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Erick Alves Pereira Lopes Filho

Filogenia e filogeografia de espécies de *Dictyota* Lamouroux (Dictyotales: Phaeophyceae)

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Dissertação apresentada ao Programa de Pós-Graduação em Ciências Biológicas (Biodiversidade Neotropical) da Universidade Federal do Estado do Rio de Janeiro como requisito parcial para obtenção do título de Mestre.

Orientador: Prof. Dr. Joel Campos de Paula
Co-orientador: Prof. Dr. Fabiano Salgueiro

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Dr.ª Maria Beatriz Barbosa de Barros Barreto
Universidade Federal do Rio de Janeiro

Dr.ª Valéria Cassano
Universidade de São Paulo

Dr. Joel Campos de Paula
Universidade Federal do Estado do Rio de Janeiro

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“L'homme en général ne prend intérêt qu'aux objets qui frappent ses regards, ou qu'il emploi aux divers usages de la vie. Il n'en est pas de même de l'observateur naturaliste: tout est, pour lui, sujet d'etude ou de méditation; et il voi dans le plus petit insect, dans le moindre lichen, un des anneaux de cette grande chaine dont il a plu à l'auteur de la nature de lier tout les êtres.”

(Jean Vincent Félix Lamouroux)

“The genus *Dictyota* is a prime example of […] a taxonomic nightmare”

(Olivier De clerck)

RESUMO

Dictyota J.V. Lamouroux é um gênero de algas pardas que habita ambientes tropicais a temperados quentes, com quase uma centena de espécies ao redor do globo. Apesar de sua importância ecológica e biotecnológica, a taxonomia de *Dictyota* se apresenta como desafio em razão da pouca delimitação de espécies e registros igualmente precários e duvidosos na literatura. No Brasil são reconhecidas 14 espécies de *Dictyota*, sendo a maioria delas já estudada por meio de produtos naturais, enquanto trabalhos taxonômicos e de filogenia molecular são quase inexistentes. Esta dissertação está dividida em capítulos, tendo sido o capítulo um publicado em 2017 no New Zealand Journal of Botany, e o segundo, submetido ao European Journal of Phycology. O capítulo um trata da *D. dichotoma*, espécie-tipo do gênero, que foi comumente aceita como cosmopolita por quase duzentos anos, devido à sua distribuição geográfica imprecisa, como consequência de sua identificação errônea em várias partes do mundo. Fato este, comprovado falso em trabalhos anteriores. A análise filogenética confirmou a ocorrência desta espécie na Argentina, mas não no Brasil. Por meio de análise filogeográfica, e de acordo com as correntes paleoceanográficas, a natureza introduzida de *D. dichotoma* foi indicada na Argentina e na África do Sul. O capítulo dois trata do *status* taxonômico de *D. ciliolata, D. menstrualis* e *D. plectens*. Um estudo prévio sugeriu a sinonimia entre esses táxons. Os dados químicos e moleculares do presente estudo e todas as informações disponíveis na literatura suportaram que *D. ciliolata* e *D. menstrualis* são duas espécies diferentes. Como resultado, a sinonímia é injustificável. No entanto, a ausência de mais dados da localidade-tipo de *D. plectens* impede conclusões adicionais sobre seu *status* taxonômico.

Palavras-Chaves: Dictyotaceae, Macroalgas, Espécies exóticas, Biodiversidade.

ABSTRACT

Dictyota J.V. Lamouroux is a brown algae genus that inhabits tropical to warm temperate environments and it has almost a hundred species around the globe. Despite its ecological and biotechnological importance, the taxonomy of *Dictyota* is a challenge due the poor delimitation of species and the equally poor and doubtful records in the literature. In Brazil 14 species of *Dictyota* are recognized, most of them already studied by means of natural products, while studies of taxonomy and molecular phylogenetic are almost nonexistent. This dissertation is divided into chapters, being the chapter one published in 2017 by the New Zealand Journal of Botany, and the second, submitted to the European Journal of Phycology. Chapter one is about the *D. dichotoma*, the type species of the genus, which was commonly accepted as a cosmopolitan species for almost two hundred years because of the inaccurate geographical distribution range as a consequence of its misidentification in several parts of the world. This was proved to be false by previous works. The phylogenetic analysis confirmed the occurrence of this species in Argentina, but not in Brazil. By means of phylogeographical analysis and according to paleoceanographic currents the introduced nature of *D. dichotoma* was indicated in Argentina and South Africa. Chapter two is about the taxonomical status of *D. ciliolata, D. menstrualis* and *D. plectens*. Previous study suggested the synonomy between them. The chemical and molecular data from the present study and all available information in the literature supported that *D. ciliolata* and *D. menstrualis* are two different species. As a result, the synomym is injustifiable. Nevertheless, the absence of more data from the type locality of *D.* plectens precludes further conclusions about its taxonomical status.

Keywords: Dictyotaceae, Macroalgae, Exotic species, Biodiversity

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As algas são importantes produtores primários em todos os tipos de ambientes, desde aquáticos (dulcícolas e marinhos) até terrestres (Oliveira 2003, Marinho-Soriano, Carneiro & Soriano 2009, Nassar 2012). O termo "alga" é artificial, pois abrange organismos de diversas linhagens de procariontes e eucariontes, uni a multicelulares (micro e macroalgas), cujas únicas características em comum são de possuírem clorofila *a* e apresentarem estrutura vegetativa considerada como talo, isto é, um corpo com pouca diferenciação celular ou nenhuma (Lourenço 2006, Neto & Fujii 2016).

As algas pardas (Phaeophyceae, Ochrophyta) pertencem a uma linhagem eucariótica distinta das demais macroalgas (*i.e.* reino Plantae) e são relacionadas à numerosas linhagens uni e pluricelulares, heterotróficas livre-natantes, parasitas ou semelhantes a fungos, sendo seu cloroplasto proveniente de um evento de endossimbiose secundária, ao invés de uma primária, como o das algas verdes e vermelhas (Van den Hoek, Mann & Jahns 1995, De Reviers 2010, Ruggiero *et al.* 2015a,b).

Atualmente são reconhecidas cerca de 2040 espécies de algas pardas distribuídas em 323 gêneros, por sua vez divididos em 4 subclasses (Silberfeld, Rousseau & De Reviers 2014, Guiry 2017). A classe contém organismos quase exclusivamente marinhos (poucas e mal estudadas espécies filamentosas de água doce), bentônicos (fixos ao substrato consolidado ou como epífitas ou endófitas), raros flutuantes, que ocorrem desde a zona superior do mesolitoral até o infralitoral, algumas vezes alcançando grandes profundidades de cerca de 100m (Graham & Wilcox 2000, Lourenço 2006, De Reviers 2010).

A ordem Dictyotales é a terceira mais diversa dentre as algas pardas, possui ampla distribuição ao redor do mundo e significante papel ecológico (Graham & Wilcox 2000, Bittner *et al.* 2008). Nas áreas tropicais ou subtropicais, caracterizadas por maior diversidade e dominância de macroalgas dos filos Rhodophyta e Chlorophyta, algas da família Dictyotaceae (Dictyotales) e *Sargassum* C. Agardh (Fucales) são importante componente nas comunidades bentônicas principalmente devido a sua biomassa (Abbott & Hollenberg 2001, Santelices, Bolton & Meneses 2009, Nassar, Pedrini & Nunes 2013, Gallardo 2015). No Brasil, por exemplo, Oliveira-Filho (1977) estimou que as Dictyotales corresponderiam a 51% das espécies de algas pardas do Brasil, sendo a mais importante quanto a biomassa na região nordeste.

As Dictyotales possuem tamanho moderado e são caraterizadas pelo talo laminar parenquimatoso, ereto ou prostrado, foliáceo simples, flabelado ou ramificado em forma de fitas estreitas por fendilhamento irregular ou dicotomia, em um único plano, com nervura central ou não, constituindo um ou vários eixos a partir de uma base espessada e aveluda, fixos ao substrato por rizoides filamentosos basais, às vezes em forma de tufo maciço de rizoides, por estruturas parenquimatosas cilíndricas ou por rizoides ao longo do talo, no casos de exemplares prostrados (Van den Hoek, Mann & Jahns 1995, Graham & Wilcox 2000, Abbott & Hollenberg 2001, Dawes & Mathieson 2008).

A família Dictyotaceae é a única reconhecida para a ordem Dictyotales e compreende 21 gêneros e cerca de 280 espécies (Silberfeld, Rousseau & De Reviers 2014, Guiry 2017). A elevada plasticidade morfológica (típica de algas pardas e fonte de desentendimento entre taxonomistas) é bastante pronunciada em Dictyotales, uma vez que é uma rápida resposta do genótipo a fatores, bióticos e abióticos, capaz de gerar diferentes fenótipos, porém de modo reversível (Beebee & Rowe 2008, Charrier, Bail & De Reviers 2012). As características da família e da ordem são as mesmas (Abbott & Hollenberg 2001, Dawes & Mathieson 2008).

2. O gênero *Dictyota* J.V. Lamouroux

No segundo volume de *Species plantarum*, Lineu reconheceu 14 gêneros de algas, apesar de haver briófitas, liquens e mesmo, animais, nesse total (Papenfuss 1950). Embora não tenha sido o primeiro a perceber a artificialidade dos gêneros de Lineu (Papenfuss 1950, Silva 1980), Lamouroux (1809a,b) transferiu algumas espécies de *Fucus* Linnaeus e *Ulva* Linneus para um novo gênero, *Dictyota* (do grego: *Dictyon*, rede, reticulado).

Ao longo do século XIX e do século XX, a circunscrição de suas espécies e o próprio o conceito do gênero *Dictyota* J.V. Lamouroux envolveram uma longa e problemática história taxonômica e nomenclatural. Numerosas descrições de táxons e variedades levaram à, igualmente, numerosas sinonímias, sobretudo com *Dictyota dichotoma* (Hudson) J.V. Lamouroux (Hörnig & Schnetter 1988), havendo também táxons erroneamente atribuídos à essa espécie e posteriormente reconhecidos, como *D. menstrualis* (Hoyt) Schnetter, Hörning & Weber-Peukert (Figura 1A). Além disso, as características utilizadas para distinguir *Dictyota* dos outros gêneros da antiga tribo Dictyoteae (Figura 1B), *Dilophus* J. Agardh, *Glossophora* J. Agardh, *Glossophorella* Nizamuddin & Campbell e *Pachydictyon* J. Agardh, eram compartilhadas entre as espécies desses gêneros em maior ou

menor grau, o que tornava difícil posicionar uma espécie em um gênero ou outro (De Clerck 2003).

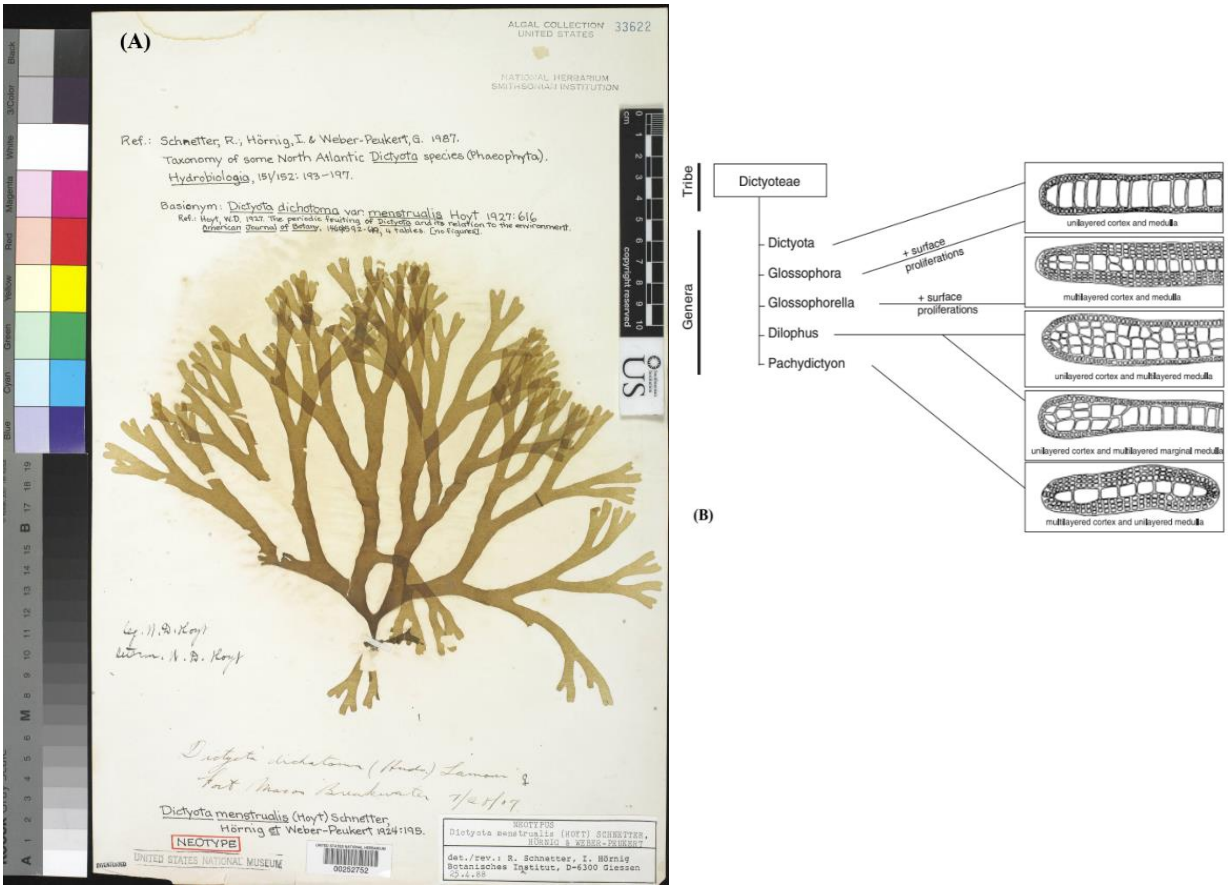

Figura 1: Exemplos de problemas taxonômicos de *Dictyota*. (A) *Dictyota menstrualis.* A intricada história da espécie é tratada brevemente nos dois capítulos desta dissertação (Imagem do neótipo do táxon enviada pelo Smithsonian Institute). (B) Representação caracteres anteriormente utilizados para diferenciar os gêneros da antiga tribo Dictyoteae (Retirado de De Clerck *et al*. 2006)

A revisão taxonômica de *Dictyota* no final do século XX, com os trabalhos de R. Schnetter e I. Hörnig no Atlântico Norte (Schnetter, Hörnig and Weber-Peukert 1987, Hörnig and Schnetter 1988, Hörnig *et al.* 1992, Hörnig, Schnetter and Prud'homme van Reine 1992), trouxe grandes mudanças no entendimento do gênero. Os autores compilaram toda a informação disponível para a região e introduziram numerosas mudanças taxonômicas baseadas em dados de cultivo, número cromossômico, conteúdo de DNA e morfometria de 18 taxa de *Dictyota* e *Dilophus*, resultando na sinonímia desses gêneros e, inclusive, na descrição de novas espécies.

Entre o final do século XX e o início do século XXI, o desenvolvimento da filogenética molecular ou sistemática molecular, com o advento da técnica da reação em cadeia da polimerase (*Polymerase Chain Reaction* - PCR), permitiu estudar as relações de ancestralidade entre espécies de acordo com os polimorfismos entre sequências de DNA através de algoritmos diversos (Ferreira & Grattapaglia 1995, Beebee & Rowe 2008, Miyaki, Russo & Pereira 2012, Russo, Miyaki & Pereira 2012). Nesse momento foram publicados os três trabalhos iniciais de filogenia molecular mais importantes em Dictyotaceae, Lee & Bae (2002), Hoshina *et al.* (2004) e Kraft *et al.* (2004), que utilizaram o 18S-rDNA (e também o *rbc*L, no caso de Lee & Bae 2002), onde verificaram que *Dictyota* e *Pachydictyon* eram estreitamente relacionados e formavam um clado irmão com *Dilophus*, ao contrário do proposto por Hörnig *et al.* (1992).

Nesse período De Clerck (2003) publicou uma extensa revisão das espécies de *Dictyota* no oceano Índico, após minuciosa re-examinação da literatura e de diversos espécimes de vários herbários. Como resultado, muitos registros de espécies foram considerados duvidosos, dezenas de exemplares foram corretamente determinados e as distribuições de muitas espécies foram alteradas. Por fim, o autor manifestou suas ressalvas na distinção entre os cinco gêneros, uma vez que as características anatômicas utilizadas para diferenciá-los (Figura 1B) eram variáveis demais e observadas, de forma sobreposta, em diversas espécies de gêneros distintos.

Em seguida, Hwang, Kim & Lee (2004) utilizaram os *loci rbc*L, *psa*A e o *psb*A do DNA do cloroplasto (cpDNA) para avaliar o status taxonônimo de *Pachydictyon coriaceum* (Holmes) Okamura. Seus resultados posicionaram a espécie entre 2 clados de *Dictyota*, levando à sua transferência para *Dictyota*. Os autores ainda observaram que a *D. coriacea* (Holmes) Wang, Kim & Lee apresentava características morfo-anatômicas de *Dictyota* e *Dilophus*, porém este último gênero aparecia como grupo irmão, assim como observado em trabalhos anteriores (Lee & Bae 2002, Hoshina *et al.* 2004, Kraft *et al.* 2004).

Por meio de uma ampla amostragem de espécies e de análises moleculares baseadas nos genes *rbc*L e 26S-rDNA, e contrariando os autores supracitados, De Clerck *et. al.* (2006) concluíram que os gêneros *Dilophus*, *Glossophora*, *Glossophorella* e *Pachydictyon* deveriam ser sinonimizados com o gênero *Dictyota*, visto que ao melhor circunscreverem *Dictyota*, como contendo espécies que apresentam esporângios nus e anterídios circundados por paráfises unicelulares hialinas, foi possível descrever dois novos gêneros: *Canistrocarpus* De Paula & De Clerck (espécies com esporângios circundados por coroa de

células corticais mais altas e anterídios circundados por paráfises multicelulares e pigmentadas) e *Rugulopteryx* De Clerck & Coppejans (espécies com esporângios circundados com coroa de células e anterídios circundados por paráfises unicelulares hialinas, além de apresentarem superfície ondulada). Esses dois gêneros abrangem cerca de uma dezena de espécies que não se agrupavam com as demais de *Dictyota* (Hwang *et al.* 2009, De Clerck *et al.* 2006).

Posteriormente, Tronholm *et al.* (2008, 2010a,b, 2012, 2013) realizaram a revisão de *Dictyota* para o Atlântico nordeste (costas atlânticas da Europa, do Mediterrâneo e da Macaronésia), incluindo novas amostras do Caribe e do Indo-Pacífico, e utilizando os genes 26S-rDNA, *rbc*L, *psb*A, *cox*1 e *nad*1. Como resultado das análises moleculares, redefiniram, revalidaram e descreveram novas espécies, incluindo *D. canariensis* (Grunow) Tronholm, *D. cyanoloma* Tronholm, De Clerck, Gómez Garreta & Rull Lluch, *D. cymatophila* Tronholm, M. Sansón & Afonso-Carrillo, *D. pleiacantha* Tronholm e *D. jamaicensis* Taylor.

Por fim, Lozano-Orozco *et al.* (2014, 2015, 2016), utilizando *psb*A e *cox*1, reportaram a ocorrência de *Dictyota canariensis* no Caribe mexicano e descreveram *Dictyota mayae* Lozano-Orozco & Sentíes, *D. pedrochei* Lozano-Orozco & Sentíes e *D. chalchicueyecanensis* Lozano-Orozco &d Sentíes.

3. Escolha do tema

No Brasil, *Dictyota* é o gênero de algas pardas mais estudado biotecnologicamente, apesar de não contemplar sua ecologia (Nassar, Pedrini & Nunes 2013, Pedrini 2013), ou mesmo sua taxonomia. Os registros mais antigos do gênero no país estão em trabalhos de ficólogos estrangeiros com materiais coletados esparsa e aleatoriamente por naturalistas e enviados para o exterior (*e.g.* Martius 1828, Martius, Eschweiler & Esenbeck 1833, Greville 1833, Dunal 1833, Montagne 1839, Martens 1870, 1871, Dickie 1874a,b,c,d, Zeller 1876, Möbius 1890, Luetzelburg 1922-23, Schmidt 1924, Howe 1928, Taylor 1930, 1931, Williams & Blomquist 1947).

Apesar do desenvolvimento da ficologia brasileira por pesquisadores nativos a partir da década de 1950 (Joly 1951, Oliveira 1951, Joly 1957), os estudos de *Dictyota* no Brasil foram basicamente inexistestes até o final do século XX, sendo as espécies do gênero apenas mencionadas em trabalhos de flora (*e.g.* Joly 1965, Yoneshigue-Braga 1970, Baptista 1977, Yoneshigue, Boudouresque & Figueiredo 1986, Széchy & Cordeiro-Marino 1991, Berchez & Oliveira 1992) e em trabalhos de dissertação e de tese, não publicados. Oliveira-

Filho (1977) em seu trabalho "Algas marinhas bentônicas do Brasil" apresenta um compilado de todo o conhecido das espécies de algas da costa brasileira até aquele momento, apresentando extenso catálogo de citações, de sinonímias de nomes e de registros duvidosos, inclusive para espécies de *Dictyota*.

No final da década de 1980 começaram a surgir os estudos de quimiotaxonomia de *Dictyota* no Brasil, ainda que em decorrência dos resultados de estudos internacionais contínuos desde a década anterior, cujo objetivo era a descoberta de novos produtos naturais e ensaios biológicos de organismos marinhos (Kelecom 1989). Nesse momento, a literatura de Dictyoteae fora do Brasil já se encontrava bastante extensa, com muitos estudos para *Dictyota* (*e.g.* Fattorusso *et al.* 1976, Faulkner *et al.* 1977, Amico *et al.* 1980, 1981, Ishitsuka, Kusumi & Kakisawa 1988).

A primeira publicação brasileira com o tema de quimiotaxonomia de Dictyotales foi produzida por Teixeira, Tomassini and Kelecom (1985). Esse estudo se consistiu de uma revisão bibliográfica, em português, e das primeiras considerações sobre a biogênese dos diterpenos (agrupados nos 3 grupos químicos) do grupo quimiotaxonômico *Dictyota* (Fenical 1980), que abrangia *Dictyota, Dilophus, Pachydictyon, Glossophora* e *Spatoglossum*. Pioneiramente, os autores propuseram a utilização dos diterpenos como marcadores taxonômicos de *Dictyota*.

No ano seguinte, Teixeira *et al.* (1986) publicaram o primeiro trabalho de quimiossistemática com material brasileiro a partir de *Canistrocarpus cervicornis* (Kütz.) De Paula & De Clerck (como *D. cervicornis* Kützing) coletada no Rio de Janeiro (RJ), observando que os produtos encontrados eram conhecidos de *D. divaricata* J.V. Lamouroux e *D. linearis* (C. Agardh) Greville do Japão e do Caribe. Outros produtos identificados de *C. cervicornis* (como *D. cervicornis*) do RJ foram publicados posteriormente (Teixeira, Tomassini & Kelecom 1986).

O uso dos diterpenos como marcadores taxonômicos do grupo *Dictyota* voltou a ser defendido por Kelecom & Teixeira (1986), Teixeira, Kelecom & Gottlieb (1987), Teixeira & Kelecom (1987) e Kelecom (1989), que realizaram as primeiras comparações dos dados químicos conhecidos para algumas espécies.

Esses trabalhos permitiram que Teixeira, Almeida & Kelecom (1990) realizassem uma abordagem quimiossistemática e biogeográfica para *D. dichotoma*, dita como cosmopolita à época, e concluissem que, do ponto de vista químico, tratava-se de um complexo de espécies morfologicamente semelhanças, porém distintas entre si.

No final do século XX, Dictyotales havia se tornado a ordem mais estudada quimicamente, dentre as algas pardas (Teixeira, Kelecom and Gottlieb 1991, Vallim *et al.* 2005). Destaca-se que no Brasil, apesar de alguns trabalhos ficoquímicos com outros gêneros da família (*e.g.* Fleury, Teixeira And Kelecom 1989, Soares *et al.* 2003, 2016, Teixeira *et al.* 2007, Gama *et al.* 2008, Domingos *et al.* 2012, Salgado *et al.* 2009), o foco dos estudos sempre foi a tribo Dictyoteae em aspectos que abrangiam da quimissistemática à ecologia química e, até mesmo, a biotecnologia (*e.g.* Cavalcanti, Bemfica and Teixeira 1998, Pereira *et al.* 2002, 2017, Barbosa *et al.* 2003, 2007, Freitas *et al.* 2007, De-Paula *et al.* 2001, De Paula *et al.* 2007, Cirne-Santos *et al.* 2006, 2008, Vallim, Teixeira and Pereira 2007, Lira *et al.* 2016, Araujo *et al.* 2017).

Não obstante, estudos taxonônimos focados em *Dictyota* permanecem quase inexistentes diante da gama de outras pesquisas realizadas. Nunes & Paula (2001) merecem ser destacados por estudarem morfologicamente as espécies de *Dictyota* ocorrentes no estado da Bahia, o primeiro estudo taxonômico do gênero no país.

Posteriormente, De Paula *et al.* (2007, 2008) descreveram *D. dolabellana* De Paula, Yoneshigue-Valentin & Teixeira para o estado da Bahia baseado em dados morfológicos e químicos. Por fim, Mesquita *et al.* (2015) publicaram o primeiro estudo combinando química de produtos naturais e biologia molecular para *D. menstrualis* (Hoyt) Schnetter, Hörnig & Weber-Peukert e *D. caribaea* Hörnig & Schnetter do Rio de Janeiro e concluíram que a segunda espécie não ocorreria no estado.

Atualmente são reconhecidas um total de 14 espécies de *Dictyota* no Brasil (Széchy & De Paula 2015), embora alguns precisem ser estudados mais detalhadamente para confirmação, como *Dictyota cuneata* Dickie; além disso, o número de nomes citados na literatura é maior do que os reconhecidos atualmente (Tabela 1), devido à, em sua maioria, se tornarem sinônimos dos nomes correntamente aceitos. O gênero possui ampla distribuição no país e, segundo a literatura, ocorre do Maranhão ao Rio Grande ao Sul (Nunes *et al.* 2013), apesar da maioria das espécies, entretanto, não possuir distribuição tão ampla (Széchy & De Paula 2015).

Tabela 1: Listagem dos táxons de *Dictyota* J.V. Lamouroux atualmente aceitos no Brasil, com a inclusão de *Canistrocarpus* De Paula & De Clerck, e seus sinônimos regionais outrora citados na literatura

Táxons atualmente aceitos para o Brasil	**Sinônimos regionais citados na literatura**
Dictyota bartayresiana J.V. Lamouroux	*Dictyota bartayresii* J.V. Lamouroux
Dictyota caribaea Hörnig & Schnetter*	*Dictyota indica* Sonder ex Kützing
Dictyota ciliolata O.G. Sond. ex Kütz.	*Dictyota ciliata* J. Agardh
Dictyota crenulata J. Agardh*	*Dictyota bartayresiana* var. *denticulata* Kützing
	Dictyota ciliolata var. *bermudensis* Taylor
Dictyota dolabellana J.C. De Paula, Yoneshigue-Valentin & V.L. Teixeira	
Dictyota friabilis Setchell	*Dictyota pfaffii* Schnetter
Dictyota guineensis (Kütz.) P. Crouan & H. Crouan	*Dictyota antigua* Sonder ex Kützing
Dictyota implexa (Desf.) J.V. Lamouroux*	
Dictyota jamaicensis W.R. Taylor	
Dictyota menstrualis (Hoyt) Schnetter, Hörnig & Weber-Peukert	*Dictyota dichotoma* (Hudson) J.V. Lamouroux
	Dictyota dichotoma var. *intricata* (C. Agardh) Greville
Dictyota mertensii (Martius) Kützing	*Dictyota brongniartii* J. Agardh
	Dictyota dentata J.V. Lamouroux
	Dictyota dentata f. *intermedia* Schmidt
	Dictyota dentata f. *mertensii* (Martius) Schmidt
Dictyota pinnatifida Kützing	*Dictyota alternans* (J. Agardh) Hörnig, Schnetter & Prud'homme van Reine
Dictyota pulchella Hörnig & Schnetter	*Dictyota divaricata* J.V. Lamouroux
	Dictyota linearis (C. Agardh) Greville
Dictyota spiralis Montagne*	
Dictyota cuneata Dickie*	
Canistrocarpus cervicornis (Kützing) De Paula & De Clerck	*Dictyota cervicornis* Kützing
	Dictyota fasciola (Roth) J.V. Lamouroux
	Dictyota pardalis Kützing
	Dictyota volubilis Kützing
Canistrocarpus crispatus (J.V. Lamouroux) De Paula & De Clerck	*Dictyota crispata* J.V. Lamouroux

*Táxons de ocorrência duvidosa pendentes de estudos detalhados

OBJETIVOS

- Estudar espécimes morfologicamente semelhantes à *Dictyota dichotoma* do Brasil e Argentina para assegurar seu *status* taxonômico e formular uma hipótese para sua origem e distribuição;
- Avaliar se a coespecificidade entre *D. ciliolata* e *D. menstrualis* proposta na literatura é sustentada à luz de novos dados de biologia molecular e produtos naturais.

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CAPÍTULO I*

* Para mais informações sobre a publicação, favor consultar o anexo da dissertação

Molecular evidence of the presence of *Dictyota dichotoma* in Argentina based on sequences from mtDNA and cpDNA and a discussion of its possible origin

Erick Alves Pereira Lopes-Filho, Fabiano Salgueiro, Silvia Mattos Nascimento, M. Cecilia Gauna, Elisa R. Parodi, Joel Campos De Paula

ABSTRACT

Dictyota is a brown alga genus inhabiting tropical to warm temperate environments where it is an important food source, shelter and substrate to several species of invertebrates and other algae. The taxonomy of this genus is troublesome, with poor species delimitation and doubtful records in the literature. *Dictyota dichotoma*, the type species of the genus, was commonly accepted as a cosmopolitan species because of the inaccurate geographical distribution range as a consequence of its misidentification in several parts of the world. Recent studies with molecular data revealed new species and a new understanding of the evolution and biogeography of the genus *Dictyota*. These studies confined populations of *D. dichotoma* to Europe (Atlantic and Mediterranean coasts) and the Macaronesian Islands (Azores, Madeira and Canary archipelagos). Also, they confirmed its presence in South Africa, but, whether the species was native or introduced in South Africa could not be verified. In the present study two regions of cpDNA (*psb*A, *rbc*L) and one region of mtDNA (*nad*1) from Argentine samples, identified morphologically as *D. dichotoma,* were analyzed and compared with other *Dictyota* species. The identity of these samples as *D. dichotoma* was confirmed. A haplotype network analysis using all available *psb*A sequences distinguished seven haplotypes divided into two geographic groups: Atlantic-Mediterranean and Canarian. In Argentina and South Africa, only the most common haplotype of the Atlantic–Mediterranean group was observed. According to the paleoceanographic currents and the presence of European haplotype, the introduced nature of *D. dichotoma* is indicated.

Keywords: Dictyotaceae; South Atlantic Ocean; Exotic Species; *psb*A; *rbc*L; *nad*1

INTRODUCTION

Dictyota J.V. Lamouroux is an important component of the marine flora in tropical and subtropical environments and is commonly found from the lower range of the intertidal

zone to deeper areas (~80m) of the subtidal zone (Littler & Littler 2000; De Clerck et al. 2006; Bittner et al. 2008). The genus has attracted the attention of researchers for several reasons, including the production of bioactive metabolites (Vallim et al. 2005; De Paula et al. 2011) and its ecological role, such as the high biomass that may be used as a food source, shelter and that serves as a substrate to several species of invertebrates and other algae (Genzano & Rodríguez 1998; Stachowicz & Hay 2000; Gauna et al. 2015; Moore & Eastman 2015), as well as the high number of species that make this genus very diverse (Tronholm et al. 2010b). The identification of *Dictyota* species may be challenging due to phenotypic plasticity, simple morphology and poor delineation between species, which is the reason for the description of hundreds of names for new taxa and doubtful geographical distributional ranges (Schnetter et al. 1987; De Clerck 2003; Tronholm et al. 2010a, 2010b; Gauna et al. 2013). In the southwestern Atlantic, the genus *Dictyota* remains understudied and the species recorded have never been the subject of a formal review, although there have been some nomenclatural corrections (Oliveira Filho 1977; Széchy & De Paula 2016).

Dictyota dichotoma (Hudson) J.V. Lamouroux was described as *Ulva dichotoma* in England in 1762 and later it was transferred to *Dictyota* in 1809 (Lamouroux 1809). During the 19th and 20th centuries, *D. dichotoma* was considered to be widely distributed from tropical to warm temperate areas of the world (Hwang et al. 2005; Tronholm et al. 2008, 2010b) and it was placed in an eurythermic group of species (Van den Hoek 1982). Tronholm et al. (2010b) reviewed the genus *Dictyota* for Europe using molecular data and a large dataset with sequences from several places of the world and they restricted the occurrence of *D. dichotoma* to the northeastern Atlantic (Europe and Africa). The specimens from other oceans, previously identified as *D. dichotoma,* were assigned to other species and so this taxon should not be considered as a cosmopolitan species. So, the native range of *Dictyota dichotoma* on the European Atlantic coasts was established, from Scotland and southern Norway to Portugal, the Mediterranean Sea and most of the Macaronesian islands, except for the tropical Cape Verde where it was not found (Van den Hoek 1982; Schnetter et al. 1987; Tronholm et al. 2010b). Despite the occurrence of *D. dichotoma* in South Africa there had been questioned by De Clerck (2003), Tronholm et al. (2010b) confirmed its presence using a *psb*A marker. This intriguing record could not be attributed to natural or introduced origin by these authors.

On the Atlantic coast of South America, there are many records of misidentification of species of *Dictyota* as *D. dichotoma* in earlier phycological studies (Saint-Hilaire 1833;

Dunal 1833; Martius et al. 1833; Montagne 1839). Recently, *D. dichotoma* has been considered as a cryptogenic species in Argentina (Gauna et al. 2015; Raffo et al. 2014; Schwindt et al. 2014).

Exotic species are one of the major threats to biodiversity and one of the major concerns throughout the oceans (Schwindt et al. 2014; Abreu et al. 2016). Invasion of marine macroalgae have been reported around the world in recent decades, such as *Undaria pinnatifida* (Harvey) Suringar, *Sargassum muticum* (Yendo) Fensholt, *Codium fragile* ssp. *fragile* (Suringar) Hariot, *Caulerpa taxifolia* (M. Vahl) C. Agardh and *Schizymenia dubyi* (Chauvin ex Duby) J. Agardh (Ramírez et al. 2002; Casas et al. 2004, 2008; Raffo et al. 2009; Irigoyen et al. 2011). Recently, Schwindt et al. (2014) sampled six of the ten main marine ports in Argentina and found the presence of 32 non-indigenous taxa, including exotic and cryptogenic taxa.

This study aims to (i) confirm the molecular identity of specimens previously identified as *Dictyota dichotoma* from Argentina and (ii) discuss the possible origin of the South Atlantic populations.

MATERIALS AND METHODS

Dictyota specimens were collected from Las Grutas, Argentina (San Matías Gulf, 40º 48' S, 64º 48' W) in 2014 from a population previously studied by Gauna et al. (2013, 2015) with respect to the morphology of the specimens, phenology and ecology (epiphytic communities). The algae were collected by SCUBA diving from the subtidal zone and then screened in the field to remove possible epiphytes. Each individual was separated into two sub-samples, one of which was preserved in silica gel for molecular studies, and the other preserved in 4% formalin solution, and deposited at the BBB - Herbarium of Universidad Nacional del Sur (Bahia Blanca, Argentina).

DNA was extracted using HiPuraTM Plant Genomic DNA Miniprep Purification Kit (MolBioTM HIMEDIA). The Plastid-encoded PSII reaction center D1 (*psb*A), NADH *dehydrogenase subunit* 1 (*nad*1) and RUBISCO large Subunit (*rbc*L) were amplified via Polymerase Chain Reaction (PCR) utilizing the primers from Tronholm et al. (2010b) and Bittner et al. (2008) and then sequenced by Macrogen Inc. Korea.

The sequences were edited on Mega 6.0 (Tamura et al. 2013) and then analyzed with others retrieved from Genbank (www.ncbi.nlm.nih.gov/genbank) (Appendix 1). Three datasets were generated with alignments of 695bp for *nad*1, 775bp for *psb*A and 1149bp for

*rbc*L. The phylogenetic reconstructions were performed for each gene separately. The concatenation would not be reliable in this case because sequences available on Genbank are from distinct vouchers and from different locations.

The evolution model of GTR+I+G was obtained by jModelTest 2.14 for each marker (Darriba et al. 2012) and then used in the Bayesian Inference (BI) analysis on MrBayes 3.1.2 (Ronquist et al. 2012). For *nad*1 and *psb*A, BI was carried out with 1 million generations in 2 runs and 4 chains, sampling every 1000th generation, discarding the first 30 and 50 trees for *nad*1 and *psb*A, respectively. For *rbc*L, BI was carried out with 2 million generations in 2 runs and 4 chains, sampling every 1000th generation, discarding the first 50 trees. The Maximum Likelihood (ML) analysis was performed on Mega 6.0, using the GTR+I+G model with bootstrap of 1000 replications.

The gene with a higher number of *Dictyota dichotoma* sequences available from Genbank was *psb*A and therefore it was used to build a haplotype network with Dnasp v.5 (Librado & Rozas 2009) and Network v.5 by Median Joining. The initial alignment used the 220 available sequences (Appendix 2). Then, the shorter sequences and those with many missing data were removed from the analysis, leaving 149 sequences. To account for the disparity in the number of sequences available from different geographic regions/localities, up to 10 sequences/haplotypes per population were used in the analysis, considering that sequences retrieved from samples collected from up to 100 km apart were considered as part of the same population. The final dataset used in the haplotype network analysis included 68 sequences with 638bp (Appendix 2).

RESULTS

The topology of the trees for *psb*A, *rbc*L and *nad*1 obtained in the present study agreed with previous studies (Tronholm et al. 2010a, 2010b). The samples from Argentina formed a clade with genuine European sequences of *D. dichotoma.* For *psb*A the clade with sequences from Argentina and from the neotype elected by Tronholm et al. (2010b) obtained bootstrap values of 100% (ML) and 1.00 (BI) (Figure 2).

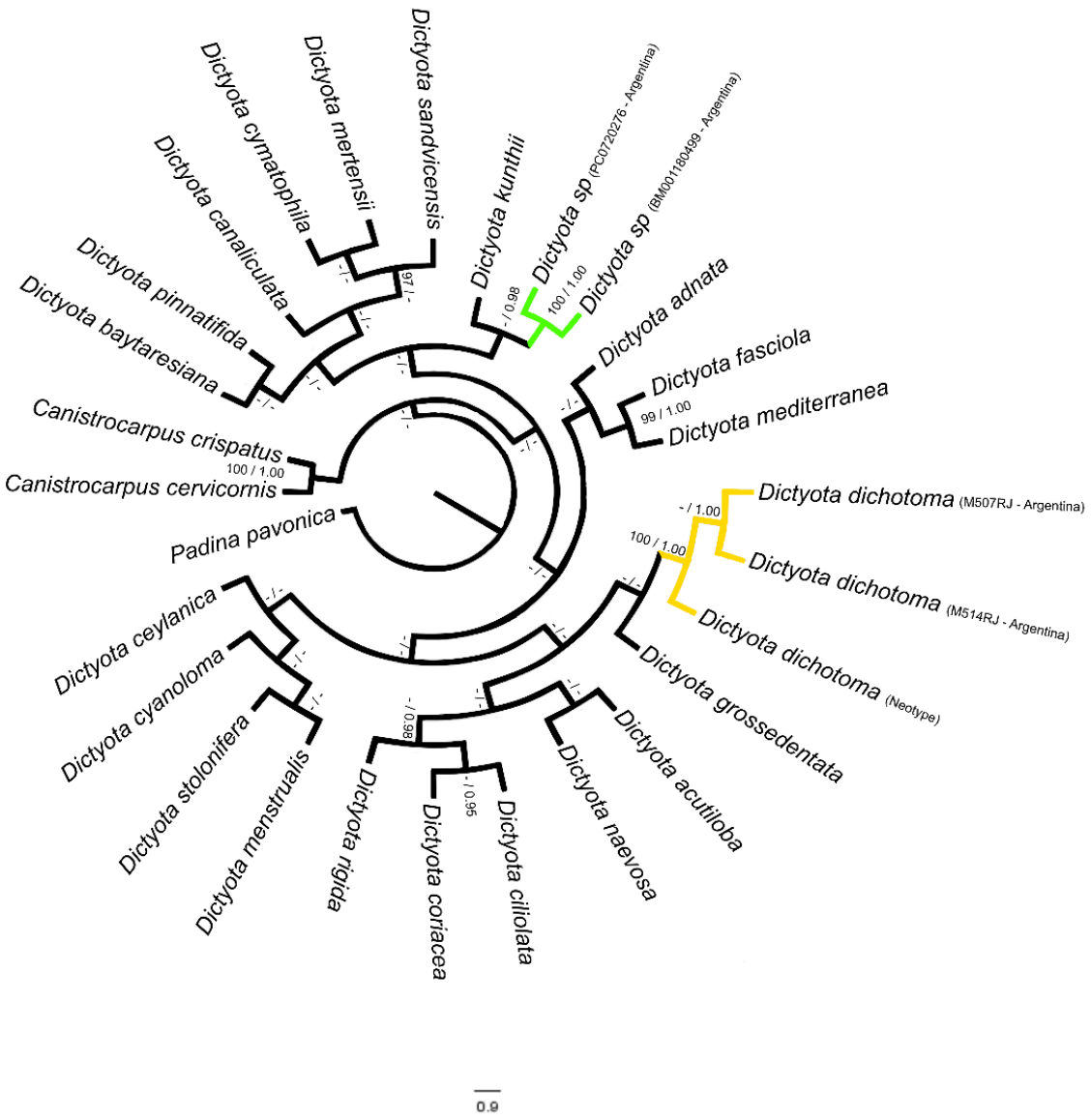

Figure 2: Phylogenetic tree based on *psb*A sequences, presenting a consensus topology estimated by Maximum Likelihood (ML) and Bayesian Inference (BI) analyses. The numbers associated with each branch represent the statistical support values (only values above 95% are shown), where the first is the bootstrap values from ML and the second is the posterior probability from BI.

For *rbc*L (Figure 3) high values of bootstrap and posterior probability were obtained for the clade with sequences from Argentina and Ireland. High values were also observed for *nad*1 (Figure 4) for the clade with sequences from Argentina and France.

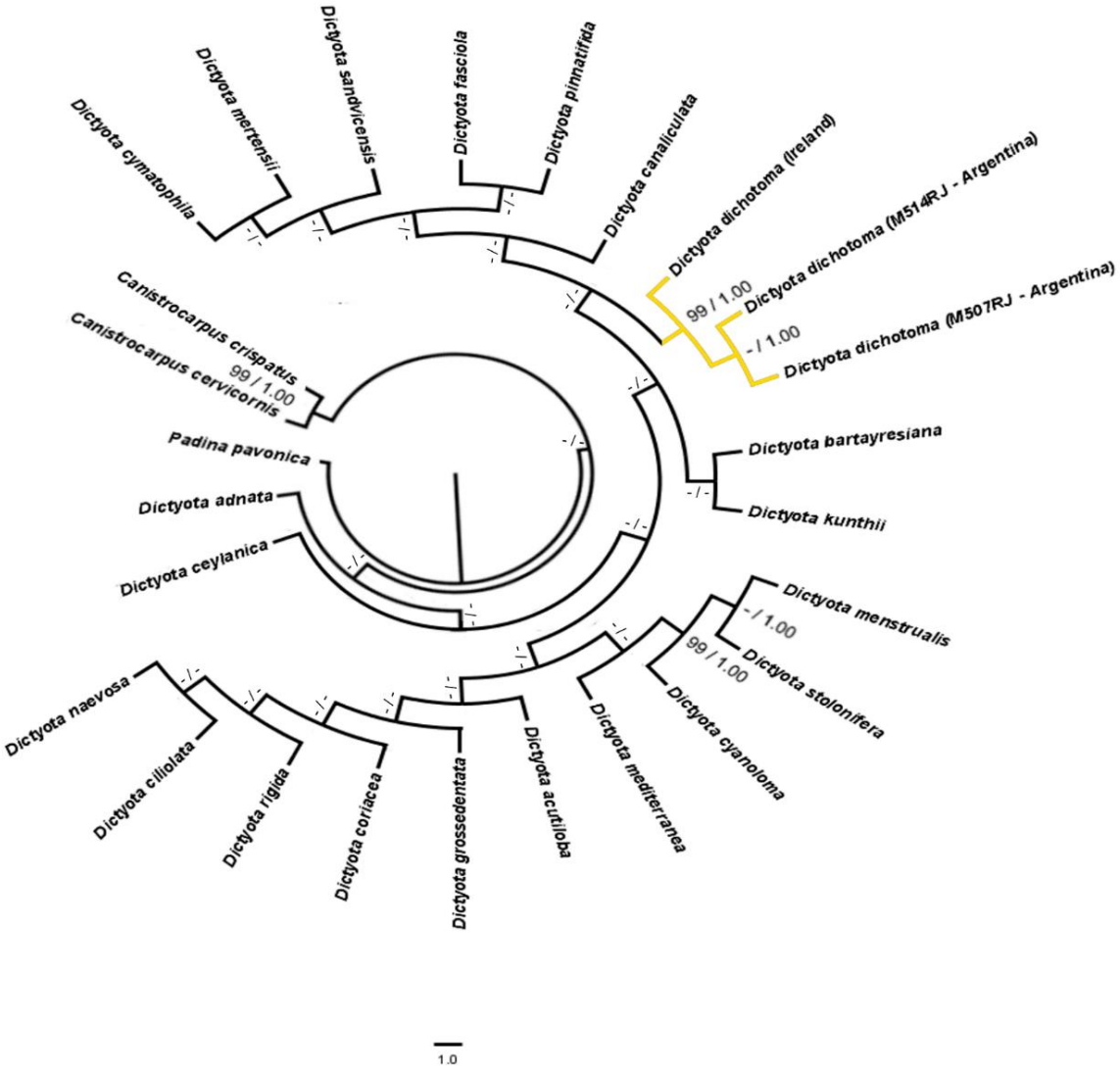

Figure 3: Phylogenetic tree based on *rbc*L sequences, presenting a consensus topology estimated by Maximum Likelihood (ML) and Bayesian Inference (BI) analyses. The numbers associated with each branch represent the statistical support values (only values above 95% are shown), where the first is the bootstrap values from ML and the second is the posterior probability from BI.

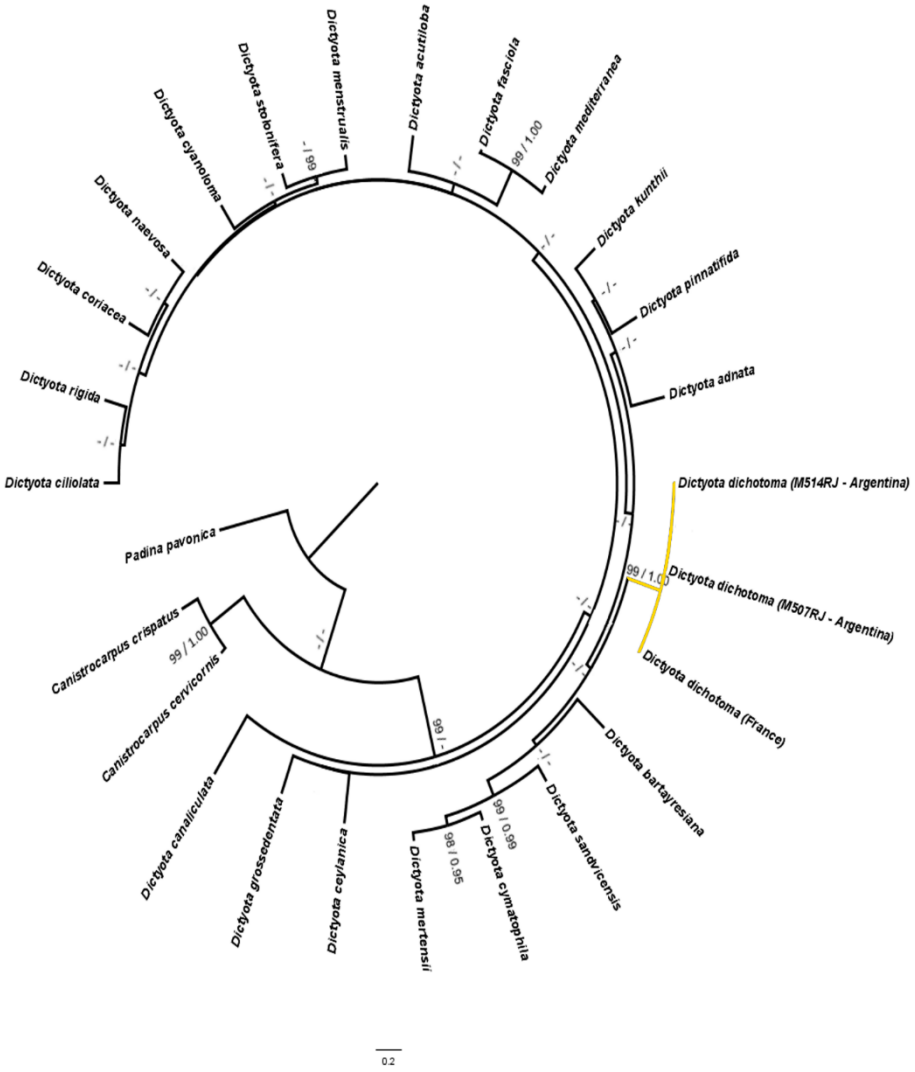

Figure 4: Phylogenetic tree based on *nad*1 sequences, presenting a consensus topology estimated by Maximum Likelihood (ML) and Bayesian Inference (BI) analyses. The numbers associated with each branch represent the statistical support values (only values above 95% are shown), where the first is the bootstrap values from ML and the second is the posterior probability from BI.

The haplotype network (Figure 5) revealed seven haplotypes in the northeast Atlantic Ocean that were geographically divided into two groups: Atlantic-Mediterranean and Canarian. The Atlantic-Mediterranean group consisted of two haplotypes, with H1 being the most widespread and present on the Atlantic coasts of the Iberian Peninsula, France, the British Islands and the North Sea, the entire Mediterranean Sea and part of the Macaronesia Islands (Azores and Madeira Archipelagos). The second haplotype (H2) seems to be less frequent in general and was only detected in the Gulf of Lion (France), in the Mediterranean Sea. Samples from Argentina and South Africa corresponded to the H1 haplotype. The

Canarian group consisted of five haplotypes (H3, H4, H5, H6 and H7) that are almost restricted to Macaronesia (Canary and Madeira Islands), whereas H5 is the most common one, widely found throughout these islands. The H3 haplotype from the Canarian group is the only one that was detected away from these islands in the Gulf of Lion.

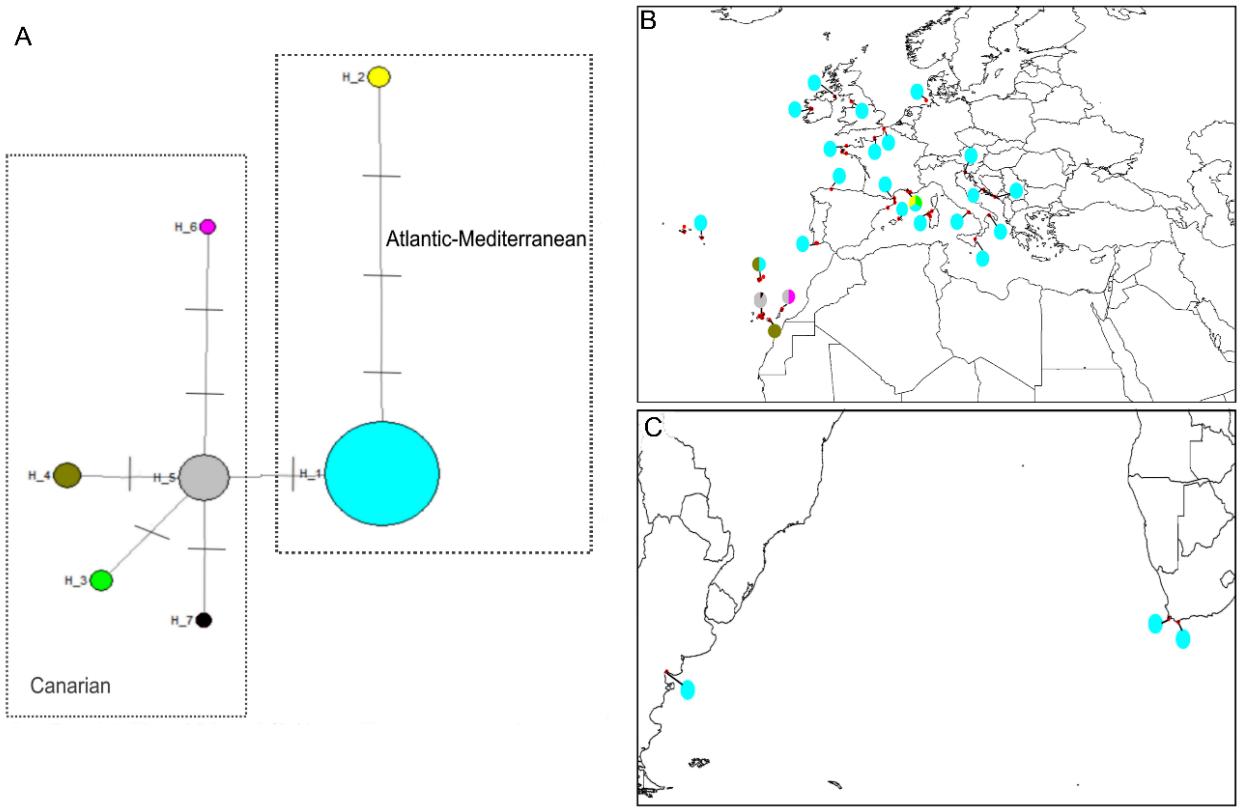

Figure 5: Haplotype diversity of *psb*A from *Dictyota dichotoma*. The red dots are the locations where the sequences of *D. dichotoma* on GenBank come from. A) Haplotype network of *psb*A showing the two groups: Atlantic-Mediterranean and Canarian. B) Distribution of the seven haplotypes in the North Atlantic population. C) South Atlantic populations with the single haplotype H1.

DISCUSSION

The higher haplotype diversity observed for *D. dichotoma* in the northeastern Atlantic (Figure 5) is consistent with the hypothesis presented by Tronholm et al. (2010b) explaining the low diversity of the genus *Dictyota* in Europe. This hypothesis states that following the desiccation of the Mediterranean Sea, which caused the extinction of most of the marine biota during the Messinian salinity crisis (6.8 - 5.3 Ma), the Mediterranean Sea was recolonized by Atlantic species from adjacent areas, such the Macaronesian Islands and the northwestern African coast when it was re-flooded (Coll et al. 2010; Tronholm et al. 2010b). The results from the present study demonstrated that European Atlantic and Macaronesian populations of *D. dichotoma* were probably separated during this vicariant

event and, later, northern populations (haplotype H1) were successful in recolonizing the Mediterranean Sea and subsequently reached Macaronesia (Azores and Madeira Archipelagos). Despite having a greater diversity, the Canarian group remained restricted to Macaronesia with the only exception of the haplotype H3, in contrast to what seems to have happened with other *Dictyota* species from Macaronesia that were able to recolonize the Mediterranean Sea (Tronholm et al. 2010b). However, the presence of the H1 haplotype in the South Atlantic would contradict this scenario.

The results of Tronholm et al. (2012), using the relaxed molecular clock for the genus, revealed *D. dichotoma* as the only extant species of one of the oldest lineages in the genus, that split early from the others circa 44.37 Ma (53-34 Ma) and being one of the first clades to disperse through the Tethys Seaway to the westernmost part of the Tethys realm, where it most likely evolved and, later dispersed to the Atlantic coast of Europe and Macaronesia. Since the opening of the South Atlantic (100 – 80 Ma) the northward paleocurrents along the African coast allowed the water transport of the Tethys sea to the Atlantic via Southern Africa while most of the transport continued on account of the circum-equatorial circulation directly to the North Atlantic until 12-18 myr (Stille 1992; Stille et al. 1996; Cowman & Bellwood 2013), when the circulation in the North Atlantic was governed by the Pacific-North Atlantic current (Iturralde-Vinent 2006). Therefore, the colonization of the South Atlantic coast of Africa by *D. dichotoma* would have been prevented because it would have been against the direction of the ocean currents.

Furthermore, there was no connection between the westernmost part of Tethys realm and South America, thereby a warm paleocurrent (probably originating in the Caribbean) crossed the Atlantic coast of South America to Patagonia and Tierra del Fuego, where the marine communities were tropical until middle-late Miocene (Del Río 2004a, 2004b; Le Roux 2012). The hypotheses of trans-oceanic dispersal in this scenario fail mainly due to biology of *D. dichotoma* demonstrated by culture experiments in which this species does not possess affinities to tropical conditions (Biebl 1959; Bogaert et al. 2016) which would be required for it to be successfully dispersed along the South American coast until the late Miocene. The adequate temperate marine conditions for *D. dichotoma* in the southwestern Atlantic were only established after the complete development of the Circumpolar Antarctic Current which lead to the full operation of the Malvinas/Falklands Current and the establishment of the Benguela Upwelling System in the Middle-Late Miocene (10 – 9 Ma). As a consequence, there was a decrease in the seawater temperature

in Patagonia and along the southwestern African coast (Heinrich et al. 2011; Rommerskirchen et al. 2011; Le Roux 2012), the extinction of the Patagonian tropical marine communities and the retraction of the warm Brazilian current to the north of Argentina/Uruguay (Del Río 2004a, 2004b). Therefore, it is difficult to explain how *D. dichotoma* would have reached the coast of Argentina through natural dispersion.

Those facts agree with the current data that do not show any exclusive haplotypes in the South Atlantic populations (Argentina and South Africa) of *D. dichotoma*, which would be expected in the case of an old dispersal from the northeastern Atlantic (over 10 myr), or any haplotype shared with the Canarian group, which would be expected in the case of a recent dispersal (less than 6 myr) and so, against the direction of the ocean currents. The occurrence of the H1 haplotype in the South Atlantic ocean is inconsistent with the hypothesis of natural dispersal with subsequent genetic differentiation and supports the hypothesis of human-mediated introduction, where propagules of *D. dichotoma* settled successfully in Argentina and in South Africa because both areas belong to temperate provinces, similar to its native area in the northeastern Atlantic (Spalding et al. 2007).

The first evidence of the presence of *D. dichotoma* in Argentina based on chemosystematics, rather than just morphology, is presented by Palermo et al. (1994) who studied a population from Nuevo Gulf and identified three prenylated diterpenes expected to occur (and its precursors) in this species (Amico et al. 1976; Fattorusso et al. 1976; Faulkner et al. 1977; Siamopoulou et al. 2004; Vallim et al. 2005). The locations where *D. dichotoma* was collected by Palermo et al. (1994) and for this study are near to two of the six main marine ports studied by Schwindt et al. (2014). These authors demonstrate that the collection areas are in natural bays with anthropic influences (but with abiotic conditions adequate for *Dictyota dichotoma,* such as salinity, surface water temperature and low environmental impact of the city) and have high maritime activities, which enable the high percentage of non-indigenous marine taxa found in them. Port areas provide artificial structures that favor the introduction of exotic fouling/benthic species (recruitment, survival and dispersal) which are mainly transported by ballast water (Schwindt et al. 2014; Abreu et al. 2016; Lin & Zhan 2016). In South Africa, most of the introduced species reported in both the cool and warm temperate provinces are from the Northern hemisphere (65%). At the Agulhas ecoregion, where the presence of *D. dichotoma* was confirmed (Tronholm et al., 2010b), 73 non-indigenous (alien, invasive or cryptogenic) taxa have been reported (Mead et al. 2011; Robinson 2015).

Introduction of exotic species may be overlooked for decades (Abreu et al. 2016), especially when a group (such as *Dictyota*) has not been formally revised. It is not clear at present how *D. dichotoma* has affected the marine species in Argentina, especially on the northern parts of the Patagonian coast where the genus *Dictyota* (reported as *D. dichotoma*) is abundant (Casas et al. 2004; Gauna et al. 2015). For example, in the Gulf of San José and nearby areas (e.g. Nuevo Gulf and San Matias Gulf) *D. dichotoma* may cover up to 30% of the entire area at depths up to 10 meters (Boraso de Zaixso & Zaixso 2007; A. Boraso pers. comm.). In the same way, the impact on native *Dictyota* species could not be estimated. Using the ecoregions proposed by Spalding et al. (2007), the known distribution of the genus *Dictyota* in Argentina (Figure 6) covers the final part of the Warm Temperate Southwestern Atlantic province and the Atlantic part of the Magallanic province.

Figure 6: Localities where *Dictyota* has been reported from Argentina (Google Earth® Image). The locations where are from the *D. dichotoma* populations discussed in this paper are marked with red stars next to their names (Map elaborated according to A. Boraso (pers.comm.); Montagne 1839; Taylor 1939; Barrales & Lobban 1975; Halperin & Wenzel 1987; Palermo et al. 1994; Boraso de Zaixso 1995; Roux et al. 1995; Eyras et al. 1998; Genzano & Rodríguez 1998; Boraso de Zaixso et al. 1999; Häder et al. 2002; Eyras & Sar 2003; Piríz et al. 2003; Casas et al. 2004; Zaixso 2004; Boraso de Zaixso & Zaixso 2007; Casas et al. 2008; Eyras et al. 2008; Storero & Gonzalez 2008; Bigatti et al. 2009; Raffo et al. 2009; Irigoyen et al. 2011; Asensi & Küpper 2012; Gauna et al. 2013; Martín et al. 2013; Becherucci et al. 2014; Gauna et al. 2015; Rabanal et al. 2014; Schwindt et al. 2014; Boraso de Zaixso et al. 2015; Bravo et al. 2015; Croce et al. 2015; Varisco et al. 2015; Zaixso et al. 2015; Becherucci & Benavides 2016; Mystikou et al. 2016).

The persistent misidentification for almost two centuries (since Montagne 1839) resulted in *D. dichotoma* being considered as the only species in Argentina and the reports of other species, such as *Canistrocarpus cervicornis* (Kützing) De Paula & De Clerck (as *Dictyota cervicornis* Kützing), *D. divaricata* J.V. Lamouroux and *D. dichotoma* var. *intricata* (C.Agardh) Greville (Taylor 1939; Asensi 1966; Van den Hoek 1982; Boraso de Zaixso 1995; Mendoza & Nizovoy 2000; Piriz et al. 2003; Croce et al. 2015), were considered as representing a wide morphological variation of it (Boraso de Zaixso 2012). Although the genus has also been found on the Beagle Channel (A. Boraso, pers. comm.), Mystikou et al. (2016) published the southernmost records of *Dictyota* in the southwestern Atlantic. Their molecular data confirmed that the species are distinct from *D. dichotoma* (as also verified in Figure 2), which is the first step towards uncovering the diversity of the genus in Argentina.

The spread of *D. dichotoma* northward along the southwestern Atlantic from the Argentine populations is unexpected because of (i) the Confluence Zone of the southward warm Brazilian current and northward cold Malvinas/Falklands current - that spans from about 25ºS to 45ºS-, where the water masses are reflected eastward as a South Atlantic current (approximate average axis at 39ºS, Bisbal 1995), and (ii) the La Plata river (at 35ºS), which results in brackish and turbid water, as well as the lack of a suitable substrate that prevents the occurrence of seagrass and marine benthic macroalgae in the La Plata estuary region, which is the reason for the depauperate flora on the Argentine, Uruguayan and Brazilian coasts under its influence (Coll & Oliveira 1999; Calliari et al. 2003; Acha et al. 2008; Braga et al. 2008; Campos et al. 2008). Additionally, the only Uruguayan record of *Dictyota* (as *D. dichotoma*) was questioned by Coll & Oliveira (1999) because no specimens were found in any of the mentioned herbaria in the original study and no other specimens have been collected subsequently. Therefore, *Dictyota* species are separated by more than 1200 km between Mar del Plata (Argentina) and Torres (Brazil) due to the lack of any hard substrate (Baptista 1977; Oliveira Filho 1977).

In the southeastern Brazil ecoregion, which includes two important Brazilian harbors, there are seasonal coastal upwelling events and the cold (< 18 ºC) water masses may reside throughout the year in a deep benthic system (Coelho-Souza et al. 2012). These waters could sustain organisms with cold waters affinities, such as the brown alga *Laminaria abyssalis* Joly & Oliveira, which occurs below 50 meters (Guimarães et al. 1986). Moreover, the intertidal *Jolyna laminarioides* Guimarães and *Elachistiella leptonematoides* Cassano, Yoneshigue-Valentin & Wynne (Valentin 2001; Cassano et al. 2004) only occur during the

upwelling period. This can promote a temporary niche for the introduction of species with cold water affinities. There is no evidence, so far, of the presence of *D. dichotoma* and most of the morphologically similar specimens are *D. menstrualis* (Hoyt) Schnetter, Hörning & Weber-Peukert (unpublished data). Recent reports of *D. dichotoma* and *D. dichotoma* var. *intricata* by Villaça et al. (2010) and Crespo et al. (2014) are due to the citation of old studies.

In conclusion, the natural dispersal of the species from the northeast Atlantic to Argentina and South Africa would be unlikely, as this temperate species would have to cross the whole equatorial and tropical Atlantic Ocean against the direction of the currents. The occurrence of a single, and the most common, haplotype of the Atlantic–Mediterranean group in the South Atlantic populations suggests that *D. dichotoma* was introduced. The human-assisted introduction of other taxa of Dictyotaceae has already been reported elsewhere, such as the cases of *Rugulopteryx okamurae* (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim (Verlaque et al. 2009), *Dictyota cyanoloma* Tronholm, De Clerck, A. Gómez-Garreta & Rull Lluc (Tronholm et al. 2010b; García et al. 2016) and *Dictyota furcellata* (C.Agardh) Greville (Nelson & Wilcox 2010). Future studies including a more comprehensive sampling are necessary and may reveal whether the introduction of *D. dichotoma* has occurred once or multiple times, its actual geographical range in Argentina and how it has affected the benthic marine community.

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Appendix 1: Sequences used on the phylogenetic analyses

Taxa	Locality	Herbarium ID	Voucher	Genbank Acession Number			References
				*psb*A	*rbc*L	*Nad*1	
Canistrocarpus cervicornis	Phillipines, Leyte Island, Municipality of Isabel, Apale	N.D.	DAP021	_	DQ472073.1	_	De Clerck et al. 2006
	Spain, Canary Islands, Tenerife Island, Punta Hidalgo	N.D.	D192	_	_	GQ425184.1	Tronholm et al. 2010
	Tanzania, Zanzibar Island, Matemwe	N.D.	TZ0714C	GQ466069.1	_	_	Tronholm et al. 2010
Canistrocarpus crispatus	Philippines, Bohol Island, Panglao	N.D.	HV721	_	GQ425119.1	_	Tronholm et al. 2010
	Philippines, Province of Negros Oriental, Dumaguete	N.D.	ODC1444	_	_	GQ425176.1	Tronholm et al. 2010
Dictyota acutiloba	Kenya, Tiwi	N.D.	ODC1545	GU265787.1	_	_	Tronholm et al. 2010
	USA, Hawaii Islands, Oahu Island, Honolulu, Ala Moana beach	N.D.	ODC888	EU395602.1	DQ472056.1	GU290247.1	Hwang et al. 2009 / Tronholm et al. 2010
Dictyota adnata	Philippines, Province of Negros Oriental, Bais	N.D.	ODC1485	GQ425188.1	_	GQ425178.1	Tronholm et al. 2010
	Indonesia, Raja Ampat Islands, Gam Island	N.D.	SD712204	_	GQ425106.1	_	Tronholm et al. 2010
Dictyota bartayresiana	Kenya, Diani Beach	N.D.	ODC1513	_	_	GQ425183.1	Tronholm et al. 2010
	Kenya, Kinondo Reef	N.D.	ODC1588	_	GQ425107.1	_	Tronholm et al. 2010
	Dominican Republic, Province of La Altagracia, Punta Cana, Playa Bávaro	N.D.	DR7	GQ425189.1	_	_	Tronholm et al. 2010
Dictyota canaliculata	Indonesia, Raja Ampat Islands, Yeffam Island	N.D.	SD712709	_	GQ425108.1	_	Tronholm et al. 2010
	Philippines, Siquijor Island, Dapdap	N.D.	ODC1477	_	_	GQ425177.1	Tronholm et al. 2010
	Indonesia, Raja Ampat Islands, Gam Island, Desa Besir	N.D.	SD712400	GQ466072.1	_	_	Tronholm et al. 2010
Dictyota ceylanica	French Polynesia, Tahiti Island, Faaa	N.D.	HV214a	_	DQ472067.1	_	Tronholm et al. 2010
	Philippines, Province of Negros Oriental, Dumaguete	N.D.	ODC1442	_	_	GQ425175.1	Tronholm et al. 2010
	French Polynesia, Tahiti Island, Faaa	N.D.	HV231a	EU395607.1	_	_	Hwang et al. 2009
Dictyota ciliolata	Spain, Canary Islands, Tenerife Island, Punta Hidalgo	N.D.	D191	_	GQ425109.1	GQ425173.1	Tronholm et al. 2010
	Spain, Canary Islands, Gran Canaria Island, Faro de Maspalomas	N.D.	D396	JX312643.1	_	_	Tronholm et al. 2012
Dictyota coriacea	Japan, Honshu Island, Shizuoka Prefecture, Yumigahama beach	N.D.	SZKIZ039	_	AB096889.1	_	Genbank
	USA, California State, Dana Point	N.D.	CSUF003	_	_	GU290251.1	Tronholm et al. 2010
	Japan, Honshu Island, Chiba Prefecture, Choshi	N.D.	JALee11	AY748323.1	_	_	Hwang et al. 2004
Dictyota cyanoloma	Portugal, Province of Algarve, City of Portimão, Praia da Rocha	N.D.	D544	_	JQ061123.1	JQ061114.1	Tronholm et al. 2012
	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS405	GU255710.1	_	_	Tronholm et al. 2010
Dictyota cymatophila	Spain, Canary Islands, Gran Canaria Islands, El Berriel	N.D.	D397	_	GQ425111.1	_	Tronholm et al. 2010

Dictyota dichotoma	Spain, Canary Islands, Tenerife Island, Punta Hidalgo	N.D.	D403	_	_	GQ425179.1	Tronholm et al. 2010
	Spain, Canary Islands, Tenerife Island, Punta Hidalgo	N.D.	D306	GQ425193.1	_	_	Tronholm et al. 2010
	Argentina, Province of Río Negro, San Antonio Oeste, San Matías Gulf, Las Grutas Beach	BBB-Gauna669	M507RJ	KY008768.1	KY012330.1	KY012327.1	This study
	Argentina, Province of Río Negro, San Antonio Oeste, San Matías Gulf, Las Grutas Beach	BBB-Gauna676	M514RJ	KY008769.1	KY012329.1	KY012326.1	This study
	Ireland, Galway County, Galway Bay, Spiddal	N.D.	IK81	_	AY527200.1	_	Hwang et al. 2004
	France, Brittany, Department of Finistère, Pointe de Mousterlin	N.D.	Cultivated	_	_	NC_007685.1	Secq et al. 2006
	England, City of Barrow-in-furness, Walney Island	N.D.	ODC1689	GU255542.1	_	_	Tronholm et al. 2010
Dictyota fasciola	France, Occitanie, Department of Pyrénées-Orientales, Port Vendres, Les Paulilles	N.D.	ODC1049	_	DQ472078.1	_	De Clerck et al. 2006
	France, Occitanie, Department of Pyrénées-Orientales, Côte Vermeille, Cerbere, Cap Peyrefitte	N.D.	ODC1065	GQ466074.1	_	GQ425172.1	Tronholm et al. 2010
Dictyota grossedentata	Tanzania, Zanzibar, Mnemba atoll	N.D.	TZ0490	JQ061043.1	JQ061125.1	JQ061116.1	Tronholm et al. 2012
Dictyota kunthii	Chile, Pan de Azúcar National Park	N.D.	Faugeron_ Chile-M1	–	DQ472057.1	–	De Clerck et al. 2006
	Chile, Pan de Azúcar National Park	N.D.	D102	EU395618.1	_	GU290250.1	Hwang et al. 2009 / Tronholm et al. 2010 / Tronholm et al. 2012
Dictyota mediterranea	Spain, Balearic Islands, Mallorca Island	N.D.	D595	_	GU290254.1	_	Tronholm et al. 2010
	Spain, Murcia, City of Cartagena, Cabo de Palos, Cala Flores beach	N.D.	Sanchez2	GU255612.1	_	_	Tronholm et al. 2010
Dictyota menstrualis	Croatia, Hvar Island	N.D.	LLGO224	_	_	GU290246.1	Tronholm et al. 2010
	Brazil, Rio de Janeiro State, City of Armação dos Búzios, Rasa beach, Ponta do Pai Vitório	HUNI 1372	JPC058	KM101060.1	KY012328.1	KY012325.1	Mesquita et al. 2015 / This study
Dictyota mertensii	Jamaica, St. Ann Parish, Drax Hall, East of St. Ann's Bay	N.D.	HV923	_	DQ472060.1	_	De Clerck et al. 2006
	Dominican Republic, Province of La Altagracia, Punta Cana, Playa Bávaro	N.D.	DR31	GQ425215.1	_	GQ425180.1	Tronholm et al. 2010
Dictyota naevosa	South Africa, Province of Kwazulu-Natal, District of Ugu, Port Edward, Palm Beach	N.D.	KZNb2345	–	–	JQ061118.1	Tronholm et al. 2012
	South Africa, Province of Kwazulu-Natal, District of uMkhanyakude, iSimangaliso Wetland Park, Mission Rocks	N.D.	KZN2241	EU395609.1	DQ472084.1	_	Hwang et al. 2009 / Tronholm et al. 2012
Dictyota pinnatifida	Venezuela, Margarita Island, El Tirano beach	N.D.	Sole3	_	GQ425115.1	_	Tronholm et al. 2010
	Jamaica, St. Ann Parish, Priory, Chris Cove	N.D.	HV932	_	_	GQ425171.1	Tronholm et al. 2010
	Dominican Republic, Province of La Altagracia, Punta Cana, Playa Bávaro	N.D.	DR6	JQ061072.1	_	_	Tronholm et al. 2012

Dictyota rigida	Kenya, Mombasa, McKenzie Point	N.D.	ODC1623	–	GQ425117.1	–	Tronholm et al. 2010
	Kenya, Mombasa, McKenzie Point	N.D.	ODC1657	GQ466077.1	–	GQ425181.1	Tronholm et al. 2010
Dictyota stolonifera	Taiwan, City of Keelung, Batouzi Harbor	N.D.	D264	–	GQ425118.1	–	Tronholm et al. 2010
	Tanzania, Zanzibar, Mnemba atoll	N.D.	TZ0488	JQ061082.1	–	GQ425182.1	Tronholm et al. 2010
Dictyota sandvicensis	USA, Hawaii Islands, Oahu Island, Lanikai	N.D.	ODC896	EU395611.1	DQ472063.1	–	Hwang et al. 2009 / Tronholm et al. 2010 / Tronholm et al. 2012
	USA, Hawaii Islands, Oahu Island, Honolulu, Ala Moana beach	N.D.	ODC889	–	–	GU290248.1	Tronholm et al. 2010
Dictyota sp	Argentina, Tierra del Fuego, Bahia Thetis	PC0720276	N.D.	KU708626.1	–	–	Mystikou et al. 2016
	Malvinas/Falklands, Isla Soledad/East Falkland, San Carlos, Playa Azul/Blue Beach	BM001180499	N.D.	KU708625.1	–	–	
Padina pavonica	France, Provence-Alpes-Côte d'Azur, Department of Alpes-Maritimes, Cannes City	N.D.	CAN2	–	AB512551.1	–	Ni-Ni-Win et al. 2011
	France, Provence-Alpes-Côte d'Azur, Department of Var, Ile des Embiez	PC0171175	FRA0509	EU681649.1	–	EU681498.1	Silberfeld et al. 2010

Appendix 2: Sequences used on haplotype network of *psb*A from *Dictyota dichotoma*. Sequences used on the final haplotype network are featured with an asterisk (*)

	Genbank Acession Number	Taxon	Locality	Herbarium ID	Voucher	Latidude	Longitude	References
*	KY008768.1	*Dictyota dichotoma*	Argentina, Province of Río Negro, San Antonio Oeste, San Matías Gulf, Las Grutas Beach	BBB-Gauna669	M507RJ	-40,8	-64,8	This study
*	KY008769.1	*Dictyota dichotoma*	Argentina, Province of Río Negro, San Antonio Oeste, San Matías Gulf, Las Grutas Beach	BBB-Gauna676	M514RJ	-40,8	-64,8	This study
	GU255768.1	*Dictyota dichotoma*	Croatia, Dubrovnik–Neretva County, City of Dubrovnik	N.D.	D662	42,641	18,104	Tronholm et al. 2010
*	GU255819.1	*Dictyota dichotoma*	Croatia, Dubrovnik–Neretva County, City of Dubrovnik	N.D.	D663	42,641	18,104	Tronholm et al. 2010
	GU255820.1	*Dictyota dichotoma*	Croatia, Dubrovnik–Neretva County, City of Dubrovnik	N.D.	D664	42,641	18,104	Tronholm et al. 2010
	GU255821.1	*Dictyota dichotoma*	Croatia, Dubrovnik–Neretva County, City of Dubrovnik	N.D.	D665	42,641	18,104	Tronholm et al. 2010
*	GU255822.1	*Dictyota dichotoma*	Croatia, Dubrovnik–Neretva County, City of Dubrovnik	N.D.	D666	42,641	18,104	Tronholm et al. 2010
	GU255827.1	*Dictyota dichotoma*	Croatia, Dubrovnik–Neretva County, City of Dubrovnik, Lapad beach	N.D.	D671	42,654	18,069	Tronholm et al. 2010
*	GU265775.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS350	43,5	16,446	Tronholm et al. 2010
	GU265776.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS376	43,5	16,446	Tronholm et al. 2010
	GU265777.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS387	43,5	16,446	Tronholm et al. 2010
	GU265778.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS388	43,5	16,446	Tronholm et al. 2010
	GU265779.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS391	43,5	16,446	Tronholm et al. 2010
	GU265780.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS397	43,5	16,446	Tronholm et al. 2010
	GU265781.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS412	43,5	16,446	Tronholm et al. 2010
*	GU255659.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS344	43,5	16,446	Tronholm et al. 2010
	GU255660.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS345	43,5	16,446	Tronholm et al. 2010
	GU255661.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS346	43,5	16,446	Tronholm et al. 2010
	GU255662.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS347	43,5	16,446	Tronholm et al. 2010
	GU255663.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS348	43,5	16,446	Tronholm et al. 2010
	GU255664.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS349	43,5	16,446	Tronholm et al. 2010
	GU255665.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS351	43,5	16,446	Tronholm et al. 2010
	GU255666.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS352	43,5	16,446	Tronholm et al. 2010
	GU255667.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS353	43,5	16,446	Tronholm et al. 2010
	GU255668.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS354	43,5	16,446	Tronholm et al. 2010
	GU255669.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS355	43,5	16,446	Tronholm et al. 2010
	GU255670.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS356	43,5	16,446	Tronholm et al. 2010
	GU255671.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS359	43,5	16,446	Tronholm et al. 2010
	GU255672.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS360	43,5	16,446	Tronholm et al. 2010
	GU255673.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS361	43,5	16,446	Tronholm et al. 2010

	GU255674.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS362	43,5	16,446	Tronholm et al. 2010
	GU255675.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS363	43,5	16,446	Tronholm et al. 2010
	GU255676.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS364	43,5	16,446	Tronholm et al. 2010
	GU255677.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS365	43,5	16,446	Tronholm et al. 2010
*	GU255678.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS366	43,5	16,446	Tronholm et al. 2010
*	GU255679.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS367	43,5	16,446	Tronholm et al. 2010
	GU255680.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS368	43,5	16,446	Tronholm et al. 2010
	GU255681.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS370	43,5	16,446	Tronholm et al. 2010
	GU255682.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS371	43,5	16,446	Tronholm et al. 2010
	GU255683.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS372	43,5	16,446	Tronholm et al. 2010
	GU255684.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS373	43,5	16,446	Tronholm et al. 2010
	GU255685.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS374	43,5	16,446	Tronholm et al. 2010
	GU255686.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS375	43,5	16,446	Tronholm et al. 2010
	GU255687.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS377	43,5	16,446	Tronholm et al. 2010
	GU255688.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS378	43,5	16,446	Tronholm et al. 2010
	GU255689.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS379	43,5	16,446	Tronholm et al. 2010
	GU255690.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS380	43,5	16,446	Tronholm et al. 2010
	GU255691.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS381	43,5	16,446	Tronholm et al. 2010
	GU255692.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS382	43,5	16,446	Tronholm et al. 2010
	GU255693.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS383	43,5	16,446	Tronholm et al. 2010
	GU255694.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS384	43,5	16,446	Tronholm et al. 2010
*	GU255695.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS385	43,5	16,446	Tronholm et al. 2010
*	GU255696.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS386	43,5	16,446	Tronholm et al. 2010
*	GU255697.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS390	43,5	16,446	Tronholm et al. 2010
*	GU255698.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS392	43,5	16,446	Tronholm et al. 2010
	GU255699.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS393	43,5	16,446	Tronholm et al. 2010
	GU255700.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS394	43,5	16,446	Tronholm et al. 2010
	GU255701.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS395	43,5	16,446	Tronholm et al. 2010
	GU255702.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS396	43,5	16,446	Tronholm et al. 2010
	GU255703.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS398	43,5	16,446	Tronholm et al. 2010
	GU255704.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS399	43,5	16,446	Tronholm et al. 2010
	GU255705.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS400	43,5	16,446	Tronholm et al. 2010
	GU255706.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS401	43,5	16,446	Tronholm et al. 2010
	GU255707.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS402	43,5	16,446	Tronholm et al. 2010
	GU255708.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS403	43,5	16,446	Tronholm et al. 2010
	GU255709.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS404	43,5	16,446	Tronholm et al. 2010
	GU255711.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS406	43,5	16,446	Tronholm et al. 2010

	GU255712.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS407	43,5	16,446	Tronholm et al. 2010
*	GU255713.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS408	43,5	16,446	Tronholm et al. 2010
	GU255714.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS409	43,5	16,446	Tronholm et al. 2010
	GU255715.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS410	43,5	16,446	Tronholm et al. 2010
	GU255716.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS411	43,5	16,446	Tronholm et al. 2010
	GU255717.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS413	43,5	16,446	Tronholm et al. 2010
	GU255718.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS414	43,5	16,446	Tronholm et al. 2010
	GU255719.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS415	43,5	16,446	Tronholm et al. 2010
	GU255720.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS416	43,5	16,446	Tronholm et al. 2010
	GU255721.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS417	43,5	16,446	Tronholm et al. 2010
	GU255722.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS418	43,5	16,446	Tronholm et al. 2010
	GU255723.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS419	43,5	16,446	Tronholm et al. 2010
	GU255724.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS420	43,5	16,446	Tronholm et al. 2010
	GU255725.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS421	43,5	16,446	Tronholm et al. 2010
	GU255726.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS422	43,5	16,446	Tronholm et al. 2010
*	GU255727.1	*Dictyota dichotoma*	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS423	43,5	16,446	Tronholm et al. 2010
*	FJ869842.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère , Pointe de Mousterlin	N.D.	FS160	47,844	-4,012	Verlaque et al. 2009
*	FJ869843.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère , Pointe de Mousterlin	N.D.	FS161	47,844	-4,012	Verlaque et al. 2009
	GU255813.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère , Pointe de Mousterlin	N.D.	FS162	47,844	-4,012	Tronholm et al. 2010
	GU255814.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère , Pointe de Mousterlin	N.D.	FS163	47,844	-4,012	Tronholm et al. 2010
	GU255809.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère, Pointe de Raz, Anse de Loc'h	N.D.	FS114	48,028	-4,635	Tronholm et al. 2010
	GU255810.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère, Pointe de Raz, Anse de Loc'h	N.D.	FS115	48,028	-4,635	Tronholm et al. 2010
	GU255811.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère, Pointe de Raz, Anse de Loc'h	N.D.	FS116	48,028	-4,635	Tronholm et al. 2010
	GU255812.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère, Pointe de Raz, Anse de Loc'h	N.D.	FS117	48,028	-4,635	Tronholm et al. 2010
	GU255531.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère , Roscoff, Ile Verte	N.D.	HEC15604	48,731	-3,989	Tronholm et al. 2010
*	GU255532.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère , Roscoff, Ile Verte	N.D.	HEC15613	48,731	-3,989	Tronholm et al. 2010
	GU255774.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère , Roscoff, Ile Verte	N.D.	FS094	48,727	-3,984	Tronholm et al. 2010
*	GU255803.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère , Roscoff, Ile Verte	N.D.	FS088	48,727	-3,984	Tronholm et al. 2010
	GU255806.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère , Roscoff, Ile Verte	N.D.	FS089	48,727	-3,984	Tronholm et al. 2010
	GU255807.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère , Roscoff, Ile Verte	N.D.	FS090	48,727	-3,984	Tronholm et al. 2010
	GU255808.1	*Dictyota dichotoma*	France, Brittany, Department of Finistère , Roscoff, Ile Verte	N.D.	FS091	48,727	-3,984	Tronholm et al. 2010
*	EU395606.1	*Dictyota dichotoma*	France, Hauts-de-France, Department of Pas-de-Calais, Point du Nid de Corbet, Audresselles	N.D.	ODC1027	50,828	1,589	Hwang et al. 2009/ Tronholm et al. 2012
*	GU255571.1	*Dictyota dichotoma*	France, Hauts-de-France, Department of Pas-de-Calais, Wimereux, Ancien Fort de Croi	N.D.	ODC1387	50,764	1,604	Tronholm et al. 2010

	GU255804.1	*Dictyota dichotoma*	France, Normandy, Department of Seine-Maritime, Etretat	N.D.	FS001	49,706	0,196	Tronholm et al. 2010
*	GU255805.1	*Dictyota dichotoma*	France, Normandy, Department of Seine-Maritime, Etretat	N.D.	FS002	49,706	0,196	Tronholm et al. 2010
*	GU255540.1	*Dictyota dichotoma*	France, Occitanie, Banyuls, Cap du Troc	N.D.	ODC1055	42,48	3,142	Tronholm et al. 2010
	GU265774.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS249	43,329	5,105	Tronholm et al. 2010
*	GU255775.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS244	43,329	5,105	Tronholm et al. 2010
	GU255776.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS250	43,329	5,105	Tronholm et al. 2010
	GU255777.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS254	43,329	5,105	Tronholm et al. 2010
	GU255778.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS255	43,329	5,105	Tronholm et al. 2010
	GU255779.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS256	43,329	5,105	Tronholm et al. 2010
	GU255780.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS258	43,329	5,105	Tronholm et al. 2010
	GU255782.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS251	43,329	5,105	Tronholm et al. 2010
	GU255783.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS253	43,329	5,105	Tronholm et al. 2010
	GU255815.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS240	43,329	5,105	Tronholm et al. 2010
*	GU255816.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS241	43,329	5,105	Tronholm et al. 2010
*	GU255817.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS242	43,329	5,105	Tronholm et al. 2010
*	GU255818.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS243	43,329	5,105	Tronholm et al. 2010
	GU255847.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS260	43,329	5,105	Tronholm et al. 2010
	GU255848.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Carry-le-Rouet, Sausset les Pins	N.D.	FS261	43,329	5,105	Tronholm et al. 2010
*	GU255793.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Cassis, Cap Canaille	N.D.	FS325	43,206	5,547	Tronholm et al. 2010
	GU255794.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Cassis, Cap Canaille	N.D.	FS326	43,206	5,547	Tronholm et al. 2010
	GU255795.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Cassis, Cap Canaille	N.D.	FS327	43,206	5,547	Tronholm et al. 2010
*	GU255796.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Cassis, Cap Canaille	N.D.	FS329	43,206	5,547	Tronholm et al. 2010
	GU255797.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Cassis, Cap Canaille	N.D.	FS330	43,206	5,547	Tronholm et al. 2010
	GU255851.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Cassis, Cap Canaille	N.D.	FS321	43,206	5,547	Tronholm et al. 2010
	GU255852.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Cassis, Cap Canaille	N.D.	FS322	43,206	5,547	Tronholm et al. 2010
	GU255854.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Cassis, Cap Canaille	N.D.	FS324	43,206	5,547	Tronholm et al. 2010
	FJ869840.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Sausset les Pins	N.D.	FS247	43,329	5,105	Verlaque et al. 2009
	FJ869841.1	*Dictyota dichotoma*	France, Provence-Alpes-Côte d'Azur, Sausset les Pins	N.D.	FS252	43,329	5,105	Verlaque et al. 2009
*	GU255538.1	*Dictyota dichotoma*	Germany, Helgoland Archipelago	N.D.	LB1676	54,181	7,885	Tronholm et al. 2010

*	GU255539.1	*Dictyota dichotoma*	Ireland, County Clare, Finavarra	N.D.	D953	53,158	-9,11	Tronholm et al. 2010
*	AY528442.1	*Dictyota dichotoma*	Ireland, Galway County, Galway Bay, Spiddal	N.D.	IK81	53,242	-9,2848	Hwang et al. 2004
*	GU255536.1	*Dictyota dichotoma*	Italy, Campania, City of Naples, Posilipo	N.D.	Kooistra2	40,794	14,193	Tronholm et al. 2010
*	GU255537.1	*Dictyota dichotoma*	Italy, Campania, Naples City, Posilipo	N.D.	Kooistra3	40,794	14,193	Tronholm et al. 2010
	GU255523.1	*Dictyota dichotoma*	Italy, Province of Catania, Sicily Island, Acicastello	N.D.	D635	37,554	15,15	Tronholm et al. 2010
*	GU255524.1	*Dictyota dichotoma*	Italy, Province of Catania, Sicily Island, Acicastello	N.D.	D637	37,554	15,15	Tronholm et al. 2010
*	GU255525.1	*Dictyota dichotoma*	Italy, Province of Catania, Sicily Island, Acicastello	N.D.	D638	37,554	15,15	Tronholm et al. 2010
*	GU255526.1	*Dictyota dichotoma*	Italy, Province of Catania, Sicily Island, Acicastello	N.D.	D639	37,554	15,15	Tronholm et al. 2010
*	GU255732.1	*Dictyota dichotoma*	Italy, Sardinia Island, Province of Oristano, Bosa Marina	N.D.	FL1205	40,287	8,474	Tronholm et al. 2010
*	GU255735.1	*Dictyota dichotoma*	Italy, Sardinia Island, Province of Sassari, Alghero City	N.D.	FL1208	40,546	8,32	Tronholm et al. 2010
	GU255736.1	*Dictyota dichotoma*	Italy, Sardinia Island, Province of Sassari, Alghero City	N.D.	FL1209	40,546	8,32	Tronholm et al. 2010
	GU255739.1	*Dictyota dichotoma*	Italy, Sardinia Island, Province of Sassari, Alghero City	N.D.	FL1212	40,546	8,32	Tronholm et al. 2010
*	GU255728.1	*Dictyota dichotoma*	Italy, Sardinia Island, Province of Sassari, Capo Caccia, Cala Dragunara, Punta del Bollo	N.D.	FL1200	40,573	8,164	Tronholm et al. 2010
	GU255729.1	*Dictyota dichotoma*	Italy, Sardinia Island, Province of Sassari, Capo Caccia, Cala Dragunara, Punta del Bollo	N.D.	FL1201	40,573	8,164	Tronholm et al. 2010
*	GU255754.1	*Dictyota dichotoma*	Italy, Sardinia Island, Province of Sassari, Castelsardo	N.D.	FL1227	40,918	8,712	Tronholm et al. 2010
*	GU255755.1	*Dictyota dichotoma*	Italy, Sardinia Island, Province of Sassari, Castelsardo	N.D.	FL1228	40,918	8,712	Tronholm et al. 2010
*	GU255756.1	*Dictyota dichotoma*	Italy, Sardinia Island, Province of Sassari, Castelsardo	N.D.	FL1229	40,918	8,712	Tronholm et al. 2010
	GU255757.1	*Dictyota dichotoma*	Italy, Sardinia Island, Province of Sassari, Castelsardo	N.D.	FL1230	40,918	8,712	Tronholm et al. 2010
	GU255758.1	*Dictyota dichotoma*	Italy, Sardinia Island, Province of Sassari, Castelsardo	N.D.	FL1231	40,918	8,712	Tronholm et al. 2010
*	GU255613.1	*Dictyota dichotoma*	Italy, Province of Taranto, Mar Piccolo	N.D.	Petrocelli1	40,437	17,211	Tronholm et al. 2010
	GU255614.1	*Dictyota dichotoma*	Italy, Province of Taranto, Mar Piccolo	N.D.	Petrocelli2	40,437	17,211	Tronholm et al. 2010
*	GU255769.1	*Dictyota dichotoma*	Italy, Province of Trieste	N.D.	DP001	45,605	13,713	Tronholm et al. 2010
	GU255520.1	*Dictyota dichotoma*	Portugal, Province of Algarve, City of Albufeira, Gale	N.D.	D541	37,077	-8,312	Tronholm et al. 2010
	GU255521.1	*Dictyota dichotoma*	Portugal, Province of Algarve, City of Albufeira, Gale	N.D.	D542	37,077	-8,312	Tronholm et al. 2010
	GU255529.1	*Dictyota dichotoma*	Portugal, Province of Algarve, Carvoeiro, A Boneca	N.D.	FAO004	37,092	-8,465	Tronholm et al. 2010
*	GU255530.1	*Dictyota dichotoma*	Portugal, Province of Algarve, Carvoeiro, A Boneca	N.D.	FAO005	37,092	-8,465	Tronholm et al. 2010
	GU255762.1	*Dictyota dichotoma*	Portugal, Azores Archipelago, Graciosa Island, Ponta Caldeirinha da Graciosa	N.D.	GRW06104	39,064	-28,067	Tronholm et al. 2010
	GU255765.1	*Dictyota dichotoma*	Portugal, Azores Archipelago, Pico Island, Manhenha	N.D.	PIX071332	38,41	-28,032	Tronholm et al. 2010
*	GU255764.1	*Dictyota dichotoma*	Portugal, Azores Archipelago, São Miguel Island, Vila Franca	N.D.	SMG03190	37,712	-25,439	Tronholm et al. 2010
*	GU255533.1	*Dictyota dichotoma*	Portugal, Madeira Archipelago, Madeira Island, City of Funchal, Cais de Carvão	N.D.	HEC15671	32,633	-16,94	Tronholm et al. 2010
	GU255528.1	*Dictyota dichotoma*	Portugal, Madeira Archipelago, Madeira Island, Ponta do Sao Lourenço	N.D.	D684	32,75	-16,734	Tronholm et al. 2010
*	GU255535.1	*Dictyota dichotoma*	Portugal, Madeira Archipelago, Madeira Island, Porto da Cruz	N.D.	HEC15818	32,773	-16,827	Tronholm et al. 2010
	GU255534.1	*Dictyota dichotoma*	Portugal, Madeira Archipelago, Porto Santos Island	N.D.	HEC15759	33,057	-16,314	Tronholm et al. 2010
*	GU255514.1	*Dictyota dichotoma*	South Africa, Western Cape Province, Cape Peninsula, Bortjesrif	N.D.	D185	-34,3967	18,4555	Tronholm et al. 2010

*	GU255527.1	*Dictyota dichotoma*	South Africa, Western Cape Province, Struisbaai	N.D.	D656	-34,794	20,06	Tronholm et al. 2010
*	GU255541.1	*Dictyota dichotoma*	Spain, Balearic Islands, Menorca Island	N.D.	ODC1688	40,02	3,78	Tronholm et al. 2010
*	GQ425208.1	*Dictyota dichotoma*	Spain, Canary Islands, Gran Canaria Island, Arinaga, Zoco del Negro	N.D.	D503	27,866	-15,384	Tronholm et al. 2010
*	GU255519.1	*Dictyota dichotoma*	Spain, Canary Islands, Gran Canaria Island, Arinaga, Zoco del Negro	N.D.	D507	27,866	-15,384	Tronholm et al. 2010
*	GQ425203.1	*Dictyota dichotoma*	Spain, Canary Islands, La Graciosa Island, Playa de las Cocinas	N.D.	D284	29,22	-13,542	Tronholm et al. 2010
*	GU255515.1	*Dictyota dichotoma*	Spain, Canary Islands, Lanzarote Island, Famara	N.D.	D272	29,119	-13,563	Tronholm et al. 2010
*	GU255516.1	*Dictyota dichotoma*	Spain, Canary Islands, Lanzarote Island, Famara	N.D.	D274	29,119	-13,563	Tronholm et al. 2010
	GU255618.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV78	28,136	-16,441	Tronholm et al. 2010
	GU255619.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV79	28,136	-16,441	Tronholm et al. 2010
	GU255620.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV80	28,136	-16,441	Tronholm et al. 2010
	GU255621.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV82	28,136	-16,441	Tronholm et al. 2010
*	GU255622.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV83	28,136	-16,441	Tronholm et al. 2010
*	GU255623.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV84	28,136	-16,441	Tronholm et al. 2010
	GU255624.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV85	28,136	-16,441	Tronholm et al. 2010
	GU255625.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV86	28,136	-16,441	Tronholm et al. 2010
	GU255626.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV87	28,136	-16,441	Tronholm et al. 2010
	GU255627.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV88	28,136	-16,441	Tronholm et al. 2010
	GU255628.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV89	28,136	-16,441	Tronholm et al. 2010
	GU255629.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV90	28,136	-16,441	Tronholm et al. 2010
	GU255630.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Abades	N.D.	ATV91	28,136	-16,441	Tronholm et al. 2010
*	GQ425204.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, La Guancha, Charco del Viento	N.D.	D297	28,401	-16,673	Tronholm et al. 2010
	GU255517.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, La Guancha, Charco del Viento	N.D.	D296	28,401	-16,673	Tronholm et al. 2010
	GU255634.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Playa de Las Arenas	N.D.	ATV98	28,371	-16,871	Tronholm et al. 2010
*	GU255635.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Playa de Las Arenas	N.D.	ATV99	28,371	-16,871	Tronholm et al. 2010
*	GU255636.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Playa de Las Arenas	N.D.	ATV100	28,371	-16,871	Tronholm et al. 2010
	GU255637.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta de Teno	N.D.	ATV101	28,341	-16,923	Tronholm et al. 2010
*	GQ425205.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	D313	28,579	-16,325	Tronholm et al. 2010
*	GQ425206.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	D314	28,579	-16,325	Tronholm et al. 2010
*	GQ425207.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	D334	28,579	-16,325	Tronholm et al. 2010
	GU255639.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV106	28,579	-16,325	Tronholm et al. 2010
	GU255640.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV107	28,579	-16,325	Tronholm et al. 2010
	GU255641.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV108	28,579	-16,325	Tronholm et al. 2010
	GU255642.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV109	28,579	-16,325	Tronholm et al. 2010
	GU255643.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV110	28,579	-16,325	Tronholm et al. 2010

	GU255644.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV111	28,579	-16,325	Tronholm et al. 2010
	GU255645.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV112	28,579	-16,325	Tronholm et al. 2010
	GU255646.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV113	28,579	-16,325	Tronholm et al. 2010
	GU255647.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV114	28,579	-16,325	Tronholm et al. 2010
	GU255648.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV115	28,579	-16,325	Tronholm et al. 2010
*	GU255649.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV116	28,579	-16,325	Tronholm et al. 2010
	GU255650.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV117	28,579	-16,325	Tronholm et al. 2010
	GU255651.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV118	28,579	-16,325	Tronholm et al. 2010
	GU255652.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV119	28,579	-16,325	Tronholm et al. 2010
	GU255653.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV120	28,579	-16,325	Tronholm et al. 2010
	GU255654.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV121	28,579	-16,325	Tronholm et al. 2010
	GU255655.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV122	28,579	-16,325	Tronholm et al. 2010
	GU255656.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV123	28,579	-16,325	Tronholm et al. 2010
	GU255657.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV124	28,579	-16,325	Tronholm et al. 2010
	GU255658.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	ATV125	28,579	-16,325	Tronholm et al. 2010
	GQ425202.1	*Dictyota dichotoma*	Spain, Canary Islands, Tenerife Island, Punta del Hidalgo	N.D.	D190	28,578	-16,328	Tronholm et al. 2010
	GU255511.1	*Dictyota dichotoma*	Spain, Catalunya, Province of Barcelona	N.D.	D973	41,331	2,173	Tronholm et al. 2010
	GU255522.1	*Dictyota dichotoma*	Spain, Catalunya, Province of Barcelona	N.D.	D624	41,331	2,173	Tronholm et al. 2010
*	GU255543.1	*Dictyota dichotoma*	Spain, Catalunya, Province of Girona, Begur, Sa Tuna	N.D.	ODC1695	41,96	3,23	Tronholm et al. 2010
*	GU255518.1	*Dictyota dichotoma*	Spain, Asturias, Municipality of Cudillero, Concha de Artedo beach	N.D.	D389	43,56549	-6,19	Tronholm et al. 2010
	GU255542.1	*Dictyota dichotoma*	United Kingdom, England, Barrow-in-furness, Walney Island	N.D.	ODC1689	54,079	-3,244	Tronholm et al. 2010
*	GU265784.1	*Dictyota dichotoma*	United Kingdom, England, Barrow-in-furness, Walney Island	N.D.	ODC1689	54,079	-3,244	Tronholm et al. 2010
*	GU255513.1	*Dictyota dichotoma*	United Kingdom, Northern Ireland, North Down, Bangor, Crawfordsburn	N.D.	D707	54,67	-5,709	Tronholm et al. 2010

CAPÍTULO II

Chemosystematics and molecular phylogenetics of *Dictyota ciliolata* (Dictyotales, Ochrophyta) and its taxonomical status

Joel Campos De-Paula, Erick Alves Pereira Lopes-Filho, Fabiano Salgueiro, Yocie Yoneshigue-Valentin, Diana Negrão Cavalcanti, Roberto Campos Villaça, Carlos Eduardo Leite Ferreira, Valéria Laneuville Teixeira

ABSTRACT

Dictyota ciliolata was recently the subject of a study that confirmed its pantropical distribution and suggested that *D. menstrualis* and *D. plectens* would be synonomyns of it by means of a molecular marker. As the molecular markers, the diterpenes may contribute to solve taxonomic problems. In this sense, the diterpenes of three Brazilian populations of *D. ciliolata* were analyzed by ^{1}H-NMR spectroscopy and HRGC-MS techniques. In addition, Brazilian specimens of *D. ciliolata* and *D. menstrualis* were compared to other *Dictyota* species in phylogenetic analyses using cpDNA (two genes) and mtDNA (one gene) sequences. Eleven diterpenes were detected: dictyol B acetate, dictyol B, dictyol C, dictyoxide, isopachydictyol A, pachydictyol A, 4β-acetoxydictyodial A, and four crenulidanes. The diterpene dictyol B acetate was the major metabolite for all. The three molecular markers placed *D. ciliolata* and *D. menstrualis* in distinct clades while the available sequences attributed to *D. plectens* placed them within *D. ciliolata*. The chemical comparison between *D. ciliolata* and *D. menstrualis* demonstrated differences between these species, while to *D. plectens* from China the skeletons identified were partially comparable to those from *D. ciliolata*. Therefore, the chemical and molecular data from the present study and all available information in the literature supported the taxonomical independence of *D. ciliolata* and *D. menstrualis*. Although the chemical and molecular data indicate a synonymy between *D. ciliolata* and *D. plectens,* the absence of more data from the type locality of *D. plectens* precludes further conclusions about its taxonomical status.

Key index words: Chemotaxonomy, Dictyotaceae, *nad*1, Natural products, Phaeophyceae, *psb*A, *rbc*L

INTRODUCTION

The genus *Dictyota* J.V. Lamouroux is well-known due to its ecological and biotechnological importance and the taxonomical difficulties of differentiating among species (Hornsey & Hide, 1974, 1976; Piazzi *et al*., 2002; Barbosa *et al.,* 2004; Cirne-Santos *et al.,* 2006, 2008; Vallim *et al.,* 2010; De Paula *et al.,* 2011; Lara-Isassi *et al.,* 2000; Fernandes *et al.,* 2014; Othmani *et al.,* 201

4; Lira *et al.,* 2016). For the last three decades, chemical studies have indicated that the diterpenes from the *Dictyota* species may have an important role as taxonomic markers (*e.g*. Kelecom & Teixeira, 1986; Teixeira & Kelecom, 1989; Teixeira *et al.,* 2001; De-Paula *et al.,* 2001, 2007*a*, 2012; Barbosa *et al.,* 2003; Vallim *et al.,* 2005; Cavalcanti *et al.,* 2006, Freitas *et al.,* 2007; Ortiz-Ramirez *et al.,* 2008), including for the description of new species (De Paula *et al.,* 2007*b*, 2008*b*).

The diterpene's biogenetic scheme (Figure 7) for compounds isolated from populations of the *Dictyota and Canistrocarpus* have been distributed into three chemical groups, depending on the first formal cyclization of the geranyl-geraniol precursor (Vallim *et al.,* 2005): those species that produce diterpenes of chemical Groups I and III (*e.g.* prenylated guaianes and xenianes respectively); species that produce exclusively diterpenes type dolabellane and its derivatives from Group IIa; and those species that produce dolastane and seco-dolastane diterpenes from Group IIb.

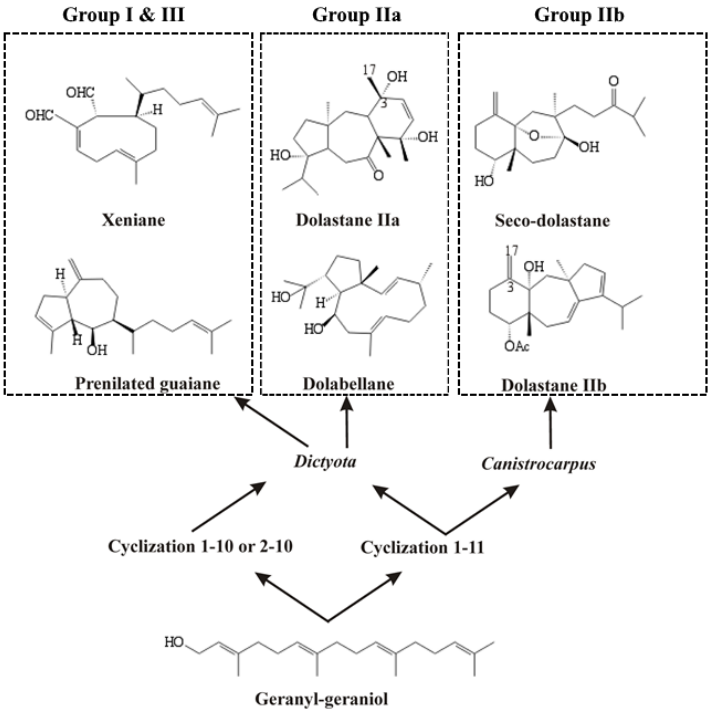

Figure 7: Hypothetical biogenetic pathways for *Dictyota* and *Canistrocarpus* diterpenes.

While diterpenes from Groups I, IIa and III are found on *Dictyota*, the diterpenes from Group IIb are restricted to the genus *Canistrocarpus* De Paula & De Clerck (Table 2).

Table 2: Chemotaxonomic Groups of *Canistrocarpus* and *Dictyota* species from Brazil*

Group I and III	Group IIa	Group IIb
Dictyota ciliolata O.G. Sond. ex Kütz.	*Dictyota pfaffii* Schnetter	*Canistrocarpus cervicornis* (Kützing) De Paula & De Clerck
Dictyota jamaicensis W. R. Taylor	*Dictyota dolabellana* De-Paula, Yoneshigue-Valentin and Teixeira	*Canistrocarpus crispatus* (J.V. Lamouroux) De Paula & De Clerck
Dictyota guineënsis (Kützing) P. Crouan & H. Crouan		
Dictyota menstrualis (Hoyt) Schnetter, Hörning & Weber-Peukert		
Dictyota mertensii (C. Martius) Kützing		

*Kelecom and Teixeira 1988; Kelecom et al. 1991; Teixeira et al. 2001; Barbosa et al. 2003, 2004; De Clerck et al. 2006; Cavalcanti et al. 2006, 2010; Freitas et al. 2007; De-Paula et al. 2001, 2007a, 2008, 2012; De Paula et al. 2007b; Oliveira et al. 2008; Ortiz-Ramirez et al. 2008

Among the producer species of diterpenes from Groups I and III, *D. ciliolata* O.G. Sond. ex Kützing stands out because of its pantropical distribution (Tronholm *et al.,* 2012), which may be interesting to bioprospection due to the biological activities of its substances (Caamal-Fuentes *et al.,* 2014; Lira *et al.,* 2016; Zubia *et al.,* 2017). Described from the Venezuelan Caribbean Sea (Kützing 1859), the species geographical distribution in the Western Atlantic ranges from the USA (North Carolina) to Brazil (Lobos Island, Rio Grande do Sul - ICN 013745). The taxonomy of this species has been troublesome for decades due to difficulties to distinguishing it from other taxa with similar habitus (Taylor, 1960; De May *et al.,* 1977), such as the dentate species *D. crenulata* J. Agardh and the smoothed margin species *D. dichotoma* (Hudson) J.V. Lamouroux and *D. menstrualis* (Hoyt) Schnetter, Hörnig & Weber-Peukert.

Recently, Tronholm *et al.* (2012, 2013) investigated the *Dictyota ciliolata-crenulata* complex by means of morphology and molecular phylogenetics, discovering the restriction of *D. crenulata* to the Mexican Pacific coast, the reinstatement of the Atlantic species *D. jamaicensis* W.R. Taylor, the raise of *D. canariensis* (Grunow) Tronholm from variety to the species level and the description of *D. pleiacantha* Tronholm. The researchers also observed that *D. ciliolata* constituted of a single lineage that included specimens identified as *D. menstrualis* (North Carolina) and *D. plectens* (Allender & Kraft) Kraft (Australia), which would result in a synonym of the latter two. In the case of *D. menstrualis*, this conclusion followed the questioning of authors such as Earle (1969) and was supported because many

forms of *D. ciliolata* ranges from clearly dentate margins (*i.e*, as the type specimens MEL 537265 and MEL 537266) to smoothed ones, and many forms of *D. ciliolata* and *D. menstrualis* can show abundant marginal proliferations, causing confusion in taxonomic determination (Taylor, 1942; Williams, 1948; Joly, 1965; Schneider & Searles, 1973; Széchy & Cordeiro-Marino, 1991, Solé & Foldats, 2003). As a result, other authors followed Tronholm *et al.* (2013) and synonymized both taxa in their works (Wynne *et al.,* 2014; Delnatte & Wynne, 2016). In the case of *D. plectens*, the possible synonym resulted from the obvious resemblance to *D. ciliolata* (as noted in the protologue by Allender & Kraft, 1983) and the molecular phylogenetic hypothesis on De Clerck *et al.* (2006).

In the present study, the diterpenes of three Brazilian populations of *D. ciliolata* were examined and the chemosystematic and phylogenetic differences among *D. ciliolata, D. menstrualis* and *D. plectens* were discussed. This way, this work contributes to the knowledge of the diversity of *Dictyota* by combing the literature records with morphological, chemical and molecular data to match the correct species identification and their correspondent bioactive compounds.

MATERIALS AND METHODS

Dictyota ciliolata was sampled during July 1999/March 2003 at Preta beach (23º00' 24" S, 44º19'05" W), Ilha Grande, city of Angra dos Reis, Rio de Janeiro state; at Itapuã beach (12º58'16" S, 38º30'39" W), city of Salvador, Bahia state; and at Atol das Rocas reef (03º51' S, 33º40' W), Rio Grande do Norte state, the only atoll in the South Atlantic. The algae were collected at depths ranging from 2 to 5 m and screening in the field to remove possible epiphytes. The algae for chemical analyses was dried at room temperature and the specimens selected as vouchers were deposited at the Herbarium of the Universidade do Estado do Rio de Janeiro (Preta beach: HRJ10415; Itapuã beach: HRJ8.846; Atol das Rocas reef: HRJ5.516). For the molecular analyses, *D. ciliolata* was sampled during August/September 2011 at Prainha beach (22° 57′ 58″ S, 42° 1′ 44″ W), city of Arraial do Cabo, Rio de Janeiro State, and *D. menstrualis* was sampled in December 2011 at Ponta do Pai Vitório (22° 43' 59" S, 41° 57' 26" W) and Forno beach (22° 45' 42" S, 41° 52' 32" W), city of Armação dos Búzios, Rio de Janeiro state, and in February 2014 at São Pedro and São Paulo Archipelago/ St. Paul's Rocks (0° 55' 01" N, 29° 20' 44" W). Each individual specimen was separated in the field into two sub-samples: the first was preserved in silica gel and the other of which was preserved in 4% formalin solution. Vouchers were deposited

at the Herbarium of the Universidade Federal do Estado do Rio de Janeiro (Prainha beach: HUNI 5010, HUNI 5011; Ponta do Pai Vitório: HUNI 1372; Forno beach: HUNI 1371; São Pedro and São Paulo Archipelago: HUNI 3215).

1 - Chemical analysis

The air-dried *D. ciliolata* (100 g each, dry weight) was extracted with acetone (100%) at room temperature. Evaporation of the solvent under reduced pressure yielded the crude extract as a brownish residue. The crude extract of the Atol das Rocas and Angra dos Reis specimens (1 g) were subjected to silica gel column chromatography eluted with *n*-hexane/ethyl acetate to give a total of 55-60 fractions each. The fractions yielded three compounds, the major being identified as dictyol B acetate (Figure 8, product **1**), with isopachydictyol A (Figure 8, product **5**) and pachydictyol A (Figure 8, product **6**) as minor components. The identification of diterpenes **1**, **5** and **6** was based on the comparison of Proton Nuclear Magnetic Resonance (^{1}H-NMR) spectroscopic data with literature values (Cavalcanti *et al.,* 2006, 2008). The crude extract from Itapuã (Salvador, BA) was analyzed using only the HRGC-MS technique.

The amounts were diluted in Ethyl Acetate (EtOAc) and analyzed by High Resolution Gas Chromatography coupled to Mass Spectrometry (HRGC-MS) on a HP 6890 series GC system, coupled to a HP 5973 mass selective detector set to the electron impact mode (70 eV), equipped with an HP-1 MS capillary column (30 m x 0.25 mm; film thickness 0.25 μm). Injector and detector temperatures were set at 270ºC and 290ºC, respectively. The temperature program was kept at 160ºC, then programmed to 260ºC at a rate of change of 4ºC/min and finally raised at a rate of 15ºC/min to 290ºC for 15 min. Hydrogen at a flow rate of 1 mL/min was used as the carrier gas. Diluted samples were injected manually in split mode (1/10). The chemical components were identified based on comparisons of their mass spectra data with data found in standards and/or literature data, by co-injecting these samples in the HRGC, and from Wiley 275 library data of the HRGC-MS system.

All solvents were HPLC grade. Analytical Thin-layer chromatography (TLC) separations were carried out on Merck silica gel 60 F-254 (0.2 mm) percolated aluminum plates. Once developed, the plates were visualized by spraying them with 2% ceric sulphate in sulfuric acid, followed by gentle heating. Silica gel 60 (Merck, 70-230 and 230-400 mesh) was used for column chromatography. ^{1}H-NMR spectra were recorded in deuterated

chloroform (CDCl3 100% Aldrich) on a Varian Unity Plus 300 spectrometer using tetramethyl silane (TMS) as an internal standard.

2 – Molecular analysis

The genomic DNA was extracted using a HiPurA^{TM} Plant Genomic DNA Miniprep Purification Kit (MolBioTM HIMEDIA). Two regions from cpDNA and one from mtDNA were amplified via the Polymerase Chain Reaction (PCR) utilizing the primers from the literature (Bittner *et al.,* 2008; Tronholm *et al.,* 2010): the Plastid-encoded PSII reaction center D1 (*psb*A), the RUBISCO large Subunit (*rbc*L) and the NADH *dehydrogenase subunit* 1 (*nad*1). The products were purified and sequenced by Macrogen Inc., Korea.

The sequences were edited and aligned by ClustalW on Mega 7.0 (Kumar *et al.,* 2016) and then analyzed with others retrieved from Genbank (www.ncbi.nlm.nih.gov/genbank). As the sequences available through Genbank are from distinct vouchers and from different locations, the three genes were not concatenated, and so, the phylogenetic reconstructions for the three datasets (with alignments of 685bp for *nad*1, 698bp for *psb*A and 1121bp for *rbc*L) were performed for each gene separately (Appendix 3).

The evolution model of GTR+I+G was obtained using jModelTest 2.14 for each marker (Darriba *et al.,* 2012) and analysed for BI (Bayesian inference) and ML (Maximum Likelihood). The BI analysis was performed on MrBayes 3.1.2 (Ronquist *et al.,* 2012) using two parallel runs (each consisting of four chains) with three million generations. The sampling took place every 3000th generation, and the first 100 trees were discarded. The ML was performed on Mega 7.0 with a bootstrap of 1000 replications.

RESULTS

The three populations of Brazilian *D. ciliolata* furnished eleven different diterpenes, of which six belonged to group I and five to group III (Table 3 and Figure 8). The extract from *D. ciliolata* collected in Angra dos Reis yielded four prenylated guaiane diterpenes, one xeniane and four crenulidanes (Table 3). In this extract was observed small amounts (traces) of other crenulidane diterpenes. In the extract from Salvador three prenylated guaianes and four crenulidanes were detected, while in the samples of Atol das Rocas six prenylated guaianes, one xeniane and four crenulidanes were detected (Table 3). The crenulidane diterpenes (Figure 8, products **10-13**) were identified using HRGC-MS and ^{1}H-NMR conjugated techniques.

Table 3: Diterpenes detected from *D. ciliolata* and *D. menstrualis*.

Identified compounds	*Dictyota ciliolata*				*Dictyota menstrualis*		
	Preta beach, Ilha Grande, Angra dos Reis, RJ (Brazil)[b]	Itapuã beach, Salvador, BA (Brazil)[b]	Atol das Rocas reef, RN (Brazil)[b]	Radio Island, Beaufort, NC (USA)[a]	Radio Island, Beaufort, NC (USA)	Rasa beach, Armação dos Búzios, RJ, (Brazil)	São Pedro and São Paulo Archipelago (Brazil)
		present study		Cronin et al. (1995) Cronin and Hay (1996)	Cronin et al. (1995) Taylor et al. (2003)	Ortiz-Ramírez et al (2008)	Ortiz-Ramírez et al (2008)
Long. Lat.	23º00'24" S, 44º19'05" W	12º58'16" S, 38º30'39" W	03º51' S, l33º40' W	34º 42' 39" N, 76º 40' 74" W	34º 42' 39" N, 76º 40' 74" W	22º 44' 49" S, 41º 52' 54" W	00º 55' N, 29º 21' W
Dictyol B acetate (**1**)	XX	XX	XX	XX			
Dictyol B (**2**)	Tr		X				
Dictyol C (**3**)	X		X			X	X
Dictyoxide (**4**)			X			tr	
Isopachydictyol A (**5**)		X	X			X	X
Pachydictyol A (**6**)	X	X	X	X	X	X	X
Dictyodial (**7**)				X	X		
4β-Acetoxydictyodial (**8**)	X		X				
4β-Hydroxy-dictyodial A (**9**)					X		
Crenulidanes (**10-13**)	Tr	X	X				
Dictyotadiol (**14**)					X	X	X
Dictyol E (**15**)					XX		X
18-*O*-Dihydro-4β-hydroxydictyodial A 18 acetate (**16**)					X		
9-Hydroxy-dichotoma-2,13-diene-16,17-dial (**17**)						XX	X
9-Acetoxy-dichotoma-2,13-diene-16,17-dial (**18**)						X	X
5-Hydroxy-1,6-cycloxenia-2,13-diene-16,17-dial (**19**)						X	X
5-Acetoxy-1,6-cycloxenia-2,13-diene-16,17-dial (**20**)						X	X

[a]Diterpenes isolated and identified by spectroscopic methods (UV, IR, NMR and MS).[b]Diterpenes detected by GC/MS and confirmed by NMR spectra. Diterpenes 1, 5 and 6 were isolated and identified by NMR spectra. XX correspond to an abundance of more than 10% of the total diterpenes), X correspond to an abundance of more than 1% of the total diterpenes; tr = trace amonts

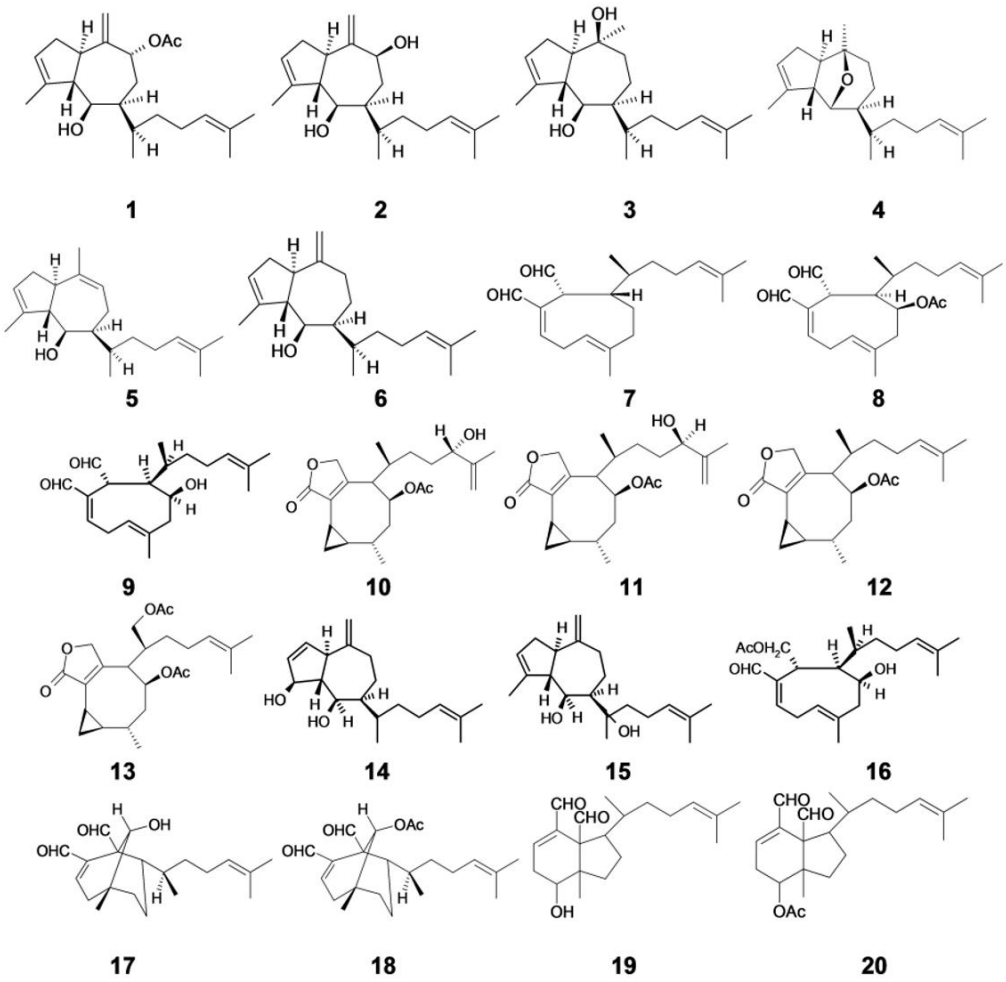

Figure 8: Diterpenes detected from *D. ciliolata* and *D. menstrualis*.

The topology of the trees for *psb*A (Figure 9A), *rbc*L (Figure 9B), and *nad*1 (Figure 10) placed *D. ciliolata* and *D. menstrualis* on distinct clades. For *psb*A *D. ciliolata* sequences from Brazil (individuals with smoothed margin and sparsely minute dentate margin) and from several other places grouped in a single clade with bootstrap values of 100% (ML) and 1.00 (BI). Despite that the clade appeared to be a sister group of *D. coriacea* for *psbA* (Figure 9A), this relation to the other two genes was not clear (Figures 9B and 10). For *rbc*L and *nad*1, Brazilian *D. ciliolata* specimens were grouped with specimens from the Canary Islands and the Philippines with high values of bootstrap and posterior probability. For the three genes *D. ciliolata* was distinct from other dentate species. *Dictyota menstrualis* specimens from Armação dos Búzios and from São Pedro and São Paulo Archipelago (St. Paul`s rocks) were grouped with bootstrap values of 99% (ML) and 1.00 (BI) on *rbc*L and

*nad*1 trees (Figures 9B and 10). The three genes supported the hypothesis that this species is a sister group of *D. stolonifera* and *D. cyanoloma*. The sequences attributed to *D. plectens* for *psb*A (Australia) and for *rbc*L (Australia and China) were placed within the clade of *D. ciliolata* for the respective trees (Figures 9A and 9B).

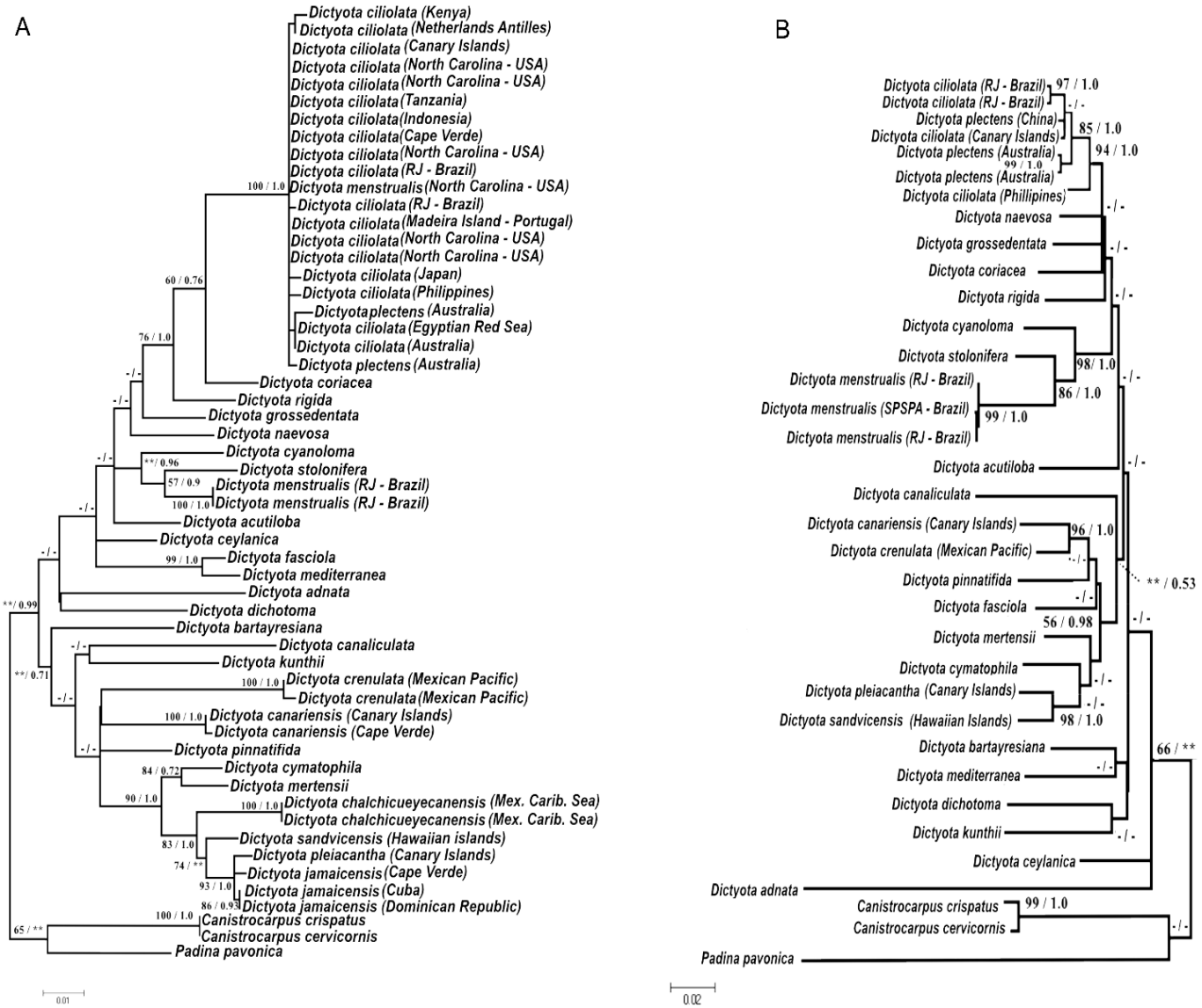

Figure 9: Phylogenetic tree based on *psb*A (A) and *rbc*L (B) sequences, presenting a consensus topology estimated by Maximum Likelihood (ML) and Bayesian Inference (BI) analyses. The numbers associated with each branch represent the statistical support values (only values above 50% are shown), where the first is the bootstrap values from ML and the second is the posterior probability from BI.

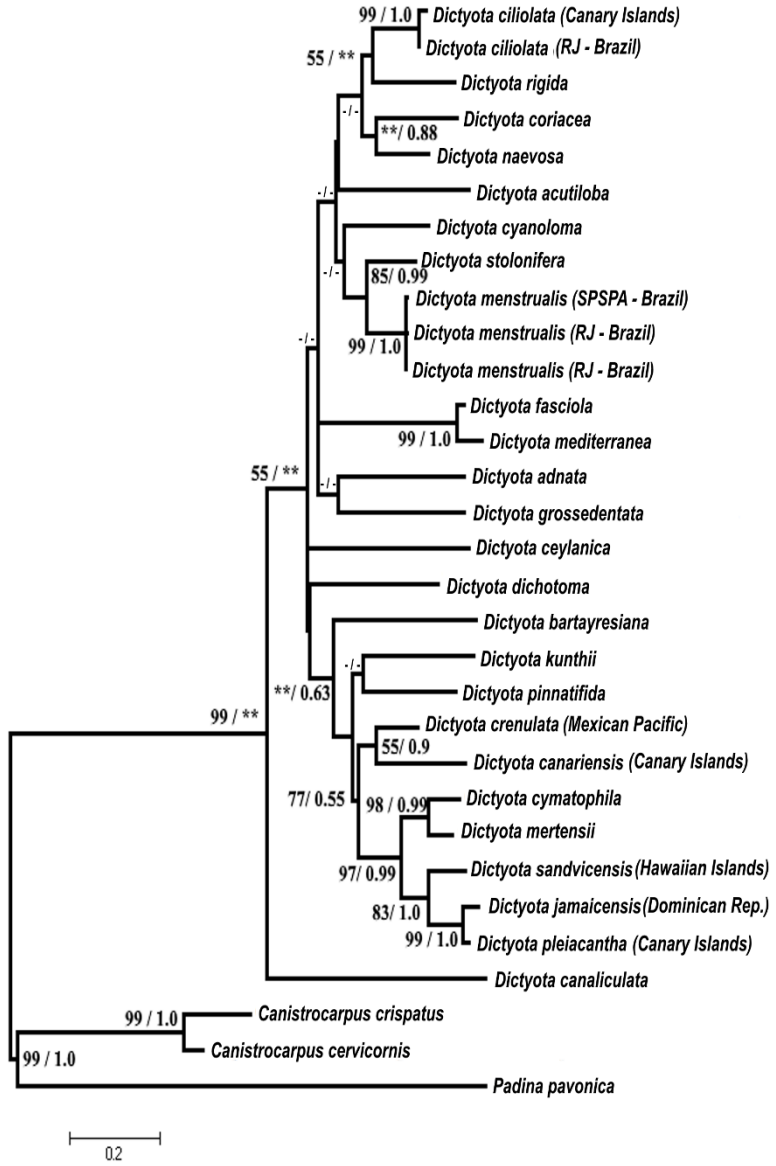

Figure 10: Phylogenetic tree based on *nad*1 sequences, presenting a consensus topology estimated by Maximum Likelihood (ML) and Bayesian Inference (BI) analyses. The numbers associated with each branch represent the statistical support values (only values above 50% are shown), where the first is the bootstrap values from ML and the second is the posterior probability from BI.

DISCUSSION

Table 3 and Figure 8 present the comparative results between the diterpenes detected from the brown alga *D. ciliolata* collected in three different localities from Brazil and one from North Carolina (34º 42' 39" N, 76º 40' 74" W), USA (Cronin *et al.,* 1995; Cronin & Hay, 1996). In addition to the prenylated guaiane diterpenes dictyol B acetate (Figure 8, product **1**) and the pachydictyol A (Figure 8, product **6**) and the xeniane diterpene, the dictyodial (Figure 8, product **8**), described to North America, the present study reveals other

nine products, all of them belong to the Groups I and III, in agreement with previous studies. Therefore, from eleven products known to *D. ciliolata,* six belong to Group I (prenylated guaiane skeleton) and other five belong to Group III (one xeniane skeleton and four crenulidanes). The main products from Brazilian populations is the same found in the North Carolina (USA), in which the dictyol B acetate was the major diterpene (Cronin *et al.,* 1995; Cronin & Hay, 1996).

It was not possible to detect the presence of dictyodial in the Brazilian material, but other product based on the same skeleton, 4β-acetoxydictyodial (Figure 8, product **8**), was as abundant in Atol das Rocas as in Rio de Janeiro. *Dictyota ciliolata* presents many other products, especially prenylated guaianes, in which structure were not possible to be elucidated in the present study due small amount isolated. In the crude extracts the second most abundant product to Rio de Janeiro and Atol das Rocas populations was 4β-acetoxydictyodial (Figure 8, product **8**) while to Salvador population was the mixture of crenulidanes (Figure 8, products **10-13**). The crenulidanes were identified by ^{1}H-NMR and HRGC-MS from Atol das Rocas. Their proposals here place this species as the most important source of these products for the Atlantic.

The crenulidane diterpene, the 13 β-hydroxy-acetoxycrenulide (Figure 8, product **10**) and the 14-hydroxy-acetoxycrenulide (Figure 8, product **11**) were reported previously in the Canary Islands (Spain) by Zarraga *et al.* (1998) and the 4-hydroxycrenulide (Figure 8, product **12**), was noted in the Senegal by Guella & Pietra (1993), all from an unidentified *Dictyota*. Analysis of the diterpenes content of brown alga *D. ciliolata* collected from Qualidia lagoon, Morocco, revealed the presence of three xenianes and two prenylated guaiane diterpenes (Manzo *et al.,* 2009). The prenylated guaiane diterpenes, dictyol B acetate (Figure 8, product **1**) and pachydictyol A (Figure 8, product **6**), characteristic metabolites from *D. ciliolata*, were not detected in the Moroccan population. On the other hand, the authors isolated dictyol H, a typical diterpene from *D. mertensii* (C. Martius) Kützing. The products isolated by Guella & Pietra (1993) and Zarraga *et al.* (1998) appear to confirm the presence of *D. ciliolata* along the African coast, in agreement with the molecular data for Macaronesia (Tronholm *et al.,* 2013) and the literature from the Atlantic African coast (John *et al.,* 2004).

Although there are six taxa with dentate margin recognized for the Atlantic Ocean, the chemical studies are available to only three of them: *D. ciliolata* presents the dictyol B acetate (Figure 8, product **1**) as major diterpene in all populations, with an abundance of

more than 10% of the crude extract, while *D. jamaicensis* (De-Paula *et al.,* 2008, as *D. crenulata*) presents a product from Group III, 4β-Acetoxydictyodial (Figure 8, product **9**) being the main component, and *D. dolabellana* (De Paula *et al.,* 2007b), with 4-hydroxi-7,8-epoxy-2-dolabellane, a product from Group IIa as a major compound. More studies are necessary for *D. canariensis* (Tronholm *et al.,* 2013; Lozano-Orozco *et al.,* 2014), *D. chalchicueyecanensis* Lozano-Orozco and Sentíes (Lozano-Orozco *et al.,* 2016) and *D. pleiacantha* (Tronholm *et al.,* 2013) to fully understand their chemotaxonomy.

Dictyota menstrualis is a very common species in the Western Atlantic, and it is one of the most studied species in Brazil in terms of the chemical ecology and biotechnology (*e.g.* Pereira *et al.,* 1994, 2000*a*, 2000*b*, 2004, 2005; Teixeira *et al.,* 2001; Cavalcanti *et al.,* 2006, 2008, 2011; Abrantes *et al.,* 2010; Fonseca *et al.,* 2013; Moura *et al.,* 2014; Simas *et al.,* 2014*a*, 2014*b*; Mesquita *et al.,* 2015). Despite the observations of Earle (1969) and Tronholm *et al.,* (2012, 2013) about the morphological resemblance, not only are the main products of *D. ciliolata* and *D. menstrualis* distinct, but also the terpenoid compositions of both species show significant differences (Table 3 and Figure 1). *Dictyota menstrualis* was extensively studied for three different populations from the Atlantic Ocean – Radio Island (34º 42' 39" N, 76º 40' 74" W; near the type locality of this species at Beaufort), Armação dos Búzios (22º 44' 49" S, 41º 52' 54" W) and São Pedro and São Paulo Archipelago (00º 55' N, 29º 21' W) – with respect to chemotaxonomy and biotechnology resulting in six prenylated guaianes (Figure 8, products **3-6, 14-15**), three xenianes (Figure 8, products **7, 9,** and **16**), two dichotomanes (Figure 8, products **17-18**), and two cyclexenianes (Figure 8, products **19-20**) (Cronin *et al.,* 1995; Taylor *et al.,* 2003; Ortiz-Ramirez *et al.,* 2008). *Dictyota menstrualis* is characterized by the production of more complex, oxidized and specialized diterpenes, such as the dichotomanes and cyclexenianes, both derived from xeniane diterpenes (Figure 1). The prenylated guaiane dictyol E (Figure 8, product **15**) is the major compound in the populations from São Pedro and São Paulo Archipelago and North Carolina, while dichotomane (Figure 8, product **17**) is the major compound in the population from Rio de Janeiro (Cavalcanti *et al.,* 2008; Ortiz-Ramírez *et al.,* 2008). Additionally, Simas *et al.* (2014*a*) reported the presence of dictyol B acetate to *D. menstrualis* (as *D. caribaea* Hörnig & Schnetter) corresponding to the first report of this product to this species, although the occurrence of this product for this taxon must be reevaluated. Ortiz-Ramírez *et al.,* (2008) considered the environmental conditions of the locales sand how they influenced the qualitative and quantitative variations of natural products among populations; the study

concluded that the production of more "oxygenated" diterpenes occurs at this species' limits of distribution.

The conclusion of Tronholm *et al.* (2012, 2013) about the taxonomical status between *D. ciliolata* and *D. menstrualis* was based on the *psb*A sequence of a single specimen identified as *D. menstrualis,* which is also from Radio Island. On Genbank there are other five sequences named *D. ciliolata* from Beaufort and Onslow Bay (North Carolina). Unfortunately, it was not allowed to us to study the vouchers by the curator of algae from GENT, either by loan neither by photos. In the present study, both species are placed in two distinct clades for three genes (Figures 2A, 2B and S2); even the Brazilian *D. ciliolata* specimens with smoothed and sparsely dentate margins do not merge with those of *D. menstrualis* from Armação dos Búzios and São Pedro and São Paulo Archipelago. The Brazilian specimens of *D. menstrualis* agreed with the neotype (US 00252752), other Hoyt's original materials from North Carolina (such as DUKE 0210404, FH 789016, FH 789017, MICH 633882, MICH 633883, MICH 633887, MICH 633890, WTU-A-014373) and the photos (Plate XCIV, fig. 1 a and b, fig. 2 c and d, fig.3) on Hoyt (1920) and the ones (fig. 5 and 6) on Schnetter *et al.* (1987).

Tronholm *et al.* (2013) examined some specimens in W.R. Taylor's herbarium and concluded that there were no morphological differences between *D. menstrualis* and *D. ciliolata.* However, none of the examined specimens were from the type locality of *D. menstrualis*, but from the Caribbean Sea. Morphologically, both species have dichotomous branching patterns and the sporophytes have scattered solitary sporangia (rarely in small groups in some points of thallus) distributed over both their surfaces that, when densely distributed, create sterile margins (Széchy & Cordeiro-Marino, 1991; Schneider & Searles, 1991; Littler & Littler, 2000; Nunes & Paula, 2001; Solé & Foldats, 2003; Dawes & Mathieson, 2008; Tronholm *et al.,* 2013). However, there are several features that distinguish them. *Dictyota ciliolata* is attached to the substrate by rhizoids or a conspicuous rhizoidal stupose base, while *D. menstrualis* is attached by basal polystichous terete surface branches (as "stoloniferous holdfast" in De Clerck, 2003). The typical yellow iridescence and transversal darker bands on the fronds of *D. ciliolata in* vivo (an important feature to distinguish this species from other dentate species and that may be visible when dried, as observed in one of the herbarium's specimens by Tronholm *et al.* 2013), were never reported in *D. menstrualis* or observed in the field by the authors of the present study. Another important feature that often occurs on the thallus surface of *D. ciliolata, in situ* germinating

sporangia (Tronholm *et al.,* 2013), was never reported in *D. menstrualis*. Finally, *D. ciliolata* and *D. menstrualis* differ by chromosome number (16 and 24, respectively) and did not generate sporophytes in interbreeding experiments (Schnetter *et al.,* 1987; Lewis, 1996).

The comparison of all data, including our molecular and chemical data, allowed us to conclude that the specimen named *D. menstrualis,* collected in North Carolina and used for phylogenetic analysis by Tronholm *et al.,* (2012, 2013), is a misidentified one of *D. ciliolata,* because both species are reported in the area (Schneider and Searles 1991). Also, most of the determination of the *Dictyota* specimens examined by Tronholm *et al.,* (2013) in W.R. Taylor's Herbarium were made before important works were published on *Dictyota* for the Western Atlantic Ocean (*e.g.* Schnetter *et al.,* 1987; Hörnig & Schnetter, 1988; Hörnig *et al.,* 1992*a*, 1992*b*; Nunes & Paula, 2001; Solé & Foldats, 2003). It is not improbable that many *Dictyota* specimens in W.R. Taylor's herbarium are incorrectly identified. The revision of this precious collection is urgent, as are new studies for the genus in the Western Atlantic.

Finally, the morphological resemblance between *D. ciliolata* and *D. plectens* has been obvious since the description of *D. bartayresii* var. *plectens* Allender & Kraft, including marginal cilia and the horizontal dark bands *in vivo*, typical of *D. ciliolata* (Tronholm *et al.* 2013), as noted in the protologue by Allender & Kraft (1983). The authors did not assign this variety to *D. ciliolata* due the enlarging cortical cells surrounding the sporangia that were similar to the involucrum observed in sporangia of *Canistrocarpus* (according to De Clerck 2003, *D. bartayresiana* Lamouroux and *D. bartayresii* Lamouroux were names erroneously used to refer to *C. crispatus* (Lamouroux) De Paula & De Clerck). Kraft (2009) raised this variety to species status level, even without a conclusive taxonomical status between *D. ciliolata* and *D. plectens,* because previous studies on *Dictyota* re-defined the genus (De Clerck *et al.,* 2006). It was later resumed by Tronholm *et al.* (2013), despite having no morphological information about the voucher.

The available chemical data on literature for *D. plectens* is restricted to one population from China (Cheng *et al.,* 2014; Zhao *et al.,* 2015). The crude extracts, performed with ethanol, furnished polar fractions of the Chinese *D. plectens*, resulting in more oxidative products (or transformed ones), while acetone or dichloromethane extracts of the Atlantic populations resulted in more nonpolar compounds. This way the final set of compounds isolated from Chinese *D. plectens* has skeletons partially comparable to *D. ciliolata*, *i.e.,* prenylated guaianes, xenianes and crenulidanes, despite the fact that they are not the same products known to *D. ciliolata.*

The phylogenetic analysis using *rbc*L sequences (Figure 2B) grouped the Chinese *D. plectens* population with *D. ciliolata* (Brazil, Canary Islands and Philippines) and two Australian sequences of *D. plectens*, including one from Lord Howe Island (the type locality of this species), the same specimen used by De Clerck *et al.* (2006) and Tronholm *et al.* (2012, 2013). Although *D. plectens* was known only for its type locality (Kraft, 2009) prior to the Chinese chemical works, *D. ciliolata* and some synonyms (*Dictyota beccariana* Zanardini and *Dictyota maxima* Zanardini) have been recorded to the South China Sea (Phang *et al.,* 2016). Since no chemical information is available from the type locality of *D. plectens,* and no further morphological comparisons between *D. ciliolata* and *D. plectens* was carried by recent works, the chemical data from China did not allow any further conclusions about the taxonomical status of this taxon, especially because this study also furnished dolabellane and dolastane products which clearly indicate this population was composed of at least two *Dictyota* species.

CONCLUSION

Concluding, the terpenes from *Dictyota ciliolata* distinguished it from the dentate species *D. jamaicensis* and *D. dolabellana,* but it was not possible to compare with *D. canariensis*, *D. chalchicueyecanensis* and *D. pleiacantha* due the lack of chemical studies for these species. In spite of the great morphological variation that may lead to misidentification in *D. ciliolata* and *D. menstrualis*, there are sufficient arguments to consider both species as distinct taxa, including the chemical and the molecular phylogenetics. Nevertheless, the taxonomical status of *D. plectens* is inconclusive. A combined study of *D. plectens* with chemical, morphological and phylogenetics approaches from the type locality is necessary to solve the status between this species and *D. ciliolata*. Also, due to the discrepancies among morphological, chemical, molecular and literature records of *Dictyota*, future research should combine these tools to improve the knowledge of the diversity of this genus and others from Dictyotaceae, a process necessary for biotechnological purposes.

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Appendix 3: Sequences used on the phylogenetic analyses

Taxa	Locality	Herbarium ID	Voucher	Genbank Acession Number			References
				*psb*A	*rbc*L	*Nad*1	
Canistrocarpus cervicornis	Phillipines, Leyte Island, Municipality of Isabel, Apale	N.D.	DAP021	--	DQ472073.1	--	De Clerck et al. 2006
	Spain, Canary Islands, Tenerife Island, Punta Hidalgo	N.D.	D192	--	--	GQ425184.1	Tronholm et al. 2010
	Tanzania, Zanzibar Island, Matemwe	N.D.	TZ0714C	GQ466069.1	--	--	Tronholm et al. 2010
Canistrocarpus crispatus	Philippines, Bohol Island, Panglao	N.D.	HV721	--	GQ425119.1	---	Tronholm et al. 2010
	Philippines, Province of Negros Oriental, Dumaguete	N.D.	ODC1444	--	--	GQ425176.1	Tronholm et al. 2010
	Kenya, Tiwi	N.D.	ODC1545	GU265787.1	--	--	Tronholm et al. 2010
Dictyota acutiloba	USA, Hawaii Islands, Oahu Island, Honolulu, Ala Moana beach	N.D.	ODC888	EU395602.1	DQ472056.1	GU290247.1	Hwang et al. 2009 / Tronholm et al. 2010
Dictyota adnata	Philippines, Province of Negros Oriental, Bais	N.D.	ODC1485	GQ425188.1	--	GQ425178.1	Tronholm et al. 2010
	Indonesia, Raja Ampat Islands, Gam Island	N.D.	SD712204	--	GQ425106.1	--	Tronholm et al. 2010
Dictyota bartayresiana	Kenya, Diani Beach	N.D.	ODC1513	--	--	GQ425183.1	Tronholm et al. 2010
	Kenya, Kinondo Reef	N.D.	ODC1588	--	GQ425107.1	--	Tronholm et al. 2010
	Dominican Republic, Province of La Altagracia, Punta Cana, Playa Bávaro	N.D.	DR7	GQ425189.1	--	--	Tronholm et al. 2010
Dictyota canaliculata	Indonesia, Raja Ampat Islands, Yeffam Island	N.D.	SD712709	--	GQ425108.1	--	Tronholm et al. 2010
	Philippines, Siquijor Island, Dapdap	N.D.	ODC1477	--	--	GQ425177.1	Tronholm et al. 2010
	Indonesia, Raja Ampat Islands, Gam Island, Desa Besir	N.D.	SD712400	GQ466072.1	--	--	Tronholm et al. 2010
Dictyota canariensis	Spain, Canary Islands, Tenerife Island, Playa de Las Arenas	N.D.	D319	JQ061018.1	--	JQ061111.1	Tronholm et al. 2012
	Cape Verde, Sal Island, Pedra Lume	N.D.	FS927	JQ061084.1	--	--	Tronholm et al. 2012
	Spain, Canary Islands Islands, Tenerife Island, Playa de Las Arenas	N.D.	D504	--	JQ061121.1	--	Tronholm et al. 2012
Dictyota ceylanica	French Polynesia, Tahiti Island, Faaa	N.D.	HV214a	--	DQ472067.1	--	Tronholm et al. 2010
	Philippines, Province of Negros Oriental, Dumaguete	N.D.	ODC1442	--	--	GQ425175.1	Tronholm et al. 2010
	French Polynesia, Tahiti Island, Faaa	N.D.	HV231a	EU395607.1	--	--	Hwang et al. 2009
Dictyota chalchicueyecanensis	Mexico, Veracruz state, Playa Hermosa,	N.D.	UAMIZ1237	KX819255.1	--	--	Lozano-Orozco et al. 2016
	Mexico, Veracruz state, Punta Puntillas	N.D.	UAMIZ1236	KX819256.1	--	--	Lozano-Orozco et al. 2016
Dictyota ciliolata	Spain, Canary Islands, Tenerife Island, Punta Hidalgo	N.D.	D191	--	GQ425109.1	GQ425173.1	Tronholm et al. 2010
	Philippines, Province of Bohol, Balicasag Island	N.D.	DAP029	--	DQ472071.1	--	De Clerck et al 2006
	Spain, Canary Islands, Gran Canaria Island, Faro de Maspalomas	N.D.	D396	JX312643.1	--	--	Tronholm et al 2013
	Philippines, Provice of Negros Oriental, Dumaguete	N.D.	ODC1441	JQ061022.1	--	--	Tronholm et al. 2012
	Kenya, Kinondo Reef	N.D.	ODC1563	JQ061024.1	--	--	Tronholm et al. 2012
	Indonesia, Raja Ampat Islands, Gam Island	N.D.	SD712150	JQ061025.1	--	--	Tronholm et al. 2012

	Tanzania, Zanzibar, Matemwe	N.D.	TZ0733	JQ061029.1	--	--	Tronholm et al. 2012
	Portugal, Madeira Island, Ponta do Sao Lourenco	N.D.	D687	JX312644.1	--	--	Tronholm et al 2013
	Netherlands Antilles, Saba, Saba Bank	N.D.	DML67457	JX312645.1	--	--	Tronholm et al 2013
	Cape Verde, Sao Vicente, Baia da Salamansa	N.D.	FS1033	JX312646.1	--	--	Tronholm et al 2013
	Egypt, El Quseir, Mangrove Bay	N.D.	HV1005	JX312650.1	--	--	Tronholm et al 2013
	Japan, Kyushu Island, Kagoshima Prefecture, Nangunn-Motomachi	N.D.	JAP118	JX312652.1	--	--	Tronholm et al 2013
	Australia, Western Australia, Ningaloo Reef	N.D.	RD90067	JX312657.1	--	--	Tronholm et al 2013
	USA, North Carolina, town of Beaufort, Radio Island	N.D.	Searles.1	JX312658.1	--	--	Tronholm et al 2013
	USA, North Carolina, Onslow Bay, Northwest places	N.D.	WNC156	JX312661.1	--	--	Tronholm et al 2013
	USA, North Carolina, Onslow Bay, Northwest places	N.D.	WNC166	JX312662.1	--	--	Tronholm et al 2013
	USA, North Carolina, Onslow Bay, Southeast Tower	N.D.	WNC311	JX312663.1	--	--	Tronholm et al 2013
	USA, North Carolina, Onslow Bay, Southeast Tower	N.D.	WNC424	JX312664.1	--	--	Tronholm et al 2013
	Brazil, Rio de Janeiro state, City of Arraial do Cabo, Prainha beach	HUNI 5010	JCP 026	MF182634.1	MF182639.1	MF182635.1	This study
	Brazil, Rio de Janeiro state, City of Arraial do Cabo, Prainha beach	HUNI 5011	JCP 105	MF182633.1	MF182635.1	--	This study
Dictyota ciliolata (as D. menstrualis)	USA, North Carolina, town of Beaufort, Radio Island	N.D.	Searles-2	JQ061064.1	--	--	Tronholm et al. 2012
Dictyota ciliolata (as D. plectens)	Australia, Lord Howe Island, Ned's Beach	N.D.	GWS1029	JQ061074.1	DQ472052.1	--	De Clerck et al 2006 / Tronholm et al. 2012
	Australia, Queensland state, Yeppoon town, Keppel Bay	N.D.	TC2	JQ061075.1	DQ472085.1	--	De Clerck et al 2006/ Tronholm et al. 2012
	China, Guangdong province, prefectural city of Zhanjiang, Xuwen County	N.D.	GZ201301	--	*	--	Cheng et al 2014
Dictyota coriacea	Japan, Honshu Island, Shizuoka Prefecture, Yumigahama beach	N.D.	SZKIZ039	--	AB096889.1	--	Genbank
	USA, California State, Dana Point	N.D.	CSUF003	--	--	GU290251.1	Tronholm et al. 2010
	Japan, Honshu Island, Chiba Prefecture, Choshi	N.D.	JALee11	AY748323.1	--	--	Hwang et al. 2004
Dictyota crenulata	Mexico, Baja California Sur state, City of Cabo San Lucas, Santa Maria beach	N.D.	HV1074	GU265782.1	GU290253.1	GU290252.1	Tronholm et al. 2012
	Mexico, Oaxaca state, Bahia de Huatulco, Togolunda	N.D.	CFMX206	JQ061089.1	--	--	Tronholm et al. 2012
Dictyota cyanoloma	Portugal, Province of Algarve, City of Portimão, Praia da Rocha	N.D.	D544	--	JQ061123.1	JQ061114.1	Tronholm et al. 2012
	Croatia, Split-Dalmatia County, City of Split, Bacvice beach	N.D.	FS405	GU255710.1	--	--	Tronholm et al. 2010
Dictyota cymatophila	Spain, Canary Islands, Gran Canaria Islands, El Berriel	N.D.	D397	--	GQ425111.1	--	Tronholm et al. 2010
	Spain, Canary Islands, Tenerife Island, Punta Hidalgo	N.D.	D403	--	--	GQ425179.1	Tronholm et al. 2010
	Spain, Canary Islands, Tenerife Island, Punta Hidalgo	N.D.	D306	GQ425193.1	--	--	Tronholm et al. 2010
Dictyota dichotoma	Ireland, Galway County, Galway Bay, Spiddal	N.D.	IK81	--	AY527200.1	--	Hwang et al. 2004
	France, Brittany, Department of Finistère, Pointe de Mousterlin	N.D.	Cultivated	--	--	NC-007685.1	Secq et al. 2006
	England, City of Barrow-in-furness, Walney Island	N.D.	ODC1689	GU255542.1	--	--	Tronholm et al. 2010
	France, Occitanie, Department of Pyrénées-Orientales, Port Vendres, Les Paulilles	N.D.	ODC1049	--	DQ472078.1	--	De Clerck et al. 2006

Dictyota fasciola	France, Occitanie, Department of Pyrénées-Orientales, Côte Vermeille, Cerbere, Cap Peyrefitte	N.D.	ODC1065	GQ466074.1	--	GQ425172.1	Tronholm et al. 2010
Dictyota grossedentata	Tanzania, Zanzibar, Mnemba atoll	N.D.	TZ0490	JQ061043.1	JQ061125.1	JQ061116.1	Tronholm et al. 2012
Dictyota jamaicensis	Dominican Republic, Province of La Altagracia, Punta Cana, Playa Bávaro	N.D.	DR27	--	--	JQ061112.1	Tronholm et al. 2012
	Cuba, Havana, Miramar	N.D.	D631	JQ061054.1	--	--	Tronholm et al. 2012
	Dominican Republic, Province of La Altagracia, Punta Cana, Playa Bávaro	N.D.	DR28	JQ061056.1	--	--	Tronholm et al. 2012
	Cape Verde, Sal Island, Baia da Murdeira	N.D.	FS881	JQ061083.1	--	--	Tronholm et al. 2012
Dictyota kunthii	Chile, Pan de Azúcar National Park	N.D.	Faugeron-Chile-M1	--	DQ472057.1	--	De Clerck et al. 2006
	Chile, Pan de Azúcar National Park	N.D.	D102	EU395618.1	--	GU290250.1	Hwang et al. 2009 / Tronholm et al. 2010 / Tronholm et al. 2012
Dictyota mediterranea	Spain, Balearic Islands, Mallorca Island	N.D.	D595	--	GU290254.1	--	Tronholm et al. 2010
	Spain, Murcia, City of Cartagena, Cabo de Palos, Cala Flores beach	N.D.	Sanchez2	GU255612.1	--	--	Tronholm et al. 2010
	Croatia, Hvar Island	N.D.	LLGO224	--	--	GU290246.1	Tronholm et al. 2010
Dictyota menstrualis	Brazil, Rio de Janeiro State, City of Armação dos Búzios, Rasa beach, Ponta do Pai Vitório	HUNI 1372	JPC058	KM101060.1	KY012328.1	KY012325.1	Mesquita et al. 2015 / Lopes-Filho et al. 2017
	Brazil, Rio de Janeiro State, City of Armação dos Búzios, Forno beach	HUNI 1371	JCP 073	KM101061.1	MF182640.1	MF182637.1	This study
	Brazil, São Pedro and São Paulo Archipelago	HUNI 3215	JCP 1079	--	MF182641.1	MF182636.1	This study
Dictyota mertensii	Jamaica, St. Ann Parish, Drax Hall, East of St. Ann's Bay	N.D.	HV923	--	DQ472060.1	--	De Clerck et al. 2006
	Dominican Republic, Province of La Altagracia, Punta Cana, Playa Bávaro	N.D.	DR31	GQ425215.1	--	GQ425180.1	Tronholm et al. 2010
Dictyota naevosa	South Africa, Province of Kwazulu-Natal, District of Ugu, Port Edward, Palm Beach	N.D.	KZNb2345	--	--	JQ061118.1	Tronholm et al. 2012
	South Africa, Province of Kwazulu-Natal, District of uMkhanyakude, iSimangaliso Wetland Park, Mission Rocks	N.D.	KZN2241	EU395609.1	DQ472084.1	--	Hwang et al. 2009 / Tronholm et al. 2012
Dictyota pinnatifida	Venezuela, Margarita Island, El Tirano beach	N.D.	Sole3	--	GQ425115.1	--	Tronholm et al. 2010
	Jamaica, St. Ann Parish, Priory, Chris Cove	N.D.	HV932	--	--	GQ425171.1	Tronholm et al. 2010
	Dominican Republic, Province of La Altagracia, Punta Cana, Playa Bávaro	N.D.	DR6	JQ061072.1	--	--	Tronholm et al. 2012
Dictyota pleiacantha	Spain, Canary Islands, Tenerife Island, El Médano	N.D.	D404	--	--	JQ061113.1	Tronholm et al. 2012
	Spain, Canary Islands, Tenerife Island, Punta Hidalgo	N.D.	D401	JQ061053.1	--	--	Tronholm et al. 2012
	Spain, Canary Islands, Tenerife Island, Buenavista, Playa de Las Arenas	N.D.	D324	--	JQ061122.1	--	Tronholm et al. 2012
Dictyota rigida	Kenya, Mombasa, McKenzie Point	N.D.	ODC1623	--	GQ425117.1	--	Tronholm et al. 2010
	Kenya, Mombasa, McKenzie Point	N.D.	ODC1657	GQ466077.1	--	GQ425181.1	Tronholm et al. 2010
Dictyota sandvicensis	USA, Hawaii Islands, Oahu Island, Lanikai	N.D.	ODC896	EU395611.1	DQ472063.1	--	Hwang et al. 2009 / Tronholm et al. 2010 /

							Tronholm et al. 2012
Dictyota stolonifera	USA, Hawaii Islands, Oahu Island, Honolulu, Ala Moana beach	N.D.	ODC889	--	--	GU290248.1	Tronholm et al. 2010
	Taiwan, City of Keelung, Batouzi Harbor	N.D.	D264	--	GQ425118.1	--	Tronholm et al. 2010
	Tanzania, Zanzibar, Mnemba atoll	N.D.	TZ0488	JQ061082.1	--	GQ425182.1	Tronholm et al. 2010
Padina pavonica	France, Provence-Alpes-Côte d'Azur, Department of Alpes-Maritimes, Cannes City	N.D.	CAN2	--	AB512551.1	--	Ni-Ni-Win et al. 2011
	France, Provence-Alpes-Côte d'Azur, Department of Var, Ile des Embiez	PC0171175	FRA0509	EU681649.1	--	EU681498.1	Silberfeld et al. 2010

* The sequence was not deposited in Genbank but is available in the supplementary material of Cheng et al 2014

- O presente trabalho corrobora a literatura acadêmica ao confirmar que *Dictyota dichotoma* tem sua distribuição natural para Mediterrâneo, Atlântico Europeu e grande parte da Macaronésia. Populações disjuntas na América do Sul e Africa do Sul devem ser tratadas como casos de introdução, embora seus efeitos nas comunidades locais não sejam conhecidos.

- Os dados atuais baseados em biologia molecular, produtos naturais e morfologia refutam a hipótese de sinonímia entre *Dictyota ciliolata* e *D. menstrualis*, evidenciando que a presença de denteações marginais ainda é um bom critério para a separação destas espécies em conjunto com o tipo de base de fixação. Embora haja dados moleculares e de produtos naturais publicados sob o nome *D. plectens*, mais estudos são necessários para se reconhecer seu real *status* taxonômico.

- Genes do cpDNA (psbA e rbcL) e do mtDNA (Nad1) se mostraram informativos para discutir as relações entre as espécies do gênero *Dictyota*.

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RESEARCH ARTICLE

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Molecular evidence of the presence of *Dictyota dichotoma* (Dictyotales: Phaeophyceae) in Argentina based on sequences from mtDNA and cpDNA and a discussion of its possible origin

Erick Alves Pereira Lopes-Filho[a], Fabiano Salgueiro[a], Silvia Mattos Nascimento[a], M. Cecilia Gauna[b], Elisa R. Parodi[b] and Joel Campos De Paula [a]

[a]Programa de Pós-Graduação em Biodiversidade Neotropical, Universidade Federal do Estado do Rio de Janeiro, Rio de Janeiro, Brazil; [b]CONICET- Instituto Argentino de Oceanografía, Universidad Nacional del Sur, Bahía Blanca, Argentina

ABSTRACT

Dictyota is a brown algae genus inhabiting tropical to warm temperate environments where it is an important food source, shelter and substrate to several species of invertebrates and other algae. The taxonomy of this genus is troublesome, with poor species delimitation and doubtful records in the literature. *Dictyota dichotoma*, the type species of the genus, was commonly accepted as a cosmopolitan species because of the inaccurate geographical distributional range as a consequence of misidentification in several parts of the world. Recent studies with molecular data revealed new species and a new understanding of the evolution and biogeography of the genus *Dictyota*. These studies confined natural populations of *D. dichotoma* to Europe (Atlantic and Mediterranean coasts) and Macaronesian islands (Azores, Madeira and Canary archipelagos). Also, they confirmed its presence in South Africa, but whether the species was native or introduced in South Africa could not be verified. In the present study two regions of cpDNA (*psb*A, *rbc*L) and one region of mtDNA (*nad*1) from Argentinian samples, identified morphologically as *D. dichotoma*, were analysed and compared to other *Dictyota* species. The identity of these samples as *D. dichotoma* was confirmed. A haplotype network analysis using all available *psb*A sequences distinguished seven haplotypes divided into two geographic groups: Atlantic–Mediterranean and Canarian. In Argentina and South Africa only the most common haplotype of the Atlantic–Mediterranean group was observed. According to the paleoceanographic currents and the presence of a European haplotype, the introduced nature of *D. dichotoma* is indicated.

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CONTACT Joel Campos De Paula depaula.joelc@gmail.com
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