Botanical Sciences 98(4): 624-643. 2020
DOI: 10.17129/botsci.2610

Received: April 07, 2020, Accepted: June 18, 2020
On line first: October 12, 2020

Taxonomy and Floristics / Taxonomía y Florística

Chondrophycus anabeliae and *Laurencia digitata* (Ceramiales, Rhodophyta) are recorded for the first time for Venezuela expanding their geographic distributions beyond the type localities

Chondrophycus anabeliae y *Laurencia digitata* (Ceramiales, Rhodophyta) se registran por primera vez para Venezuela expandiendo sus distribuciones geográficas más allá de las localidades tipo

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Abstract

Background: Over the course of approximately 12 years, the species of the *Laurencia* complex have been systematically studied in the tropical and subtropical Atlantic Ocean, showing high diversity (48 species), which has been underestimated for the coast of Venezuela.
Questions: What is the species diversity of the *Laurencia* complex in Venezuela?
Studied species: *Chondrophycus anabeliae*, *Laurencia digitata*.
Study site and dates: Cayo Muerto, Parque Nacional Morrocoy, Estado Falcón, Venezuela, 2015.
Methods: For molecular studies, the plastid *rbc*L gene and the mitochondrial DNA barcode marker COI-5P were used, combined with the study of current morpho-anatomical characters used for the identification of the species of the complex.
Results: The occurrence of *Chondrophycus*, as currently circumscribed, was confirmed for the first time for Venezuela. *Chondrophycus anabeliae* and *Laurencia digitata* are reported for the first time beyond the type localities. Tetrasporophytes are described for the first time for *L. digitata*.
Conclusions: Our findings expand the geographic distribution of *Ch. anabeliae* and *L. digitata* for the Venezuelan Caribbean and the Atlantic Ocean, respectively.
Keywords: COI-5P, phylogeny, *rbc*L, Rhodomelaceae, taxonomy.

Resumen

Antecedentes: A lo largo de aproximadamente 12 años se han estudiado de manera sistemática a las especies del complejo *Laurencia* en el Océano Atlántico tropical y subtropical, evidenciando una alta diversidad (48 especies), misma que se ha subestimado para la costa de Venezuela.
Preguntas: ¿Cuál es la diversidad de especies del complejo *Laurencia* en Venezuela?
Especies de estudio: *Chondrophycus anabeliae*, *Laurencia digitata*.
Sitio y años de estudio: Cayo Muerto, Parque Nacional Morrocoy, Estado Falcón, Venezuela, 2015.
Métodos: Para los estudios moleculares, se utilizaron el gen del plástido *rbc*L y el marcador mitocondrial del código de barras de ADN, COI-5P, combinado con el estudio de los caracteres morfoanatómicos actuales utilizados para la identificación de las especies del complejo.
Resultados: La presencia del género *Chondrophycus*, como se circunscribe actualmente, se confirmó por primera vez para Venezuela. *Chondrophycus anabeliae* y *Laurencia digitata* se registran por primera vez fuera de sus localidades tipo. Los tetrasporofitos se describen por primera vez para *L. digitata*.
Conclusiones: Nuestros hallazgos amplían la distribución geográfica de *Ch. anabeliae* y *L. digitata* para el Caribe venezolano y el Océano Atlántico, respectivamente.
Palabras clave: COI-5P, filogenia, *rbc*L, Rhodomelaceae, taxonomía.

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The *Laurencia* complex encompasses an extremely diverse group of marine red macroalgae in which new species and genera have been defined in the last three decades (Nam *et al.* 1994, Garbary & Harper 1998, Nam 2007, Martin-Lescanne *et al.* 2010, Cassano *et al.* 2012b, 2019, Metti *et al.* 2015, Machín-Sánchez *et al.* 2016, Sentíes *et al.* 2016, 2019, Francis *et al.* 2017, Rousseau *et al.* 2017, Collado-Vides *et al.* 2018, Bibi *et al.* 2019). The complex is comprised of 394 species, of these, 211 have been taxonomically accepted at this time (Guiry & Guiry 2020), distribuited in eight genera: *Laurencia sensu stricto* J.V.Lamouroux, *Osmundea* Stackhouse, *Chondrophycus* (Tokida & Y.Saito) Garbary & J.T.Harper, *Palisada* K.W.Nam, *Yuzurua* (K.W.Nam) Martin-Lescanne, *Laurenciella* Cassano, Gil-Rodríguez, Sentíes, Díaz-Larrea, M.C.Oliveira & M.T.Fujii, *Corynecladia* J.Agardh, and *Ohelopapa* F.Rousseau, Martin-Lescanne, Payri & L.Le Gall. *Laurencia s.s.* is the most speciose genus of the complex, with 138 species accepted taxonomically around the world (Guiry & Guiry 2020), whereas *Chondrophycus* is much less representative, with 16 species accepted taxonomically, mostly cited for the Indo-Pacific Ocean. *Chondrophycus anabeliae* Sentíes, M.T.Fujii, Cassano & Dreckmann is the only species of the genus reported for the western Atlantic Ocean (Sentíes *et al.* 2016, Wynne 2017).

Venezuela is an important area of occurrence of species of the *Laurencia* complex in the Atlantic. To date, 16 species and one variety have been reported: nine of *Laurencia*, four of *Palisada*, two of *Osmundea* and one of *Yuzurua*. However, the genera *Chondrophycus* (as currently circumscribed), *Corynecladia*, *Laurenciella* and *Ohelopapa* were not mentioned in the region (Rodríguez de Ríos 1979, Ganesan 1989, Gómez *et al.* 2020). Of the species cited for Venezuela, some are rare or endemic. *Laurencia foldatsii* N.Rodríguez Ríos is endemic to Venezuela (Rodríguez de Ríos 1981, Hernández *et al.* 2017); *Laurencia gracilis* J.D. Hooker & Harvey [as *Laurencia filiformis* J.D.Hooker & Harvey *nom. illeg.*] is rare in the Atlantic; apart from Venezuela it is quoted only for the Indo-Pacific; and *Osmundea pinnatifida* (Hudson) Stackhouse and *Osmundea oederi* (Gunnerus) G.Furnari (= *Laurencia bolivarii* N.Rodríguez Ríos) are rare in the western Atlantic. The citations of the *Laurencia* complex species in Venezuela are mostly based on morpho-anatomical characters; only *Laurencia natalensis* Kylin was studied based on molecular data (García-Soto & Lopéz-Bautista 2019).

During our study of the *Laurencia* complex in the tropical and subtropical Atlantic, we identified two species not yet reported for the Venezuelan coast using molecular markers, *rbc*L and COI-5P, combined with morphological data. Our findings confirm the occurrence of the genus *Chondrophycus* for Venezuela, expanding the geographic distribution of *Ch. anabeliae* beyond the type locality, and of *Laurencia digitata* Francis, Bolton, Mattio & R.J. Anderson to the Atlantic Ocean.

Materials and methods

Samples of *Chondrophycus anabeliae* and *Laurencia digitata* were collected in Cayo Muerto, Parque Nacional Morrocoy, Estado Falcón, Venezuela (10° 55' 48.08" N, 68° 15' 31.73" W) in 2015. For each sample, small fragments of the thallus were dried in silica gel for molecular analyses, and the remaining material was preserved in 4 % formalin-seawater or pressed as herbarium vouchers for morphological studies. For morphological examination, transverse and longitudinal hand sections were stained with 0.5 % aqueous aniline blue and acidified with 1N HCl. For each specimen studied, a minimum of 20 measurements of each morphometric character were made. Measurements are given as length × diameter. Images of whole specimens were taken with a Sony W5 digital camera (Sony, Tokyo, Japan), and details of branches and branchlets were captured with Sony W5 coupled to a Stemi SV 6-Zeiss stereomicroscope (Zeiss, Göttingen, Germany). Microscopic diagnostic features were taken with the Sony W5 coupled to a Nikon Eclipse E-200 optical microscope (Nikon, Tokyo, Japan). Voucher specimens were deposited in the herbaria of University of São Paulo (SPF) and Botanical Institute, São Paulo (SP), University of Carabobo, Venezuela (LUC), and Metropolitan Autonomous University (UAMIZ). Abbreviations follow Index Herbariorum (Thiers 2020).

For molecular studies, DNA extraction followed manufacturer´s instructions of the DNeasy Plant Mini Kit (Qiagen, Valencia, USA). PCR protocols for both markers followed Cassano *et al.* (2019), using for *rbc*L the following pairs of primers: F*rbc*Lstart-R492, F492-R1150 and F993-R*rbc*S (Freshwater & Rueness 1994), and for COI-5P the primer pair GAZF1-GAZR1 (Saunders 2005). For PCR amplification was used the PCR Master Mix (Promega, Madison, Wisconsin USA) in a final volume of 25 µl. The reactions were performed in a Techne TC-4000 thermocycler (Bibby Scientific, Staffordshire, UK). All PCR products were analyzed by electrophoresis in 1 % agarose to check product size and were purified with MicroSpinTMS-300 HR Columns (GE Healthcare Life Sciences, Piscataway, New Jersey, USA) as per manufacturer's instructions.

Sequencing reactions were made using the same PCR primers mentioned above, and the BigDye Terminator Cycle Sequencing Ready Reaction kit (Applied Biosystems, Foster City, California, USA) on an ABI PRISM 3730 Genetic Analyzer (Applied Biosystems). Consensus sequences and multiple sequence alignments for both *rbc*L and COI-5P were generated using BioEdit 7.0.4.1 software (Hall 1999). Multiple sequence alignment for *rbc*L consisted of 93 sequences, including three newly generated sequences from Cayo Muerto, Venezuela; the remaining

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sequences were downloaded from GenBank (Appendix 1). Three Rhodomelacean species were used as outgroups, *Chondria acrorhizophora* Setchell & N.L.Gardner, *Chondria collinsiana* M.Howe, and *Chondria dasyphylla* (Woodward) C.Agardh (Appendix 1). Neighbor-joining (NJ) analysis was conducted in PAUP v4.0 beta10 (Swofford 2002) with 2,000 bootstrap replicates. The most appropriate model of sequence evolution for maximum likelihood (ML) and Bayesian inference (BI) was selected using jModeltest v2.1.10 (Darriba *et al.* 2012) under the Akaike information criterion (AIC) as implemented on the online server CIPRES Science Gateway v3.3 (Miller *et al.* 2010). The model selected was the general-time-reversible model of nucleotide substitution with invariant sites and gamma-distributed rates for the variable sites (GTR+I+G). Maximum likelihood (ML) analysis was performed using IQ-Tree v1.4.3 (Nguyen *et al.* 2015) with 1,000 boostrap replicates on the IQ-Tree web portal. BI analysis was performed using MrBayes v3.2.2 (Ronquist *et al.* 2012). For BI analysis, two runs with four MCMC chains (one hot and three cold) were conducted with 4,000,000 generations and sampling every 1,000 generations, starting with a random tree. The first 100,000 generations in both runs were discarded as burn-in to build the consensus tree.

Multiple sequence alignment for COI-5P consisted of 69 sequences, including three newly generated sequences; the remaining were downloaded from GenBank (Appendix 1). One Rhodomelacean species was used as outgroup, *Chondria baileyana* (Montagne) Harvey (Appendix 1). The neighbor-joining (NJ) analysis was conducted in PAUP with 2,000 bootstrap replicates. Intra- and interspecific divergence values of *rbc*L and COI-5P were calculated using uncorrected "p" distances in PAUP.

Results

Molecular study. The *rbc*L final alignment included 93 sequences of 1,448 bp in length.

The *Chondrophycus* clade had full support (Figure 1). The two *rbc*L sequences of *Chondrophycus anabeliae* from Venezuela were identical and formed a subclade with *Ch. anabeliae* from Mexico, its type locality, with high to moderate supports (Figure 1), diverging by 1.34 %. This subclade was sister to *Chondrophycus* sp. 3 from New Caledonia plus *Chondrophycus* sp. from Australia from which it diverged by 5.17-5.9 %. The subclade formed by *Chondrophycus* cf. *undulatus* (Yamada) Garbary & J.T.Harper, *Ch.* sp.1, *Ch.* sp. 2 from New Caledonia, *Chondrophycus dotyi* (Y.Saito) K.W.Nam from Hawaii, and *Chondrophycus tronoi* (E.Ganzon-Fortes) K.W.Nam from Philippines diverged by 1.86 % (*Ch.* sp.1 vs *Ch.* cf. *undulatus*) to 6.4 % (*Ch. doyti* vs *Ch. tronoi*). The interspecific divergence within *Chondrophycus* genus ranging from 1.86 % to 7.8 % (*Ch. anabeliae* from Mexico vs *Ch.* sp.1 from New Caledonia).

Laurencia s.s. clade was highly supported (Figure 1). The *rbc*L sequence of *L. digitata* from Venezuela joined with *L. digitata* from South Africa, its type locality, with high to moderate support, diverging by 0.85 %. *Laurencia digitata* is sister to *Laurencia* cf. *kuetzingii* A.J.K.Millar from New Caledonia, diverging by 2.14-2.19 %. This subclade was resolved as sister to *Laurencia pumila* (Grunow) Papenfuss plus *L. pumila* var. *dehoopiensis* Francis, Bolton, Mattio & R.J.Anderson from South Africa plus *Laurencia karachiana* Bibi, Cassano & Rasheed from Pakistan with high to moderate supports. The interspecific divergence between sequences of *L. digitata* and *L. pumila* plus *L. pumila* var. *dehoopiensis* was 4.36-4.89 %, whereas *L. digitata* diverged from *L. karachiana* by 4.7-4.9 %.

The COI-5P final alignment included 69 sequences of 644 bp in length (Figure 2). We were unable to obtain COI-5P sequence for *L. digitata* from Venezuela due to contamination, even after several amplification attempts. The two identical COI-5P sequences of *Ch. anabeliae* fromVenezuela joined to the sequence of *Ch. anabeliae* from the type locality generated in this study (MN597440), diverging only by 0.3 % (Figure 2). This subgroup joined to *Chondrophycus succisus* (A.B.Cribb) K.W.Nam (as *Laurencia succisa* A.B.Cribb) from Molokai (Hawaii, USA) with 5.4-5.7 % of divergence. The subgroup formed by one sequence of *Ch. dotyi* and four of *Ch.* cf. *undulatus*, all from the Hawaiian Islands, showed low genetic divergence (0.16-0.48 %) suggesting that these samples represent the same taxonomic entity. The divergence between these two subgroups (*Ch. anabeliae-Ch. succisus* and *Ch. dotyi-Ch.* cf. *undulatus*) ranging from 8.13 % to 8.76 %.

Morphological study. Chondrophycus anabeliae Sentíes, M.T.Fujii, Cassano & Dreckmann in Sentíes *et al.* 2016: 261, figures 1-18. (Figures 3A, 4A-E, 5A-D, 6A-D)

Type locality. Mexico, Quintana Roo, Isla Mujeres, Garrafón de Castilla; holotype UAMIZ 1240!

Description. Plants forming erect tufts up to 5 cm high, reddish-brown to yellowish-brown, terete to partially compressed axes (Figures 3A, 4A), cartilaginous in texture, not adhering to herbarium paper when dried. Thalli attached to the substratum by a discoid holdfast. Erect branches irregularly alternate and spirally arranged, usually with 2-3 (4) orders of branches. The main axes are terete and first-order branches partially compressed mainly in the upper third portion of the thalli, up to 2,000 µm in diameter, and slightly narrowing towards the terete apices. Ultimate branchlets cylindrical to clavate and truncate at the apices, 500-2,800 µm long and 525-1,000 µm in diameter.

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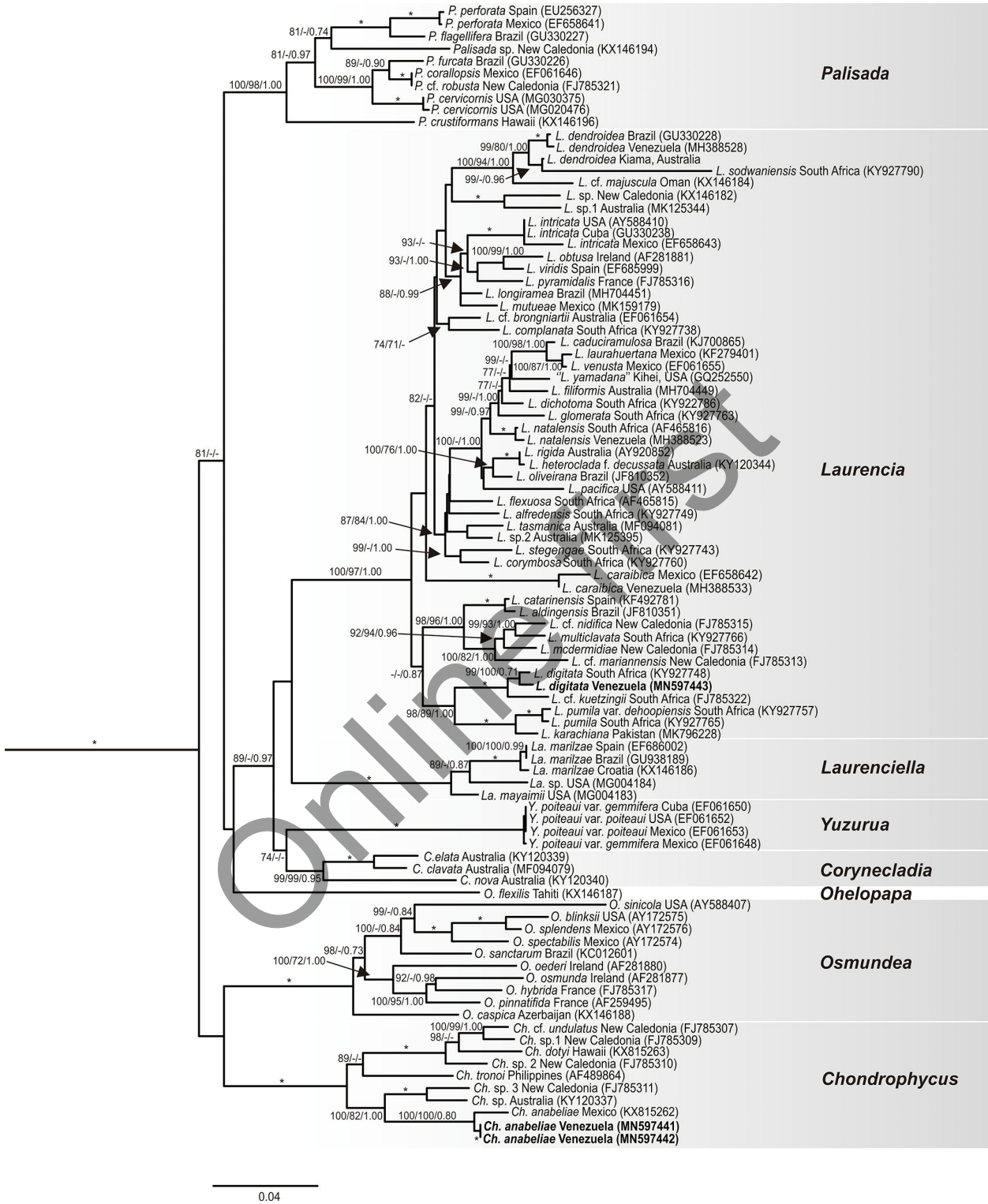

Figure 1. Consensus tree derived from Maximum likelihood (ML) analyses of *rbc*L sequences. Bootstrap supports for NJ (2000 replicates)/ML (1000 replicates)/posterior probabilities, PP < 0.95 are given at the nodes. Sequence generated in this study in bold; - indicates lack of bootstrap support or values under 70; *indicates full support. Outgroups were removed from the figure only for better ingroups viewing.

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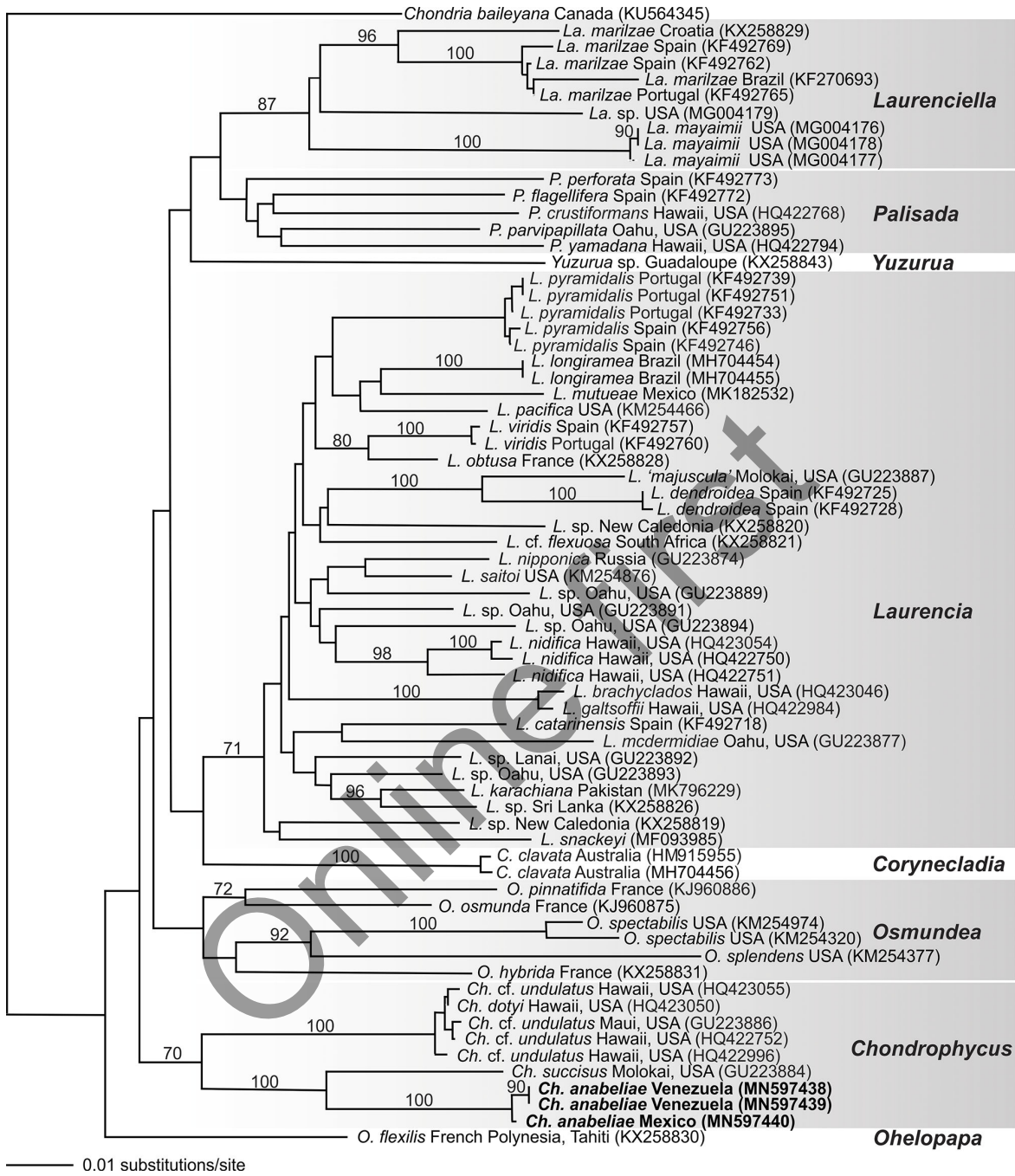

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Figure 2. NJ analysis for COI-5P sequences. Bootstrap values (2000 replicates) are shown at nodes; values under 70 were not considered. Sequence generated in this study in bold.

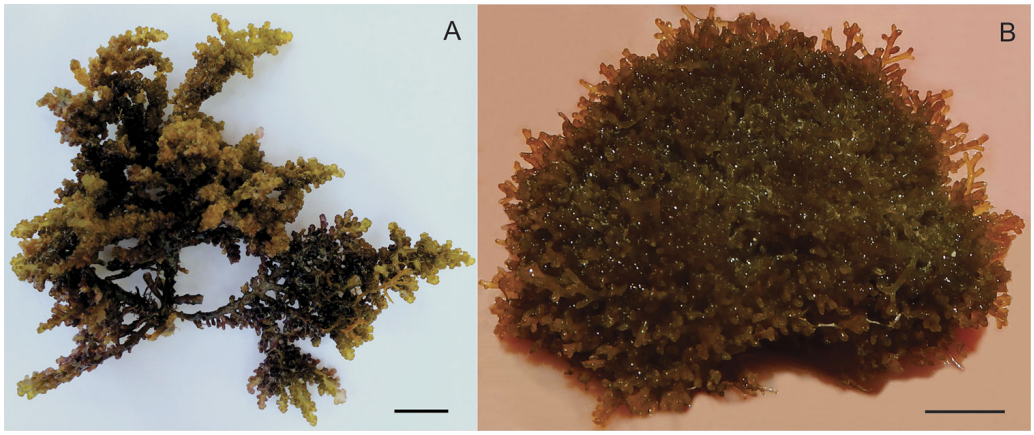

Figure 3. A) Habit of *Chondrophycus anabeliae*. B) Habit of *Laurencia digitata*. Living materials. Scale bar: A and B, 1 cm.

In surface view, the outermost cortical cells are translucent, isodiametric-polygonal in the middle portions, 17.5-32.5 × 17.2-37.5 µm without secondary pit connections (Figure 4B). Subcortical cells are pigmented, larger and connected to each other by secondary pit connections (Figure 4C). Outermost cortical cells translucent and subcortical cells present 1 (-2) crystals per cell (Figure 4C, D). In transverse section, thalli formed by two cortical cell layers, and four or five layers of medullary cells (Figure 4E). The cortical cells of translucent outer layer are quadratic, cuneiform to rectangular, smaller than the inner layer cells, measuring 17.5-30 × 22.5-30 µm in the ultimate branchlets (Figure 5A), and elongated, 47.5-55 × 27.5-35 µm in the middle portions of main axes. The inner layer of cortical cells is composed of pigmented and elongated cells, measuring 40-65 × 35-50 µm (Figure 5B) in the middle portions of main axes. Medullary cells are rounded or slightly radially elongated, measuring 65-145 × 47.5-107.5 µm in the middle portions of the main axes. Medullary cell walls uniformly thickened, but lenticular wall thickenings are absent. Each vegetative axial segment cuts off two pericentral cells (Figure 5C) that are slightly smaller than the medullary cells of the surrounding layer. In median longitudinal sections through a branchlet, the outer cortical cell walls near the apices are markedly projecting beyond the surface (Figure 5D).

Tetrasporangial branchlets are cylindrical or slightly compressed, simple or compound, 500-1,500 × 575-825 µm (Figure 6A). At the apex of fertile branches, each axial segment produces one fertile additional pericentral cell situated oppositely to the pre-existing two pericentral cells which remain vegetative (Figure 6B). The additional cell cuts off two pre-sporangial cover cells distally abaxially positioned in relation to the tetrasporangial initial (Figure 6C). Subsequently, one post-sporangial cover cell is produced and continues to divide, contributing to cortication around the tetrasporangia. Tetrasporangia are arranged in a right-angled pattern in relation to fertile branchlets (Figure 6D). Mature tetrasporangia are tetrahedrally divided, 50-100 µm in diameter. Gametangia were not observed.

Examined material. Venezuela. Estado Falcón: Parque Nacional Morrocoy, Cayo Muerto, 19 May 2015, tetrasporophyte, *S. Ardito, M.T. Fujii, A. Sentíes, V. Cassano* (SPF58487, SP470468, LUC7611, UAMIZ 1405). GenBank accession number for *rbc*L (MN597441, MN597442) and for COI-5P (MN597438, MN597439).

Distribution and habitat. This species is currently recorded only for Mexico (Sentíes *et al.* 2016), and Venezuela (this study). Epilithic specimens were collected growing in shallow waters on rocky coastline, northeast of Cayo Muerto. The environment is considered as an intertidal zone with medium-sized rocks and moderately strong waves.

Laurencia digitata Francis, Bolton, Mattio & R.J.Anderson in Francis *et al.* 2017: 812, Figure 5. (Figures 3B, 7A-F, 8A-D)

Type locality. South Africa, KwaZulu-Natal, Cape Vidal; holotype BOL150572.

Description. Plants forming small, very intricate cushion-like tufts, up to 5 cm high, yellowish-brown, terete, cartilaginous in texture, adhering to herbarium paper when dried (Figure 3B). Thallus attached to the substratum by a discoid holdfast, and basal descending branches. Erect branches irregularly alternate and spirally arranged, with up to 3 orders of branches (Figure 7A). Main axes 275-525 µm in diameter in middle portion of the thallus. Ultimate branchlets are cylindrical to clavate with truncated tips, 452-950 × 225-325 µm in diameter.

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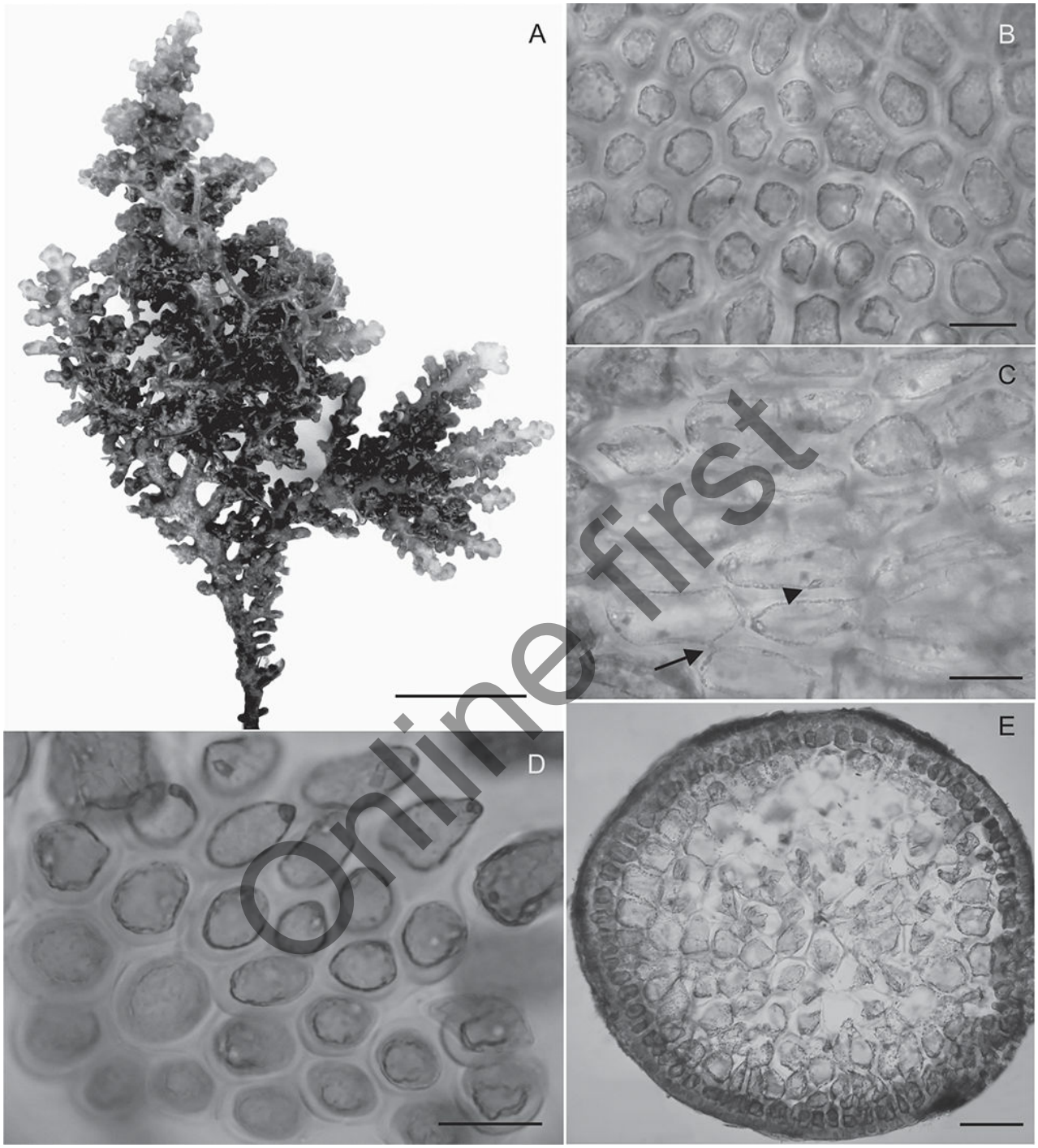

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Figure 4. *Chondrophycus anabeliae.* A) Part of branches of a sterile plant. B) Surface view of translucent cortical cells. C) Surface view of subcortical cells. Note secondary pit connections between subcortical cells (arrow) and crystals (arrowhead). D) Surface view of translucent cortical cells showing one crystal per cell. E) Transverse section of the thallus. Scale bar: A, 1 cm; B and D, 25 µm; C, 50 µm; E, 100 µm.

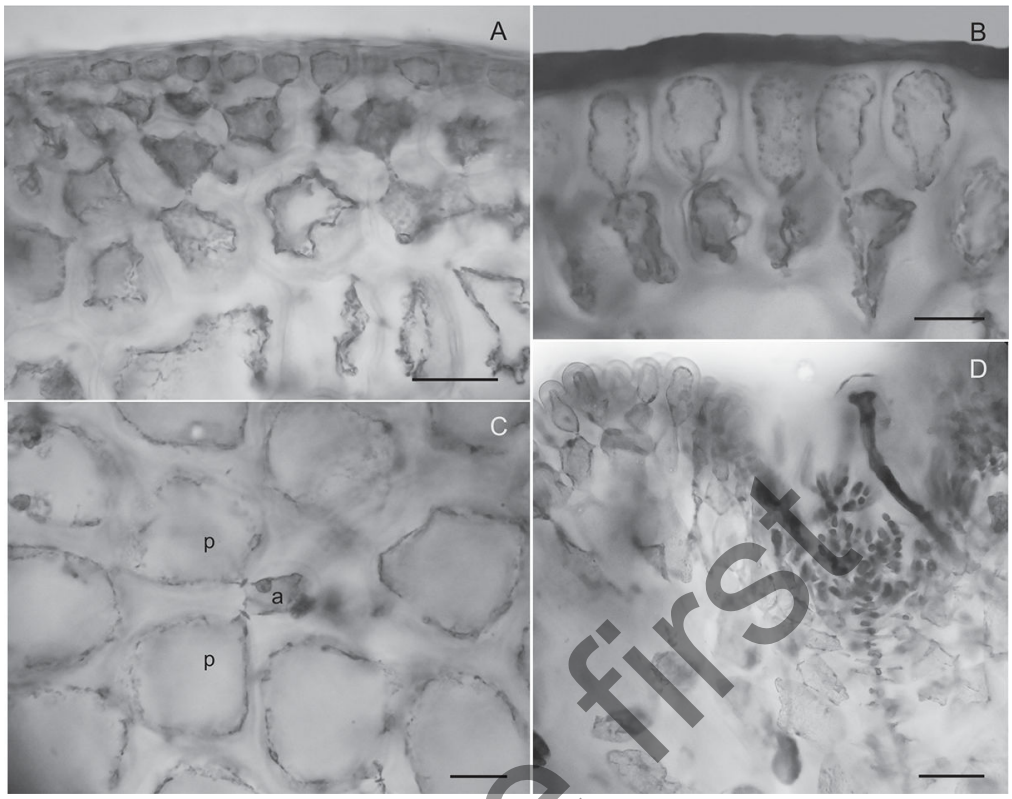

Figure 5. *Chondrophycus anabeliae.* A) Detail of the two-layered cortical cells of ultimate branchlets. Note small translucent outer cortical cells and large pigmented inner cortical cells with secondary pit connections between them. B) Detail of the two-layered cortical cells of main axes in the middle portions of the thallus. Note elongated translucent outer cortical cells. C) Transverse section of upper portion of branch showing an axial cell (a) with two pericentral cells (p). D) Longitudinal section through to a branchlet showing projecting cortical cells. Scale bar: A, D, 50 µm; B and C, 25 µm.

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In surface view, cortical cells have 1 (-2) *corps en cerise* per cell (Figure 7B). Cortical cells are arranged regularly in longitudinal rows and connected to each other by longitudinally oriented secondary pit-connections (Figure 7C). Cortical cells are rounded to polygonal and slightly longitudinally elongated in middle portions of main axes, 37.5-57.5 × 27.5-50 µm. In transverse section, the thallus has 1-2 layers of pigmented cortical cells and 3-4 layers of hyaline medullary cells (Figure 7D). Cortical cells are quadrate, cuneiform to rectangular, not arranged as a palisade, and 25-35 × 22.5-37.5 µm in the middle portions of thalli. Medullary cells are rounded to slightly radially elongated, and 55-90 × 42.5-52.5 µm, gradually increasing in size toward the center of the thallus. Each vegetative axial segment cut off four pericentral cells slightly larger than the other surrounding cells (Figure 7E). In median longitudinal sections through a branchlet, the outer cortical cell walls near the apices projecting beyond the surface (Figure 7F). Lenticular thickening absent.

Tetrasporangial branchlets are cylindrical, simple or compound, 575-2,125 × 225-400 µm (Figure 8A). At the apex of fertile branches, each axial segment produces one fertile pericentral cell, the fourth ones (Figure 8B), the other pericentral cells remain sterile. Fertile pericentral cell cuts off two pre-sporangial cover cells distally abaxially positioned in relation to the tetrasporangial initial (Figure 8D). Subsequently, one post-sporangial cover cell is produced and continues to divide, contributing to cortication around the tetrasporangia. Tetrasporangia are arranged in a parallel pattern in relation to fertile branchlets (Figure 8A, C). Mature tetrasporangia are tetrahedrally divided, 47.5-75 µm in diameter. Gametangia were not observed.

Material examined. Venezuela. Estado Falcón: Parque Nacional Morrocoy, Cayo Muerto, 19 May 2015, tetrasporophyte, *S. Ardito, M.T. Fujii, A. Sentíes, V. Cassano* (SPF58488, SP470469, UAMIZ 1406). GenBank accession number for *rbc*L (MN597443).

Distribution and habitat. This species is currently recorded only for South Africa (Francis *et al.* 2017) and Venezuela (this study). *Laurencia digitata* was collected as drift specimens in shallow waters on rocky coastline, northeast of Cayo Muerto. The environment is considered as an intertidal zone with medium-sized rocks and moderately strong waves.

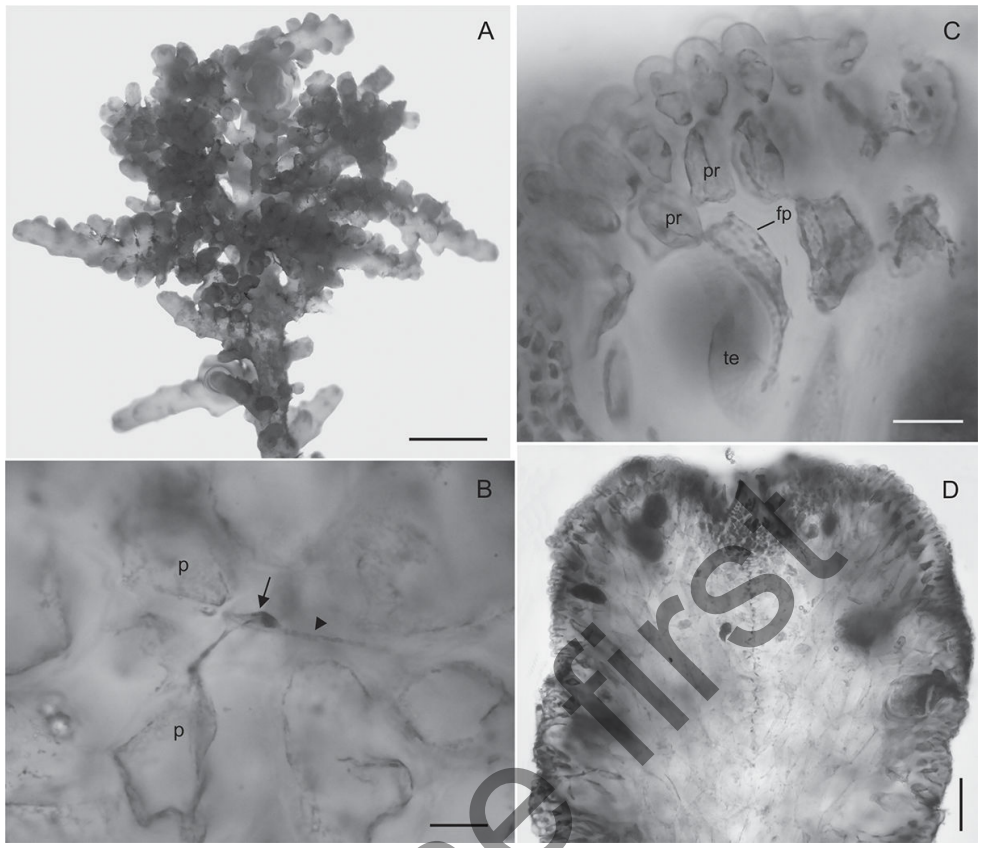

Figure 6. *Chondrophycus anabeliae.* A) Detail of tetrasporangial branches. B) Transverse section of tetrasporangial axial segment showing an axial cell (arrow) and two vegetative pericentral cells (p); an additional third fertile pericentral cell is formed in the opposite position (arrowhead). C) Detail of fertile pericentral cell (fp) with two pre-sporangial cover cells (pr), tetrasporangium (te, out of focus); post-sporangial cover cell not shown. D) Longitudinal section through tetrasporangial branchlet showing right-angle arrangement of the tetrasporangia. Scale bar: A, 3 mm; B and C, 25 µm; D, 100 µm.

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Discussion

Comparison of *rbc*L and COI-5P sequences of *Ch. anabeliae* from the type locality (Mexico) with our material confirmed the occurrence of this species on the Venezuelan coast, whereas *L. digitata* was confirmed only by comparison with *rbc*L sequence from the type locality (South Africa), since we were unable to generate COI-5P sequences and there are also no sequences available of this marker in databases.

Considering our results for *rbc*L, intraspecific value between the Venezuelan and South African *L. digitata* (0.85 %) is within the range observed in previous works for *Laurencia s.s.* (0-1.35 %) reported by Cassano *et al.* (2012a, b), Metti *et al.* (2013), and Collado-Vides *et al.* (2018). Interspecific divergences for the *rbc*L gene between *L. digitata* and *Laurencia* species closest molecularly (*i.e.,* *L.* cf. *kuetzingii*, *L. pumila*, *L. pumila* var. *dehoopiensis*, and *L. karachiana*, 2.14-4.9 %) were within the variation observed for *Laurencia s.s.* by Cassano *et al.* (2012b, 1.0-6.8 %) and Cassano *et al.* (2019, 2.4-3.7 %).

There are no data available in the literature for the *rbc*L gene to compare the intraspecific divergence for *Chondrophycus*. However, the intraspecific value obtained for *Ch. anabeliae* (1.34 %) is below the interspecific variation range described for the genus by Cassano *et al.* (2012b, 1.8-6.9 %), by Sentíes *et al.* (2016, 3.4-7.8 %), and that found in this study (1.86-7.8 %).

For COI-5P gene, the intraspecific divergence values reported for the *Laurencia* complex are low, not exceeding 1 %. The lowest range of intraspecific divergence was observed in this study (0-0.3 %) for samples of *Ch. anabeliae* from the Caribbean Sea (Venezuela and Mexico), whereas divergences up to 0.52 % were reported by Machín-Sánchez *et al.* (2014) for *Laurencia*, up to 0.67 % by Machín-Sánchez *et al.* (2016) for *Osmundea*, and up to 0.7 % by Cassano *et al.* (2012b), Machín-Sánchez *et al.* (2014), and Collado-Vides *et al.* (2018) for *Laurenciella*. The interspecific divergence obtained in this study for COI-5P (5.4-8.76 %) is within the range found for other genera of the complex, i.e. for *Laurenciella* species (7.4-9.2 %, Collado-Vides *et al.* 2018), and for *Laurencia* species (2.6-10.2 %, Cassano *et al.* 2019).

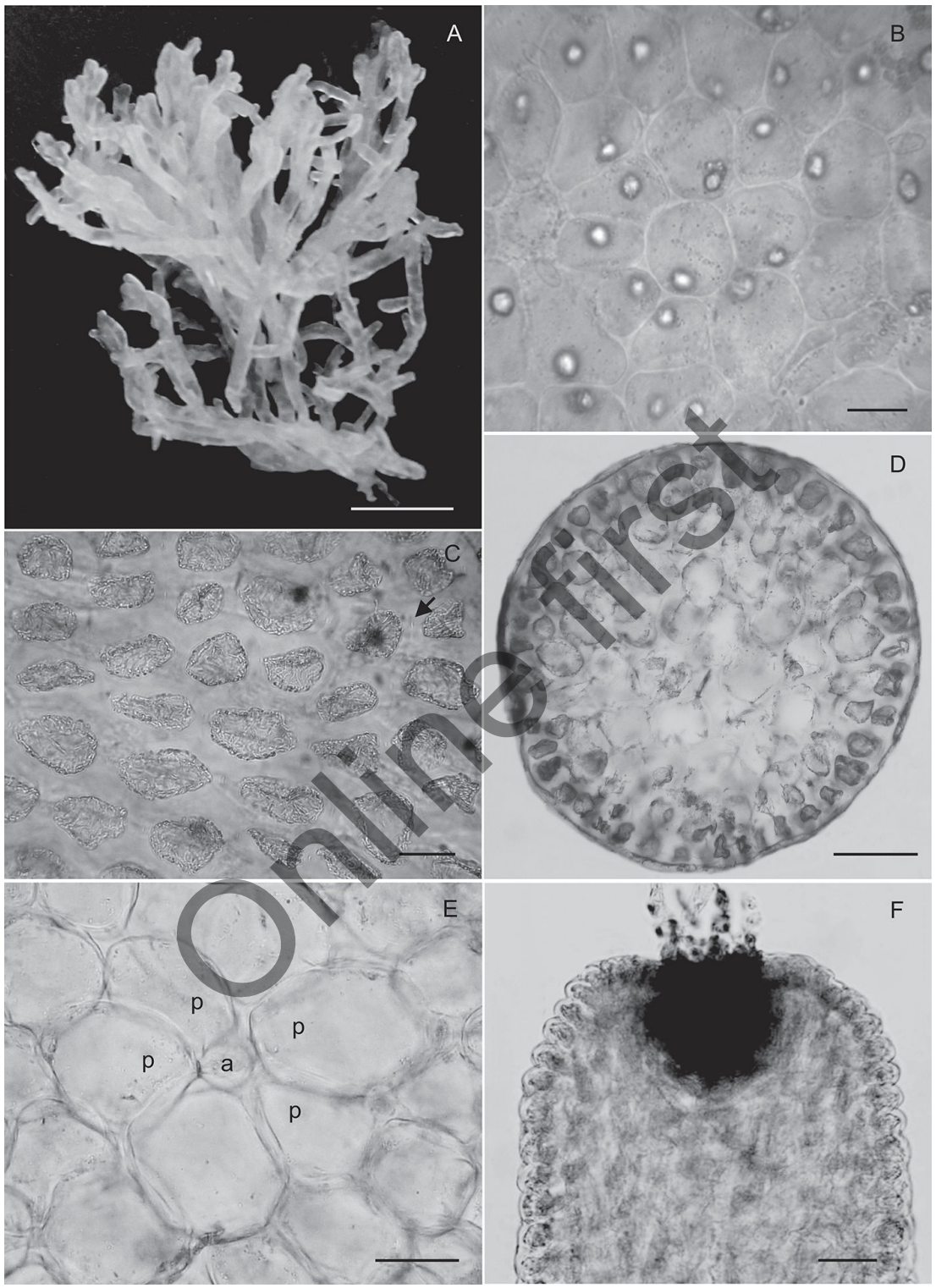

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Figure 7. *Laurencia digitata*. A) Part of branches of a sterile plant. B) Surface view of cortical cells showing *corps en cerise* in living material. C) Surface view of cortical cells showing secondary pit-connections (arrow). D) Transverse section of the thallus. E) Transverse section of upper portion of branch showing an axial cell (a) with four pericentral cells (p). F) Longitudinal section through to a branchlet showing projecting cortical cells. Scale bar: A, 3 mm; B and C, 25 µm; D, 100 µm; E and F, 50 µm.

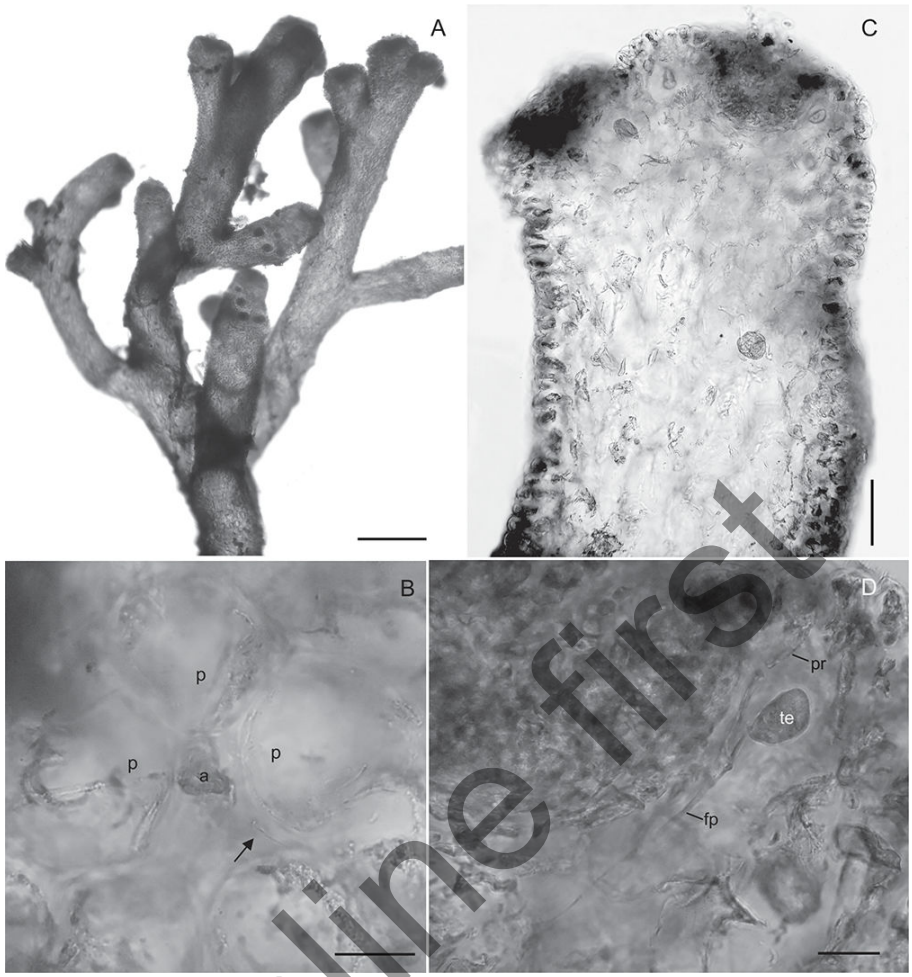

Figure 8. *Laurencia digitata* A) Detail of tetrasporangial branches. B) Transverse section of two superimposed tetrasporangial segments showing an axial cell (a) and one fertile pericentral cell, the fourth (arrow); the other pericentral cells (p) remain sterile (pit connections between axial and pericentral cells, out of focus). C) Longitudinal section through a tetrasporangial branchlet showing parallel arrangement of tetrasporangia. D) Detail of fertile pericentral cell (fp) with two pre-sporangial cover cells (pr, only one visualized), tetrasporangium (te); post-sporangial cover cell not shown. Scale bar: A, 500 µm; B and D, 25 µm; C, 40 µm.

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Morphologically, Venezuelan *Ch. anabeliae* shares all diagnostic characters described for the species by Sentíes *et al.* (2016), such as: (i) thallus slightly compressed; (ii) two cortical cell layers, the outmost layer formed by translucent cells with conspicuous cell wall projections near the apices and absence of secondary pit connections, and the inner layer formed by pigmented and pit connected cells; and (iii) tetrasporangia produced from one additional fertile pericentral cell. The presence of 1 (-2) crystals per cortical and subcortical cells is a characteristic unique for *Ch. anabelia*e from Venezuela; they were not found in Mexican *Ch. anabelia*e and were not described for other *Chondrophycus* species.

Venezuelan and South African *Laurencia digitata* share the cushion-like tufted habit and absence of lenticular thickenings. However, the South African material differed from ours by color (reddish-brown), branching pattern (alternate but subopposite and/or subverticillate at the tips of some branches), and absence of cortical cell walls projections near the apices (Francis *et al.* 2017). The tetrasporophyte has typical features of the genus *Laurencia* and is described for the first time for this species.

Chondrophycus anabeliae seems to be restricted to the Caribbean Sea so far. The range of distribution of *Ch. anabeliae* represents the limits from the western to the southeast Caribbean, whereas *L. digitata*, previously considered endemic to South Africa by Francis *et al.* (2017), presents a disjunct distribution in the Indian and Atlantic Oceans. The disjunct distribution of *L. digitata* is similar to that of *L. natalensis* whose occurrence was recorded only for the Indian Ocean, nevertheless with wider distribution [South Africa, Mozambique, Kenya, Mauritius, Sri Lanka and Vietnam (Guiry & Guiry 2020)], and it was cited for Venezuela by García-Soto & Lopéz-Bautista

(2019). However, more studies of biogeography and phylogeography are needed in the area, which will allow us to explain this further.

Although macroalgal floristic studies have been carried out for the Venezuelan coast (*e.g.,* Gómez *et al.* 2017), the diversity for this region is still underestimated. Similar underestimations have already been reported for other groups of red algae (*e.g.,* Adey *et al.* 2015, Basso *et al.* 2015, Hind *et al.* 2015, Ardito *et al.* 2017, Núñez-Resendiz *et al.* 2018). For this reason, it is necessary to continue performing floristic surveys that incorporate molecular-assisted alpha taxonomy to accurately identify all and potential new species from this region, especially for ecologically and economically important taxonomic groups such as those included in the *Laurencia* complex.

The use of *rbc*L gene for phylogenetic inference, and the COI-5P barcode marker for species delimitation allied to morphological study revealed the presence of two species of the *Laurencia* complex for Venezuela, *Chondrophycus anabeliae* and *Laurencia digitata*. Both constitute new records for the region and their first occurrence outside the type localities. Our findings expand the geographic distribution of *Ch. anabeliae* to the southeast of the Caribbean Sea, where the species seems to be restricted so far, whereas the first report of *L. digitata* for the Atlantic Ocean established a disjunct distribution of this species in the Atlantic and Indian Oceans.

Acknowledgements

We wish to thank the Faculty of Science and Technology of the University of Carabobo, Venezuela and the Faculty of Science of the Central University of Venezuela, for the field and laboratory logistical support. We also thank Marion Cordero, Yugreisy Polanco and Jorge Escobar for help with field material. We are very grateful to Michael Wynne for revising the English and for his helpful comments that improved the manuscript. VC thanks Funding from São Paulo Research Foundation (FAPESP, 2018/06085-1). VC and MTF thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil) for the Productivity Fellowship (302549/2017-0 and 304899/2017-8, respectively). AS thanks the partial support of the projects: UAMI-CBS2019-2022: session 15.18-281118 and UAMI-CA-117, PRODEP.

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Associate editor: José Antonio Zertuche González

Author contributions: VC, conceptualization, field work, formal analysis, investigation, writing - original draft preparation, project administration, funding acquisition; LPS, investigation, writing - reviewing and editing; BEVV, investigation, writing - reviewing and editing; SA, field work, investigation, writing - reviewing and editing; SG, investigation, writing- reviewing and editing; AS, field work, investigation, writing - reviewing and editing; MTF, field work, investigation, writing - reviewing and editing.

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Appendix 1. Taxa used in this study for molecular analysis.

Samples	Collection data	GenBank accession numbers	
		COI-5P	*rbc*L
Chondria baileyana (Montagne) Harvey	Canada, Nova Scotia, Pomquet (far on Monks Head Road), 16 Aug. 2012, G.W. Saunders, A. Savoie, C. Longtin, K. Dixon, M. Bruce	KU564345	-
C. californica (Collins) Kylin	USA, California, San Diego Co., Beach Club Reef (La Jolla Shores), 1 Jul. 1996, M. Volovsek	-	AY172578
C. collinsiana M.A. Howe	Brazil, Rio de Janeiro, Armação dos Búzios, Praia Rasa, 13 Jan. 2005, V. Cassano, J.C. De-Paula	-	GU330225
C. dasyphylla (Woodward) C. Agardh	USA, North Carolina, Carteret Co., Bogue Sound	-	U04021
Chondrophycus anabeliae Sentíes, M.T.Fujii, Cassano & Dreckmann	Mexico, Quintana Roo, Isla Mujeres, Garrafón de Castilla, 12 Feb. 2007, A. Sentíes, M.C. Gil-Rodríguez	MN597440	KX815262
Ch. anabeliae	Venezuela, Estado Falcón, Parque Nacional Morrocoy, Cayo Muerto, 19 May 2015, S. Ardito. M.T. Fujii, A. Sentíes, V. Cassano	MN597438 MN597439	MN597441 MN597442
Ch. dotyi (Y. Saito) K.W. Nam	USA, Hawaii	HQ423050	-
Ch. dotyi	USA, Hawaii, Oahu, Sandy Beach, 31 May 2015, E.M. Stein	-	KX815263
Ch. cf. *undulatus* (Yamada) Garbary & J.T. Harper	New Caledonia, Loyalty Is., Maré, 22 Mar. 2005, C. Payri	-	FJ785307
Ch. cf. *undulatus*	USA, Maui, 12 Dec. 2007	GU223886	-
Ch. cf. *undulatus*	USA, Hawaii	HQ422752 HQ423055 HQ422996	-
Ch. succisus (A.B. Cribb) K.W. Nam	USA, Molokai, 11 Feb. 2007	GU223884	-
Ch. tronoi (E. Ganzon-Fortes) K.W. Nam	Philippines, A.O. Lluisma	-	AF489864
Ch. sp.	Australia, Norfolk Island, Collins Head, 21 Mar. 2005, Y. Metti, A. Millar		KY120337
Ch. sp. 1	New Caledonia, Loyalty Is., Lifou, 26 Mar. 2005, C. Payri	-	FJ785309
Ch. sp. 2	New Caledonia, Loyalty Is., Maré, 21 Mar. 2005, C. Payri	-	FJ785310
Ch. sp. 3	New Caledonia, Loyalty Is., Beautemps/Beaupré, 06 Apr. 2005, C. Payri	-	FJ785311
Corynecladia clavata J. Agardh	Australia, Victoria, Walkerville, 20 Jan. 2015, P. Díaz-Tapia, M. Brookes	-	MF094079
C. clavata	Australia, Victoria, The Caves, 21 Jan. 2015, P. Díaz-Tapia, M. Brookes	MH704456	-
C. clavata (as Ceramiales sp.)	Australia, Tasmania, 24 Jan. 2004, G.W. Saunders, R. Withall	HM915955	-
C. elata (C. Agardh) Cassano, M.C. Oliveira & M.T. Fujii	Australia, Western Australia, Rottnest Island, 15 Nov. 2008, J. Eu	-	KY120339
C. nova (Metti) Cassano, M.C. Oliveira & M.T. Fujii	Australia, NSW, Jervis Bay, Plantation Point, 15 Feb. 2005, Y. Metti, A. Millar	-	KY120340
Laurencia aldingensis	Brazil, Rio de Janeiro, Armação dos Búzios, Praia Rasa, 13 Jan. 2005, V. Cassano, J.C. De-Paula	-	JF810351
L. alfredensis Francis, Bolton, Mattio & Anderson	South Africa, 04 Jul. 2008, R.J. Anderson, J.J. Bolton	-	KY927749
L. brachyclados Pilger	USA, Hawaii	HQ423046	-

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Samples	Collection data	GenBank accession numbers	
		COI-5P	*rbc*L
L. cf. *brongiartii* J. Agardh	Australia, Tarcoola Beach, 1996, S. Fredericq	-	EF061654
L. caduciramulosa Masuda & Kawaguchi	Brazil, Rio de Janeiro, Angra dos Reis, Praia do Velho, 19 Apr. 2006, V. Cassano, J.C. De-Paula	-	KJ700865
L. caraibica P.C. Silva	Mexico, Quitana Roo, Cancún, Isla Mujeres, 2006, A. Sentíes	-	EF658642
L. caraibica	Venezuela, Falcon, Cabo San Roman, 06 Oct. 2012, G. Garcia-Soto		MH388533
L. catarinensis Cordeiro-Marino & M.T. Fujii	Spain, Canary Islands, Tenerife, Punta del Hidalgo, 02 Jun. 2012, M.C. Gil-Rodríguez, M. Machín-Sánchez	-	KF492781
L. catarinensis	Spain, Canary Islands, Lanzarote, Pechigueras, 15 Jan. 2013, M.C. Gil-Rodríguez, M. Machín-Sánchez	KF492718	-
L. complanata (Suhr) Kützing	South Africa, 09 Dec. 2010, R.J. Anderson, J.J. Bolton	-	KY927738
L. corymbosa J. Agardh	South Africa, 19 Aug. 2008, R.J. Anderson, J.J. Bolton	-	KY927760
L. dendroidea J. Agardh	Brazil, Bahia, Lauro de Freitas, Praia Vilas do Atlântico, 08 Jan. 2008, A. Oliveira	-	GU330228
L. dendroidea	Venezuela, Falcon, Playa Buchuacos, 06 Oct. 2012, G. Garcia-Soto	-	MH388528
L. dendroidea (as *L. majuscula*)	Australia, NSW, Kiama Harbour, North side, 03 Apr. 2004, Y. Metti, D. Williams	-	-
L. dendroidea	Spain, Canary Islands, La Gomera, Punta de La Dama, 21 Sept. 2009, E. Aylagas, M.C. Gil-Rodríguez, M. Machín-Sánchez	KF492725	-
L. dendroidea	Spain, Canary Islands, Lanzarote, Pechigueras, 15 Jan. 2013, M.C. Gil-Rodríguez, M. Machín-Sánchez	KF492728	-
L. dendroidea (as *L. majuscula*)	USA, Molokai, 10 Feb. 2007	GU223887	-
L. dichotoma Francis, Bolton, Mattio & Anderson	South Africa, 22 Mar. 2011, J.J. Bolton	-	KY927786
L. digitata Francis, Bolton, Mattio & Anderson	South Africa, 04 Jul. 2008, R.J. Anderson, J.J. Bolton	-	KY927748
L. digitata	Venezuela, Estado Falcón, Parque Nacional Morrocoy, Cayo Muerto, 19 May 2015, S. Ardito, M.T. Fujii, A. Sentíes, V. Cassano	-	MN597443
L. flexuosa Kützing	South Africa, S. KwaZulu-Natal, Palm Beach, 07 Feb. 2001, S. Fredericq	-	AF465815
*L.*cf. *flexuosa*	South Africa, Eastern Cape Province, 15 Jun. 2003, O. De Clerck	KX258821	-
L. filiformis (C. Agardh) Montagne	Western Australia, Geraldton, Tarcoola Beach, 21 Sept. 1995, M.H. Hommersand, F.H. Hommersand	-	MH704449
L. galtsoffii M.A. Howe	USA, Hawaii	HQ422984	-
L. glomerata (Kützing) Kützing	South Africa, 03 Mar. 2009, R.J. Anderson, J.J. Bolton	-	KY927763
L. heteroclada Harvey f. *decussata* Cribb	Australia, NSW, Arrawarra headland, 28 Jul. 2004, Y. Metti	-	KY120344
L. intricata J.V. Lamouroux	Cuba, Ciego de Ávila, Cayo Coco, 25 Sept. 2005, M.T. Fujii	-	GU330238
L. intricata	USA, Florida, Long Key, Channel 5 (ocean side), 10 Dec. 1998, B. Wysor, T. Frankovich	-	AY588410
L. karachiana Bibi, Cassano & Rasheed	Pakistan, Karachi, French Beach (Buleji), 13 Aug. 2018, R. Bibi	MK796229	MK796228
L. cf. *kuetzingii* A. Millar	New Caledonia, Loyalty Is., Ouvéa, 31 Mar. 2005, C. Payri	-	FJ785322

Online first

Samples	Collection data	GenBank accession numbers	
		COI-5P	*rbc*L
L. laurahuertana Mateo-Cid, Mendoza-González, Sentíes & Díaz-Larrea	Mexico, Quintana Roo, Punta Herrero, 12 Apr. 2012, A.C. Mendoza González, L.E. Mateo-Cid	-	KF279401
L. longiramea Cassano, G.N. Santos, J.M.C. Nunes, M.C. Oliveira & M.T. Fujii	Brazil, Espírito Santo, Anchieta, Ilhote de Ubu, 30 Jun. 2007, E.M. Stein	MH704454	-
L. longiramea	Brazil, Rio de Janeiro, Armação dos Búzios, Praia Rasa, 13 Jan. 2005, V. Cassano, J.C. De-Paula	MH704455	MH704451
L. cf. *majuscula* (Harvey) A.H.S. Lucas	Oman, Dhofar, Sept. 2001, M. Wynne	-	KX146184
L. cf. *mariannensis* Yamada	New Caledonia, Lagon Sud-Ouest, Ilot Larégnère, 11 Jul. 2003, C. Payri	-	FJ785313
L. mcdermidiae I.A. Abbott	USA, Oahu, 08 Apr. 2007	GU223877	-
L. mcdermidiae	New Caledonia, Ile des Pins, 09 Nov. 2005, C. Payri	-	FJ785314
L. multiclavata Francis, Bolton, Mattio & Anderson	South Africa, 29 Mar. 2010, R.J. Anderson	-	KY927766
L. mutueae Sentíes, Cassano & Dreckmann	Mexico, Guerrero, Acapulco, Isla la Roqueta, 07 Jun. 2017, A. Sentíes, K.M. Dreckmann	MK182532	MK159179
L. natalensis Kylin	South Africa, S. KwaZulu-Natal, Palm Beach, 07 Feb. 2001, S. Fredericq	-	AF465816
L. natalensis	Venezuela, Falcon, Cabo San Roman, 06 Oct. 2012, G. Garcia-Soto		MH388523
L. nidifica J. Agardh	USA, Hawaii	HQ422750	-
L. nidifica	USA, Hawaii	HQ422751	
L. nidifica	USA, Hawaii	HQ423054	-
L. cf. *nidifica*	New Caledonia, Ile des Pins, 30 Nov. 2005, C. Payri	-	FJ785315
L. nipponica	Russia, Sakhalin, 23 Jun. 2003	GU223874	-
L. obtusa (Hudson) J.V. Lamouroux	Ireland, County Donegal, Fanad Head, C.A. Maggs	-	AF281881
L. obtusa	France, Languedoc-Roussillon, Pyrenees-Orientales, Cap Beart, Banyuls-sur-Mer, 11 Jul. 2007, L. Bittner	KX258828	-
L. oliveirana Yoneshigue	Brazil, Rio de Janeiro, Arraial do Cabo, Ponta da Cabeça, Praia Grande, 07 Jul. 2008, V. Cassano, J.C. De-Paula	-	JF810352
L. pacifica Kylin	USA, California, Stillwater Cove, Pebble Beach, 20 May 2010, B. Clarkston, K. Hind, S. Toews	KM254466	-
L. pacifica	USA, California, Moss Beach, Central Beach, 17 Feb. 1992, S. Fredericq	-	AY588411
L. pumila (Grunow) Papenfuss	South Africa, 10 Jun. 2009, R.J. Anderson, J.J. Bolton	-	KY927765
L. pumila var. *dehoopiensis* Francis, Bolton, Mattio & Anderson	South Africa, 19 Aug. 2008, R.J. Anderson	-	KY927757
L. pyramidalis Bory ex Kützing	France, Brittany, Roscoff, 05 Dec. 2002, F. Rousseau	-	FJ785316
L. pyramidalis	Portugal, Madeira, Seixal, Praia da Laje, 07 Jul. 2011, E. Nogueira, V. Cassano, A. Sentíes	KF492733	-
L. pyramidalis	Portugal, Madeira, Porto Muniz, 07 Jul. 2011, M.T. Fujii, A. Neto, M. Machín-Sánchez	KF492739	-

Online first

Samples	Collection data	GenBank accession numbers	
		COI-5P	*rbc*L
L. pyramidalis	Portugal, Azores, São Miguel, Mosteiros, 27 Jun. 2011, M.T. Fujii, A. Prestes, A. Pacheco, M. Machín-Sánchez	KF492751	-
L. pyramidalis	Spain, Canary Islands, Fuerteventura, Garcey, 10 Sept. 2012, M. Machín-Sánchez	KF492756	-
L. pyramidalis	Spain, Canary Islands, Tenerife, Puerto de La Cruz, 20 May 2011, M.C. Gil-Rodríguez, M. Machín-Sánchez	KF492746	-
L. rigida J. Agardh	Australia, NSW, Botany Bay, 11 May 2000, G.C. Zuccarello, J.A. West	-	AY920852
L. saitoi Perestenko	USA, California, Monterey, McAbee Beach, 21 May 2010, B. Clarkston, K. Hind, S. Toews	KM254876	-
L. snackeyi (Weber van Bosse) M. Masuda	Unspecified	MF093985	-
L. sodwaniensis Francis, Bolton, Mattio & Anderson	South Africa, 22 Mar. 2011, C.M. Francis	-	KY927790
L. stegengae (Stegenga, Bolton & Anderson) Francis, Bolton, Mattio & Anderson	South Africa, 18 Mar. 2010, R.J. Anderson	-	KY927743
L. tasmanica J.D. Hooker & Harvey	Australia, Victoria, Tween Reef, between Cape Paterson and Inverloch, P. Díaz-Tapia	-	MF094081
L. venusta Yamada	Mexico, Quintana Roo, Puerto Morelos, Punta Brava, 2004, J. Díaz-Larrea, A. Sentíes	-	EF061655
L. viridis Gil-Rodríguez & Haroun	Spain, Canary Islands, Tenerife, Punta del Hidalgo, Roca Negra, 06 Oct. 2005, M.C. Gil-Rodríguez	-	EF685999
L. viridis	Spain, Canary Islands, Fuerteventura, El Cotillo, 07 Mar. 2011, M.C. Gil-Rodríguez	KF492757	-
L. viridis	Portugal, Azores, Santa Maria, Boca de Ribeira Seca, 02 Jul. 2011, M.T. Fujii, A. Neto, J. Pombo, M. Machín-Sánchez	KF492760	-
"L. yamadana" M.A. Howe	USA, HI, Maui, Kihei, 05 Apr.2006, A.L. Carlile, J.R.Waaland	-	GQ252550
Laurencia sp.	New Caledonia, Loyalty Islands, Maré, 21 Mar. 2005, C. Payri	KX258820	KX146182
Laurencia sp.	New Caledonia, Loyalty Islands, Maré, 19 Mar. 2005, C. Payri	KX258819	-
Laurencia sp.	USA, Oahu	GU223889 GU223891 GU223893 GU223894	-
Laurencia sp.	USA, Lanai	GU223892	-
Laurencia sp.	Sri Lanka, Odayapiti lagoon, 08 Nov. 2006, E. Coppejans	KX258826	-
Laurencia sp.1	Australia, Victoria, Mallacoota, H. Verbruggen, K.Dixon	-	MK125344
Laurencia sp.2	Australia, Victoria, Mallacoota, H. Verbruggen, K. Dixon	-	MK125395
Laurenciella marilzae (Gil-Rodríguez *et al.*) Gil-Rodríguez *et al.*	Spain, Canary Islands, Tenerife, Punta del Hidalgo, 12 Jul. 2006, M.C. Gil-Rodríguez, M.T. Fujii, A. Sentíes	-	EF686002
La. marilzae	Spain, Canary Islands, Lanzarote, Pechigueras, 15 Jan. 2013, M.C. Gil-Rodríguez, M. Machín-Sánchez	KF492762	-

Online first

Samples	Collection data	GenBank accession numbers	
		COI-5P	*rbc*L
La. marilzae	Portugal, Azores, São Miguel, Cerco da Caloura-Baía, E. Nogueira, V. Cassano, A. Sentíes	KF492765	-
La. marilzae	Spain, Canary Islands, Tenerife, Punta del Hidalgo, 13 Jan. 2012, M.C. Gil-Rodríguez, M. Machín-Sánchez	KF492769	-
La. marilzae	Brazil, São Paulo, Laje de Santos Marine State Park, Parcel do Sul, 25 Mar. 2007, R. Rocha-Jorge	KF270693	GU938189
La. marilzae	Croatia, Scedro, 11 Jun. 2007, J. Utge, L. Le Gall	KX258829	KX146186
La. mayaimii L. Collado-Vides, Cassano & M.T. Fujii	USA, Florida, Biscayne Bay at Deering Estate, 12 Aug. 2013, L. Collado-Vides, V. Cassano, M.T. Fujii	MG004176 MG004177	-
La. mayaimii	USA, Florida, Key Largo, John Pennekamp Park, 14 Aug. 2013, L. Collado-Vides, V. Cassano, M.T. Fujii	MG004178	MG004183
Laurenciella sp.	USA, Florida, Key Biscayne, Crandon Park, 12 Aug. 2013, L. Collado-Vides, V. Cassano, M.T. Fujii	MG004179	MG004184
Ohelopapa flexilis (Setchell) F. Rousseau, Martin-Lescanne, Payri & L. Le Gall	French Polynesia, Tahiti, Tahara reef, 24 Mar. 2007, A. Apham	KX258830	KX146187
Osmundea blinksii (Hollenberg & I.A. Abbott) K.W. Nam	USA, California, San Mateo Co., Año Nuevo, Greyhound Rock, 17 Jul.1996, M.H. Hommersand	-	AY172575
O. caspica (Zinova & Zaberzhinskaya) Maggs & L.M. McIvor	Azerbaijan, Sangachal Bay, 01 Sept. 2003	-	KX146188
O. hybrida (A.P. de Candolle) K.W. Nam	France, Brittany, St. Lunaire, 20 Mar. 1999, F. Rousseau	-	FJ785317
O. hybrida	France, Brittany, Roscoff, Finistere, 12 May 2002, F. Rousseau	KX258831	-
O. oederi (Gunnerus) G. Furnari	Ireland, Co. Donegal, St. John´s Point, 12 Oct. 1999, C.A. Maggs	-	AF281880
O. osmunda (S.G. Gmelin) K.W. Nam & Maggs	Ireland, Co. Donegal, St. John´s Point, 12 Oct. 1999, C.A. Maggs	-	AF281877
O. osmunda	France, Brittany, Le Loup, 19 May 2011, L. Couceiro, M. Robuchon	KJ960875	-
O. pinnatifida (Hudson) Stackhouse	France, Brittany, Penmarch	-	AF259495
O. pinnatifida	France, Brittany, Le Loup, 08 Mar. 2012, L. Couceiro, M. Robuchon	KJ960886	-
O. sanctarum M.T. Fujii & R. Rocha-Jorge	Brazil, São Paulo, Laje de Santos Marine State Park, Parcel do Sul, 19 Aug. 2012, R. Rocha-Jorge, M.B. Barros-Barreto	-	KC012601
O. sinicola (Setchell & N.L. Gardner) K.W. Nam	USA, California, Orange Co., Crescent Beach, 28 May 2002, S. Murray	-	AY588407
O. spectabilis (Postels & Ruprecht) K.W. Nam var. *spectabilis*	Mexico, Baja California, Punta Santo Thomas, 02 Jul. 1996, M.H. Hommersand	-	AY172574
O. spectabilis	USA, California, Aquarium Reef, Monterey Bay, 23 May 2010, B. Clarkston, S. Toews	KM254974	-
O. spectabilis	USA, California, Monterey, McAbee Beach, 21 May 2010, B. Clarkston, K. Hind, S. Toews	KM254320	-
O. splendens (Hollenberg) K.W. Nam	Mexico, Baja California, Drift, Bahia Colnett, 02 Jul. 1996, M.H. Hommersand, J. Hughey	-	AY172576
O. splendens	USA, California, Santa Cruz (Four Mile), 19 May 2010, B. Clarkston, K. Hind, S. Toews	KM254377	-

Online first

Samples	Collection data	GenBank accession numbers	
		COI-5P	*rbc*L
Palisada cervicornis (Harvey) Collado-Vides, Cassano & M.T. Fujii	USA, Florida, Key Largo, Pickles Reef, 14. Aug. 2013, A. Duran	-	MG030375 MG020476
P. corallopsis (Montagne) Sentíes, M.T. Fujii & Díaz-Larrea	Mexico, Yucatán, Cancún, Chaac Mool Beach, 2005, J. Díaz-Larrea, A. Sentíes	-	EF061646
P. crustiformans (McDermid) A.R. Sherwood, A. Kurihara & K.W. Nam	USA, Hawaii	HQ422768	-
P. crustiformans	USA, Hawaii, Oahu, Makapuu, 26 May 2007, A. Kurihara	-	KX146196
P. flagellifera (J. Agardh) K.W. Nam	Brazil, Rio de Janeiro, Rio das Ostras, Praia do Cemitério, 03 Aug. 2005, V. Cassano, M.B.B. Barreto	-	GU330227
P. flagellifera	Spain, Canary Islands, Tenerife, Punta del Hidalgo, 13 Jan. 2012, M.C. Gil-Rodríguez, M. Machín-Sánchez	KF492772	-
P. furcata (Cordeiro-Marino & M.T. Fujii) Cassano & M.T. Fujii	Brazil, Paraíba, Praia de Tambaú, 24 Feb. 2004, M.T. Fujii	-	GU330226
P. parvipapillata (C.K. Tseng) K.W. Nam	USA, Oahu,18 Sept. 2007	GU223895	-
P. perforata (Bory) K.W. Nam	Spain, Canary Islands, Tenerife, Punta del Hidalgo, Faro, Bahía Izquierda, 06 Oct. 2005, M. Gil-Rodríguez	-	EU256327
P. perforata	Mexico, Quintana Roo, Isla Mujeres, 2007, A. Sentíes, M.C. Gil-Rodríguez	-	EF658641
P. perforata	Spain, Canary Islands, Tenerife, Punta del Hidalgo, 13 Jan. 2012, M.C. Gil-Rodríguez, M. Machín-Sánchez	KF492773	-
P. cf. *robusta* (Yamada) K.W. Nam	New Caledonia, Lifou, 23 Mar. 2005, C. Payri	-	FJ785321
P. yamadana (M.A. Howe) K.W. Nam	USA, Hawaii	HQ422794	-
Palisada sp.	New Caledonia, Ilot Bayes, 01 Jan. 2001, C. Payri	-	KX146194
Yuzurua poiteaui (J.V. Lamouroux) Martin-Lescanne var. *gemmifera* (Harvey) M.J. Wynne	Mexico, Quintana Roo, Puerto Morelos, Ojo de Agua, 2004, J. Díaz-Larrea, A. Sentíes	-	EF061648
Y. poiteaui var. *gemmifera*	Cuba, La Havana, Rincon de Guanabo, 2005, J. Díaz-Larrea, A. Areces	-	EF061650
Y. poiteaui var. *poiteaui*	USA, Florida, Long Key, Ovan Side, 1998, S. Fredericq	-	EF061652
Y. poiteaui var. *poiteaui*	Mexico, Quitana Roo, Cancún, Playa del Carmen, 2005, J. Díaz-Larrea, A. Sentíes	-	EF061653
Yuzurua sp.	West Indies, Guadeloupe, Grand Cul-de-Sac Marin, Chenal ilet Colas, 03 May 2012, F. Rousseau, Y. Buske, J. Espinosa, M. Snyder, G. Dirberg	KX258843	-

Online first