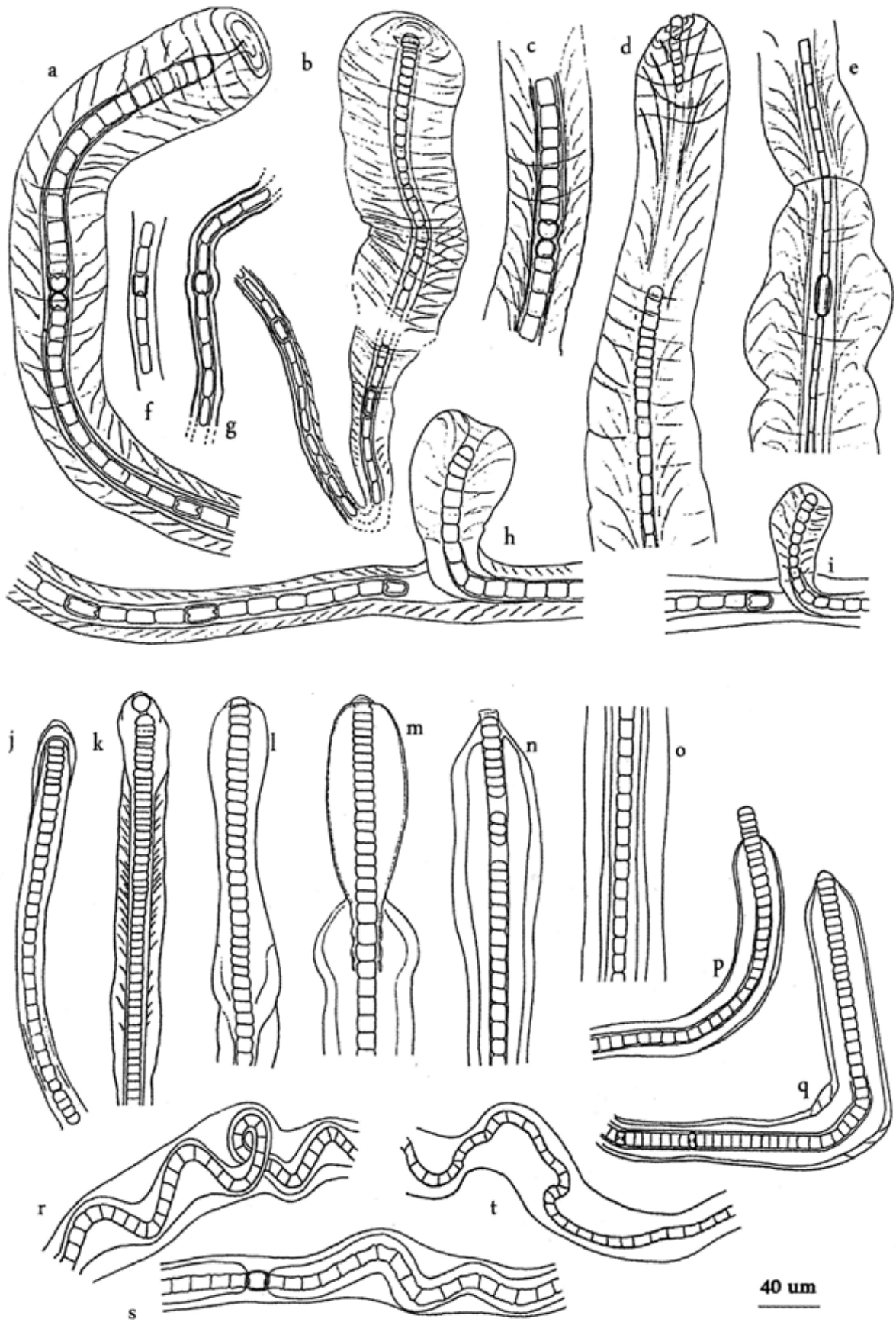


Fig. 2. Iconographs of *Petalonema alatum*: (a–i) natural sample; (j–s) culture; (a–c, e–g, j–m, o–q) heteropolarity of filaments and sheath stratification; (d, n) hormogonia formation; (r–s) trichome spiral–curved in culture. Scale bar 40 μm

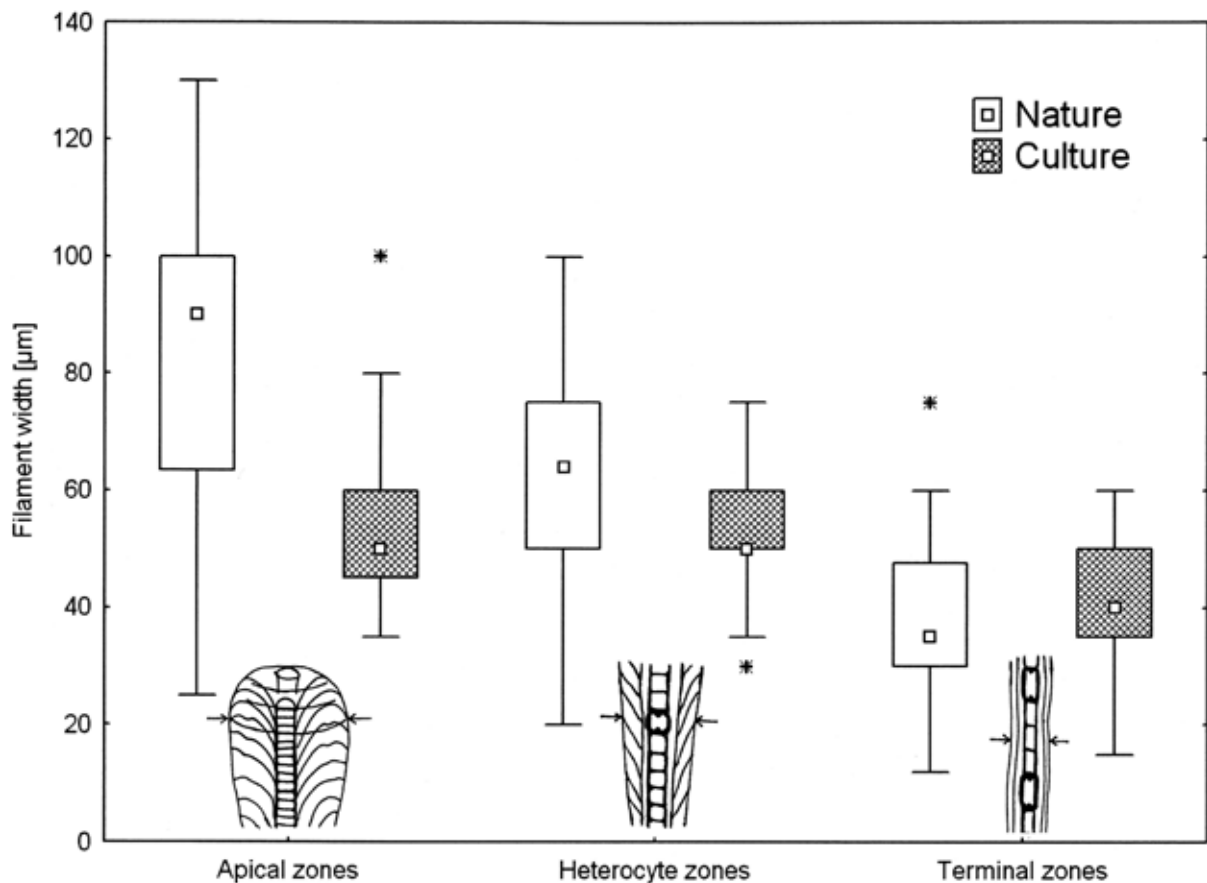


Fig. 3. Comparison of the filament measurements of *Petalonema alatum* – in nature vs. culture, * outliers, □ median, ⊥ non outlier, box border quantil 25% and 75%

of the species *Petalonema alatum* or the genus *Petalonema* motivated me to do a comparative study based on cultivation and the use of statistical methods to illustrate some suggestions on often discussed diacritical features.

Results presented here confirm that morphological variation of *Petalonema alatum* under different conditions is broad and the study of similar taxa is still required in order to definitively establish that they do not belong to a life-history stage of *P. alatum*.

I would like to more definitively say that I agree with KOMÁREK & ANAGNOSTIDIS 1989 that *Petalonema* is a valid genus, and that *P. alatum* is more closely affiliated with *Tolypothrix* in the Microchaetaceae than *Scytonema* (Figs 1–3). The taxon is defined by the copious sheath with funnel-like lamellations, and while the feature is variable, it still persists in culture (Figs 1-2). The Microchaetaceae and Scytonemataceae are possibly confused, and we certainly need some molecular data to resolve these families. The preliminary phylogenies that exist seem

to indicate that the Microchaetaceae are a monophyletic group (ŘEHÁKOVÁ et al. 2007; KAŠTOVSKÝ & JOHANSEN 2008; LUKEŠOVÁ et al. 2009), and *Scytonema* falls outside of this group (Flechtner et al. 2002). There is currently only one *Petalonema* that has been sequenced, *Petalonema* cf. *involvens* from Antarctica (TATON et al. 2006). Unfortunately, TATON et al. (2006) did not include many Microchaetaceae in their phylogeny. They placed their *Petalonema* in the *Nostoc* clade. Furthermore, the other putative member of Microchaetaceae (an Antarctic *Coleodesmium*) was close to the *Nostoc* clade, sister to *Nostoc* Fin 152, a taxon demonstrated elsewhere to not be *Nostoc* (ŘEHÁKOVÁ et al. 2007; KAŠTOVSKÝ & JOHANSEN 2008; LUKEŠOVÁ et al. 2009). The TATON phylogeny does show *Scytonema hofmannii* distant from *Petalonema* and *Coleodesmium*, consistent with FLECHTNER et al. (2002).

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Table 1. Overview of development of main diacritical taxonomic features of species *Petalonema alatum* through history.

Taxonomic stream (origin)	Mentioned as species	Preferred main diacritical taxonomic features	Classification results	References
BERKELEY 1833	<i>Petalonema alatum</i> first definition	the funnel structures of sheath apex of the filament type of heterocytes type of branching (asymmetric) germination of hormogonia filament lined by lamella	Family: Microchaetaceae Subfamily: Tolypotrichoidae	CORRENS (1889) MIGULA (1907, 1915) LEMMERMANN (1910) GEITLER (1932, 1942) SKUJA 1964 ZEHNDER (1985) SANT'ANNA (1988) KOMÁREK & ANAGNOSTIDIS (1989) JAAG 1943 GOLUBIĆ (1967) BOURELLE (1970) KANN (1978) HOFFMANN & DEMOULIN (1985) HOFFMANN (1986) ABDELAHAD (1989) BORNET & FLAHAULT (1887) FORTI (1907) TILDEN (1910), KOSINSKAJA (1926) KOSSINSKAJA IN ELENKIN (1938) FRÉMY (1927, 1942) GUPTA & NAIR(1963) ACLETO (1966) STARMACH (1966) KONDRATYEVA (1968) HINDÁK (1978) KUKK ET AL. (2001)
ITZIGSOHN 1855	inside species <i>Scytonema myochrous</i> as morphotypes	type of branching (symmetric) width of the filament and structure of the sheaths depends on the environment	Family: Scytonemataceae	
BORZI 1879	<i>Scytonema alatum</i> Synonymous to <i>P. alatum</i> or genus <i>Petalonema</i> does not exist	branching in pairs or individually, structured sheath, filament lined by lamella, wide apex of filament and the cells become thinner from apex to the base asymmetric filaments broad apex symmetric branching short branches structured sheath	Family: Scytonemataceae	

Table 2. Published morphometric data of *Petalonema* taxa.

Petalonema species	Cell length (μm)	Cell width (μm)	Filament width (μm)	Heterocytes length \times width (μm)	Ecology	References
<i>P. densum</i> (A. BRAUN) MIGULA	?	6–12	24–40	?	Humid stones, soil	GEITLER 1932
	5–6	5–6	24–30	6 \times 4.5	Aerial on the rock	BOURELLE & MARGUIN 1954
	7.5	10–12	?	?	?	CHOLNOKI 1952
	7–9	5–10	30–45	4–12 \times 6–9	Humid soil	KAMAT 1963
	?	6–12	24–40	?	Humid rocks, soil	KOSSINSKAJA 1926
	?	6–12	24–40	?	Humid rocks, soil	FRÉMY 1927
<i>P. pulchrum</i> (FRÉMY) GEITLER	?	6–12	(19)24–40	?	Humid rocks	STARMACH 1966
	6–7	15–20	Ad 65	?	Humid rocks	GEITLER 1932
	6–7	15–20	Ad 65	?	Humid sandstone	GEITLER 1925
	6–7	15–20	Ad 65	?	?	FRÉMY 1924
<i>P. involvens</i> (A. BRAUN) MIGULA	?	6–12	15–30	?	Epiphytic in a swamp	GEITLER 1932
	3–5	10	20–22	10 in diam.	Epiphytic in a swamp	WOODHEAD & TWEED 1959
	?	6–12	15–30	?	Epiphytic in a swamp	FRÉMY 1927
	4	5–6	12–15	15 \times 7	?	SERPETTE 1955
	3.4–14	6–12	13–30	9–16 \times 7–8.5	Epiphytic and epilithic in a swamp	STARMACH 1966
	?	5.7–9.2	13–30	9.2–13.8 \times 5.7–9.2	Epiphytic in a swamp, humid rocks	KOSSINSKAJA 1926
<i>P. velutinum</i> (C. AGHARD) KIRCHIN.	4–10	6–8	15–30	?	Humid soil	GEITLER 1932
	3.4–6.9	5.7–11.5	13–35	9.2–12.6 \times 3.4–6.9	Humid soil, thermal waters	KOSSINSKAJA 1926
	?	10	?	?	Humid soil, thermal waters	FRÉMY & RAYSS 1938
	?	9–15	12–30	?	Humid soil, thermal waters	FRÉMY 1927
	5–8	10–13	30–50	10–13 \times 13–15	Soil	JAO 1944
	?	10	?	?	Thermal waters	RAYSS 1944

Table 2 Cont.

<i>P. crustaceum</i> (C. AGHARD) KIRCHN.									
3.7-7	5.7-13	12-35	?	Humid soil		STARMACH 1966			
4-10	6-8	15-30	12×6	Soil		BISWAS 1934			
?	6-12	(15)18-22	?	Humid rocks		GEITLER 1932			
?	7.5-10	20-27	?	In a swamp		WHELDEN 1947			
4.6-6.9	4.6-8	13-30	5.7-9 × 5.7-6.9	Soil, humid rocks		KOSSINSKAJA 1926			
?	6-8	15-30	?	Soil, in mosses		FRÉMY 1927			
4.5-7	5.7-8	13-30	5.7-8 in diameter	Calcareous rocks, in mosses		STARMACH 1966			
?	7	15-18.5	?	In a swamp		NIELSEN & MADSEN 1956			
?	7-9	22-50	?	?		NAKANO 1971			
?	4.5-7	?	?	On rocks, in mosses		STARMACH 1975			
4.6-15	4.6-11.5	25.3-75	11.5-12.6 in diam.	Humid rocks, swamps		KOSSINSKAJA 1926			
?	11-14	42-53	19-21 × 9.5	?		ACLETO 1966			
?	?	24-66	?	In a water, on rocks		FRÉMY 1927			
4.6-15	4.6-11.5	24-75	12.5 in diameter	In a water, on humid rocks		STARMACH 1966			
4-9.5	5-11	24-92.5(138)	18-22 × 8-15	Rocks		GUPTA & NAIR 1963			
?	8-18	30-80	14-19×13-15	On water mosses, on submersed rocks		SKUJA 1929			
?	9-15	24-66	17 in diameter	Humid rocks		GEITLER 1932			
(5)6-15(18)	(4)5-8(9)	25-100(130)	(12.5)15-17.5 × (5)7.5-10.5	Humid limestones by water-falls		*UHER			

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