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A taxonomic account of species in the tribe Spongoclonieae (Ceramiaceae, Ceramiales, Rhodophyta) reported from Atlantic and Pacific Mexico

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ABSTRACT

The tribe Spongoclonieae (Ceramiaceae subfam. Spongoclonioideae) is represented on the Atlantic and Pacific coasts of Mexico by two genera: *Pleonosporium* with eight species and *Spongoclonium* with a single species. *Pleonosporium boergesenii* and *P. borreri* are both new records for Atlantic Mexico. Known in Pacific and Atlantic Mexico, *P. rhizoideum* has the widest distribution, while *P. pygmaeum* and *P. vancouverianum* have only a few records in the study area. *Pleonosporium mexicanum* is found mainly in tropical Pacific Mexico, and *P. globuliferum* has a discontinuous distribution in the Gulf of California and then in Salina Cruz, Oaxaca. In the case of *P. squarrulosum* morphological and genetic comparisons are needed to verify its presence in Mexico. The report of *Spongoclonium caribaeum* from intertidal Veracruz (Gulf of Mexico) represents the second record of this species for the Atlantic coast of Mexico. Detailed descriptions, information on nomenclature, collections studied, distribution and habitat are provided for each of the species. Measurements of vegetative characters and reproductive structures provide a consistent basis for identifying Atlantic and Pacific Mexican species of *Pleonosporium* and *Spongoclonium*.

Key words: comparative morphology, Ceramiaceae, Mexican marine algae, new records, *Pleonosporium*, *Spongoclonium*

INTRODUCTION

The red algal family Ceramiaceae Dumortier (1822) is composed of more than 120 genera in 24 tribes, and represented in most marine habitats throughout of the world (Choi *et al*., 2008; Guiry and Guiry, 2017). The tribe Spongoclonieae F. Schmitz et Hauptfleisch (1897) of Ceramiaceae subfam. Spongoclonioideae De Toni (1903) is composed of four genera: *Halothamnion* J. Agardh, *Lophothamnion* J. Agardh, *Pleonosporium* Nägeli and *Spongoclonium* Sonder. Thus far only the latter two genera have been recorded from the Atlantic and Pacific coasts of Mexico.

The genus *Pleonosporium* Nägeli (1862) described based on *Conferva borreri* Smith (1807; = *Callithamnion borreri* (Smith) C. Agardh, 1828) is characterized by a filamentous thallus, distichous alternate branching, polysporous meiosporangia, and terminally borne cystocarps. The generic concept of *Pleonosporium* was redefined by Norris (1985) who considered *Mesothamnion* Børgesen (1917) and *Compsothamnionella* Itono (1977) to be congeneric with *Pleonosporium* on the basis of their similar female reproductive structures. Previously used features of branching mode and polysporangia are no longer useful as generic characters (Norris, 1985; Kim and Lee, 1988).

Spongoclonium Sonder (1855) was described based on *Spongoclonium conspicuum* Sonder (generitype; = *Callithamnion conspicuum* (Sonder) Harvey, 1859). The genus is distinguished by its subapical procarps on short determinate branches; carpogonial branches 4-celled, borne on the subterminal cell of short, lateral, 3 (–5)-celled branches, with 2 periaxial cells on the third cell; the 3 sterile cells (terminal cell and 2 periaxial cells) enlarge and become rounded. Post-fertilization the auxiliary cell, cut off from supporting cell, leading to carposporophyte with produces successive rounded groups of carposporangia surrounded by involucral filaments and spermatangial clusters pedicellate on filamentous branches (Norris, 1985; Womersley and Wollaston, 1998; Guiry and Guiry 2017).

The tribe Spongoclonieae includes 42 species represented in tropical and subtropical seas of the world (Guiry and Guiry, 2017), of which only five are known from Atlantic, Pacific and Caribbean Mexico (Dawson, 1962a; Ortega *et*

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al., 2001). In this study, we examined the occurrence and distribution of members of the tribe Spongoclonieae along the Atlantic and Pacific coasts of Mexico, including the Gulf of México and Gulf of California, with new records for two unusual and rare species discovered in our collections.

MATERIALS AND METHODS

Specimens of *Pleonosporium* were borrowed from herbarium: ENCB (Herbario, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Mexico City, Mexico); CMMEX (Herbario de Algas, Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Ensenada, Baja California, Mexico); and US (Algae Collection, US National Herbarium, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (herbarium abbreviations follow Thiers, 2017). Additional specimens of *Pleonosporium* and *Spongoclonium* were field collected in the intertidal and by free diving, between 1–2 m depths in selected study areas. Specimens (ENCB) were liquid-preserved in 5% Formalin in seawater, and later stained with iodine green or aniline blue for anatomical examination of vegetative and reproductive structures with use of an Olympus microscope (CX31, Philippines). Photomicrographs were taken with a digital camera (CANON D20, Japan).

RESULTS

Pleonosporium* Nägeli, 1862: 326, 330, *nom. cons.

Eight species of *Pleonosporium* are now known in Mexico: six from the Eastern Pacific (1 from Pacific México, and 5 found in both Pacific México and Gulf of California); and, two in the Western Atlantic from the Gulf of Mexico.

***Pleonosporium boergesenii* (A.B. Joly) R.E. Norris, 1985: 61 (Figs. 1–4)**

Basionym: *Mesothamnion boergesenii* A.B. Joly, 1957: 142.

Type locality: Paranapoan Beach, São Vicente, São Paulo State, Brazil.

Distribution. WESTERN ATLANTIC: North Carolina, Georgia and Florida, USA; Veracruz, México; and São Paulo State, Brazil (Joly, 1957; Schneider and Searles, 1991; herein).

Specimens studied. WESTERN ATLANTIC. **Veracruz** (Gulf of Mexico), México: Playa El Pulpo, Barra de Cazones (97°11´90.72´´W, 20°43´33.98''N), coll. Mateo-Cid, Mendoza-González & Hernández Ortiz, 16-04-2016 (*ENCB 21801*; polysporangia).

Habitat. On rocks; shallow subtidal, 1–2 m deep.

Morphology, Anatomy and Reproductive structures. Thalli erect, bushy, up to 3 cm tall, rosy red, axes ecorticate; branching alternately radial and pseudodichotomous, becoming alternate in a 1/3 spiral in upper portions; branchlets incurved, with obtuse tips; attached by multicellular, uniseriate branched rhizoids arising from bases. Main axes cells in lower segments of proximal portions, cylindrical, 200–220 µm in diameter, 200–300 µm long; lateral axes gradually tapering, with middle cells 100-120 µm in diameter, 150–200 µm long; and, cells of ultimate segments, 12–15 µm in diameter, 30–50 µm long;

Polysporangia sessile, single, subglobose to slightly ellipsoid, 50–60 µm in diameter (including thick hyaline cell wall), divided into sixteen spores; borne distally and adaxially on branch cells. Gametangial thalli not observed.

Remarks. The Veracruz *P. boergesenii* is in general agreement with of Schneider and Searles (1991), and represent the first records for Atlantic México.

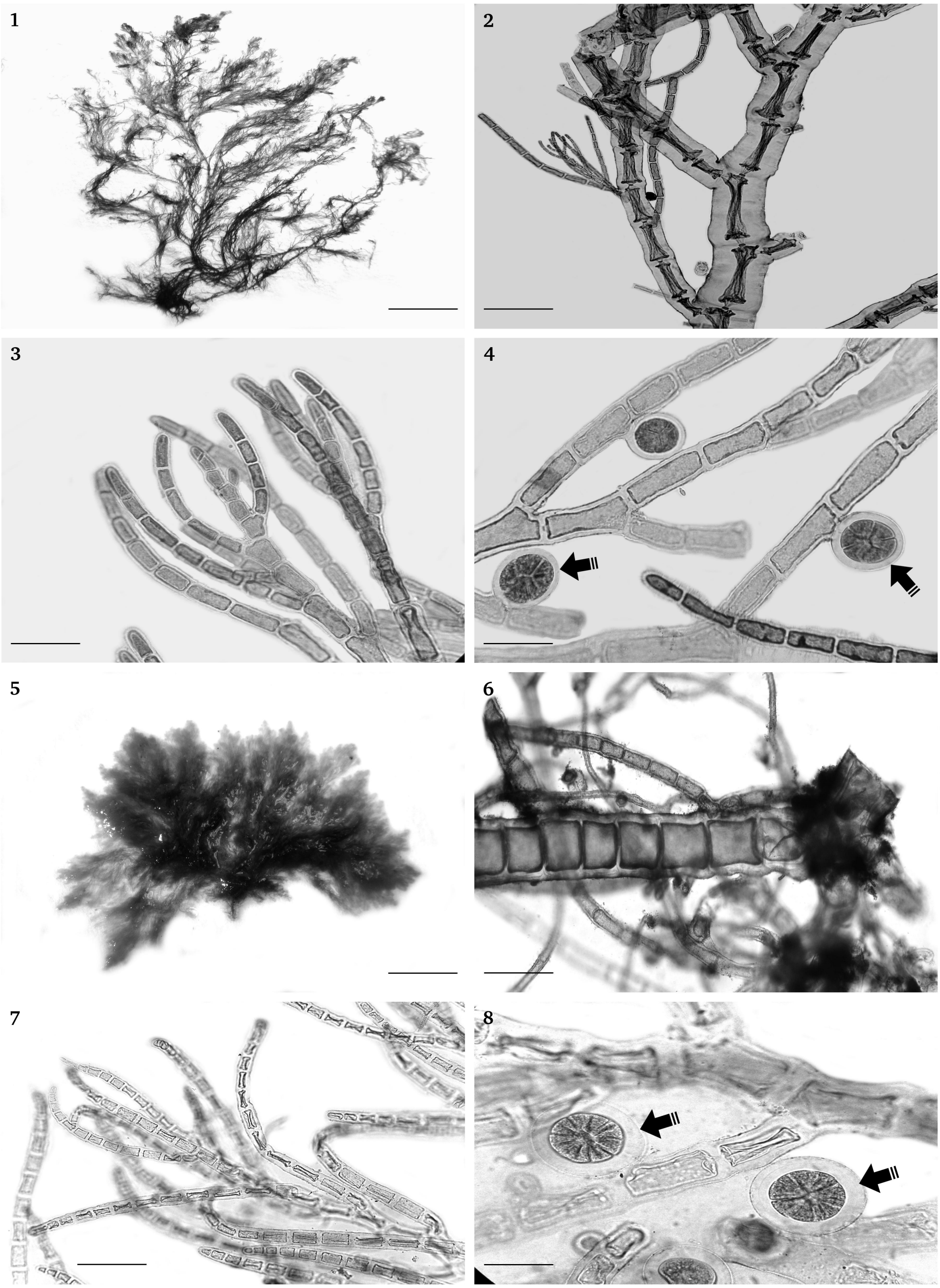
***Pleonosporium borreri* (Smith) Nägeli 1862: 342 (Figs. 5–8)**

Basionym: *Conferva borreri* Smith, 1807: pl. 1741.

Homotypic synonym: Callithamnion borreri (Smith) C. Agardh, 1828: 170.

Type locality: Yarmouth, Norfolk, England, UK (Maggs and Hommersand, 1993: 168; Silva *et al.*, 1996: 419).

Distribution. WESTERN ATLANTIC: Massachusetts to Delaware, USA (Mathieson and Dawes, 2017); Veracruz, México; and Brazil (Taylor, 1957; Guiry and Guiry, 2017; herein). WESTERN PACIFIC: Japan; South China Sea; and Vietnam (Titlyanov *et al.*, 2006; Nguyen *et al.*, 2013; Phang *et al.*, 2016).



FIGURES 1–8. Species of *Pleonosporium.* 1–4: *Pleonosporium boergesenii*, Playa El Pulpo, Barra de Cazones, Veracruz (*ENCB 21801*). 1) An entire, mature sporophyte. Scale bar: 7 mm. 2) Ecorticate branching axis and determinate lateral branch. Scale bar: 250 µm. 3) Branch tip of sporophyte showing incurving branchlets. Scale bar: 20 µm. 4) Branch of sporophyte showing sessile polysporangia (arrow). Scale bar: 60 µm. 5–8: *Pleonosporium borreri*, Playa El Pulpo, Barra de Cazones, Veracruz (*ENCB 21896*). 5) Habit of mature sporophyte. Scale bar: 8 mm. 6) Basal portion of thallus showing rhizoidal attachment. Scale bar: 150 µm. 7) Branch tip of sporophyte showing incurving and curved branchlets. Scale bar: 125 µm. 8) Branch of sporophyte with sessile polysporangia (arrows). Scale bar: 50 µm.

Specimens studied. WESTERN ATLANTIC: **Veracruz** (Gulf of Mexico), México: Playa El Pulpo, Barra de Cazones (97°11´90.72´´W, 20°43´33.98"N), coll. Mendoza-González & Mateo-Cid, 19-01-2017 (*ENCB 22896*; polysporangia).

Habitat. On rocks; shallow subtidal, 1–2 m deep.

Morphology, Anatomy and Reproductive structures. Thalli erect, dense filamentous tufts, up to 2.5 cm tall, rosy, with percurrent axes, branching alternately-distichous; branchlets incurved, with obtuse apices; lower portions lightly corticated by uniseriate filaments; attached by entangled, multicellular rhizoids. Cells cylindrical in proximal portions of main axes, 150–200 µm in diameter, 125–200 µm long; lateral axes gradually tapering, with middle cells 85–100 µm in diameter, 120–240 µm long; and cells of ultimate segments, 20–25 µm diameter, 60–75 µm long.

Polysporangia sessile, single, subglobose, 60–75 µm in greatest dimension (including thick hyaline cell wall), divided into sixteen spores; borne distally and adaxially on branch cells. Gametangial thalli not observed.

Remarks. Pleonosporium borreri (generitype) was originally described from temperate waters of Yarmouth, Norfolk, England (Smith, 1807). Since then *P. borreri* has been reported from a wide ranging regions and habitats: sub-boreal to subtropical eastern Atlantic, temperate to tropical western Atlantic, temperate to subtropical western Pacific, and from subtropical to tropical Indian Ocean (e.g., Silva *et al.*, 1996; Guiry and Guiry, 2017). Schneider and Searles (1991: 391) noting *P. borreri* was from cooler northerly waters removed it from the marine flora of the Carolinas, western Atlantic.

In general, the features observed in our specimens are similar to those described from northern Spain (Secilla, 2012) and the British Isles (Maggs and Hommersand, 1993), which had spherical to ovoid, polysporangia that were larger, 72–104 µm wide, 80–106 µm long; whereas in our Mexican specimens the polysporangia were subglobose and smaller, 60–75 µm. Further morphological and phylogenetic analyses will enable verification of its identification. Our report of *P. borreri* in the southwestern Gulf of Mexico represents the first report of its occurrence in Atlantic México.

***Pleonosporium globuliferum* Levring 1941: 647 (Figs. 9–14)**

Type locality: Quebrada Sánchez (Ausserhalb Sanchez), Isla Alejandro Selkirk (Isla Más Afuera; Masafuera), Islas Juan Fernández, Valparaíso Región, Chile.

Distribution. EASTERN PACIFIC: Gulf of California, México (Sonora, and Baja California Sur); Pacific México: Baja California (Isla Guadalupe), Jalisco, Colima, and Oaxaca; El Salvador; Costa Rica; and Chile (Dawson, 1961, 1962a, 1962b; Mateo-Cid *et al.*, 2000; Bucher and Norris, 2014; Norris *et al.*, 2017; herein). WESTERN PACIFIC: South China Sea, and Philippines (Silva *et al.*, 1987; Phang *et al.*, 2016).

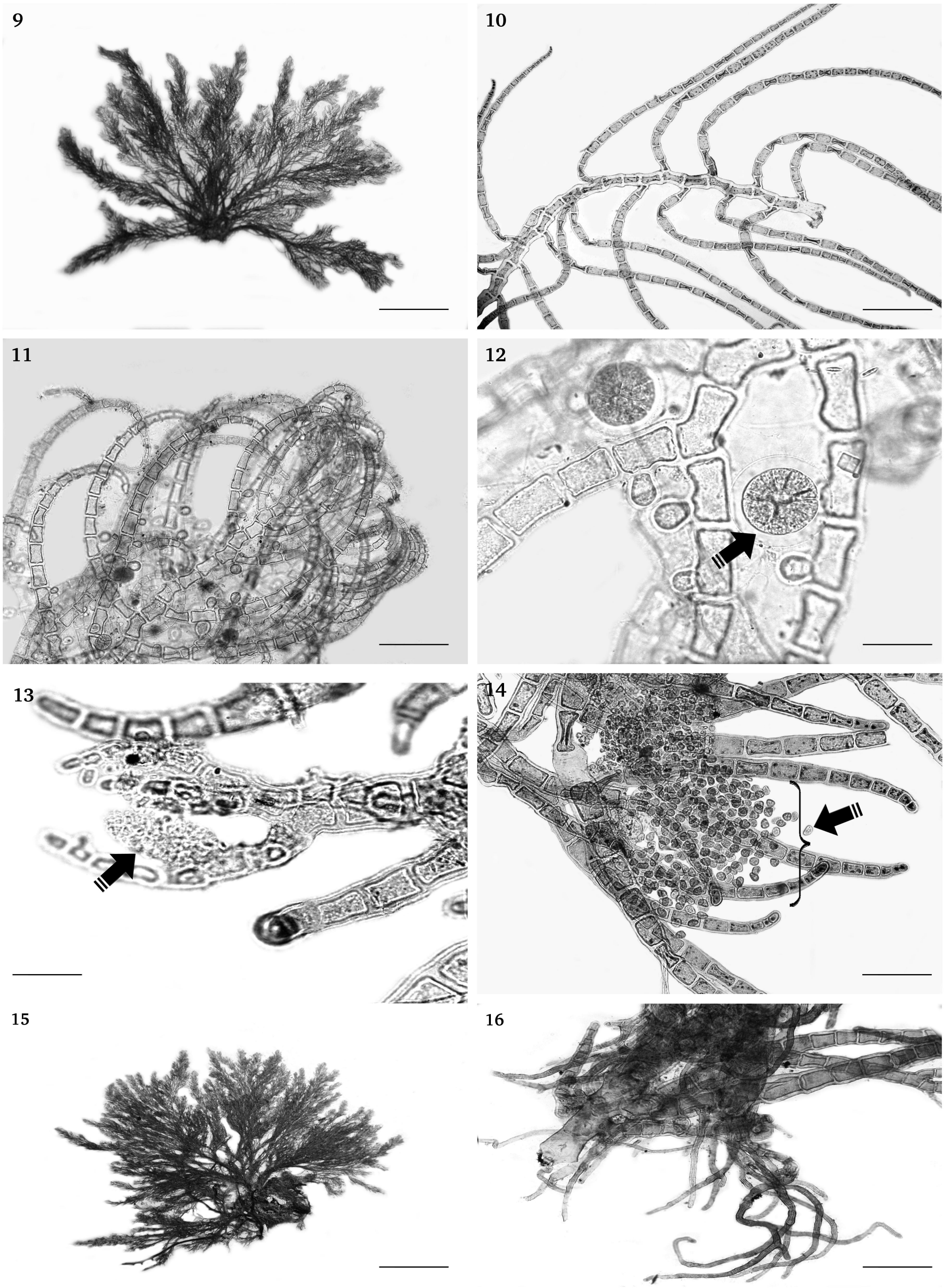
Specimens studied. GULF OF CALIFORNIA. **Baja California Sur**: Punta Arenas (109°48'17"W, 23°59'51"N), coll. Mateo-Cid & Mendoza-González, 26-04-1994 (*ENCB 12386*; ♀, polysporangia). PACIFIC MÉXICO. **Jalisco**: Chamela (105°05'00"W, 19°31'45"N), coll. Mateo-Cid & Galicia García, 06-10-1991 (*ENCB 18859*; ♀, ♂); **Colima**: Manzanillo (104°20'51"W, 19°06'18"N), coll. Mendoza-González & Mateo-Cid, 14-12-1985 (*ENCB 8267*; polysporangia); and, **Oaxaca**: Salina Cruz (95°12'11"W, 16°09'37"N), coll. Mateo-Cid & Mendoza-González, 08-08-1992 (*ENCB 14958*; ♂, ♀, polysporangia).

Habitat. On rocks, and epiphytic on species of *Codium* and *Sargassum*, or sometimes entangled with other algae; intertidal to shallow subtidal; on rocks, tidal platforms, and in tidal pools.

Morphology, Anatomy and Reproductive structures. Thalli tufted, of several erect, axes multifariously branched throughout, up to 2 cm tall, rosy; primary axes ecorticate; ultimate branchlets alternately divided, upcurved, with blunt apical cell; attached by a group of branched, multicellular, penetrating rhizoids. Cells of main filaments 140–150 µm in diameter and 120–200 µm long; middle cells 70–80 µm in diameter and 100–120 µm long; determinate lateral branches 1 mm long or more, ascending and mostly curved, about 26–30 µm in diameter, 30–60 µm long, with blunt apices.

Polysporangia sessile, subspherical, (25–) 40–90 (–100) µm in diameter (including thick hyaline cell wall); divided into thirty-two spores; scattered along lateral branches, mainly adaxial. Gametangial thalli dioecious. Spermatangial clusters subcylindrical, 70–80 µm long, 30–40 µm in diameter; sessile along adaxial side of lateral branchlets. Cystocarps subspherical, 450–500 µm in diameter; developed in the terminal portions of thallus.

Remarks. Although our SW Gulf of California and Pacific Mexico specimens are mostly in agreement with descriptions of Dawson (1962a) and Bucher and Norris (2014), they are taller and the cells of the main axes are larger.



FIGURES 9–16. Species of *Pleonosporium: Pleonosporium globuliferum*, Salina Cruz, Oaxaca (*ENCB 14958*). 9) Habit, female gametophyte. Scale bar: 9 mm. 10) Ecorticate axis with determinate lateral branches. Scale bar: 150 µm. 11) Detail of upper portions showing strongly curved ultimate branchlets. Scale bar: 150 µm. 12) Branch of sporophyte with polysporangia (arrows) sessile. Scale bar: 75 µm. 13) Spermatangial cluster (arrow). Scale bar: 45 µm. 14) Mature carposporophyte (bracket) with carposporangia (arrows). Scale bar: 230 µm. *Pleonosporium mexicanum,* Santa Elena Cozoaltepec, Oaxaca (*ENCB 14964*). 15) Habit of male gametophyte. Scale bar: 9 mm. 16) Basal portion of thallus showing rhizoidal attachment. Scale bar: 450 µm.

***Pleonosporium mexicanum* E.Y. Dawson 1962a: 41 (Figs. 15–21)**

Type locality: Lowermost intertidal on small reef 3 km. north of Belmar Hotel, Playa de Olas Altas, Mazatlán, Sinaloa, Gulf of California, México.

Distribution. EASTERN PACIFIC. Gulf of California, México: Sonora, Baja California Sur, Sinaloa, and Nayarit. Pacific México: Baja California (Isla Guadalupe), Baja California Sur, Jalisco, Michoacán, Guerrero, and Oaxaca; El Salvador; and Costa Rica (Mendoza-González *et al.*, 1994; Mateo-Cid *et al.*, 2006; Bucher and Norris, 2014; Norris *et al.* 2017; herein). WESTERN ATLANTIC: Brazil (Oliveira Filho, 1977).

Specimens studied. GULF OF CALIFORNIA: **Nayarit**: Lo de Marcos (105°21'20" W, 20°57'17" N), coll. Huerta Múzquiz, Casas Valdés & Hernández, 25-05-1973 (*ENCB 3016*; polysporangia). PACIFIC MÉXICO: **Jalisco**: Playa Conchas Chinas (105°14'02"W, 20°36'45"N), coll. Mendoza-González & Mateo-Cid, 08-10-1997 (*ENCB 16739*; ♀, ♂); **Michoacán**: Playa La Salada (102°62'63" W, 18°05'16" N), coll. Mendoza-González & Mateo-Cid, 16-12-2006 (*ENCB MICH-A/1*; ♀, ♂, polysporangia); **Guerrero**: Las Peñitas (102°03'88"W, 17°98'91"N), coll. Mateo-Cid & Mendoza-González, 17-12-2009 (*ENCB 19551*; ♀, polysporangia); Playa Manzanillo-La Majahua (101°44'55"W, 17°48'08"N), coll. Mendoza-González & Mateo-Cid, 24-09-2007 (*ENCB 19535*; polysporangia); Playa Las Gatas, Zihuatanejo (101°33'05"W, 17°37'12"N), coll. Mateo-Cid & Mendoza-González, 08-11-1996 (*ENCB 19434*; polysporangia); and, **Oaxaca**: Morro de Cerro Hermoso (97°33'30"W, 15°57'34"N), coll. Mendoza-González & Mateo-Cid, 23-02-1996 (*ENCB 14961*; polysporangia), Santa Elena Cozoaltepec (96°44'38"W, 15°43'14"N), coll. Mateo-Cid & Mendoza-González, 22-02-1996 (*ENCB 14964*; ♂, ♀, polysporangia), Playa Agua Blanca (96°48'50"W, 15°43'58"N), coll. Mendoza-González & Mateo-Cid, 08-08-1992 (*ENCB 14962*; polysporangia), Puerto Ángel (96°29'42"W, 15°39'46"N), coll. Mendoza-González & Mateo-Cid, 26-02-1996 (*ENCB 14960*; polysporangia), and Tangolunda (96°05'58"W, 15°46'10"N), coll. Mendoza-González & Mateo-Cid, 08-08-1993 (*ENCB 14959*; polysporangia).

Habitat. On rocks, and epiphytic on *Amphiroa beauvoisii* J.V. Lamouroux; intertidal to subtidal.

Morphology Anatomy and Reproductive structures. Thalli erect, bushy, tufts 2-5 cm tall, reddish green; primary axes ecorticate, commonly barren of branches in lower and mid-portions; upwards alternate, distichously branched (but not from every cell); branches bearing distichous, alternate, determinate lateral, mostly unbranched, branchlets from each cell, somewhat incurved; attached by a group of long, little-divided, multicellular, rhizoids. Axial cells of main filaments (110–) 150–190 (–225) µm in diameter and 240–300 µm long; middle cells 70–80 µm in diameter and (100–)120–160 µm long; determinate lateral branchlets usually simple, of 15–30 cells, 40–60 µm in diameter basally, becoming strongly incurved upwards, somewhat corymbose, outwards cells 25–40 in diameter and 40–60 µm long, ultimate cell, about 25 µm in diameter with blunt apices.

Polysporangia sessile, broadly ovoid, about (70–) 80–100 µm in diameter (including thick hyaline cell wall); divided into thirty-two spores; borne in mainly adaxial series along lateral branches. Gametangial thalli dioecious. Spermatangial clusters about 75–80 µm long, 30–35 µm in diameter; sessile, adaxial on lateral branchlets. Cystocarps subspherical, about 250–280 µm in diameter; borne on the terminal portions of thallus.

Remarks. Although mostly in agreement with *P. mexicanum* E.Y. Dawson (1962a), our specimens were taller and the main axes had larger cells than those he described. It is now reported for the first time for the coast of Michoacán in Pacific México.

***Pleonosporium pygmaeum* N.L. Gardner 1927: 379, pl. 79: fig. 2, pl. 80 (Figs. 22–25)**

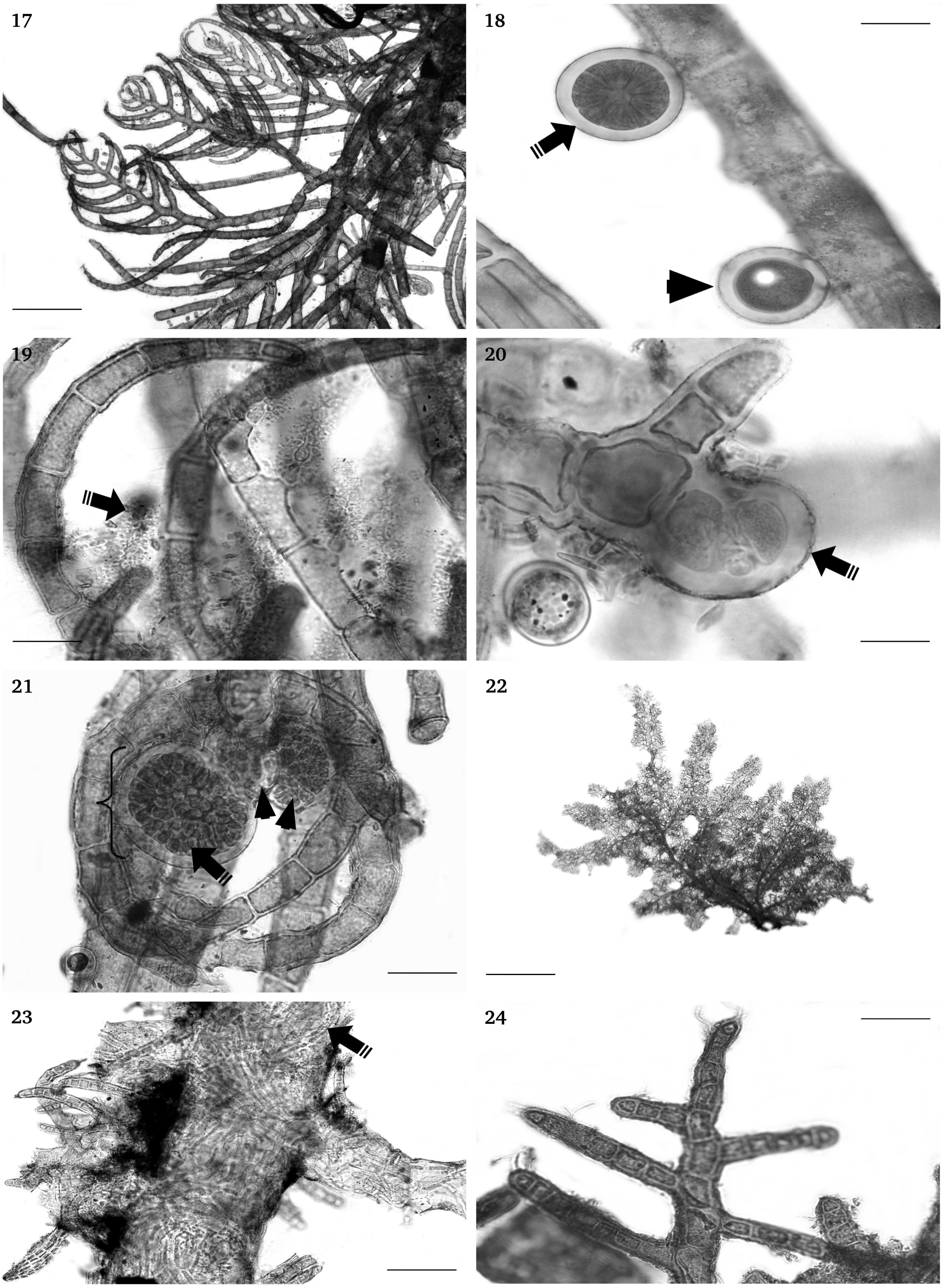
Type locality: cast ashore; on seagrass, *Phyllospadix*; La Jolla, San Diego County, California, USA.

Distribution. EASTERN PACIFIC. California, USA; Baja California, México; and El Salvador (Dawson 1961, Guiry and Guiry 2017; herein).

Specimens studied. PACIFIC MÉXICO: **Baja California**: Punta Morro (116°39'45"W, 31°51'41"N), coll. Mendoza-González & Mateo-Cid, 31-07-1987 (*ENCB 9570*; polysporangia); and, Raul´s, north of Ensenada (116°39'34" W, 31°51'36" N), coll. R. Aguilar Rosas, 12-04-2000 (*CMMEX 3698*; polysporangia).

Habitat. Epiphytic on *Osmundea spectabilis* (Postels & Ruprecht) K.W. Nam; intertidal, in tide pools.

Morphology, Anatomy and Reproductive structures. Thalli flaccid, soft pink, 1.5–2.5 cm high, with percurrent axes, branching more or less alternate-distichously; upper main branches often longer than the lower ones; lower portions of thallus lightly corticated by slender, descending rhizoidal filaments; attached by numerous rhizoids. Primary axes 300–350 µm in diameter and 300–500 µm long; primary axes and branches of first and second orders corticated by slender, branched, descending rhizoidal filaments from the basal cell of lateral branches; ultimate indeterminate branchlets 30–40 µm in diameter at the base, upward becoming tapered and adaxially curved, with blunt apices.



FIGURES 17–24. Species of *Pleonosporium*: *Pleonosporium mexicanum,* 17) Apical portion of a sporophyte with incurved branchlets. Scale bar: 600 µm. 18) Sessile mature polysporangium (arrows), and an immature polysporangium (arrowhead). Scale bar: 65 µm. 19) Sessile spermatangial cluster (arrow). Scale bar: 40 µm. 20) Young procarp (arrow); note that the trichogyne has not developed. Scale bar: 50 µm. 21) Mature carposporophyte (key), note the carposporangia (arrow) and mature carposporophyte (arrowheads). Scale bar: 130 µm. *Pleonosporium pygmaeum,* Punta Morro, Baja California (*ENCB 9570*). 22) Habit of sporophyte. Scale bar: 8 mm. 23) Basal portion of thallus showing strong rhizoidal cortication (arrow). Scale bar: 160 µm. 24) Branch tip of sporophyte with straight branchlets. Scale bar: 120 µm.

Polysporangia spherical, 60–70 µm in diameter (including thick hyaline cell wall), divided into 32 spores; borne adaxial on simple third-order branchlets. Gametangial plants not observed.

Remarks. Uncertain if *Pleonosporium pygmaeum* should be recognized as a distinct species, Dawson (1962a:42) observed material from Cortes Bank, California Channel Islands (*EYD-8010*) in agreement with *P. pygmaeum* N.L. Gardner (1927). He noted the species could be characterized by its small size, 0.6–2.0 cm, and the corticating filaments restricted to its lowermost base. Although Dawson (1962a) also suggested it could be a dwarfish, little corticated, variant of *P. dasyoides* (J. Agardh) De Toni, he did not treat it as a synonym. Later, Abbott (1972) considered both *P. pygmaeum* and *P. dasyoides* as being conspecific with *P. squarrulosum* (Harvey) I.A. Abbott.

Our Mexican specimens are much smaller than of *P. dasyoides* as reported from Pacific Baja California, i.e., 5–10 cm tall (Dawson, 1962a) and 5–20 cm tall from California (Abbott and Hollenberg,1976). We tentatively refer our Mexican specimen to *P. pygmaeum*, pending phylogenetic analyses to test its taxonomic status and verify its presence in Pacific Mexico.

***Pleonosporium rhizoideum* E.Y. Dawson 1962a: 42 (Figs. 22–26)**

Type locality: Salina Cruz, Oaxaca, México.

Distribution. EASTERN PACIFIC. Gulf of California, México: Baja California Sur, Sonora, Sinaloa, Nayarit, and Jalisco. Pacific México: Colima, Michoacán, Guerrero and Oaxaca. (Dawson, 1962a; Mendoza-González *et al.* 1994; Mateo-Cid *et al.* 2006; Mateo-Cid and Mendoza-González, 1992, 2001, 2012; Bucher and Norris, 2014; Norris *et al.*, 2017; herein).

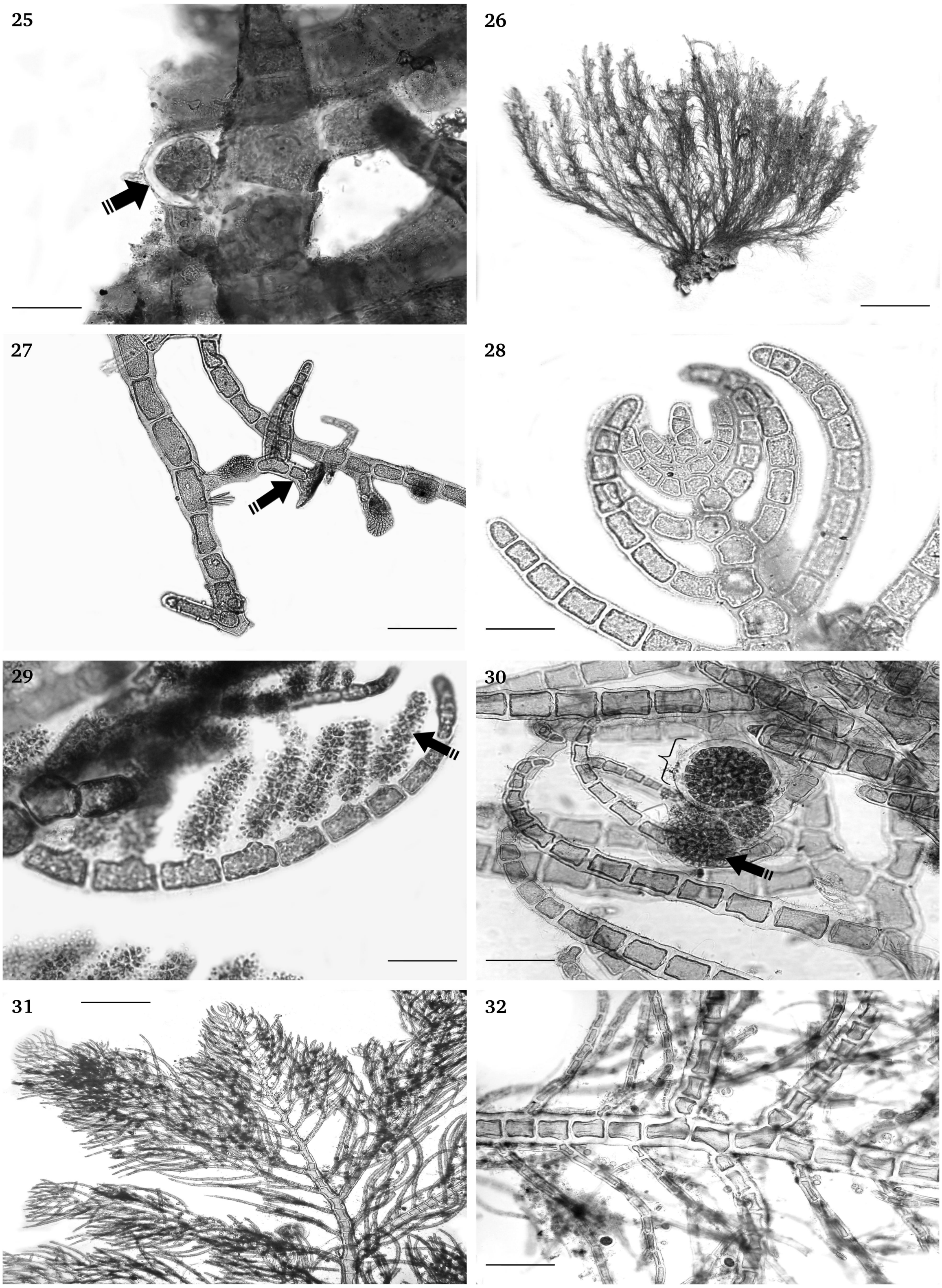
Specimens studied. Gulf of California, México: **Sonora**: Puerto Peñasco (113°34'48"W, 31°17'42"N), coll. Mendoza-González, Mateo-Cid, Aguilar Rosas L.E. & Aguilar Rosas R., 03-06-1997 (*ENCB 16338*; polysporangia). **Sinaloa**: Mazatlán (Playa Norte) (106°26'23"W, 23°12'06"N), coll. Mendoza-González & Mateo-Cid, 27-07-1987 (*ENCB 8114*; polysporangia). **Baja California Sur**: Bahía Concepción (Santispack) (111°53'06" W, 26°45'32" N), coll. Mateo-Cid, 14-03-1990 (*ENCB 10880*; polysporangia). **Nayarit**: Punta Mita (105°32'09"W, 20°46'12"N), coll. Mateo-Cid & López Sánchez, 23-06-1989 (*ENCB 8116*; ♂, polysporangia). PACIFIC MÉXICO: **Colima**: Manzanillo (104°20'51"W, 19°06'18"N), coll. Mendoza-González & Mateo-Cid, 05-10-1987 (*ENCB 8268*; polysporangia). **Michoacán**: Bahía de Maruata (103°20'29"W, 18°16'55"N), coll. López Sánchez, 17-05-1986 (*ENCB 15555*; polysporangia). **Guerrero**: Playa Las Gatas, Zihuatanejo (101°33'05" W, 17°37'12" N), coll. Mateo-Cid & Mendoza-González, 03-09-1995 (*ENCB 16794*; polysporangia); and, Las Peñitas (102°03'88"W, 17°98'91"N), coll. Chávez Barrera, 03-01-1971 (*ENCB 2727*; ♀, polysporangia). **Oaxaca**: Santa Elena Cozoaltepec (96°44'38"W, 15°43'14"N), coll. Mateo-Cid & Mendoza-González, 08-05-1997 (*ENCB 97-56/01*; ♂, polysporangia); Playa Agua Blanca (96°48'50" W, 15°43'58" N), coll. Mendoza-González & Mateo-Cid, 08-05-1997 (*ENCB 21832*; polysporangia); Puerto Ángel (96°29'42"W, 15°39'46"N), coll. Mendoza-González & Mateo-Cid, 08-12-1994 (*ENCB 14956*; polysporangia); and, Tangolunda (96°05'58"W, 15°46'10"N), coll. Mendoza-González & Mateo-Cid, 08-08-1993 (*ENCB 14959*; polysporangia).

Habitat. On rocks, and epiphytic on *Jania* sp.; intertidal.

Morphology, Anatomy and Reproductive structures. Thalli erect, bushy, up to 2.5 cm tall, reddish green; primary axes ecorticate; attached by numerous, descending, branched, multicellular rhizoids that become densely entangled to form a felt-like basal attachment. Erect axes more or less loosely clothed in lower portions by entangled rhizoids; branching principally distichous; branches mostly simple and very long, at first strongly incurved, then becoming irregularly curved or recurved, somewhat entangled; terminating in blunt apices (may sometimes form a terminal hook, or become prolonged to form a rhizoid). Cells of main filaments (125–)140–150 (–170) µm in diameter and (180–) 220–450 µm long; middle cells of filaments, 60–70 µm in diameter and 90–100 µm long; determinate lateral branchlets usually simple, 10–20 cells in length, strongly incurved, about 30–45 µm in diameter and 45–50 µm long, with blunt apices.

Polysporangia sessile, spherical, (60–) 90–110 µm in diameter (including thick, hyaline cell wall), divided into 32 spores; borne in densely branched portions of thallus, on short, irregular specialized branches bearing groups of alternate, polysporangia. Gametangial thalli dioecious. Spermatangial clusters about 110–130 µm long, 40–50 µm in diameter; briefly pedicellate, adaxial on lateral branchlets. Cystocarps subspherical, in terminal portions of thallus, 200–210 µm in diameter.

Remarks. Our specimens are similar to *Pleonosporium rhizoideum* E.Y. Dawson (1962a), described from Salina Cruz, Oaxaca on the coast of Pacific México. However, the cell diameter of the main filaments and the sizes of polysporangia and cystocarps are larger than those described by Dawson (1962a; see also: Bucher and Norris, 2014). Specimens from Bahía de Maruata represent new distribution records from the coast of Michoacán.



FIGURES 25–32. Species of *Pleonosporium*: *Pleonosporium pygmaeum,* 25) Branch of sporophyte showing sessile polysporangia (arrow). Scale bar: 90 µm. *Pleonosporium rhizoideum,* Puerto Peñasco, Sonora (*ENCB 16338*). 26) Habit of sporophyte. Scale bar: 5 mm. 27) Basal portion of the thallus; note the attachment structure (arrow). Scale bar: 280 µm. 28) Branch tip of a sporophyte with curved branchlets. Scale bar: 100 µm. 29) Group of spermatangial clusters (arrow) borne on a single branch. Scale bar: 80 µm. 30) Group of mature carposporophytes (key), with carposporangia (arrow). Scale bar: 200 µm. Species of *Spongoclonium*: *Spongoclonium caribaeum*, Escolleras Tuxpan, Veracruz (*ENCB VER-2017/A*). 31) Branch tips from sporophyte showing branching axis and determinate lateral branchlets. Scale bar: 600 µm. 32) Ecorticate axis and determinate lateral branches. Scale bar: 300 µm.

***Pleonosporium squarrulosum* (Harvey) I.A. Abbott, 1972: 262**

For illustrations see: Dawson, 1962a, as *P. dasyoides*: 40, pl. 13: figs.1–2; Abbott and Hollenberg, 1976: 618, fig. 561.

Basionym: *Callithamnion squarrulosum* Harvey, 1853: 232.

Heterotypic synonyms: *Pleonosporium dasyoides* (J. Agardh) De Toni, 1903: 1310; *Callithamnion dasyoides* β *californicum* J. Agardh, 1876: 31.

Type locality: "Golden Gate, California" (Harvey, 1853: 233); [entrance to San Francisco Bay], San Francisco, California, USA (Abbott, 1972; Abbott and Hollenberg, 1976).

Distribution. EASTERN PACIFIC. PACIFIC MÉXICO: Punta Descanso to Bahía Blanco, northern Baja California (Dawson, 1962a, as *P. dasyoides*). GULF OF CALIFORNIA: Bahía de Loreto, Baja California Sur (CONANP, 2002; Bucher and Norris, 2014; Norris *et al.*, 2017).

Habitat. Epiphytic on other algae, and epizooic on hydroids and possibly other invertebrates; intertidal to subtidal; dredged from 18–30 m depths.

Morphology, Anatomy and Reproductive structures. Thalli 5–10 cm tall, usually epiphytic; axes mostly about 300 µm in diameter (can be up to 1000 µm in diameter near base); alternately more or less distichously branched; lower thallus lightly to heavily corticated by slender descending rhizoidal filaments from basal cell of lateral branches; apices of branches attenuate; upper branches of main axis often longer than lower branches; ultimate branchlets, 11–16 cells in length, slightly tapered, more or less adaxially curved, cells about as long as broad; with basal cells about 40 µm in diameter.

Polysporangia oviform, 65–75 µm long; terminal on simple or compound branchlets of one to several cells, arising near base of determinate lateral branches. Spermatangia on upper sides of ultimate branchlets; a terminal, subcylindrical or subconical cluster above a base of 1–3 sterile cells.

Remarks. *Pleonosporium squarrulosum* is distinguished from other Mexican species of the genus by its lower thallus cortication, the large diameter of basal cells, and short terminal branches. Although reported in Pacific Mexico (Dawson, 1962a) and the southern Gulf of California from Bahia de Loreto (CONANP, 2002; Bucher and Norris, 2014) to La Paz, Baja California Sur (Norris *et al.*, 2017), the finding of reproductive thalli for morphological and genetic comparisons are needed to verify its presence in Mexico.

***Pleonosporium vancouverianum* (J. Agardh) J. Agardh, 1892: 37.**

For illustrations see: Kylin, 1925: 57, figs. 37A–C; Dawson, 1962a: 39, pl. 13: fig. 3; Abbott and Hollenberg, 1976: 618, fig. 562; Bucher and Norris, 2014: 302, figs. 149A-C.

Basionym: *Callithamnion vancouverianum* J. Agardh, 1876: 30.

Synonyms: *Pleonosporium abysicola* N.L. Gardner, 1927: 380; *Pleonosporium vancouverianum* Setchell & N.L. Gardner, 1903: 338.

Type locality: "ad insulam Vancouveri" (J. Agardh, 1876: 30; 1892: 37); Vancouver Island, British Columbia, Canada.

Distribution. EASTERN PACIFIC. PACIFIC MÉXICO: Islas Todos Santos (Bahía de Todos Santos; vicinity of Ensenada), Isla Guadeloupe, and Arrecife Sacramento, Baja California; and Isla Magdalena, Baja California Sur. GULF OF CALIFORNIA: Isla Coronado and Islas de Los Gemelos (both Bahía de Los Ángeles), Baja California; and Bahía Chacala, Nayarit (Aguilar-Rosas *et al*., 1990; Mateo-Cid and Mendoza-González, 1992; Bucher and Norris, 2014).

Habitat. Epiphytic or entangled on other algae; shallow subtidal, down to 20 m depths.

Morphology, Anatomy and Reproductive structures. Thalli of few to several erect, ecorticated, axes of uniseriate filaments, up to 1.0 (–1.8) cm tall; branching from almost every cell, distichous and alternate, up to 4 (–5) orders; each order progressively smaller than proceeding one; attached by a few, wide filament-like rhizoids at base of axes, and by long, thin (to 20 µm in diameter), unbranched, multicellular rhizoids issued singly, from the middle of some lower axial cells. Cells of main axes and primary branches, cylindrical, basally 150–240 µm in diameter and to 340–680 µm long, becoming smaller above and cuboid. Proximal cell of lateral branches slightly shorter than adjoining cells. Ultimate branchlets of 2–6 cell long; cells about 1-2 diameters long; terminal cells with rounded tips, about 10 µm in diameter.

Mature polysporangia ovate to oblong-ellipsoidal, to 75 µm in length and to 45 µm wide, divided into about 16 spores; sessile, borne alternately in position of ultimate branchlets. Sexual plants not found in Gulf of California or Pacific Mexico material.

Remarks. *Pleonosporium vancouverianum* is somewhat similar to *P. squarrosum squarrulosum* Kylin (1925: 57, figs. 37D-G), but differs primarily in having rounded to blunt branch apices, ellipsoidal polysporangia, and spermatangia alternate on both upper and lower sides of ultimate branchlets, versus the attenuated branch apices, oviform polysporangia, and spermatangia restricted to upper sides of ultimate branchlets in *P. squarrosum* (Gabrielson *et al.*, 2000).

Although *Pleonosporium abysicola* N.L. Gardner (1927) was accepted as a synonym of *P. vancouverianum* by some (Hollenberg and Abbott, 1966; Abbott and Hollenberg, 1976; Guiry and Guiry, 2016), others recognize it as a distinct species (e.g., Scagel *et al.*, 1989; Gabrielson *et al.*, 2000; Enciso-Padilla and Serviere-Zaragoza, 2006). Both species lack significant cortication and have sessile polysporangia, but differ in orders of branching; *P. abysicola* has 5 (rarely 6) orders of branching, and *P. vancouverianum* 3–4 orders (Gabrielson *et al.*, 2000: 47).

Dawson (1962a) measured cells in the type figure of *P. abysicola* N.L. Gardner (1927: pl. 81: fig. 1; TL: dredged, near Friday Harbor, San Juan Island, Washington) to be 2.5−3.0 diameters long, and noted Gardner's text description (1927: 380) mistakenly stated cell sizes of main axes as "3.0−4.0 diameters long" and primary branch as "4.0−6.0 diameters long." Northern Gulf of California specimens referred to *P. vancouverianum* by Bucher and Norris (2014) had axial cells 150−240 μm in diameter and 340−680 μm in length (about 2.3−2.83 diameters long), measurements similar to the type of *P. abysicola* (Gardner, 1927) and those reported from Pacific Baja California (Dawson, 1962a). For now, we treat the Pacific Baja California and the northern Gulf of California specimens as *P. vancouverianum*. Further comparative morphological and molecular phylogenetic studies are needed to clarify the identity of the Mexico specimens referred to *P. abysicola* (Dawson, 1962a; Mateo-Cid and Mendoza-González, 1992) and *P. vancouverianum* (Bucher and Norris, 2014) with comparisons to the type materials of these species.

***Spongoclonium* Sonder, 1855: 515**

One species known in México is now reported from another state Tamaulipas on the coast of southwestern Gulf of Mexico, Western Atlantic.

***Spongoclonium caribaeum* (Børgesen) M.J. Wynne, 2005: 23, 87 (Figs. 31–38)**

Basionym: *Mesothamnion caribaeum* Børgesen, 1917: 208.

Homotypic synonym: *Pleonosporium caribaeum* (Børgesen) R.E. Norris, 1985: 61.

Type locality: Annaberg, St. John, U.S. Virgin Islands [USVI], Leeward Islands, Caribbean Sea (Silva *et al.*, 1996: 419).

Distribution. WESTERN ATLANTIC: Bahamas; Gulf of Mexico (Veracruz; Campeche), México; Puerto Rico; U.S. Virgin Islands, Colombia, Venezuela, and Brazil (García and Gomez, 2007; Nunes *et al.*, 2008; Mendoza-González *et al.*, 2015; Ballantine *et al.*, 2016; Wynne, 2017; herein).

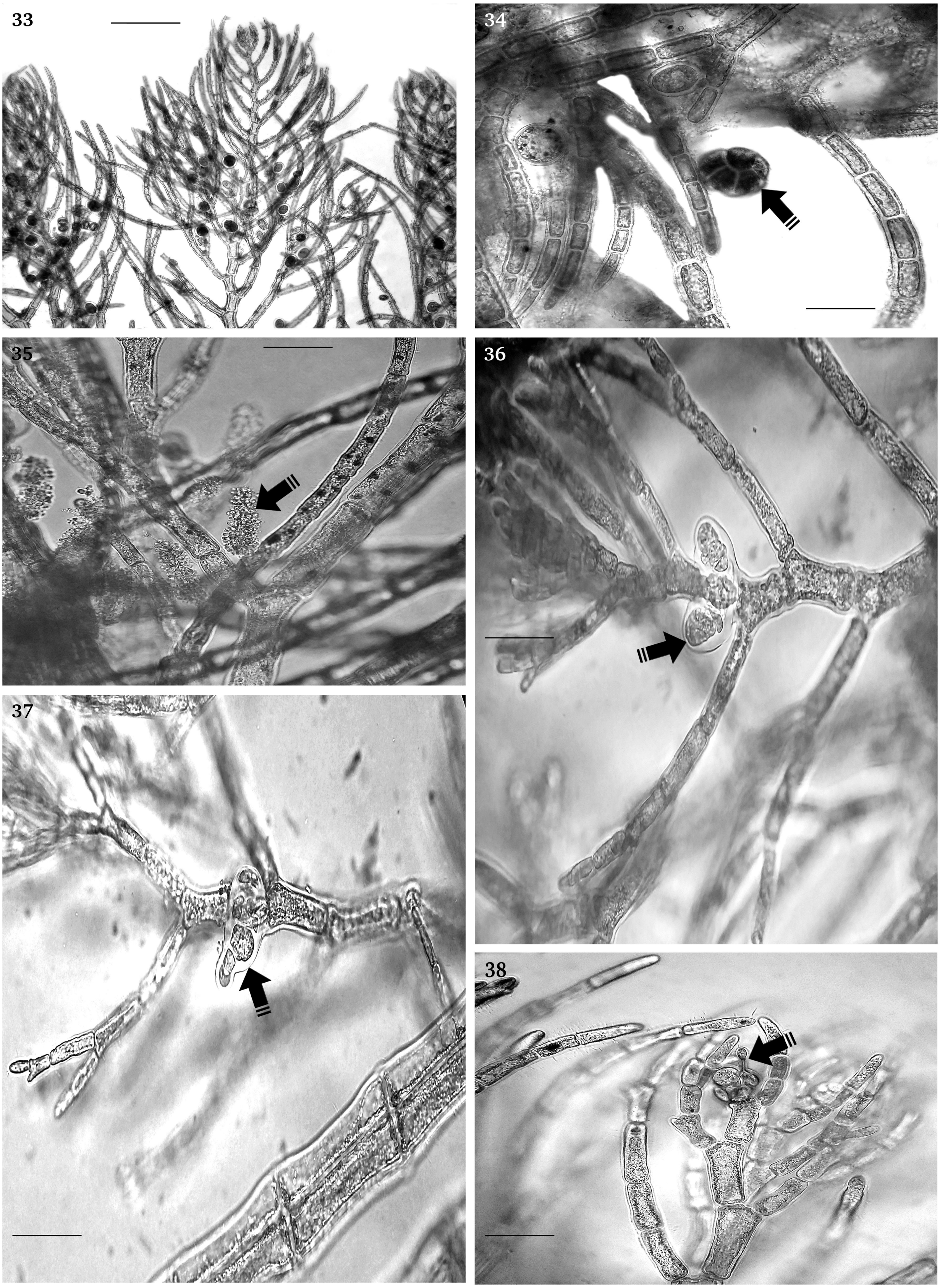
Specimens studied. ATLANTIC MÉXICO. **Veracruz**: Escolleras de Tuxpan (97°23´57´´W, 20°57´18"N), coll. Mateo-Cid, 19-08-2016 (*ENCB VER-16-LE/01*; ♂, ♀, polysporangia); and, Punta Puntillas (95°17´22´´W, 18°46´55´´N), coll. Mendoza-González & Mateo-Cid, 21-05-2016 (*ENCB VER-2017/A*; polysporangia).

Habitat. Epizoic on mollusks and corals, and epiphytic on *Acanthophora* sp.; intertidal.

Morphology, anatomy and reproductive structures. Thalli bushy, erect, up to 1.2 cm tall, reddish purple; primary axes ecorticate; branching principally distichous, regularly alternate, twisted, or polistichous, with several planes on the same axis; attached by a group of tangled rhizoid filaments. Branches near the apices extending and curving around the apical cell; branches of the second order generally simple, or may branch regularly alternate in distichous part and sometimes in abaxial series. Cells of main filaments terete, 160–175 μm in diameter, 110–125 μm long; middle cells 65–70 μm in diameter, 90–100 μm long; lateral branches with multicellular rhizoidal filaments from the basal cells that form a lightly rhizoidal cortication; middle of branch cells 120–130 μm in diameter, 90–120 μm long; determinate lateral branchlets usually simple, 10 cells in length, strongly curved; branchlet cells 35–40 μm in diameter, 70–80 μm long, with blunt tips (about half the dimensions of other cells).

Polysporangia sessile, ovoid to ellipsoid, about 74–80 μm in diameter (including thick hyaline cell wall), divided into eight or sixteen spores; borne in alternate groups on densely branched portions of thallus of short irregular branches. Gametangial thalli dioecious. Spermatangial clusters subcylindrical, 15–20 μm in diameter, 60–70 μm long, sessile, and adaxial on lateral branchlets. Procarp three-celled, apical on short branches, consisting of a basal cell bearing a carpogonial branch and a sterile cell, in the middle of both is the auxiliary cell and on it a sterile apical cell is formed. Trichogyne cylindrical and persistent. Cystocarps not observed.

Remarks. *Mesothamnion caribaeum* Børgesen (1917; basionym) was originally described from Annaberg, St. John, USVI, Caribbean Sea. Since then *Spongoclonium caribaeum* has been widely reported in temperate, subtropical to tropical regions of Eastern Atlantic, Western Atlantic, Indian Ocean, Western Pacific, Central Pacific and South Pacific (Silva *et al.*, 1996; Guiry and Guiry, 2017).



FIGURES 33–38. *Spongoclonium caribaeum*. 33) Sporophyte with numerous polysporangia. Scale bar: 450 µm. 34) Sessile mature polysporangia. Scale bar: 90 µm. 35) Sessile spermatangial cluster (arrow). Scale bar 70 µm. 36) Procarp four-celled stage (arrows). Scale bar: 75 µm. 37) Procarp at five-cell stage (arrow). Scale bar: 110 µm. 38) Young procarp with carpogonium initiating the trichogyne (arrow). Scale bar: 150 µm.

Our specimens generally agree with *S. caribaeum* as detailed by Garcia and Gomez (2007) for Venezuela, and by Secilla (2012) for Bizkaia (Biscay), Spain. Although the diameter of the cells of main filaments and the polysporangia in our Veracruz specimens are smaller than those reported by Børgesen (1917), the structure of the spermatangial clusters and the procarps agree with those of Børgesen (1917) and Norris (1985). Our specimens are the first record for Veracruz and the second report on the Mexican coast of Gulf of Mexico, Atlantic Mexico.

DISCUSSION

Currently there are 30 species recognized in *Pleonosporium* (Guiry and Guiry, 2016−2017), a genus primarily distinguished by characteristics of its female reproductive structures. However in our Atlantic and Pacific Mexico collections we observed female specimens in only 3 of the 8 species, *P. globuliferum, P. mexicanum,* and *P. rhizoideum.* A combination of morphological and reproductive characters were used to identify the Mexican specimens: uniaxial thallus, distichously or spirally arranged branches, diameter of the basal cells, type of branching, polysporangia pedicellate or sessile on determinate branches, number of spores in polysporangia, subcylindrical spermatangial clusters, and cystocarp dimensions (Table 1). Our study showed this suite of morpho-anatomical characters can be used to identify species of *Pleonosporium* in Mexico.

The number of species in *Pleonosporium* and *Spongoclonium* in Atlantic and Pacific Mexico had been uncertain due to: the absence of reproductive structures in herbarium specimens, the unknown influence of the environment on the extremely plastic phenotype of these algae, and because of their small size and inconspicuous habit they may be overlooked. This situation has changed substantially from the studies of Norris (1985) and Aponte and Ballantine (1992) which have provided solid bases for the separation of these genera.

CONCLUSIONS

Eight species of *Pleonosporium* and one of *Spongoclonium* are now recognized in Mexico. On the basis of our 36 samples, primarily in the states of 1) **Atlantic Mexico**: Veracruz, Gulf of Mexico; 2) **Pacific Mexico**: Baja California, Baja California Sur, southern Jalisco, Colima, Michoacán, Guerrero and Oaxaca; and 3) **Gulf of California**: Baja California, Baja California Sur, Sonora, Sinaloa, Nayarit, and northern Jalisco, we recognize. On the Pacific coast of Mexico, we found six species of *Pleonosporium*, including those recorded by Dawson (1962a), and those known in the Gulf of California (Bucher and Norris, 2014; Norris *et al.*, 2017). Further intertidal and subtidal collecting will likely yield other species. Of the eight species in this study, two represent new records for Atlantic Mexico: *Pleonosporium boergesenii* and *P. borreri.*

A suite of morpho-anatomical characters, particularly those associated with reproductive structures, seems to be useful in delineating Mexican species of *Pleonosporium* and *Spongoclonium*. From our finding both genera are apparently rare in distribution and abundance on both the Atlantic and Pacific coasts of México, the Gulf of Mexico and Gulf of California. More collections with allow critical genetic analyses and testing of the species, and comparative morpho-anatomical and phylogenetic studies of both genera. It is likely new taxa, overlooked species, new geographical and ecological distribution records and range extensions of the species will continue to be discovered.

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TABLE 1. Morphological and reproductive characters of the Mexican species of *Pleonosporium*.

Character	*P. boergesenii*	*P. borreri*	*P. globuliferum*	*P. mexicanum*
Branching	Alternate in upper portions; alternately radial and pseudodichotomous below	Alternate, distichous	Multifarious throughout	Alternate, distichous
Basal cells: diameter/ length	200–220µm /200–300µm	200–215µm /230–300µm	140–150µm /120–200 µm	(110–)150–190(–225)µm /240–300µm
Basal cell attachment: uniseriate rhizoids	Multicellular branched rhizoids	Multicellular, entangled branched rhizoids	Multicellular branched rhizoids	Multicellular long, little-divided, rhizoids
Rhizoidal cortication	Ecorticate	Sparse to lightly corticated	Ecorticate	Ecorticate
Ultimate branches	Incurved	Incurved	Curved	Incurved
Ultimate branches: diameter/length	12–15µm /30–50µm	20–25µm /60–75µm	25–30µm /30–60µm	25–40µm /40–60µm
Polysporangia: shape	Subglobose to slightly ellipsoid	Subglobose	Subspherical	Broadly ovoid
Polysporangia: position	Sessile; distal, adaxially on branch cells	Sessile; adaxially on branch cells	Sessile; mainly adaxial	Sessile; mainly adaxial
Polysporangia: diameter (including hyaline wall)	50–60µm	60–75µm	(25–)40–90(–100)µm	(70–)80–100µm
Polysporangia: number of spores	16	16	32	32
Spermatangial cluster: position	ND	ND	Sessile; adaxial	Sessile; adaxial
Spermatangial cluster: diameter/length	ND	ND	30–40µm /70–80µm	30–35µm /75–80µm
Cystocarps: shape and diameter	ND	ND	Subspherical; 450–500µm	Subspherical; 250–280µm

Character	*P. pygmaeum*	*P. rhizoideum*	*P. squarrulosum*	*P. vancouverianum*
Branching	More or less alternate, distichous	Alternate, distichous	Alternate, more or less distichous	Alternate, distichous
Basal cells: diameter/ length	300–350µm /300–500 µm	(125–)140–150(–170)µm /(180–)220–450 µm	300µm–up to 1000µm near base	150–240µm /340–360µm
Basal cell attachment; uniseriate rhizoids	Multicellular; numerous entangled rhizoids	Multicellular; becoming densely entangled	Multicellular; becoming entangled	Multicellular thin, long unbranched rhizoids filaments from lower cells; and, wide rhizoids at base of axes
Rhizoidal cortication	Axes, 1st & 2nd order branches, and lower portions corticated by rhizoids	Lower portions loosely corticated with entangled rhizoids	Lower portions lightly to heavily corticated by rhizoids from basal cells of branches	Ecorticate
Ultimate branches	Adaxially curved	Incurved above; below irregularly curved or recurved	Slightly curved	Mostly straight to slightly curved
Ultimate branches: diameter/length	30–40 µm	30–45 µm /45–50 µm	ND	(8–)15–20µm /15–25(–40)µm
Polysporangia: shape	Spherical	Subspherical	Oviform	Ovate to oblong-ellipsoidal
Polysporangia: position	Adaxial	Sessile; mainly adaxial	Pedicellate; mostly adaxial	Sessile; alternately abaxial and adaxial
Polysporangia: diameter (including hyaline wall)	60–70µm	(60–)90–110µm	55–70µm wide /75–85 µm long	30–45 wide /60–75µm long
Polysporangia: number of spores	32	32	32 or 64	16
Spermatangial cluster: position	ND	Pedicellate; adaxial	Pedicellate (base of 1-3 sterile cells); alternate abaxial and adaxial	ND
Spermatangial cluster: diameter/length	ND	40–50/110–130 µm	ND	ND
Cystocarps: shape and diameter	ND	Subspherical; 200–210 µm	Subsperical; adaxial and abaxial	ND

ND= Data not available.

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