

Molecular data demonstrate the occurrence of *Compsopogon caeruleus* (Compsopogonophyceae, Rhodophyta) in Bahia state, Brazil

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Key words:

- Brazilian northeast
- COI-5P
- Compsopogonales
- *rbcL*
- red algae

Palavras-chave:

- nordeste brasileiro
- COI-5P
- Compsopogonales
- *rbcL*
- algas vermelhas

Abstract

The freshwater red macroalga *Compsopogon caeruleus* is ubiquitously distributed in tropical and subtropical regions and has been reported in many Brazilian states. Here, we report the first record of this species in the state of Bahia, constituting the third record of this species in the northeast region. This population was found on an oyster farm in the Graciosa Quilombola Fishing Community, Taperoá, Bahia, Brazil. We conducted a detailed morphological assessment and analyzed of the sequences of the molecular markers COI-5P and *rbcL*.

Resumo

Embora seja ubiquamente distribuída em regiões tropicais e subtropicais, e seja relatada para muitos estados brasileiros, a macroalga vermelha de água doce *Compsopogon caeruleus* é relatada pela primeira vez para o estado da Bahia, constituindo a terceira citação para a região Nordeste. A população foi encontrada em uma fazenda de ostras na Comunidade de Pesca Quilombola Graciosa, Taperoá, Bahia, Brasil. Neste estudo, descrevemos sua morfologia em detalhes, corroborando com análises das sequências dos marcadores moleculares COI-5P e *rbcL*.

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Introduction

The freshwater macroalgae *Compsopogon caeruleus* (Balbis ex C. Agardh) Montagne (1846:154) (Compsopogonophyceae, Rhodophyta) is widely distributed in tropical and subtropical regions (Oliveira Filho & Pereira 1973; South & Skelton 2002; Liu & Wang 2004; Ratha *et al.* 2007; Sherwood *et al.* 2010; Kitayana 2011; Bautista & Necchi Junior 2014; Vis & Necchi Junior 2021). The species has even been reported in temperate regions (Nichols 1964; Chapman & Cameron 1967; Žáková *et al.* 2013; Zaburlín *et al.* 2019; Vis & Necchi Junior 2021), where it is often considered an invasive species (Žáková *et al.* 2013; Zaburlín *et al.* 2019).

Compsopogon caeruleus is well adapted to adverse environmental conditions, including aquariums and artificial lakes, natural water bodies affected by the discharge of industrial effluents (Szymanska & Krupinska 1983; Scott *et al.* 1988; Scott & Broadwater 1989; Stoyneva *et al.* 2006; Žáková *et al.* 2013; Bautista & Necchi Junior 2014),

and water discharge regions that are used to cool power plants (Chapman & Cameron 1967).

Advancements in morphological taxonomic studies and, subsequently, the emergence of molecular taxonomy have resulted in the consolidation of most *Compsopogon* taxa, with 19 heterotypic synonyms now included in *C. caeruleus* (Guiry 2022). This has expanded its global distribution, demonstrating its remarkable phenotypic plasticity and adaptability. Molecular studies have revealed that although *C. caeruleus* populations are geographically isolated, they exhibit low genetic diversity (Necchi Junior et al. 2013; Nan et al. 2016; Zaburlín et al. 2019).

According to Flora e Funga do Brasil 2025 (continuously updated), *C. caeruleus* is documented from the north to the south of Brazil, in the states of Amazonas, Pará, Maranhão, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, and Rio Grande do Sul; Necchi Junior et al. (2013) also mentioned its presence in the state of Sergipe. However, the species has not been confirmed in the state of Bahia. Here, we report the first documented occurrence of *C. caeruleus* in Bahia and provide morphological and molecular analyses.

Materials and Methods

Sample collection

A population of *Compsopogon caeruleus* was discovered growing in great abundance on an estuarine oyster farm in Graciosa, a community of quilombola fishermen (descendants of enslaved people), in the municipality of Taperoá, Bahia, Brazil (13°28'46.26"S, 39°05'34.50"W). The estuary is surrounded by mangroves, and the land is occupied by extensive palm oil plantations.

The highest occurrence of algae occurred in autumn 2022, the region's rainiest period, when local oyster farmers recorded salinities ranging from approximately 8 at low tide to 24 at high tide. The algae were growing in the oyster farming lanterns in dense populations, harming cultivation because of the weight of the floating structures.

Sampling was conducted in July 2022, and the collected material was preserved in 70% alcohol. The material was subsequently used for morphological and molecular analyses. A voucher specimen was deposited in the Herbarium Alexandre Leal Costa (ALCB) at the Federal University of Bahia, Brazil (Tab. 1).

Morphological analysis

Aspects of external and internal morphology were analyzed using a stereomicroscope Motic™-SMZ-168 Series (Hong Kong, China), and further microscopic analyses were conducted under an optical microscope (Olympus-CX 31, São Paulo, SP, Brazil), coupled to a digital camera (Motic-Motican 3.0 MP). The images were analyzed using

Motic software (Images Plus 2.0 ML). The analyses were conducted based on the observation of the filaments and cuts made with the aid of steel blades. Minimum and maximum measurements were taken for morphometric characteristics from a set of 10 measurements for each analyzed structure.

Molecular analysis

Total DNA was extracted after grinding in liquid nitrogen using the NucleoSpin® Plant II-Macherey-Nagel kit (Bethlehem, PA, USA), following the manufacturer's instructions. For polymerase chain reaction (PCR), the *rbcL* marker was amplified using three overlapping pairs of primers: *FrbLS-R492a*, *F492a-R1150a*, and *F993-RrbcS* (Freshwater & Rueness 1994; Cassano 2009). The COI-5P marker was amplified using the primer pair *GAZF1-GAZR1* (Saunders 2005). For PCR amplification, two GoTaq kits were used following the manufacturer's instructions: Flexi DNA Polymerase Kit (Promega, Madison, WI, USA) and G2 Hot Start Polymerase Kit (Promega); the final volume of the reaction was 25 µL. As a way of solving problems in the amplification, bovine serum albumin (0.5 µL) or magnesium chloride (1.5 µL at 25 mM) were added to the PCR solution, always maintaining the final volume at 25 µL. For *rbcL*, the amplification cycle involved an initial denaturation step at 94 °C for 4 min, followed by 35 cycles of 1 min at 94 °C, 1 min at 45 °C, and 1 min 30 s at 72 °C with a final 10 min extension cycle at 72 °C. For COI-5P, the amplification involved an initial denaturation step at 94 °C for 5 min, followed by 34 cycles of 30 s at 94 °C, 1 min at 45 °C, and 2 min at 72 °C with a final 7 min extension cycle at 72 °C. The reactions were performed using a Techne TC-330 thermocycler (Ramsey, MN, USA). All PCR products were analyzed via electrophoresis on 0.7% agarose gel and stained with Gel Loading Buffer GelRed™ (Biotium) to check product size. PCR products were purified using the PureLink™ PCR Purification Kit (Invitrogen, Carlsbad, CA, USA) following the manufacturer's instructions.

Purified amplicons for both markers were sequenced in both directions using the same PCR primers mentioned above, and the BigDye Terminator Cycle Sequencing Ready Reaction kit (Applied Biosystems, Foster City, CA, USA) on an ABI PRISM 3130DNA Genetic Analyzer (Applied Biosystems) using 40 cycles of 10 s at 96 °C, 20 s at 54 °C and 4 min at 60 °C.

The sequences obtained in the forward and reverse directions for each marker were compared using the BlastN algorithm of GenBank (<<http://www.ncbi.nlm.nih.gov>>), and alignment was performed using BioEdit 7.0.4.1 (Hall 1999). Ambiguous nucleotides were checked in the original electropherograms. For each marker, an alignment

Table 1 – Species, collection information, and voucher and accession numbers of COI-5P and *rbcL* sequences.

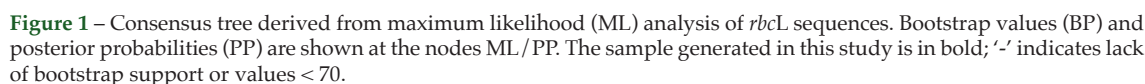
Sample	Collection data	Voucher	GenBank acc. no.	
			COI-5P	<i>rbcL</i>
<i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh	USA, California, Pebble Beach, May 1965, J. Ramus	UTEX1690	-	AF087118
<i>E. carnea</i>	Australia, Tasmania, Tinderbox	JAW4398.1	-	EF660274
<i>Sahlingia subintegra</i> (Rosenvinge) Kornmann	India, Pondicherry, July 20, 2012, F. Bast	POD-49	MH107767	-
<i>S. subintegra</i>	India, Elathur, May 25, 2012, F. Bast	ELA-11	MH107768	-
<i>Boldia erythrosiphon</i> Herndon	USA, Tennessee, Hiawassee River, June 22, 1993, R. Holton		-	AF087122
<i>B. erythrosiphon</i>	-	UTEX LB2858	-	KY709208
<i>Boldia</i> sp.	Canada, K.M. Muller	CRON	HQ699256	-
<i>Compsopogon caeruleus</i>	Vanuatu, Efate Island, June 16, 2005	JAW4530	JX028181	JF292657
<i>C. caeruleus</i>	Vanuatu, Cressionnieres Cascades, 2 km North of Eton Beach waterfall, June 16, 2005, J. West	BHO VU-4531	JX028193	-
<i>C. caeruleus</i>	Argentina, Misiones, Candelaria, High Parana River, 2016, N. Pividori, D. Aichino	-	MH638995	-
	Argentina, Misiones, Yabebiry, High Parana River, 2017, N. Pividori, D. Aichino	-	MH638996	-
<i>C. caeruleus</i>	Australia, Victoria, Hopkins River mouth, March 1995, J. West	BHO A-0893	JX028190	JX028170
<i>C. caeruleus</i>	Austria, Pernhofen, Pulkava River, October 19, 2010, Z. Žáková	BIOTES Lab, AT	JX028189	JX028148
<i>C. caeruleus</i>	Brazil, São Paulo, Conchas, Muquém River, June 13, 2008, O. Necchi Jr.	SJRP BR-CO	-	JX028149
<i>C. caeruleus</i>	Brazil, Espírito Santo, Domingos Martins, Rodovia ES 164, July 18, 2006, O. Necchi Jr.	SJRP BR-ES3	JX028172	JX028150
<i>C. caeruleus</i>	Brazil, Espírito Santo, Cachoeira, Guandú River. July 19, 2006, O. Necchi Jr.	SJRP BR-ES06	JX028173	JX028151
<i>C. caeruleus</i>	Brazil, Espírito Santo, Afonso Cláudio, Route ES-165, waterfall beside the road, July 19, 2006, O. Necchi Jr.	SJRP BR-ES7	JX028174	JX028152
<i>C. caeruleus</i>	Brazil, Espírito Santo, Santa Teresa, Country Club Waterfall. July 21, 2006, O. Necchi Jr.	SJRP BR-ES10	JX028175	JX028153
<i>C. caeruleus</i>	Brazil, São Paulo, Pereiras, near the railroad station, June 13, 2008, O. Necchi Jr.	SJRP BR-PE	JX028176	JX028154
<i>C. caeruleus</i>	Brazil, São Paulo, Pontes Gestal, Rio Preto, Cachoeira de São Roberto, June 1, 2009, O. Necchi Jr.	SJRP BR-PG2	JX028177	JX028155
<i>C. caeruleus</i>	Brazil, Sergipe, Lagarto, Route SE-110, 3,5 km from Campo de Brito, Rio das Traíras, June 8, 2006, O. Necchi Jr.	SJRP BR-SE4	JX028178	JX028156
<i>C. caeruleus</i>	Brazil, São Paulo, Ubatuba, Itamambuca Beach, Itamambuca River, 200 m from the sea, January 17, 2011, O. Necchi Jr.	SJRP BR-CI	JX028184	JX028165
<i>C. caeruleus</i>	Brazil, São Paulo, Guaraqueçaba, Sebuí Ecological Reserve, mouth of Sebuí River, September 21, 2008, O. Necchi Jr.	SJRP BR-CL	JX028185	JX028166
<i>C. caeruleus</i>	Brazil, Bahia, Taperoá, Graciosa Quilombola Fishing Community, oyster farm, 22 July 2022	ALCB 145987	PP445213	OR820778

Sample	Collection data	Voucher	GenBank acc. no.	
			COI-5P	rbcL
<i>C. caeruleus</i>	China, Shanxi province, Niangziguan	MM1	KR706536	KR706528
<i>C. caeruleus</i>	China, Shanxi province, Niangziguan	MM2	KR706537	KR706529
<i>C. caeruleus</i>	China, April 18, 2019, K. Fang	SXU-YN19045	MT649410	MT653121
<i>C. caeruleus</i>	China, December 2020, K. Fang	SXU-GD20005	-	OM171262
<i>C. caeruleus</i>	Indonesia, Central Java, downstream from hot spring near Tegal, August 19, 2011, E. Johnston, N. Buhari, F. Saint Amour	IR-34	-	KF557555
<i>C. caeruleus</i>	Guam, Mahlack River, Talofoto branch, December 1, 2007, M.L. Vis, D.L. House, C. Lobban	BHO:A-0223	JX028182	JX028160
<i>C. caeruleus</i>	Malaysia, Johor, Sungai Mupur off the highway between Kota Tinngi and Mersing, September 3, 2011, E. Johnston, F. Saint Amour	MR-16	-	KF557565
<i>C. caeruleus</i>	Federated States of Micronesia, Wachen Falls. December 3, 2007, M. Vis, D. House	BHO A-1515	JX028186	JX028167
<i>C. caeruleus</i>	Spain, Lleida, Segre River, September 13, 2010, P. Tomás	MUB ES-209	JX028191	JX028157
<i>C. caeruleus</i>	Spain, Zaragoza, Ebro River, September 8, 2010, P. Tomás	MUB ES-210	-	JX028158
<i>C. caeruleus</i>	Spain, Zaragoza, Ebro River, September 8, 2010, P. Tomás	MUB ES-211	-	JX028159
<i>C. caeruleus</i>	USA, Florida	US-FLa	-	AF087114
<i>C. caeruleus</i>	USA, Louisiana, Whiskey Chitto	US-LAa	-	AF087116
<i>C. caeruleus</i>	USA, Florida, Marion County, Juniper Springs, March 23, 2011, M.L. Vis, W.B. Chiasson, K.W. Chiasson.	BHO A-0415	JX028179	JX028161
<i>C. caeruleus</i>	USA, Hawaii, O'ahu, Kahana stream, Kahana State Park, Ko'olau Poko district, August 7, 2001, M.L. Vis, A.R. Sherwood	BHO A-1518	-	JX028162
<i>C. caeruleus</i>	USA, Covington, Virginia, Jackson River, November 2006, J. Zalack	BHO A-1445	JX028180	JX028163
<i>C. caeruleus</i>	USA, Hawaii, Kaua'i, north fork of Wailua stream, Kawaihua district, August 11, 2001, M.L. Vis, A.R. Sherwood	BHO US-HI11	JX028187	JX028168
<i>C. caeruleus</i>	USA, Louisiana, Spring Creek, Athus-Melder Rd, July 26, 2008, M.L. Vis, W.B. Chiasson	BHO A-1517	JX028188	JX028169
<i>C. caeruleus</i>	USA, Hawaii, Oahu	00216-00001	-	KC596170
<i>C. caeruleus</i>	USA, Hawaii	01159-00001	-	KC596173
<i>C. caeruleus</i>	USA, Hawaii, Maui	04155-00005	KC596325	-
<i>C. caeruleus</i>	USA, Hawaii, Maui	ARS 02676	HQ423112	-
<i>C. caeruleus</i>	Venezuela, Edo Sucre, Rio Guaire, April 10, 1991, J. West	BHO A-0894	JX028192	JX028171
<i>C. caeruleus</i>	From an aquarium, November 1, 2007, J. Bonham	BHO:A-0938	JX028183	JX028164
<i>C. caeruleus</i>	Germany, River Erft	FD Ott O646	-	DQ308425
<i>C. caeruleus</i>	Japan	FD Ott O1123	-	DQ308426

and *Sahlingia* were used as outgroups. For *rbcL* and COI-5P matrices, genetic distances were calculated using uncorrected 'p' distances in PAUP v4.0 beta10 (Swofford 2002).

Results and Discussion

For *rbcL*, 44 sequences were used in an alignment of 1117 bp, including one new accession obtained in the present study (Tab. 1). The *rbcL* consensus tree (Fig. 1) containing all global populations of *Composopogon caeruleus* sequenced thus far recovered the species as monophyletic with full support. The same was observed for COI-5P, for which 33 sequences (one new accession) were used in an alignment of 664 bp (Fig. 2). The divergence values between our sequences and those from GenBank were 0.13%–1.2% for *rbcL* and 1.15%–1.48% for COI-5P. Other studies reported similar results, demonstrating low genetic diversity in *C. caeruleus* samples from around the world (Necchi Junior *et al.* 2013; Nan *et al.* 2016).



Compsopogon caeruleus (Fig. 3a-i) has a densely branched filamentous thallus, with alternate to irregular branching, green to gray in color, and up to 30 cm. Thalli, which is heterotrichous, is composed of pluriseriate main axes and uniseriate lateral branches, corticated in older portions. The pluriseriate portion contains numerous spine-like branchlets. Uniseriate branches are 12–50 μm in diameter. Pluriseriate branches have 1–2 layers of cells, 87–300 μm thick; axial cell is 40–200 μm in diameter. In surface view, cortical cells of the outermost layer are polygonal to irregular, and of the second layer, when it occurs, are globose; cortical cells measure 12.5–50 μm in diameter and 10–50 μm length. Monosporangia present in corticated filaments, spherical to polygonal, and 9–16 μm in diameter.

Compared with other studies (for example: Thaxter 1900; Oliveira Filho & Pereira 1973; Necchi Junior *et al.* 1999, 2013; Bautista & Necchi Junior 2014), few morphological differences exist; however, some studies have highlighted the absence of spine-like branchlets (South & Skelton 2002) and the presence of more layers of cortical cells (Liu & Wang 2004; Ratha *et al.* 2007; Vis & Necchi Junior 2021). A summary of the comparison

of *C. caeruleus* characteristics from the present study with those from other regions of the world is presented in Table 2.

The hydrology of the Graciosa region, characterized by the influence of rivers, such as the Rio Graciosa and major tributaries entering the Canal de Taperoá (*e.g.*, Rio do Engenho, Rio das Almas, and Rio Una), generates a highly dynamic estuarine environment (Araujo *et al.* 2013, Ferraz & Accioly 2015). This pronounced salinity range and the transitional nature of the Graciosa/Taperoá estuarine system provide an ecological context that is consistent with the observed distribution of *C. caeruleus*. Although primarily considered a freshwater taxon, *C. caeruleus* has been recorded in estuarine and brackish lagoon environments worldwide. Early studies attested to this brackish water tolerance, reporting the species as “frequent” in tidal creeks within estuarine regions of the United States (Thaxter 1900; Taylor 1960). In India, this species has been collected directly from an estuarine channel and the brackish Chilika Lagoon (Ratha *et al.* 2007). Kitayana (2011) reported the presence of *C. caeruleus* along the Pacific coast of Japan, indicating a distribution pattern associated with coastal and estuarine habitats.

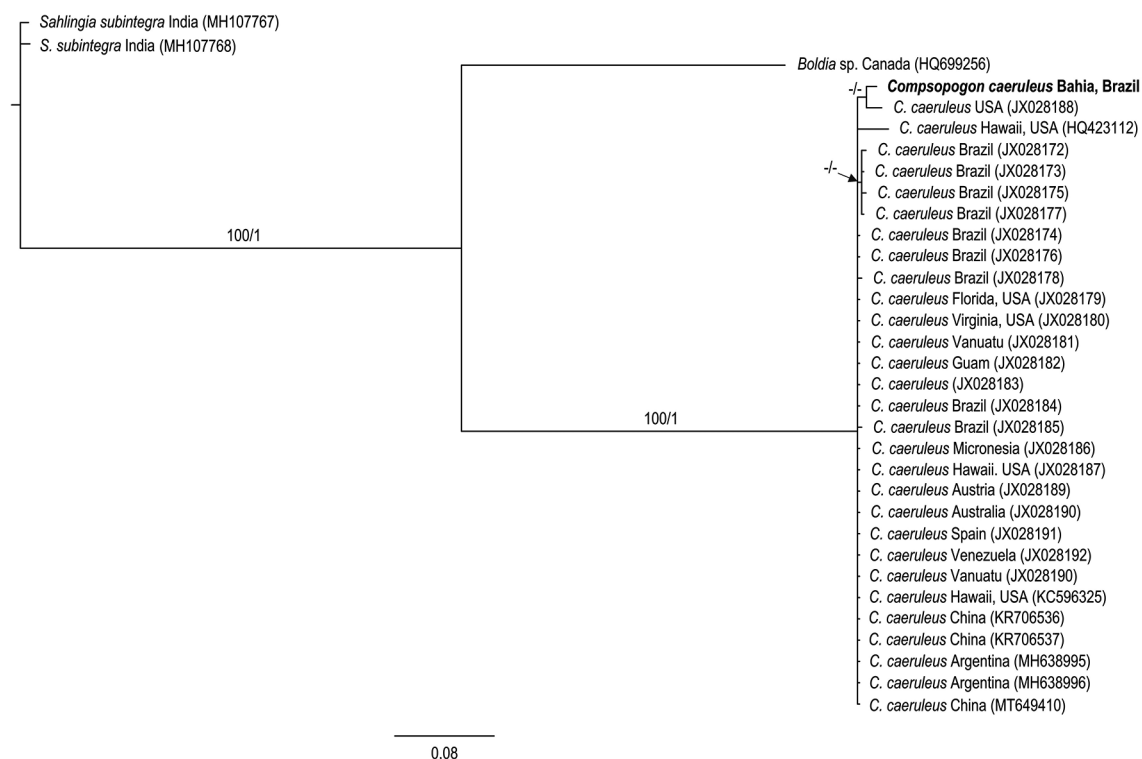


Figure 2 – Consensus tree derived from maximum likelihood (ML) analysis of COI-5P sequences. Bootstrap values and Bayesian posterior probabilities (BP/PP) are shown at the nodes. The sample generated in this study is in bold; ‘-’ indicates lack of bootstrap support or values under 70.



Figure 3 – a-i. Morphological characters of *Compsopogon caeruleus* from Taperoá, Bahia, Brazil – a. aspect of corticated and uniseriate filaments (scale bar = 200 μ m); b. details of uniseriate branches (scale bar = 100 μ m); c. aspect of spine-like branchlets (scale bar = 200 μ m); d. details of spine-like branchlets (scale bar = 200 μ m); e. cross section of an apical corticate filament, showing one layer of cortical cells (scale bar = 50 μ m); f. cross section of a corticated filament of the median portion, showing one layer of cortical cells; arrow indicates a monosporangia (scale bar = 20 μ m); g. cross section of a corticated filament of the basal portion, showing two layers of cortical cells (scale bar = 50 μ m); h. details of a corticated branch of the median portion; arrows indicate monosporangia (scale bar = 100 μ m); i. details of a corticated branch of the basal portion; arrows indicate monosporangia (scale bar = 100 μ m).

Table 2 – Comparison of morphological characters of *Compsopogon caeruleus* from the present and other studies.

Characteristics	Present study	as <i>C. aeruginosus</i>			as <i>C. chalybeus</i>			Ratha <i>et al.</i> (2007)	Kitayana (2011)	Zaburlin <i>et al.</i> (2019)	Vis and Necchi Junior (2021)
		Champpman and Cameron (1967)	South and Skelton (2002)	as <i>C. chalybeus</i> (Oliveira Filho and Pereira, 1973)	as <i>C. tenellus</i> (Liu and Wang, 2004)	Stoyneva <i>et al.</i> (2006)					
Country	Brazil	New Zealand	Brazil	Fiji	Taiwan	Belgium	India	Japan	Argentina-Paraguay	Puerto Rico	
Thallus color	Green to gray	Green, blue, gray, purplish, or variations	Greenish blue, yellowish green	Bluish green	Green	-	Bluish green, greenish grey	Bluish green or reddish brown	Violet, dark red, olive green, to bluish	-	
Thallus length (cm)	Up to 30	20–60	6–20	Up to 20	Up to 15	-	Up to 35	Up to 40	Up to 18	-	
Branch angle	Acute	Over 45°	-	45°	-	-	Acute	Acute	Acute	Acute	
Spine-like branchlets	Present	-	Present	Absent	Absent	Absent	Absent	Absent	Present	Present	
Uniseriate branches (µm, diam.)	12–50	Up to 20	17–43	Up to 35	-	7.1–21.4	5–24.5	-	20–66	10–55	
Corticated branches											
Corticated branches (diam.)	87–300 µm	Up to 1.5 mm	Up to 360 µm	1–2 mm	50–320 µm	210–220 µm	Up to 2.8 mm	Up to 360 µm	Up to 250 µm	Up to 2 mm	
Cortical layers	1–2	One to several	1–2	1–2	1–3	1	2–3	1–3	1	1–4	
Cortical cells shape	Polygonal to irregular	Polygonal	Polygonal	Rounded to angular	Polygonal to ovoid	-	Polygonal	Spherical / Cuboidal	Polygonal to irregular	Polygonal	
Cortical cells (µm, diam.)	12.5–50	20–40	10–15	Up to 20	17–30	23–38	10–33	12–32	14–22	15–30	
Cortical cells (µm, length)	10–50	-	12–20	Up to 20	22–40	23–38	14–43	15–48	16–32	15–55	
Axial cells (µm, diam.)	40–200	Up to 200	-	-	-	-	-	-	-	45–450	
Monosporangia (µm, diam.)	9–16	10–15	12–17	Absent	12–22	13–16	8.6–22.3	12–16	12–20	10–20	

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Data availability statement

In accordance with Open Science communication practices, the authors inform that all data supporting the findings of this study are included in the article.

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