

Two New Species of the Genus *Dictyota* (Phaeophyceae: Dictyotales) from the Mexican Caribbean

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Abstract

During a molecular characterization of the genus *Dictyota* J. V. Lamouroux (Phaeophyceae, Dictyotales) along the Mexican coasts of the Gulf of Mexico and the Mexican Caribbean, using *psbA* and *cox1* genes, it was found that two particular collections did not match with the sequences published for a total of 39 species of *Dictyota*. For each gene, both collections diverged in high-uncorrected “p” distance values with respect to other related species. This high genetic divergence was corroborated by morphological analysis. Hence, we proposed *Dictyota mayae* J. Lozano-Orozco & Senties and *Dictyota pedrochei* J. Lozano-Orozco & Senties as new species.

Keywords

Mexican Caribbean, *Dictyota mayae* sp. nov., *Dictyota pedrochei* sp. nov., Molecular Phylogeny, Taxonomy

1. Introduction

Floristic identification of species belong to the genus *Dictyota* J. V. Lamouroux (Phaeophyceae, Dictyotales), it

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has been a controversial issue among the community of Dictyotales specialists for at least the past two decades [1]-[3]. This scenario was the consequence of that nineteenth-century phycological school which saw the least minimal morphological difference as a diagnostic feature (the classical algorithm for that is: *if one cell, then species A; if two, then species B*), which in turn was the consequence of a very low morphological variability and phenotypic plasticity, both intra and inter species. Today, 77 specific names are recognized within the genus worldwide [4]. For the American Atlantic, for example, we recognize 15 species [5], and 11 for the Mexican Caribbean alone [6]-[9]. Fortunately, methods of modern molecular phylogenetics have allowed us to solve the problems resulting from the lack of reliable morphological characters. As an instance for genus *Dictyota*, molecular characters have been used in order to redefine intraspecific and interspecific taxonomy [10]-[16]. Recently, several authors studied the taxonomic relationships of *Dictyota* species at the interspecific level, combining morphological and molecular data [3] [17]-[20]. As a result of these studies, new species had been described within *Dictyota* [3] [18] [20]. Because of the above, we started a molecular characterization of genus *Dictyota* along the Mexican coasts of the Gulf of Mexico and the Mexican Caribbean. During the research, however, it was found that two particular sample collections did not match the sequences published for a total of 39 species of *Dictyota*. A high genetic divergence, together with morphological analyses, convinced us of the presence of two new species, which here we formally described.

2. Materials and Methods

The specimens studied in the present study were collected at Punta Brava and Puerto Morelos, Quintana Roo, in March 2012, by J.G. Lozano-Orozco and A. Sentíes. Voucher samples were fixed in 4% formalin solution for morphological analysis.

The specimens were examined using a Leica stereomicroscope (Leica MZ 12.5, Wetzlar, Germany). Transverse hand sections in the apical, middle and basal regions of the thallus were made with a stainless steel razor blade under a dissecting scope. Photomicrographs were taken with an Olympus Vg-160 digital camera (Tokyo, Japan) coupled to a Nikon Eclipse E200 microscope (Tokyo, Japan). Voucher specimens were deposited at UAMIZ Herbarium (UAMIZ1231, UAMIZ1232, UAMIZ1233 and UAMIZ1234).

Total DNA was extracted from silica gel-preserved material using a Dneasy Mini Kit (Qiagen, Valencia, CA, USA) following the manufacturers' instructions. A total of 956 bp from the *psbA* gene were amplified using the *psbA* F and *psbA* R primers [16], and 672 bp were amplified for *cox1* with Gaz1R and Gaz1F primers (adapted from [21]), using the AmpliTaq kit of the Applied Biosystems (Lincoln Centre Drive Foster City, CA, USA). All PCR products were checked for their correct length by electrophoresis on 1% agarose gel. The PCR products were sent to Macrogen (Gasan-dong, Seoul, Korea) to be purified and sequenced. Alignments for *psbA* and *cox1* sequences were constructed using MEGA version 5 [22]. Collection sites and GenBank Accession Numbers of the specimens used in the phylogenetic analysis are provided in **Table 1**.

Phylogenetic relationships were inferred using a concatenated matrix (1703 nt) of two genes from 39 taxa (*psbA* = 1031 bp; *cox1* = 672 bp; **Table 1**). *Canistrocarpus crispatus* (J. V. Lamouroux) De Paula & De Clerck, *Dictyopteris polypodioides* (A. P. De Candolle) J. V. Lamouroux, *Rugulopteryx okamurae* (E. Y. Dawson) I. K. Hwang, W. J. Lee & H. S. Kim and *Scoresbyella profunda* Womersley were included as outgroup taxa based on previous results obtained by [23]. The intraspecific and interspecific divergence values obtained for *psbA* and *cox1* were calculated using uncorrected "p" distances implemented in MEGA version 5 [22]. The Bayesian phylogenetic analysis was inferred with MrBayes v.3.0 beta 4 software [24] using the general time-reversible model of nucleotide substitution with invariant sites and Gamma-distributed rates for the variable sites (GTR + I + G). This model was selected based on Maximum Likelihood (ML) ratio test implemented by the software ModelTest 0.1.1 [25]. For the Bayesian analysis, five chains of the Markov chain Monte Carlo (one hot and four cold) were run, sampling one tree every 1000 generations for 5×10^6 generations starting with a random tree. Maximum likelihood analysis was performed using TOPALI v2 software [26] with the GTR + I + G model. The ML bootstrap analyses were conducted with 100 replicates. Support values [27] were computed, as implemented in TOPALI v2.

3. Results

3.1. Morphological Analysis

Dictyota mayae: J. Lozano-Orozco & Sentíes sp. nov. (**Figures 1(A)-(H)**).

Table 1. Taxa used in this study for phylogenetic analysis.

Samples	Collection Sites		GenBank Accession Numbers	
	<i>psbA</i>	<i>cox1</i>	<i>psbA</i>	<i>cox1</i>
<i>Canistrocarpus crispatus</i> (J. V. Lamouroux) De Paula & De Clerck	Tiwi, Kenya	Negros Oriental, Philippines	GU265787	GQ425137
<i>Dictyopteris polypidioides</i> (A. P. De Candolle) J. V. Lamouroux	France	France	EU681639	EU681404
<i>Dictyota acutiloba</i> J. Agardh	Hawaii, USA	Hawaii, USA	EU395602	GU290236
<i>Dictyota adnata</i> Zanardini	Raja Ampat, Indonesia	Raja Ampat, Indonesia	GU265788	GQ425134
<i>Dictyota bartayresiana</i> J. V. Lamouroux	Zanzibar, Tanzania	Punta Cana, Dominican Republic	GQ425129	GQ466071
<i>Dictyota binghamiae</i> J. Agardh	Baja California, Mexico	British Columbia, Canada	JQ061015	FJ409140
<i>Dictyota canaliculata</i> O. De Clerck & E. Coppejans	Siquijor, Philippines	Raja Ampat, Indonesia	GQ425190	GQ425132
<i>Dictyota canariensis</i> (Grunow) Tronholm	Veracruz, Mexico	Veracruz, Mexico	KF322229	KF322228
<i>D. caribaea</i> Hörnig & Schmetter	St. Ann Parish, Jamaica	St. Ann Parish, Jamaica	EU395608	JQ061097
<i>D. ceylanica</i> Kützing	Tahiti, French Polynesia	Tahiti, French Polynesia	EU395607	GQ425122
<i>D. ciliolata</i> (Kützing) Sonder	Canary Islands, Spain	Olango Island, Philippines	GQ425192	GQ425124
<i>D. crenulata</i> J. Agardh	Baja California, Mexico	Oaxaca, Mexico	GU265782	JQ061089
<i>D. cyanoloma</i> Tronholm, De Clerck, Gomez Garreta & Rull Lluch	Canary Islands, Spain	Algarve, Portugal	GU255590	JQ061101
<i>D. cymathophila</i> Tronholm, M. Sanson & Afonso-Carrillo	Canary Islands, Spain	Canary Islands, Spain	GQ425193	GQ425128
<i>D. dhofarensis</i> (Nizamuddin) A. C. Campbell & De Clerck	Dhofar, Oman	Dhofar, Oman.	JQ061037	JQ061102
<i>D. dichotoma</i> (Hudson) J. V. Lamouroux	Walney Island, England	Languedoc-Rousillon, France	GU255542	GQ425131
<i>D. fasciola</i> (Roth) J. V. Lamouroux	Languedoc-Rousillon, France	Languedoc-Rousillon, France	FJ869847	GQ425133
<i>D. fastigiata</i> Sonder	Esperance Bay, Australia	Esperance Bay, Australia	EU395614	GQ425125
<i>D. friabilis</i> Setchell	Tahiti, French Polynesia	Saba, Netherlands Antilles	GU265786	GU290237
<i>D. grossedentata</i> De Clerck & E. Coppejans	Zanzibar, Tanzania	Zanzibar, Tanzania	JQ061043	JQ061103
<i>D. hamifera</i> Setchell	Tahiti, French Polynesia	Tahiti, French Polynesia	GQ425213	GQ425123
<i>D. humifusa</i> Hörnig, Schmetter & Coppejans	Raja Ampat, Indonesia	Gazi, Kenia	JQ061046	JQ061104
<i>D. implexa</i> (Desfontaines) J. V. Lamouroux	Provence Cassis, France	Provence Carry-le-Rouet, France	GQ466076	GQ425135
<i>D. intermedia</i> Zanardini	Lord Howe Island, Australia	Queensland, Australia	EU395615	GQ425127
<i>D. jamaicensis</i> W. R. Taylor	Punta Cana, Dominican Republic	Punta Cana, Dominican Republic	JQ061055	JQ061099
<i>D. kunthii</i> (C. Agardh) Greville	Pan de Azucar, Chile	Pan de Azucar, Chile	EU395618	GU290240
<i>Dictyota mayae</i> sp. nov.	Puerto Morelos, Quintana Roo, Mexico		KT445275	KT445273
<i>D. mediterranea</i> (Schiffner) G. Furnari	Siracusa, Italy	Sicily, Italy	GU255569	GQ290236
<i>D. mertensii</i> (Martius) Kützing	Punta Cana, Dominican Republic	Punta Cana, Dominican Republic	GQ425215	GQ425130

Continued

<i>D. naevosa</i> (Suhr) Montagne	Kwazulu-Natal, South Africa	Kwazulu-Natal, South Africa	EU395609	JQ061105
<i>D. nigricans</i> J. Agardh	Perth, Australia	Perth, Australia	JQ061068	JQ061106
<i>Dictyota pedrochei</i> sp. nov.	Punta Brava, Quintana Roo, Mexico		KT445276	KT445274
<i>D. pinnatifida</i> Kützing	St. Ann Parish, Jamaica	St. Ann Parish, Jamaica	EU395612	GQ425126
<i>D. rigida</i> De Clerck & Coppejans	Mombasa, Kenya	Mombasa, Kenya	GQ466077	GQ425138
<i>D. sandvicensis</i> Sonder	Hawaii, USA	Hawaii, USA	JQ061078	GU290239
<i>D. spiralis</i> Montagne	Madeira, Portugal	Languedoc-Roussillon, France	GQ466078	GU290235
<i>D. stolonifera</i> E. Y. Dawson	Luzon, Philippines	Zanzibar, Tanzania	GQ425222	GQ425139
<i>Rugulopteryx okamurae</i> (E. Y. Dawson) I. K. Hwang, W. J. Lee & H. S. Kim	Choshi, Japan	Languedoc-Roussillon, France	AY748322	GQ425120
<i>Scoresbyella profunda</i> Womersley	Western Australia, Australia	Western Australia, Australia	EU395620	GQ425121

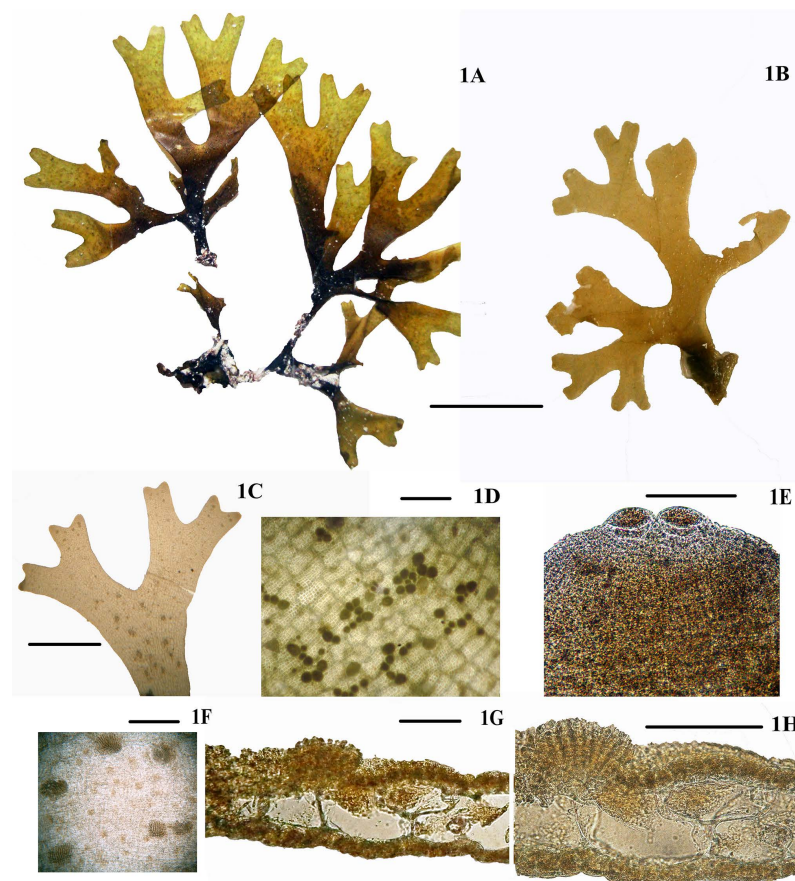


Figure 1. *Dictyota mayae* J. Lozano-Orozco & Senties sp. nov. (1) Habit of sporophyte, Puerto Morelos, Quintana Roo, designated as holotype (UAMIZ1231). Scale bar = 2 cm; (2) Sporophyte (UAMIZ1232). Scale bar = 2 cm; (3) Detail of dichotomous branching (UAMIZ1231). Scale bar = 5 mm; (4) Note sporangial zone on the surface of the thallus (UAMIZ1231). Scale bar = 500 µm; (5) Detail of the apical cells UAMIZ1231. Scale bar = 500 µm; (6) Antheridial cells of the thallus (UAMIZ1233). Scale bar = 300 µm; (7) Cross section of the middle portion of a branch (UAMIZ1233). Scale bar = 100 µm; (8) Cross section of the thallus, note spermatangia (UAMIZ1233). Scale bar = 100 µm.

Description: Thalli 22 - 40 mm long, erect, attached to the substrate by rhizoids. Sympodial and strictly dichotomous branching. Color *in situ* brown with iridescence, obtuse apices, smooth margins. Solitary or grouped sporangia in the middle of thalli. The width of the axes is uniform throughout the thalli 3 - 4 mm, apical cell protruding. Cortex unilayered, cells 40 - 43 μm long, 17 - 19 μm wide. Medulla unilayered, cells 190 - 200 μm long, 78 - 83 μm wide. Sporangia scattered singly on both thallus surfaces, dark brown. 95 - 100 μm in diameter, borne on a single stalk cells 15 - 18 μm high. Antheridia grouped in elipsoidal sori 360 - 380 μm long and 220 - 240 μm wide. The antheridia 60 - 65 μm high borne on a single stalk cell 9 - 10 μm high.

Etymology: The specific epithet honors the Mayans, a well known ethnic group in the history of southeastern Mexico and Central America.

Holotype: Voucher POK80, housed at UAMIZ under the code 1231. Material collected by J. Lozano and A. Sentíes, 12-03-2012, sporophyte.

Type locality: Puerto Morelos (18°36'22" N, 103°30'05" W), Quintana Roo, Mexican Caribbean.

Isotypes: UAMIZ1232 and UAMIZ1233.

Distribution and habitat: The species is known only from the type locality. Usually growing on coral or sand in shallow water (1 - 2 m at low tide).

***Dictyota pedrochei*:** J. Lozano-Orozco & Sentíes sp. nov. (Figures 2(A)-(F)).

Description: Thalli 40 - 50 mm long, erect, attached to the substrate by rhizoids. Sympodial and dichotomous branching to irregular. Color *in situ* dark brown. Iridescence absent, obtuse apices, smooth margins, with surface proliferations in middle segments. The width of the axes is uniform throughout the thallus 3 - 4 mm, apical cell protruding. The sporangia common on middle parts of the thallus. Cortex unilayered, cells 19 - 20 μm long, 9 - 10 μm wide. Medulla unilayered, cells 98 - 103 μm long, 55 - 60 μm wide. Sporangia scattered singly on both thallus surfaces, dark brown. 90 - 95 μm in diameter, borne on a multiple stalk cells 40 - 45 μm high.

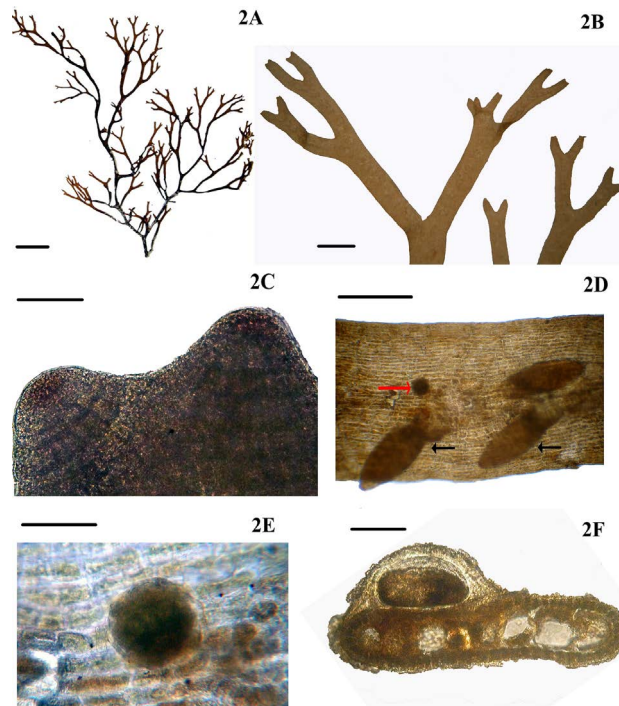


Figure 2. *Dictyota pedrochei* J. Lozano-Orozco & Sentíes sp. nov. (9) Image of sporophyte from Punta Brava, Quintana Roo, designated as holotype (UAMIZ1234). Scale bar = 1 cm; (10) Specimen from Punta Brava, Quintana Roo. Detail of dichotomy (UAMIZ1235). Scale bar = 1 mm; (11) Apical portion of thallus (UAMIZ1235). Scale bar = 150 μm ; (12) Note proliferations on the thallus and monosporangia (black arrows and red arrow, respectively; UAMIZ1235). Scale bars = 400 μm ; (13) Detail of the monosporangia. (UAMIZ1235). Scale bar = 70 μm ; (14) Monosporangia on the cortical cells in transverse sections (UAMIZ1235). Scale bar = 50 μm .

Etymology: The specific epithet honors the Mexican phycologist Francisco F. Pedroche.

Holotype: Voucher POK82, housed at UAMIZ under the code 1234. Material collected on by J. Lozano-Orozco and A. Sentías, 11-03-2012, sporophytic.

Type locality: Punta Brava (18°36'22" N, 103°30'05" W), Quintana Roo, Mexican Caribbean.

Isotype: UAMIZ1234.

Distribution and habitat: The species is known only from the type locality, growing epilithically at this locality exposed in the shallow sublittoral.

3.2. Molecular Analysis

A total of 39 sequences were analyzed (Table 1). The Maximum Likelihood and Bayesian trees obtained for each marker were similar (not shown). Additionally, a phylogenetic analysis was carried out combining the partial sequences of *psbA* and *cox1* genes of the 39 correspondent taxa, analysis of ML and IB produced highly congruent trees, differing in some positions that had poor support clades, but where the two new species are located, both analyses produced excellent support clades (Figure 3). Both new species diverged in high-uncorrected *p* distances values from the rest of the *Dictyota* representatives (>0.8% *psbA* and >11% *cox1*), confirming that these two samples constitute new taxonomic entities, or evolutionary independent lineages.

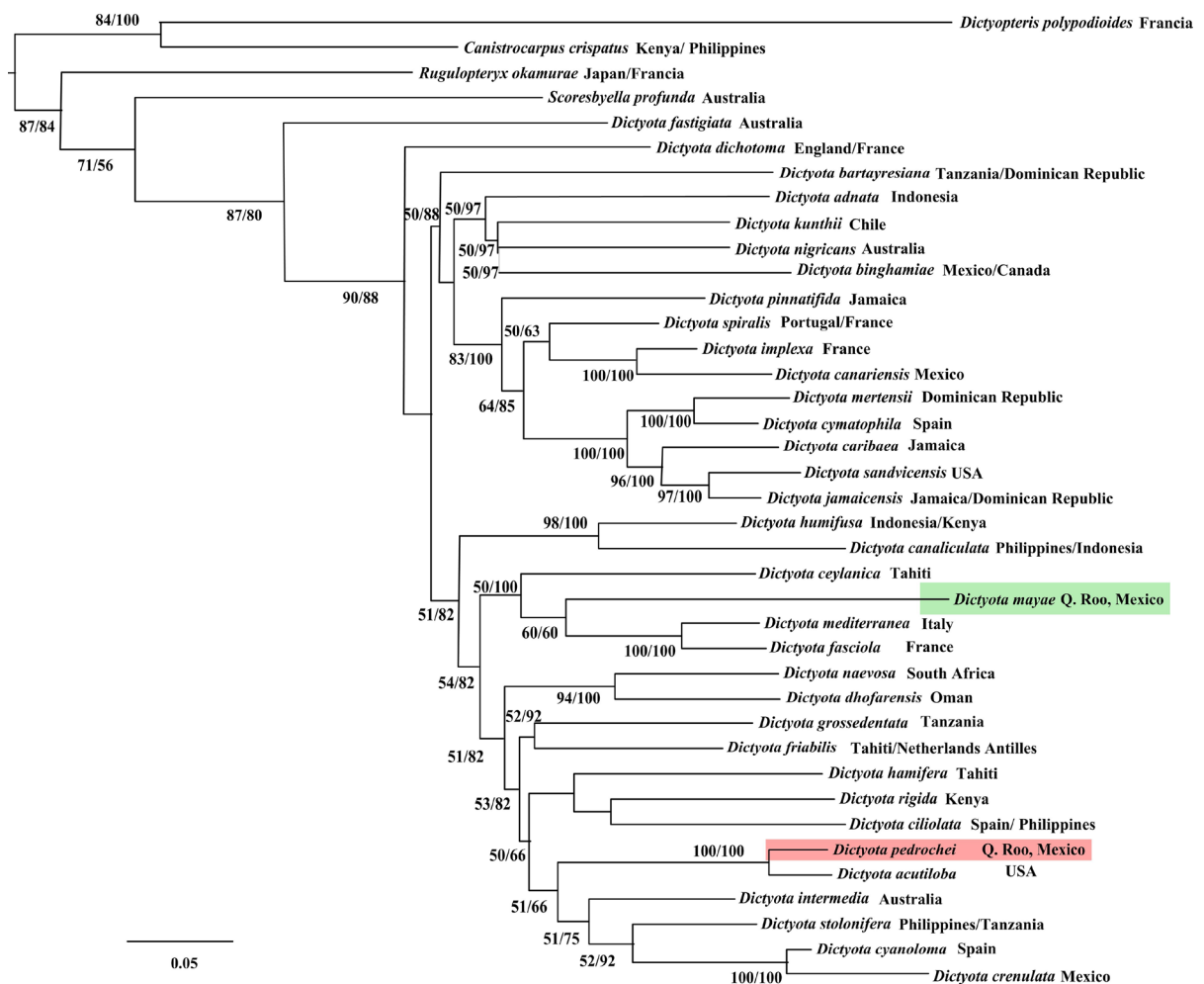


Figure 3. Phylogenetic relationship of *Dictyota* representatives based on concatenated Bayesian analysis of *psbA* and *cox1* DNA sequences. The GTR + I + G evolutionary model was used in the Bayesian Analysis, selected by a maximum-likelihood ratio test. Bayesian posterior probability (right) and ML bootstrap (left) values are indicated at the node. The localities are from the *psbA* sequences (right) and *cox1* (left); other dates are shown in Table 1.

Table 2. Morphological comparison of *D. mayae* and *D. pedrochei* with other *Dictyota* species reported for Mexican Atlantic.

	<i>D. mayae</i>	<i>D. pedrochei</i>	<i>D. hartwegiana</i>	<i>D. canariensis</i>	<i>D. caribaea</i>	<i>D. ciliolata</i>	<i>D. guineensis</i>	<i>D. hamifera</i>	<i>D. jamaicensis</i>	<i>D. menstrualis</i>	<i>D. mertensii</i>	<i>D. pinnatifida</i>	<i>D. pulchella</i>
Thallus length (cm)	2 - 4	4 - 7	5 - 20	4 - 11	20	15	30	12	12	15 - 35	20	15	10
Texture	Supple	Supple	Supple	Crisp	Crisp	Crisp	Crisp	Crisp	Crisp	Supple	Crisp	Supple	Supple
Branching	Dichotomous	Dichotomous to irregular	Dichotomous	Dichotomous	Dichotomous to irregular	Dichotomous	Dichotomous, rarely alternate	Dichotomous	Dichotomous	Dichotomous	Alternate	Alternate to irregular	Dichotomous
Habit	Erect	Erect	Erect	Erect, basal parts forming tufts	Tough, wiry, bushy.	Erect, bushy	Erect, bushy	Bushy in tangled clumps	Erect, bushy	Erect, bushy	Erect, large, bushy	Erect, bushy	Erect forming bushy tangled clumps
Iridescence	Blue-greenish	Absent	Blue and green	Sometimes blue-greenish	Absent	Sometimes yellow-greenish	Absent	Bright blue	Absent	Absent	Blue-green sheen	Absent	Green
Apices shape	Rounded	Acute	Broadly rounded	Rounded to obtuse	Acute	Rounded to acute	Acute	Blunt	Blunt	Blunt	Broadly rounded	Blunt or rounded	Blunt to pointed
Teeth	Absent	Absent	Absent	Present	Absent	Present	Absent	Absent	Present	Absent	Absent	Absent	Absent
Surface	Smooth	Smooth with leaf-like proliferations	Smooth	Smooth, leaf-like proliferations	Smooth	Smooth, sometimes leaf-like proliferations	Smooth	Smooth with lateral hooks or tendrils	Smooth	Smooth with marginal rizooids	Smooth	Smooth	Smooth with marginal rizooids
Surface hairs	Absent	Absent	Present	Absent	Present	Present	Present	Present	Present	Present	Present	Present	Present
Layers of medullary cells	Single	Single	Single	Single	Single	Single	2-4	Single	Single	Single, occasional and multiple near the base	Single	2-5	Single
Distribution	Puerto Morelos, Quintana Roo, Mexico.	Punta Brava, Quintana Roo, Mexico	Campeche, Quintana Roo, Tamaulipas, Mexico; Southern and Western Caribbean	Macaronesian Islands and Veracruz	Florida, USA; Greater Antilles, Lesser Antilles, Southern and Western Caribbean, Gulf of Mexico	Campeche, Quintana Roo, Tamaulipas, Veracruz and Yucatan, Mexico; Pantropical	Quintana Roo, Veracruz, Florida, Bahamas, Greater Antillas, Lesser Antilles, Southern and Western Caribbean, Gulf of Mexico	Cozumel, Mexico; Greater Antilles and Lesser Antilles	Campeche, Quintana Roo, Florida, Veracruz, Mexico; Greater Antilles, Lesser Antilles, Cape Verde	Campeche, Quintana Roo, Veracruz, Yucatan, Mexico; Florida, Bahamas, Greater Antilles, Lesser Antilles, Southern and Western Caribbean	Quintana Roo, Veracruz, Yucatan, Mexico; Florida, USA; Bahamas, Greater Antilles, Lesser Antilles, Southern and Western Caribbean	Quintana Roo, Yucatan, Mexico; Florida, USA; Bahamas, Greater Antilles, Lesser Antilles, Southern and Western Caribbean	Cozumel, Mexico; Florida, USA; Bahamas, Greater Antilles, Lesser Antilles, Southern and Western Caribbean
References	This study	This study	[5] [6] [28]	[13] [20]	[5] [28]	[5] [6] [20]	[5] [6] [28]	[5] [7] [28]	[5] [6] [20]	[5] [6] [20]	[5] [6] [20]	[5] [6] [20]	[5] [7] [20]

4. Discussion

4.1. Phylogenetic Analysis

Considering the problems with the identification from the majority of *Dictyota* species based solely on morphological, anatomical or reproductive characters, we performed a phylogenetic analysis based on *psbA* and *cox1* partial sequences. Two clades representing two undescribed species become apparent. These taxa, *Dictyota mayae* and *D. pedrochei*, are clearly delineated by long and highly supported branches. The divergence of *psbA* and *cox1* sequences within the new species and the other *Dictyota* species was high (>0.8% *psbA* and >11% *cox1*). We determine that are new taxonomic entities because the divergence values obtained in the *psbA* gene are within intraspecific (<1%) and interspecific limits (<7%) previously reported in the literature for Dictyotales [18] [29].

4.2. Morphological Comparison and Distribution

Table 2 shows character distribution for species previously reported, plus the two new species here proposed. The morphological comparison between *D. mayae* and the other species phylogenetically related reveal striking differences. One of the main features is that *D. mediterranea* (Schiffner) G. Furnari and *D. fasciola* (Roth) J. V. Lamouroux have a multilayered medullary layer, with no iridescence in coloration, while *D. mayae* has a single medullary layer, color *in situ* is brown, with clear iridescence. In addition, *D. fasciola* and *D. mediterranea* are distributed in the European Atlantic and Mediterranean Sea. In the case of *D. pedrochei*, it also has several discrepancies with *D. acutiloba* J. Agardh, a phylogenetically related species that has a spiraling thallus, with a height to 20 cm, tufts of hairs in centrally located irregular rows on both surfaces, while *D. pedrochei* has a flattened thallus, a height to 5 cm and, surface proliferation in the middle of thallus without hairs. Primarily, *D. acutiloba* has a greater height than that of *D. pedrochei*, which is from Mexican Caribbean while *D. acutiloba* is strictly from the Pacific Ocean.

5. Conclusion

In this study, we perform morphological and molecular analyses on several species belonging to the genus *Dictyota* with special reference to the Mexican Caribbean. Analyses of thallus construction and a concatenated matrix of two phylogenetic markers have been found successful in supporting our conclusion that *D. mayae* and *D. pedrochei* are two evolutionarily independent lineages, and consequently two different species for the science. The application of morphological and molecular tools is improving our understanding of the biodiversity in the Mexican Caribbean, and in particular, to develop a model to have a better understanding of global diversity of *Dictyota*.

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