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TESIS

**TAXONOMÍA Y BIOGEOGRAFÍA DE LAS FAMILIAS CAULERPACEAE
(CHLOROPHYTA), DICTYOTACEAE (OCHROPHYTA) Y CORALLINACEAE
(RHODOPHYTA) EN EL PACÍFICO DE CENTROAMÉRICA**

QUE COMO REQUISITO PARA OBTENER EL TÍTULO DE
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PRESENTE.

Los abajo firmantes, Miembros de la Comisión Revisora del trabajo de tesis terminado titulado:

Taxonomía y Biogeografía de las familias Caulerpaceae (Chlorophyta), Dictyotaceae (Ochrophyta) y Corallinaceae (Rhodophyta) en el Pacífico de Centroamérica

Que presentó: Cindy Fernández García

Otorgamos nuestro voto **aprobatorio** y consideramos que dicho Trabajo está listo para su defensa, a fin de obtener el **Grado de Doctor en Ciencias Marinas y Costeras**, con Orientación en **Biología Marina**

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A Chepe

A mis padres y hermanos

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RESUMEN GENERAL

El conocimiento de la diversidad de flora marina del Pacífico de Centroamérica es limitado debido a la corta historia de investigación en esta área temática y a la falta de especialistas en macroalgas marinas a lo largo de esta amplia región. Esto ha dejado como resultado una falta de actualización taxonómica de aproximadamente 50 años para muchos de los grupos de macroalgas. Por lo que los objetivos de este trabajo fueron: 1- determinar el número de especies reportadas en esta costa por medio de un catálogo taxonómico con el fin de establecer una línea base de lo que existe a hasta el momento, 2- evaluar la taxonomía de algunos géneros de las familias Caulerpaceae (Chlorophyta), Dictyotaceae (Ochrophyta) y Corallinaceae (Rhodophyta) en el Pacífico de Centroamérica comparando con otros sitios del Pacífico Tropical Oriental y 3- describir las tendencias en la distribución biogeográfica de los géneros seleccionados de las familias Caulerpaceae (Chlorophyta), Dictyotaceae (Ochrophyta) y Corallinaceae (Rhodophyta) dentro y fuera del Pacífico Tropical Oriental. En el Capítulo 1 se presenta el catálogo taxonómico, el cual es un listado que está basado en registros publicados en artículos, tesis de estudiantes y reportes oficiales. En total se reportan 379 especies de macroalgas, así como 16 taxa cuya distribución es dudosa para esta región. Las algas rojas (Rhodophyta) presentaron el mayor número de especies (252), seguidas por las algas verdes (Chlorophyta: 81), y las algas pardas (Phaeophyceae: 46). El país con el mayor número de reportes fue Costa Rica con 216 especies, seguido por Panamá con 174, El Salvador con 146, Nicaragua con 24, y Guatemala con 16. Hasta el momento, por la falta de estudios, no se han registrado macroalgas marinas para la costa Pacífica de Honduras. El análisis del número de especies reportadas por grado latitudinal de la costa Centroamericana, nos muestra que el número de especies varía entre los países y localidades, por diferencias en la geomorfología y la heterogeneidad de hábitats de la costa, así como la intensidad en el esfuerzo de investigación que se ha llevado a cabo. Seguidamente en los Capítulos 2, 3, 4 y 5 se analizan los géneros *Caulerpa*, *Padina*, *Dictyota* y *Amphiroa*, respectivamente, los cuales son géneros ecológicamente relevantes en la región. El material utilizado en el presente estudio procede de 107 sitios ubicados en

la las costas del Pacífico Tropical de México y Centroamérica. Aunado a esto se obtuvieron algunos especímenes de la costa de Colombia. Para cada género se realizó un análisis morfológico y molecular (*Caulerpa*: cinco caracteres morfológicos, gen *tufA*, *Padina*: veintidos caracteres, gen *cox3*, *Dictyota*: veintiocho caracteres, gen *cox3* y *Amphiroa*: once caracteres, gen COI-5P). Los especímenes se separaron en morfo-especies que fueron comparadas con el material tipo de las especies morfológicamente relacionadas. Finalmente se evaluó si las unidades morfológicas coincidían con los clados genéticos. Para el género *Caulerpa* se determinó la presencia de seis clados a nivel de especie: *C. verticillata*, *C. sertularioides*, *C. cupressoides*, *C. serrulata*, *C. racemosa* var. *mucronata* y *C. racemosa laetevirens/peltata/turbinata*. Estos resultados muestran una reducción del estimado de riqueza de especies en 50 % (de 13 a 6). En concordancia con otros trabajos recientes, nuestros datos morfológicos y moleculares garantizan el reconocimiento a nivel de especie del complejo *C. laetevirens/turbinata/peltata*, siendo *C. chemnitzia*, el nombre más antiguo aplicado a este grupo de especies, así mismo se propone el uso de ecadas como una solución práctica para la identificación de la diversidad morfológica de esta especie en el PTO. Aunado a esto se reconoce la sinonimia de *C. racemosa* var. *mucronata* con *C. racemosa* var. *macrophysa*. Para el género *Padina*, el análisis molecular reveló la presencia de cuatro clados a nivel específico: *P. caulescens*, *P. conrescens*, *P. durvillei* y *P. mexicana*. De acuerdo a otros trabajos recientes, los datos morfológicos y moleculares de este trabajo garantizan el reconocimiento de *P. caulescens* como un nombre válido, y no como sinónimo de *P. durvillei* como fue propuesto. Así mismo se reconoce que *P. crispata* es un sinónimo de *P. mexicana*. En el caso del género *Dictyota*, los resultados muestran que la identificación de este género, basada en la morfología ha fallado debido a la plasticidad fenotípica intrínseca del género, vaga definición en los caracteres de las especies descritas y mala identificación por el uso de claves taxonómicas no acordes con la región. De las 13 especies reportadas para el PTO, se encontraron 3 nombres válidos (*D. crenulata*, *D. humifusa*, *D. stolonifera*), 7 identificaciones erróneas (*D. baytaresiana*, *D. ciliolata*, *D. conrescens*, *D. flabellata*, *D. friabilis*, *D. linearis*, *D. pinnata*) y 3 reportes no confirmados (*D. binghamiae*, *D. major*, *D. masonii*). Aunado, se encontró una especie polifilética no

reportada antes para la región (*D. ceylanica*) y 3 especies nuevas. Asimismo, se confirma que las especies *D. divaricata*, *D. dichotoma* y *D. adnata* no están distribuidas en el PTO. Finalmente para el género *Amphiroa* se encontraron 12 especies. Debido a la falta de comparación con otros especímenes (secuencias) del mundo, para este estudio se definieron cinco complejos de especies: Complejo A con una especie; Complejo B con tres especies; Complejo C con dos especies; Complejo D con dos especies y Complejo E con cuatro especies. La mayoría de los grupos de especies mostraron consistencia morfológica, sin embargo se requieren estudios adicionales y colecta de especies nuevas para definir algunas de las especies. Al evaluar el número de especies final, luego del análisis morfológico y molecular de los cuatro géneros de este estudio, encontramos que se da una reducción de las especies que fueron reportadas. Esto debido a que muchas especies descritas son sinónimos de otras, a una mala identificación de las especies y confusión con especies de otras provincias biogeográficas, esto último posiblemente por realizar la identificación utilizando claves taxonómicas de otros sitios. Biogeográficamente a nivel mundial las especies de algas encontradas muestran dos patrones de distribución: algunas especies presentan distribución en varias provincias biogeográficas del mundo, principalmente en la zona tropical (todas las especies de *Caulerpa* y *Dictyota*) y en contraste hay especies que tienen un rango de distribución restringida en el PTO (todas las especies de *Padina* y *Dictyota*). Por otro lado a nivel latitudinal dentro del PTO encontramos especies con distribución restringida a localidades o ambientes particulares y otras especies que muestran una amplia distribución latitudinal y de ambientes.

INTRODUCCIÓN Y JUSTIFICACIÓN

Las macroalgas representan uno de los grupos más antiguos en el planeta Tierra, surgiendo durante los períodos Cámbrico y Ordovícico, hace 500 a 420 millones de años (Knoll 1994). Dado el largo espacio de tiempo sobre cuál la evolución ha ocurrido, una gran diversidad morfológica y genética ha sido detectada entre los diferentes grupos de macroalgas marinas (Saunders et al. 1995). Las macroalgas son esenciales en las interacciones del ecosistema marino, ya que como productores primarios, inician las cadenas tróficas en estos ambientes y sus praderas albergan una gran diversidad de animales asociados, que utilizan las algas como alimento, refugio y criadero de juveniles (Lee 2008a). Así mismo, las macroalgas marinas tienen importancia económica, ya que de ellas pueden extraerse sustancias que se usan en medicina, industria farmacéutica o alimenticia, o para el cultivo de microorganismos (Bold y Wynne 1978).

A nivel mundial el estudio de algas marinas es de gran interés, ya que en muchos lugares se han reportado cambios en las comunidades costeras, asociados a aumentos o disminuciones en la cobertura de estas (McCook 1999). Estas se distribuyen en todos los océanos desde las zonas polares hasta las tropicales y están confinadas a ambientes someros en la zona fótica, donde la temperatura juega un papel muy importante para delimitar la distribución de éstas (Lüning 1990, Adey y Steneck 2001). Según Lüning (1990) se han definido siete regiones ficogeográficas: Región Ártica, Región Antártica, Región Templada Fría del Hemisferio Norte, Región Templada Caliente de Hemisferio Norte, Región Templada Fría del Hemisferio Sur, Región Templada Caliente del Hemisferio Sur y Región Tropical. El límite de cada zona biogeográfica se caracteriza por un cambio drástico en la composición de especies costeras de la flora.

Dentro de estas regiones, la franja tropical presenta temperaturas estables entre los 25 y 30°C, constituyendo uno de los hábitats marinos más antiguos de la tierra, con una composición muy similar en los géneros de algas. Esto último, posiblemente debido a que durante el Mesozoico existió una franja de agua cálida alrededor de la tierra, generando una distribución global de algas tropicales. Seguidamente la flora marina tropical se separó y

procesos de especiación y colonización tuvieron lugar. Esto debido a que esta franja fue interrumpida por secciones terrestres que empezaron a emerger en el Terciario Tardío (17 millones de años), con el cierre de la conexión entre el Mediterráneo y el Océano Índico, y el surgimiento del Istmo Centroamericano (3 millones de años) (Lüning 1990). Actualmente la región Tropical se subdivide en: Atlántico Este Tropical, Atlántico Oeste Tropical, Indo-Pacífico y Pacífico Tropical Oriental (PTO) (Lüning 1990).

En las zonas costeras tropicales, las macroalgas juegan un papel importante dentro de los ecosistemas marinos. En las zonas intermareales la presencia y abundancia de las algas se usan como índices de las condiciones ambientales que caracterizan las zonas rocosas, además estas son aprovechadas por los herbívoros que viven en estas zonas (Underwood 2000). En los arrecifes coralinos y rocosos, tanto saludables como degradados, su abundancia y composición son críticas en la ecología del ambiente arrecifal (McCook 1999). Asimismo, estas contribuyen significativamente en la formación del arrecife y en la producción de arena; constituyendo parte de un ecosistema muy sensible. Por otro lado, las algas conforman hábitats particulares como los bosques de *Sargassum* y los mantos de rodolitos (algas rojas) que sostienen también una rica diversidad de especies. En estos se han encontrado especies poco abundantes, inusuales y endémicas que han sido informadas en muchos lugares tropicales (Steller et al. 2003).

En estos últimos años el PTO ha sido una región con particular interés para los estudios de su flora marina. La investigación taxonómica y biogeográfica de estos organismos ha sido mayor en las costas de México, pero menor en la región de Centroamérica. Biogeográficamente, se han propuesto dos teorías para explicar el origen de las biotas actuales del PTO. La primera propone que la biota actual es derivada de especies Pan-Téticas que por un proceso de vicarianza, como lo fue el cierre del istmo hace 3 millones de años, sobrevivieron especies que se han ido modificando por extinciones y evolución (Heck y McCoy 1978). Por otro lado, se ha propuesto que hubo una eliminación de especies y posteriormente se dio el transporte transoceánico de organismos desde otros sitios como el Indo-Pacífico (Dana 1975, Cortés 1986) y el Pacífico Central (Lessios y Robertson 2006). Para comprobar dichas teorías se han realizado trabajos con corales,

equinodermos y peces, sin embargo los estudios biogeográficos de macroalgas de esta región se han hecho por índices de similitud de la flora y estadística multivariada pero nunca se han probado estas teorías por análisis moleculares (Joosten y Hoek 1986).

Investigación de las Macroalgas Marinas en el Pacífico de Centroamérica

El conocimiento de la flora marina para el Pacífico Centroamericano inicio con las colectas de algas coralinas realizadas entre 1845 y 1848, por A.S Öersted, las cuales actualmente están almacenadas en Copenhague, sin que se hallan identificado hasta la fecha. Posteriormente, Howe (1910) y Lemoine (1929), realizaron algunas colectas adicionales de algas coralinas recientes y fósiles, en el Canal de Panamá, en la Islas Coiba y Coco. Seguidamente W.R. Taylor y E.Y. Dawson, entre las décadas de 1940 y 1960 desarrollaron colecciones del Pacífico y estos son quienes describen aproximadamente el 70% de la flora de Centroamérica, reportando la mayoría de las especies que hasta ahora conocemos para esta región.

Muchas de esas especies no han sido revisadas taxonómicamente, lo que ha dejado como resultado una desactualización taxonómica de aproximadamente 50 años para muchos de los grupos de macroalgas. A partir de estas fechas, los trabajos sobre la flora marina disminuyeron sustancialmente hasta a principios del 2000, donde se han realizado esfuerzos con recopilaciones bibliográficas, nuevas colectas, trabajos ecológicos y revisiones moleculares de algunas especies. Pero muchos de estos trabajos moleculares analizan muestras de herbarios que fueron colectadas en la década de 1960 (Santelices 1991, 1999a).

Actualmente existen aproximadamente 101 publicaciones sobre la flora marina de América Central, de la cuales 54 citan macroalgas de Costa Rica, 35 de Panamá, 28 de El Salvador, 6 de Guatemala, 6 de Nicaragua y hasta en momento no se han reportado algas para la costa Pacífica de Honduras (Nelson 1990). Sumado a estos trabajos se han desarrollado esfuerzos de colecta en la región pero los especímenes en los herbarios de la

región son escasos y están mal identificados por la falta de guías taxonómicas actualizadas (Obs. pers).

Recientemente, Wysor (2004) realizó una recopilación de algas verdes de la costa Pacífica de Panamá, en la que hace una comparación con otros países de la región, evidenciando la falta de información de la flora marina para todos los países de Centroamérica. Asimismo, encuentra que un gran porcentaje de las recolectas no concuerdan con ninguna especie identificada hasta el momento, lo que hace suponer que hay una flora marina muy específica para esta región (B. Wysor com. pers) o que lo anterior no fue identificado adecuadamente.

Aunado, a la desactualización taxonómica antes mencionada, se han reportado aproximadamente 65 especies de algas en común entre las costas del Pacífico y el Caribe de Centroamérica. Este número compartido de algas marinas entre ambas costas excede en mucho el número de la especie compartidas de otros grupos de organismos. En una recopilación realizada por Lessios (2008), indica que de las especies anfi-ístmicas se han estudiado 38 regiones de ADN en 9 clados de erizos de mar, 38 de crustáceos, 42 de peces y 26 de moluscos. De las cuales 34 se diferenciaron al final del cierre del Istmo Centroamericano, 73 se separaron antes del cierre y únicamente 8 mantienen cercanía genética después del cierre. Por lo que, en el caso de las especies de algas queda por resolver si esto es resultado de una taxonomía inadecuada o si la tasa de evolución de estos grupos es mucho menor en comparación con otros organismos o si es un efecto de inventarios incompletos de las especies en general (Wysor 2004).

Justificación de la investigación

Aunque se reconoce la importancia de las macroalgas en los ambientes tropicales del Pacífico Tropical Oriental, actualmente no se cuenta con un conocimiento real de la composición o un número aproximado de la riqueza de algas de la región, esto debido a la falta de clarificación taxonómica de las especies. En muchas investigaciones sobre el

bentos marino, estas se clasifican hasta género y en muchos casos como grupos funcionales o morfotipos y esto trae como consecuencia la poca comparación entre trabajos.

Sin embargo, aunque la taxonomía muestra un rezago importante para la zona es posible actualizarla para algunos grupos que se han estado estudiando recientemente en algunas otras regiones del Pacífico Oriental. Tal es el caso de las familias Caulerpaceae (Chlorophyta) (Wysor 2004, Fernández 2007, Ortuño-Aguirre 2007), Dictyotaceae (Phaeophyta) (Paul-Chavez 2000, Altamirano-Cerecedo 2004, Altamirano-Cerecedo y Riosmena-Rodríguez 2007, Ortuño-Aguirre y Riosmena-Rodríguez en prep) y Corallinaceae (Rhodophyta) (Riosmena-Rodríguez y Siqueiros-Beltrones 1996, Riosmena-Rodríguez y Woelkerling 2000, Riosmena-Rodríguez 2002, 2006).

Estas tres familias sobresalen entre otras en la región, debido a su alta riqueza y amplia distribución, y sobretodo, por ser elementos esenciales en la dinámica costera y arrecifal del PTO (Dawson y Beaudette 1959). Además, algunos géneros de estas familias se diversificaron en el Paleoceno, hace 65 MA, antes del cierre del istmo, lo que las hace de particular interés para el análisis biogeográfico y determinación origen de la flora de esta región. Asimismo, los grupos propuestos para este trabajo han sido estudiados morfológica y molecularmente a nivel mundial.

Actualmente la familia Caulerpaceae se distribuye a nivel mundial y se han reportado aproximadamente 88 especies distribuidas en dos géneros (Guiry y Guiry 2012). Para el PTO se han informado 14 especies pertenecientes a dos géneros (*Caulerpa* y *Caulerpella*) (Taylor 1945, Dawson 1957, 1960, 1961b, Wysor 2004, Fernández y Alvarado 2008, O. Tejada com. pers.). De estas el género con más especies distribuidas en el PTO es *Caulerpa* (13), es por esto, que para este estudio se escogió el análisis de este género. Investigaciones recientes han revelado propagaciones continuas de las algas de este género en la zona, dando como resultado una alteración en la dinámica y composición del ecosistema arrecifal (Glynn y Maté 1997, Fernández y Cortés 2005, Fernández 2007, Smith et al. 2010). Muchas especies del género *Caulerpa* han mostrado que pueden ser potencialmente invasivas si las condiciones se los permiten (Withgott 2002). Esto hace

evidente que el manejo exitoso de los ecosistemas marinos depende del descubrimiento temprano de estos eventos y de sus causas.

Por otro lado, la familia Dictyotaceae tiene a nivel mundial aproximadamente 201 especies en 22 géneros (Guiry y Guiry 2012), de las cuales 27 especies, en siete géneros, se han informado para el PTO (Pedroche et al. 2005, Bernecker 2009, Guiry y Guiry 2012). Dentro de esta familia de algas pardas, los géneros más conspicuos y dominantes en las zonas intermareales y submareales de los trópicos y en particular del PTO son *Dictyota* y *Padina* (Dawson 1950b, Dawson y Beaudette 1959, De Clerck 2003), consistiendo de aproximadamente el 60% de la especies en esta familia. El éxito de estas algas está ligado a su capacidad de evitar el pastoreo de herbívoros, por lo que compiten con corales y otros organismos bénticos sésiles por espacio y luz (De Clerck et al. 2006). Es por esto, que para este estudio se escogieron estos dos géneros para su análisis taxonómico y biogeográfico.

Finalmente, la familia Corallinaceae a nivel mundial cuenta con aproximadamente 425 especies en 51 géneros (Guiry y Guiry 2012) y para el PTO han sido reportadas aproximadamente 40 especies en 13 géneros (Taylor 1945, Dawson 1957, 1960, 1961b, González-González 1993, Tejada 2007b). Esta familia está constituida por múltiples especies, todas fuertemente calcificadas y muy comunes en las regiones tropicales. Estos organismos juegan un papel especialmente importante en el arrecife, contribuyen en la formación de arena, produciendo carbonatos y en general en la consolidación del arrecife (Hoek van den et al. 1998). Dentro de esta familia el género *Amphiroa* es uno de los más conspicuos, encontrándose desde la zona intermareal hasta los 30 m, es por esto, que para este estudio se escogieron estos dos géneros para su análisis taxonómico y biogeográfico.

Objetivos Generales

1. Determinar el número de especies reportadas en el Pacífico de Centroamérica.
2. Evaluar la taxonomía de algunos géneros de las familias Caulerpaceae (Chlorophyta), Dictyotaceae (Phaeophyta) y Corallinaceae (Rhodophyta) en el Pacífico de Centroamérica comparando con otros sitios del Pacífico Tropical Oriental
3. Describir las tendencias en la distribución biogeográfica de los géneros seleccionados de las familias Caulerpaceae (Chlorophyta), Dictyotaceae (Phaeophyta) y Corallinaceae (Rhodophyta) dentro y fuera del Pacífico Tropical Oriental.

Objetivos Específicos

- 1.1. Realizar un catálogo taxonómico de las macroalgas del Pacífico de Centroamérica, con el fin de establecer una línea base de lo que existe a hasta el momento.
- 2.1. Validar los caracteres morfológicos de las familias selectas para esclarecer la taxonomía de las especies.
- 2.2. Analizar las unidades moleculares de las familias selectas y determinar si coinciden con las unidades morfológicas.
- 3.1. Determinar con base en el catálogo la distribución de la flora del Pacífico de Centroamérica y sus afinidades.
- 3.2. Describir la distribución de las especies y sus patrones biogeográficos a nivel mundial y latitudinal en el Pacífico Tropical Oriental.

ÁREA DE ESTUDIO Y COLECTA DE ESPECIMENES

Área de Estudio

El Pacífico Tropical Oriental, comprende desde el sur de Baja California, México, hasta Ecuador (Pennington et al. 2006), sin embargo, otros autores apuntan que su límite sur es el norte de Perú (Spalding et al. 2007). El PTO tiene una extensión de aproximadamente 8800 km de línea de costa, la cuál es muy heterogénea y conformada por golfos, bahías, playas arenosas y rocosas e islas, entre otros accidentes geológicos. Debido a esta particularidad y sus características oceanográficas, la costa del PTO se caracteriza por poseer importantes ecosistemas estuarinos, extensos bosques de manglar, zonas intermareales, arrecifes de coral de desarrollo limitado, bosques de algas, camas de rodolitos y un limitado desarrollo de pastos marinos.

Los principales disturbios naturales que afectan el ETP: el calentamiento de aguas debido al fenómeno de El Niño y los afloramientos costeros de aguas frías con nutrimentos. Las temperaturas promedio de esta región pueden ser extremas durante el evento de El Niño (más de 33°C) o frías (hasta 12°C) durante el afloramiento. Este último fenómeno ocurre cuando los vientos alisios del noreste cruzan las zonas bajas del continente desde al Caribe hasta el Pacífico (Legeckis 1988; McCreary et al. 1989, Cortés 2007), lo que produce el desplazamiento de aguas superficiales en la tres zonas: zona sur México (afloramiento de Tehuantepec), entre el sur de Nicaragua y norte de Costa Rica (afloramiento de Papagayo) y en la zona del golfo de Panamá (afloramiento de Panamá) (Fig.1). Estos cambios de nutrimentos y temperatura tienen efectos directos en la composición y abundancia de las macroalgas marinas en las zonas costeras (Glynn y Stewart 1972, Fernández 2007). Para este estudio se colectaron algas marinas de un total de 107 sitios de la costa de México y de Centroamérica. Del total de sitios, 29 fueron México, 17 en El Salvador, 17 en Nicaragua, 22 en Costa Rica y 17 en Panamá (Fig. 2).

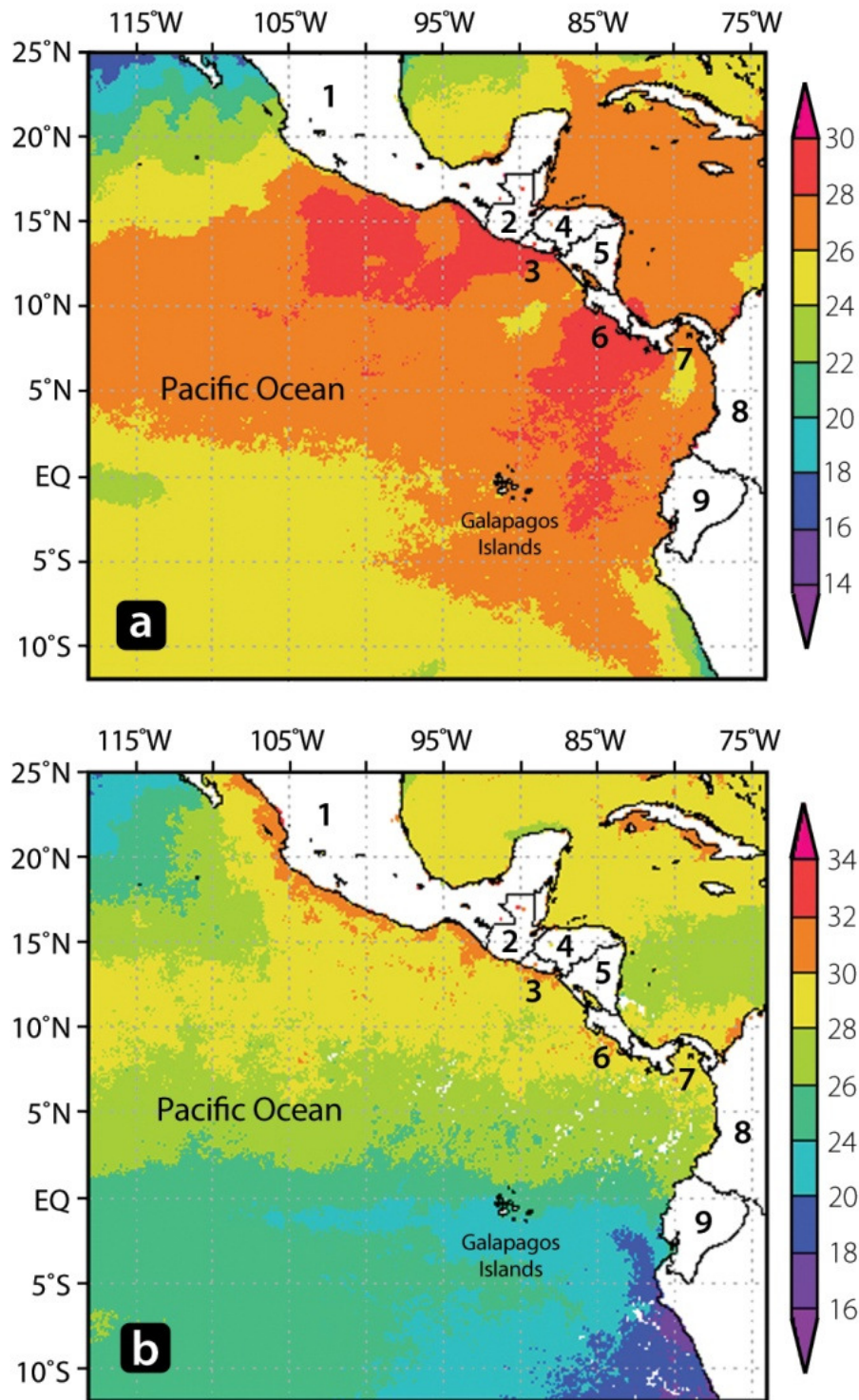


Fig.1. Mapa del Pacífico Tropical Oriental y temperatura superficial mensual. A) Febrero 2008, estación de afloramiento y, B) Julio 2008. 1-México, 2- Guatemala, 3- El Salvador, 4- Honduras, 5-Nicaragua, 6- Costa Rica, 7- Panamá, 8- Colombia, 9- Ecuador. Modificado de la NASA Giovanni (www.giovanni.gfsc.nasa.gov).

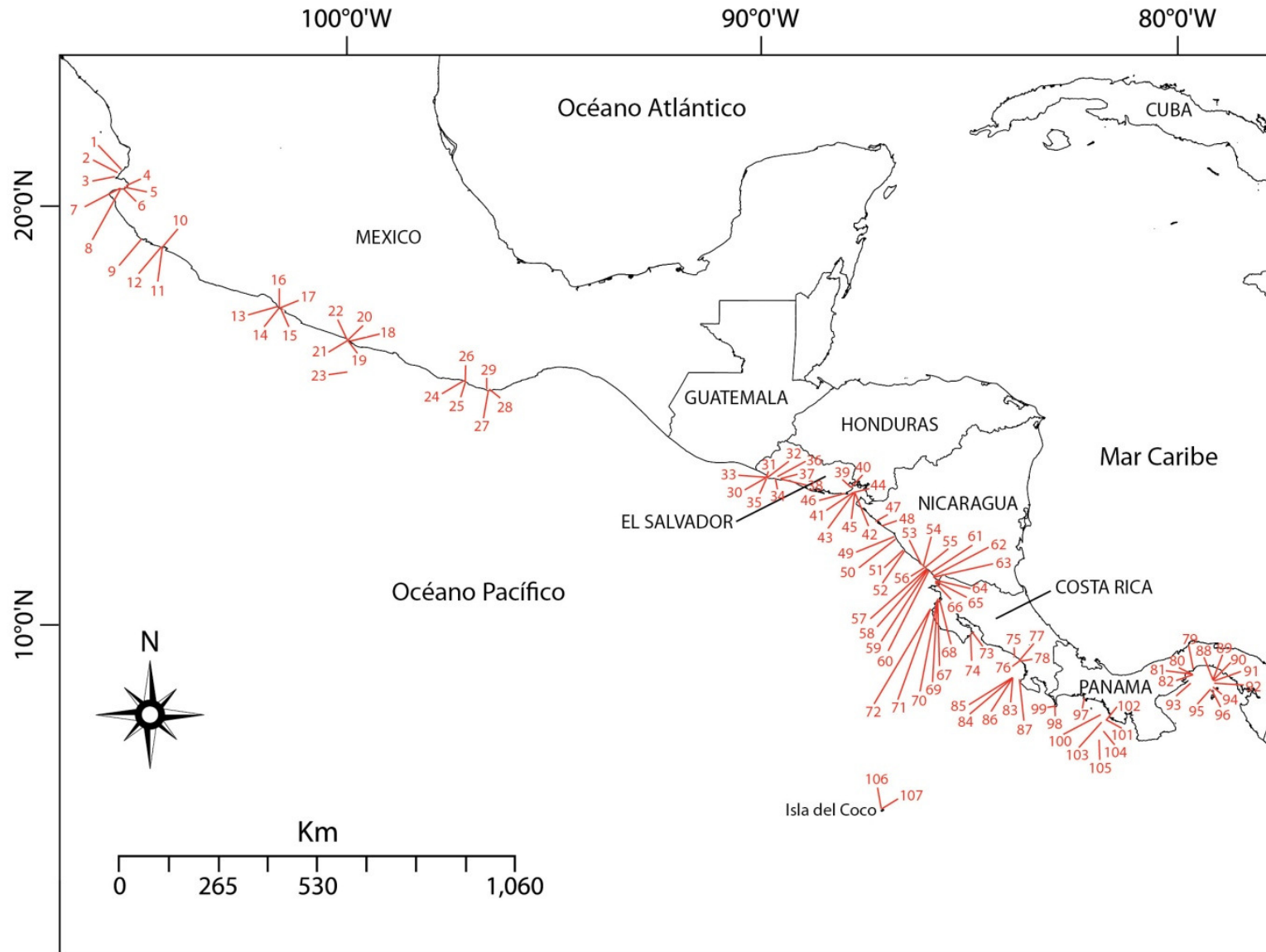


Fig. 2. Mapa de sitios de colecta

Cuadro 1. Sitios de colectas nuevos en Centroamérica y el Pacífico Tropical Mexicano

País	# Mapa	Sitio
México	1	Nayarit: Lo de Marcos: playa en Lo de Marcos
	2	Nayarit: Sayulita: Punta los Muertos
	3	Playa Careyero, Pta Mita, Puerto Vallarta
	4	Bajo del Cristo, cerca de los arcos, Puerto Vallarta
	5	Playa Mismaloya, Puerto Vallarta
	6	Colomitos, Puerto Vallarta
	7	Majahuitas, Puerto Vallarta
	8	Caletas, Puerto Vallarta
	9	Playa Tenacatita
	10	Playa La Audiencia, Manzanillo
	11	Julupan (Islote), Manzanillo
	12	Roca Elefante, Manzanillo
	13	Playa del Palmar, Ixtapa
	14	Playa Las Gatas, Zihuatanejo
	15	Manzanillo, Zihuatanejo
	16	Caleta de Chon, Zihuatanejo
	17	Caletota, Zihutanejo
	18	Isla de la Virgen
	19	Otro lado del canal (continente)
	20	NW de la Isla Roqueta 1
	21	NW Isla Roqueta
	22	NW de la Isla Roqueta 3
	23	NW de la Isla Roqueta 2
	24	Puerto Escondido 2
	25	Puerto Escondido 1
	26	Puerto Angelito
	27	Togolunda, Bahía de Huatulco
	28	Playa El Panteon, Puerto Angel, Oaxaca
	29	Mazunte
El Salvador	30	Frente al Hotel De cameron, Poza salinas, Los Cóbános
	31	Playa El Privado, Los Cóbános
	32	Playa El Faro, Los Cobanos
	33	La Loredona, Los Cobanos
	34	El Pital, La Libertad
	35	La Pared, Los Cobanos

País	# Mapa	Sitio
El Salvador	36	Punta del monte, Los Cóbano
	37	La Vega, La Libertad
	38	Playa escondida, La Libertad
	39	Chiquirin, Golfo de Fonseca
	40	Isla Zacatillo, Golfo de Fonseca, La Unión
	41	Suroeste Isla Meanguera
	42	Pirigallo Oeste, Golfo de Fonseca, La Unión
	43	Pirigallo Este, Golfo de Fonseca, La Unión
	44	Isla Meanguera, Playa Mahaua, Golfo de Fonseca, La Unión
	45	Pirigallo Sur, Golfo de Fonseca, La Unión
	46	Playa Maculiz
Nicaragua	47	Isla El Cardón, Puerto Corinto, Chinandega
	48	Poneloya, León
	49	Playa Hermosa, León
	50	Playa El Tránsito, León
	51	Masachapa, Managua
	52	Pochomil, Managua
	53	El Hueco
	54	Gigante
	55	Guacalito
	56	La Anciana
	57	Punta El Clavo
	58	Costa Blanca
	59	Marsella, Rivas
	60	El Toro, Rivas
	61	La Peña Rota, Rivas
	62	La Flor, San Juan del sur
	63	La Cagada, San Juan del Sur
Costa Rica	64	Isla Bolaños, Bahía Salinas
	65	La Paloma, Bahía Salinas
	66	Isla Despensa, Bahía Salinas
	67	Bahía Virador, Bahía Culebra
	68	Punta Arenita, Bahía Culebra
	69	La Penca, Bahía Culebra
	70	Cacique, Bahía Culebra
	71	Los Conejos, PNM Baulas

País	# Mapa	Sitio
Costa Rica	72	Cabo Vela, PNM Baulas
	73	Isla Negritos, Golfo de Nicoya
	74	Tolinga, Lado Sur de Islas Tortugas, Golfo de Nicoya
	75	Punta Domaticalito
	76	Bajo Tres Hermanas, PNMB
	77	Isla Ballena, costado sur, PNMB
	78	Roca Tres Hermanas, PNMB
	83	El Jardín, Isla del Caño
	84	Catarata 1, Isla del Caño
	85	La Cueva del Tiburón, Isla del Caño
	86	Catarata 2, Isla del Caño
	87	San Josecito
	106	Bahía Weston, Isla del Coco
	107	Punta Ulloa, Isla del Coco
Panama	79	Playa Culebra
	80	Isla Taboguilla
	81	Isla Taboga
	82	Isla Urabá
	88	Isla Pacheca
	89	Islotes antes de Saboga
	90	Isla Saboga
	91	Isla Contadora
	92	Isla Mogo-Mogo
	93	Otoque Sur
	94	Isla Bayoneta
	95	Islote Trapiche, Isla Pedro González
	96	Playa Don Bernardo, Isla Pedro Gonzalez
	97	Playa Hermosa, Chiriquí Panama
	98	Punta Burica
	99	Isla Burica
	100	Isla Uva, Golfo Chiriqui
	101	Canales de afuera
102	Isla Canales de Afuera, NE end, Golfo de Chiriquí	
103	Coiba Noreste	
104	Bahia Damas	
105	Jicarita	

Colecta de especímenes

La recolecta de las macroalgas se realizó a nivel submareal por medio de buceo SCUBA y a nivel intermareal. Las algas fueron removidas del sustrato manualmente o por medio de una cuchilla y fueron colocadas en bolsas plásticas. Parámetros como la profundidad, tipo del sustrato, así como la ubicación específica de la muestra dentro del hábitat fueron tomados en el momento de la recolección. Con una parte de los especímenes colectados se procedió a fijarlos con una solución de formalina al 4% en agua de mar, asimismo se realizaron réplicas secas que fueron depositadas en los Herbarios de cada país y replicas para otros herbarios de la región. Otra parte de las muestras se colocará en bolsas plásticas con 20-30 g de cristales de silica gel para su posterior análisis molecular.

Herbarios Consultados

Aunado a las colectas, se visitaron los herbarios de la región y los que cuentan con colecciones importantes para este estudio, citados a continuación:

- Herbario de la Universidad de Berkeley, California (UC)
- Herbario de la Universidad de Michigan, Michigan (MICH)
- Herbario de la Universidad de Costa Rica, San José (USJ)
- Herbario Nacional de Costa Rica, San José (CR)
- Herbario de la Universidad de El Salvador, San Salvador (ITIC)
- Herbario de la Universidad de Panamá, Panamá (PMA)

**CATÁLOGO DE LAS MACROALGAS MARINAS DEL PACÍFICO DE
CENTROAMÉRICA¹****Checklist of the Pacific Marine Macroalgae of Central America**

Resumen: El conocimiento de la diversidad de flora marina del Pacífico de Centroamérica es limitado debido a la corta historia de investigación en esta área temática y a la falta de especialistas en macroalgas marinas a lo largo de esta amplia región. Esto ha dejado como resultado una falta de actualización taxonómica de aproximadamente 60 años para muchos de los grupos de macroalgas. El listado que se presenta está basado en registros publicados en artículos, tesis de estudiantes y reportes oficiales. En total se reportan 379 especies de macroalgas, así como 16 taxa cuya distribución es dudosa para esta región. Las algas rojas (Rhodophyta) presentaron el mayor número de especies (252), seguidas por las algas verdes (Chlorophyta: 81), y las algas pardas (Phaeophyceae: 46). El país con el mayor número de reportes fue Costa Rica con 216 especies, seguido por Panamá con 174, El Salvador con 146, Nicaragua con 24, y Guatemala con 16. Hasta el momento, por la falta de estudios, no se han registrado macroalgas marinas para la costa Pacífica de Honduras. El análisis del número de especies reportadas por grado latitudinal de la costa Centroamericana, nos muestra que el número de especies varía entre los países y localidades, por diferencias en la geomorfología y la heterogeneidad de hábitats de la costa, así como la intensidad en el esfuerzo de investigación que se ha llevado a cabo.

Abstract: Our present knowledge of marine macroalgae diversity for the Central American Pacific coast is limited by the short history of investigations (ca. 100 years) and few algal specialists through a large geographical area. While recent checklists have emerged for other regions of the eastern Pacific, there have been virtually no attempts to inventory macroalgal diversity for the Pacific of Central America. This checklist of the marine macroalgae was developed based on published scientific literature and unpublished records in student theses. A total of 379 species records are regarded as current valid names of marine macroalgae. The red algae (Rhodophyta) had the highest species number (252 species), followed by green algae (Chlorophyta: 81 species) and brown algae (Phaeophyceae: 46 species). The country with the greatest diversity of marine macroalgae is Costa Rica with 216 species, followed by Panama with 174 El Salvador with 146, Nicaragua with 24, and Guatemala with 16. At present there are no published records for the Pacific coast of Honduras. Variation in number of species throughout the Pacific coast of Central America is likely due to differences in geomorphology, habitat heterogeneity among national coastal-marine zones, and to unbalanced research efforts.

Key Words: Chorophyta, Eastern Tropical Pacific, marine floristics, Phaeophyceae, Rhodophyta

¹ Publicado como: Fernández-García, C., Riosmena-Rodríguez, R., Wysor, B., Tejada, O. & Cortés, J. 2011. Checklist of the Pacific Marine Macroalgae of Central America. *Bot. Mar.* 54: 53-73 (Fig. S1).

Introduction

Knowledge of marine macroalgal diversity for the Central American Pacific coast (CAP) is limited by a short history of investigations (ca. 100 years) and few algal specialists throughout a large geographical area (~3829 km from Guatemala to Panama). While recent checklists have emerged for other regions of the eastern Pacific, to the north (González-González 1993, González-González et al. 1996, Riosmena-Rodríguez 2005, Payri et al. 2008) and south (Schnetter and Bula-Meyer 1982, Bula-Meyer 1995, Garske 2002), there have been virtually no attempts to inventory macroalgal diversity for the CAP. Such inventories are useful starting points for investigations of algal evolution and biogeography and are essential to monitoring efforts that seek to determine the impacts of global climate change or synanthropic transport of species, to name but two. Given the availability of Wynne's (2005) exhaustive catalogue of western Atlantic macroalgal diversity and known or projected disturbances to the Central American landscape (climate change, coastal infrastructure, expansion of the Panama Canal), a checklist Pacific Central American algae is both timely and essential.

The history of algal exploration through CAP can be divided into three stages: 1) regional exploration and documentation, 2) species checklists by country, and 3) sampling for DNA-based diversity assessments.

The first stage commenced in 1909 with Marshall Avery Howe's "*Botanical visit to the Isthmus of Panama*". During a one-week visit to the Pacific coast, Howe (1910) collected upwards of 50 species of closely encrusting, minutely filamentous and unicellular forms of marine algae, but he seemed more impressed by the apparent paucity of macroalgae at that latitude than by those that he actually encountered. Numerous later works (Grunow 1915-1916, Lemoine 1929, Setchell 1937, Setchell and Mason 1943), especially those derived from the Allan Hancock Expeditions aboard the *Velero III* (Dawson 1944, 1949, 1950a, 1950b, 1950c, 1953, 1955, 1962c, Taylor 1945, Chou 1947) and those of Dawson (Dawson 1957, 1959, 1960, 1961a, 1961b, 1962a, 1962b, Dawson and Beaudette 1959) would reveal a much more species-rich marine flora. Dawson's

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(1962b) illustrated taxonomic key documented 235 species of benthic macroalgae (167 Rhodophyta, 46 Chlorophyta and 22 Phaeophyceae) based on observations made in El Salvador, Nicaragua, Costa Rica and Panama. This work remains the only regional account of marine floristic diversity for CAP to date. The untimely death of Dawson in 1966 (Hawkes 1966) marked the end of the first stage of CAP phycology, a time period in which over 50% of the known algal taxa for the CAP were listed in the literature (Figs. 1.1, 1.2).

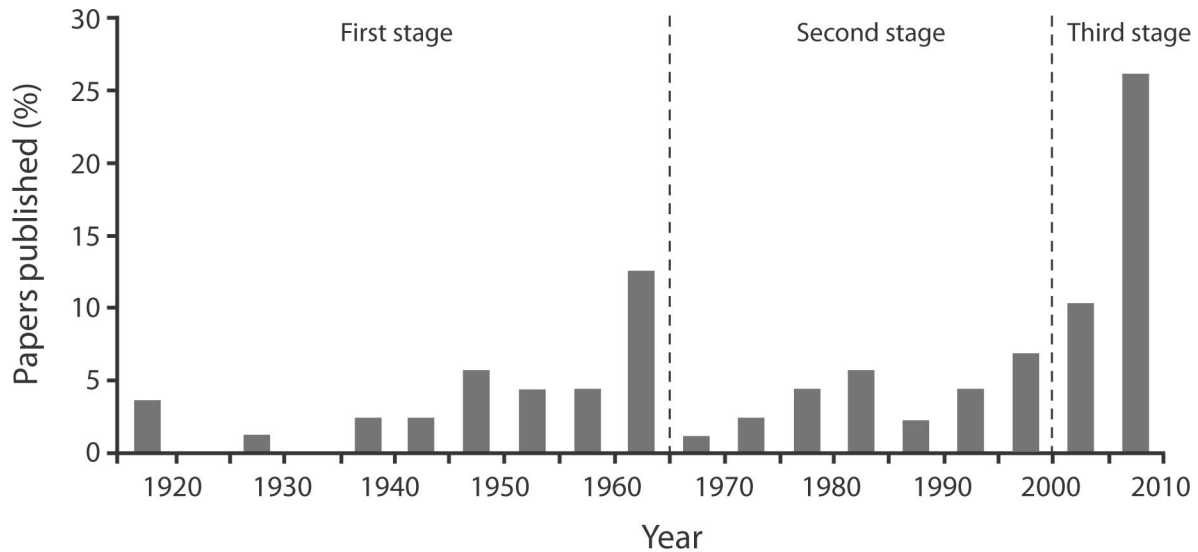


Fig. 1.1 Percentage of papers on marine macroalgae of the Pacific of Central America.

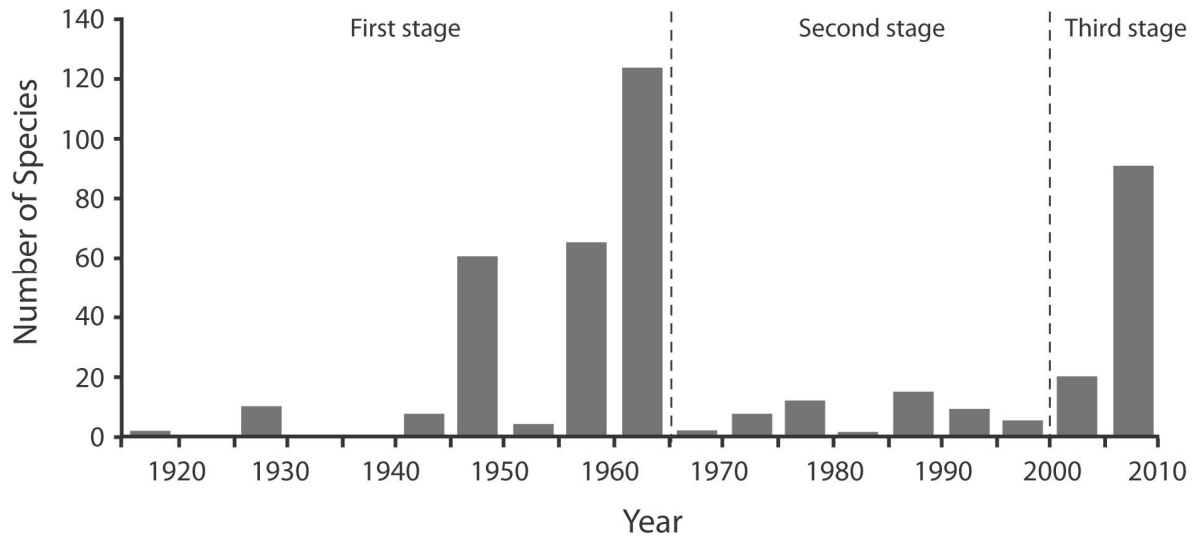


Fig. 1.2. Number of species of marine algae reported for the first time in each year.

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The second stage of algal diversity assessments in the CAP spanned more than three decades from 1965 to 1998. Numerous national marine floristic surveys were undertaken (Guatemala: Bird and McIntosh 1979, Dreckmann et al. 1998; El Salvador: Áviles and Canjura 1979, Gutiérrez 1985; Castro-Avilés and Tejada 1993; Costa Rica: Soto and Bermúdez 1990, Cortés 1993; Panama: Earle 1972). With the advent of SCUBA, deeper collections and ecological studies were also initiated (Glynn and Stewart 1973, Villalobos 1980, Gutiérrez 1985, Glynn 1990, Glynn and Maté 1997). This second stage of phycological investigation presented species records representing 23% of known algal number (Fig. 1.2).

The third stage of Central American phycology, characterized by molecular assisted assessments of algal diversity, commenced in 1999 and continues through today. During the last 12 years, some species, many of them identified by Dawson, have been included in molecular systematic studies (Hillis 1999, 2001, Zuccarello and West 2002, Gurgel et al. 2003, Kamiya et al. 2003, Zuccarello and West 2003, 2006, Gurgel and Fredericq 2004, Santelices 2004, Andreakis et al 2007, Leliaert et al. 2008). Moreover, between 2000 and 2009, more systematic and ecological studies were undertaken with new specimens collected in the Pacific region of Central America (Karsten et al. 2000, Tejada 2002, Wysor 2004, Fernández and Cortés 2005, Bezy et al. 2006, Sibaja-Cordero 2005, 2008, Tejada and Vieyetz 2006, Tejada 2007b, Fernández 2008, Fernández and Alvarado 2008, Littler and Littler 2008, 2009, Sibaja-Cordero and Cortés 2008, Bernecker 2009, Bernecker and Wehrtmann 2009).

The advent of SCUBA during the second phase of Central America phycology facilitated profound changes in the understanding of algal richness throughout the CAP at that time. Similarly, the advent of molecular tools in the current era of Central American phycology has fundamentally altered concepts of algal diversity that are amenable to testing in an evolutionary context. Not only can morphological stasis and phenotypic plasticity be evaluated in order to account for all species present, but the timing of isthmian emergence provides a geological timeframe in which speciation could have taken place (Lessios 1999, 2001). These questions are the target of continuing research in the area (e.g., C. Fernandez,

W. Freshwater, and B. Wysor unpublished data) and emphasize the need for a modern synthesis of algal species number in the CAP. This paper attempts to document and update the only previously published account (i.e., Dawson 1962b) of marine algal species number in the region, a necessary prerequisite for studies of evolutionary biology and ecology, and marine resource management.

Materials and methods

Geographical scope

The Central American Pacific coast is located in the eastern tropical Pacific (ETP), encompasses coastal and oceanic zones from Guatemala to Panama, including the offshore Isla del Coco (=Cocos Island) (Costa Rica) about 500 km southwest of Costa Rica (Fig. 1.3). The approximately 3829 km of coastline (Alvarado et al. 2010) is environmentally heterogeneous and includes important marine and estuarine ecosystems, such as extensive mangrove forests, rocky intertidal zones, coral reefs, turf algal beds, algal forests, rhodoliths beds, and extensive crustose coralline algal cover (Fig 1.4). Seagrass beds, which are common in shallow coastal ecosystems at similar latitudes elsewhere, are absent from this region, although patches of *Ruppia maritima* Linnaeus are known in isolated locations (Cortés 2007).

The CAP is both seasonally and episodically dynamic due to seasonal upwelling and El Niño-Southern Oscillation (ENSO) warming events, respectively. Upwelling occurs when northeast trade winds cross Central American lowlands from the Caribbean to the Pacific (Legeckis 1988; McCreary et al. 1989, Jiménez 2001). This results in depressed sea surface temperatures in the Gulf of Papagayo and Gulf of Panama, and elevated nutrient concentrations (i.e., nutrient concentrations can be 2-8 fold higher in upwelling regions than in other locations, Fernández 2007, Sunagawa et al. 2008, Alvarado et al. 2009); however, a warm (>30°C) pool of water is present between these gulfs where high mountains divert the trade winds that otherwise push coastal waters offshore (McClain et al. 2002; Fiedler and Talley 2006; Cortés 2007). Seasonal upwelling may be interrupted for

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periods of 6-18 months in the CAP (Glynn 1988) by episodic ENSO warming events, which occur every 4-7 years. During such times, cool, nutrient-rich upwelled waters are replaced by warm nutrient-depleted waters from a westward flowing equatorial current (Glynn 1988). Sea surface temperature range throughout the region is, consequently, very broad; temperatures can reach as high as 33°C during ENSO events and as low as 12°C during seasonal upwelling (Cortés 2007).

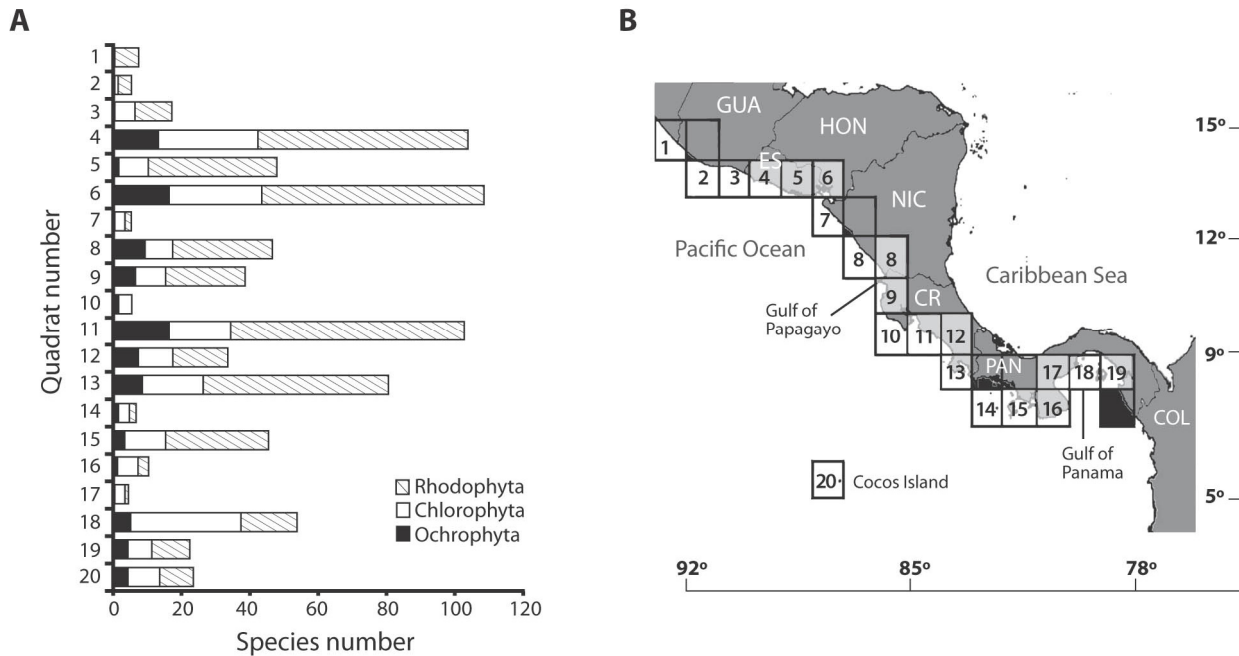


Fig. 1.3. Number of species of Rhodophyta, Chlorophyta and Ochrophyta-Phaeophyceae in each latitudinal quadrat of the Pacific coast of Central America. 1, 2, 3- Guatemala Pacific coast, 4- Sonsonate (including Los Cobanos National Park)- La Libertad coast, 5- La Paz and Usulután coast, 6- Gulf of Fonseca (including islands), 7- North Pacific of Nicaragua, 8- South Pacific of Nicaragua and Salinas Bay in Costa Rica, 9- North Pacific of Costa Rica (from Santa Elena Peninsula to Ostional), 10- Outside the Nicoya Peninsula, 11- Nicoya Gulf and central Pacific of Costa Rica (in part), 12- Central Pacific: Marino Ballena National Park, northeast part of Térraba-Sierpe mangrove, 13- South Pacific of Costa Rica: Térraba Sierpe mangrove forest, Caño Island and Golfo Dulce, 14- Islands of the Gulf of Chiriqui (in part), 15- Islands of Chiriqui Gulf and Honda Bay, 16- Azuero Peninsula, 17- Parita Bay, 18- Panama Bay and Perlas Islands (in part), 19- Perlas Islands, 20- Isla del Coco.

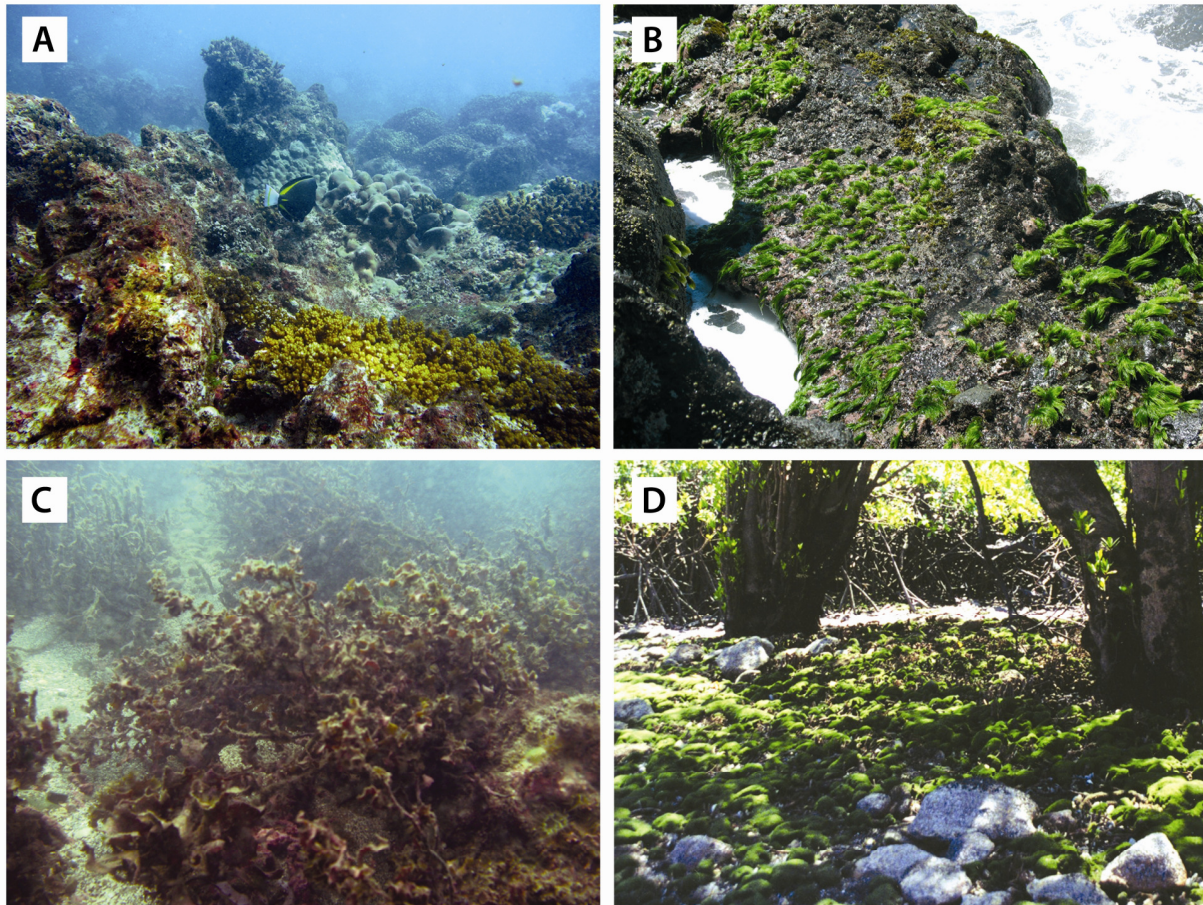


Fig. 1.4. Different algal habitats in the Pacific of Central America. A) Turf algae in coral reef, Caño Island, Costa Rica. Field: ~ 3 m across. B) Intertidal rocky shore, La Vega, El Salvador. Field: ~3.5 m across. C) *Sargassum* forest, San Juan del Sur, Nicaragua. Field: ~ 1.5 m across. D) Mangrove floor, Aguadulce, Panama. Field: ~1.5 m across.

The dynamic conditions of nutrients and temperature have direct effects on the composition and abundance of the organisms in areas across the region (Fernández 2007). For example, reduced temperatures in the Gulf of Panama during upwelling were correlated with decreased growth in some reef building corals (due perhaps to physiological response of the coral, or to reduced feeding rates). The combination of reduced coral competition,

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availability of new space (i.e., dead coral), and enhanced nutrient concentrations favored the growth of benthic algae during periods of upwelling (Glynn and Stewart 1973, Glynn and Maté 1997). Similarly, Fernández (2007) showed that the green alga *Caulerpa sertularioides* (S.G Gmelin) M.A. Howe had increased growth rates during periods of upwelling in the Gulf of Papagayo in Costa Rica.

Arrangement of the list

This checklist is based mainly on an exhaustive published literature search. We also included information from unpublished students theses and official government reports, however we excluded species reported only in this literature and included them in a separated list of unconfirmed records. Also in the unconfirmed records list we included records requiring taxonomic revision and/or further taxonomic clarification in order to establish CAP distribution.

Systematic arrangements of the Ochrophyta-Phaeophyceae, Chlorophyta and Rhodophyta follow Wynne (2005). The taxa (genera and species) within each phylum/class are arranged alphabetically.

Taxa are listed as originally reported in the literature. When no specific locality is available we refer to it as Central America. For each taxon, distribution is reported by country and numbers in parentheses refer to the references list (see consecutive numbers in boldface after the references):

Current name Author: Distribution (Reference #).

If the taxon reported is not a current name, it is followed in brackets by the current name and reference to synonymy:

Synonym Author [=*Current name* Author, Synonymy reference]: Distribution (Reference #)

When different authors report current names and synonymies, we list the current name, followed by the distribution and when authors cite a synonym, the reference number will be followed by the name reported and the synonymy reference:

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Current name Author: Distribution (Reference # that cited as current name)
(Reference # cited as *Synonym*, Synonymy reference)

When a current name is not reported and two authors cited synonyms of it, we include both synonymies separately and count only the current name for the species number estimate. This is the case for *Ulva paradoxa/Enteromorpha plumosa* and *Galaxaura arborea/Galaxaura spathulata*.

Species records with an asterisk (*) are those for which the genus has been reviewed, but for which Central American species require further taxonomic scrutiny in order to establish names validity. These species are included in the species number estimate for the CAP.

Statistical analyses

To estimate expected species number in Pacific Central America for future investigations, we built a matrix of species presence (1) and absence (0) for each country and we calculated the estimator Chao 2 (Chao Estimator \pm Variance) (Chao 1987), and traced the cumulative curves of new species reported by year in each phylum/class of macroalgae. For all statistical analyses we used the list of species regarded as current names.

The Central America Pacific coast (including Isla del Coco) was divided into a series of 20 quadrants based on a grid of 1° latitude by 1° longitude (Fig. 1.3). Quadrants with a short length of coastline and one collecting site were merged with neighbouring cells. Quadrants with no collecting sites were eliminated from the analyses and were marked in black on the map (Fig. 1.3). Quadrants were numbered sequentially from north (Guatemala) to south (Panamá and Isla del Coco).

The average taxonomic distinctness (Δ^+) and its variance (Λ^+) (Clarke and Warwick 2001) were estimated as a measure of diversity for each country. This index measures the taxonomic distance between each pair of individuals, as defined by a Linnaean classification tree (Clarke and Warwick 2001). We used six taxonomic levels based on Wynne (2005): species, genus, family, order, class and phylum, with the following weights

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ω = 16.7 (species in the same genera), 33.3 (same family but different genera), 50 (same order but different family), 66.7 (same class but different order), 83.3 (same class different phylum), and 100 (different phylum). The genera *Asteronema* and *Pilinia* were excluded from this analysis because of uncertain taxonomic position (Wynne 2005). The statistical analyses were performed with Systat 8.0 (SYSTAT 1998), PRIMER 6.0 (Clarke and Gorley 2005) and Past 1.83 (Hammer et al. 2001) software packages.

Checklist

Ochrophyta-Phaeophyceae

Chnoospora implexa J. Agardh: Costa Rica (6, 19, 22), Panama [56a as *Chnoospora pannosa* J. Agardh, Abbott and Huisman 2004], Central America (25)

Chnoospora minima (K. Hering) Papenfuss: El Salvador (5, 9, 23, 45, 77, 80), Central America (25)

Colpomenia mollis W.R. Taylor: Panama (56a)

Colpomenia phaeodactyla M.J. Wynne et J.N. Norris: Costa Rica (60, 85)

Colpomenia peregrina Sauvageau: Panama (56a)

Colpomenia ramosa W.R. Taylor: Costa Rica (6, 19, 22, 74, 75, 85), Panama (56a), Central America (25, 60)

Colpomenia sinuosa (Mertens ex Roth) Derbès et Solier: El Salvador (9, 77, 80), Costa Rica (6, 11, 19, 22, 74, 70, 72, 75), Panama (32, 56a), Central America (25)

Dictyopteris delicatula J.V. Lamouroux: Costa Rica (34), Central America (25)

Dictyopteris repens (Okamura) Børgesen: El Salvador (5, 23, 45, 77), Costa Rica (6, 19, 22), Panama (56a), Central America (25)

Dictyota binghamiae J. Agardh: Costa Rica (6), Panama (56a, 75)

Dictyota concrescens W.R. Taylor: Panama (56a)

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- Dictyota crenulata* J. Agardh: Costa Rica (6, 19, 22, 74, 75), Central America (15, 25, 60)
- Dictyota flabellata* (Collins) Setchell et N.L. Gardner: Costa Rica (15, 19, 70, 72, 74, 75), Panama (1, 15, 32, 56a), Central America (60, 87, 75)
- Dictyota friabilis* Setchell: El Salvador (77), Costa Rica (6, 19, 22), Central America (25)
- Dictyota humifusa* Hörnig, Schnetter et Coppejans: Panama (56a)
- Dictyota masonii* Setchell et N.L. Gardner: Costa Rica (6, 21, 22), Central America (25)
- Dictyota major* W.R. Taylor: Panama (56a)
- Dictyota stolonifera* Dawson: Nicaragua (24, 30), Costa Rica (6, 11, 24, 30,34), Panama (56a)
- Dilophus pinnatus* E.Y. Dawson [=*Dictyota pinnata* (E.Y. Dawson) Hörnig Schnetter et Prud'homme van Reine, Hörning et al. 1993]: El Salvador (45, 77)
- Ectocarpus breviarticulatus* J. Agardh [=*Asteronema breviarticulatum* (J. Agardh) Ouriques et Bouzon, Ouriques and Bouzon 2000]: El Salvador (5, 23, 45, 77), Costa Rica (74, 83), Central America (25)
- Feldmannia indica* (Sonder) Womersley et A. Bailey: Costa Rica (83 as *Ectocarpus indicus* Sonder, Womersley and Bailey 1970), Panama (56a), Central America (25, as *Ectocarpus indicus*)
- Giffordia rallsiae* (Vickers) W.R. Taylor [=*Ectocarpus rallsiae* Vickers, Wynne 2005]: Panama (41)
- Hincksia mitchelliae* (Harvey) P.C. Silva: Costa Rica (6a), (11 as *Giffordia mitchelliae* (Harvey) G. Hamel, Silva et al. 1987), Panama (41 as *Giffordia mitchelliae*)
- Hydroclathrus clathratus* (C. Agardh) M. Howe: Central America (25)
- Kuetzingiella elaschistaeformis* (Heydrich) M. Balakrishnan et Kinkar: Panama (56a)
- Lobophora variegata* (J.V. Lamouroux) Womersley ex E.C. Oliveira: El Salvador (23, 45, 77 as *Pocockiella variegata* (J.V. Lamouroux) Papenfuss, Oliviera 1977), Nicaragua (24 as *Pocockiella variegata*), Costa Rica (6, 34, 38), (19, 22 as *Pocockiella variegata*), Panama (32), Central America (25)
- Padina conrescens* Thivy: Panama (56a)

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Padina crispata Thivy [= *Padina mexicana* Dawson, Riosmena-Rodríguez et al. 2009]: El Salvador (4, 9, 23, 45, 77, 80), Costa Rica (4, 6, 11, 19, 34, 74, 75), Panama (22, 56a), Central America (25, 60, 75)

Padina durvillaei Bory: Nicaragua (24), (24 as *Padina caulescens* Thivy, Riosmena-Rodríguez et al. 2009), Costa Rica (6, 11, 12, 19, 74, 75) (6, 19, 22 as *Padina caulescens*), Panama (75, 56a), Central America (25, 87) (25 as *Padina caulescens*)

Padina fraseri (Greville) Greville: Panama (56a)

Padina pavonica (Linnaeus) Thivy: El Salvador (77, 80)

Padina vickersiae Hoyt [= *Padina gymnospora* (Kützinger) Sonder, Allender and Kraft 1983]: El Salvador (5, 9, 45, 77, 80)

Pilinia lunatae Collins: Panama (22, 32, 75), Central America (25)

Ralfsia pacifica Hollenberg: El Salvador (45, 77)

Ralfsia verrucosa (Areschoug) Areschoug: El Salvador (45, 77)

Rosenvingea intricata (J. Agardh) Børgesen: Costa Rica (6a, 34, 58)

Rosenvingea orientalis (J. Agardh) Børgesen: Costa Rica (6, 21, 22), Central America (25)

Sargassum brandegeei Setchell et N.L. Gardner: Costa Rica (75)

Sargassum camouii E.Y. Dawson [= *Sargassum sinicola* Setchell et N.L. Gardner subsp. *camouii* (E.Y. Dawson) J.N. Norris et Yensen, Norris 2010]: Nicaragua (24)

Sargassum liebmannii J. Agardh: El Salvador (5, 9, 23, 45, 77, 80), Nicaragua (24), Costa Rica (6, 11, 12, 19, 68, 74, 84), Panama (22, 75), Central America (25, 87)

Sargassum liebmannii J. Agardh var. *nicoyana* Grunow: Costa Rica (22, 42, 68)

Spatoglossum ecuadorenum W.R. Taylor: Panama (56a)

Spatoglossum howellii Setchell et N.L. Gardner: Nicaragua (24)

Sphacelaria novae-hollandiae Sonder: El Salvador (45, 23, 77), Costa Rica (19, 22), Central America (25, 60)

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Sphacelaria rigidula Kützing: Costa Rica (6, 11, 19) (22, as *Sphacelaria furcigera* Kützing, Prud'homme van Reine 1982), Panama (56a), Central America (25, as *Sphacelaria furcigera*)

Sphacelaria tribuloides Meneghini: Costa Rica (6a)

Chlorophyta

Acetabularia pusilla (M. Howe) Collins [= *Parvocaulis pusillus* (Howe) S. Berger et al., Berger et al. 2003]: Panama (32, 40, 86)

Acicularia shenkii (K. Möbius) Solms-Laubach [= *Acetabularia shenkii* K. Möbius, Berger et al. 2003]: Panama (86)

Boodlea composita (Harvey) F. Brand: El Salvador (45, 77) (77 as *Boodlea siamensis* Reinbold, Guiry and Guiry 2010), Costa Rica (6, 19, 35) (22 as *Boodlea siamensis*), Panama (86), Central America (25 as *Boodlea siamensis*)

Boodleopsis pusilla (Collins) W.R. Taylor, A.B. Joly et Bernatowicz: El Salvador (80)

Boodleopsis verticillata E.Y. Dawson: El Salvador (78, 79, 80), Costa Rica (6, 6a, 11, 35, 76, 79), Panama (21, 22, 32, 86), Central America (25)

Bryopsis galapagensis W.R. Taylor: El Salvador (80), Central America (25)

Bryopsis hypnoides J.V. Lamouroux: El Salvador (5, 77), Panama (22, 32, 86, 75), Central America (25)

Bryopsis pennata J.V. Lamouroux: El Salvador (5, 23, 45, 77, 80), Costa Rica (6a, 11, 19, 22, 34, 35, 74), Panama (56a, 86), Central America (25)

Bryopsis pennata var. *leprieurii* (Kützing) Collins et Hervey: Costa Rica (6)

Bryopsis rhizophora M. Howe: Panama (86)

Bryopsis salvadoreana E.Y. Dawson: El Salvador (5, 23, 45, 77), Panama (56a, 86), Central America (25)

Caulerpa cupressoides (West) C. Agardh var. *lycopodium* Weber-van Bosse: Central America (25)

Caulerpa macrophysa (Sonder ex Kützing) G Murray: Panama (56a)

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Caulerpa microphysa (Weber van Bosse) Feldmann: Panama (32, 86)

Caulerpa nummularia Harvey ex J. Agardh: Panama (56a)

Caulerpa racemosa (Forsskål) J. Agardh: El Salvador (5, 45, 77) (45, 77, 80 as *Caulerpa racemosa* var. *uvifera* (C. Agardh) J. Agardh, Wynne 2005), Costa Rica (6a, 11, 35), Panama (32, 39, 40, 86)

Caulerpa racemosa var. *peltata* (J.V. Lamouroux) Eubank: El Salvador (5, 23, 45, 77, 80) (77 as *Caulerpa peltata* J.V. Lamouroux, Wynne 2005), Costa Rica (6, 19) (11, 35, 74 as *Caulerpa peltata*), Panama (86) (32, 40 as *Caulerpa peltata*), Central America (25) (25 as *Caulerpa racemosa* var. *laetevirens* (Montagne) Weber-van Bosse, Wynne 2005)

Caulerpa serrulata (Forsskål) J. Agardh: Costa Rica (34, 35), Panama (56a, 86)

Caulerpa sertularioides (S.G. Gmelin) M. Howe: Nicaragua (24), Costa Rica (7, 33, 35, 36, 37, 73), Panama (32, 40, 56a, 86), Central America (25)

Caulerpa vickersiae Børgesen [= *Caulerpella ambigua* (Okamura) Prud'homme van Reine et Lokhorst, Prud'homme van Reine and Lokhorst 1992]: El Salvador (23, 45, 77), Central America (25)

Chaetomorpha antennina (Bory) Kützing: Guatemala (8), El Salvador (5, 23, 45, 77, 80), Nicaragua (24), Costa Rica (6, 12, 35, 74) (73 as *Chaetomorpha media* (C. Agardh) Kützing, Børgesen 1940), Panama (12, 75), Central America (25)

Chaetomorpha indica (Kützing) Kützing: Panama (21, 22, 86), Central America (25)

Chaetomorpha javanica Kützing: El Salvador (5, 23, 45, 77), Costa Rica (6, 24, 35), Panama (86), Central America (25)

Chaetomorpha linum (O.F. Müller) Kützing: Panama (86)

Chlorodesmis caespitosa J. Agardh: Costa Rica (35), Panama (56a, 86)

Chlorodesmis hildebrandtii A. Gepp et E.S. Gepp: El Salvador (5, 23, 45, 77), Costa Rica (6, 19), Central America (25)

Chlorodesmis mexicana W.R. Taylor: El Salvador (45, 77), Central America (25)

Chloropelta caespitosa Tanner [= *Ulva tanneri* H.S. Hayden et J.R. Waaland, Hayden et al. 2003]: Panama (86)

Cladophora albida (Nees) Kützing: El Salvador (5, 23, 45, 77), Central America (25)

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Cladophora coelothrix Kützing: El Salvador (23, 45, 77 as *Cladophoropsis peruviana* M. Howe, Cribb 1960), Costa Rica (35) (6, 24 as *Cladophoropsis peruviana*), Panama (86), Central America (25 *Cladophoropsis peruviana*)

Cladophora crystallina (Roth) Kützing: El Salvador (5, 45, 77), Costa Rica (6, 21, 22, 35), Central America (25)

Cladophora flexuosa (O.F. Müller) Kützing: Panama (86)

Cladophora herpestica (Montagne) Kützing: Panama (56a)

Cladophora laetevirens (Dillwyn) Kützing: Panama (86)

Cladophora lehmanniana (Lindenberg) Kützing: Costa Rica (6, 35) (21, 22 as *Cladophora utriculosa* Kützing, Hoek 1963), Central America (25 as *Cladophora utriculosa*)

Cladophora microcladioides Collins: Panama (86)

Cladophora montagneana Kützing: Panama (86)

Cladophora panamensis W.R. Taylor: Costa Rica (34), Panama (22, 32, 75, 86), Central America (25)

Cladophora perpusilla Skottsberg et Levring: Central America (25)

Cladophora prolifera (Roth) Kützing: El Salvador (5, 45, 77), Costa Rica (6, 19, 11, 22, 35, 74, 75), Central America (25)

Cladophora sericea (Hudson) Kützing: El Salvador (45, 77 as *Cladophora nitida* Kützing, Hoek 1963), Costa Rica (6, 35) (19, 22 as *Cladophora rudolphiana* (C. Agardh) Kützing, Hoek 1963), Central America (25 as *Cladophora rudolphiana*)

Cladophora socialis Kützing: Costa Rica (6, 19, 22, 35), Panama (86), Central America (25)

Cladophora vagabunda (Linnaeus) Hoek: Costa Rica (11, 35)

Cladophoropsis gracillima E.Y. Dawson: Costa Rica (6, 19, 21, 22, 35), Central America (25)

Cladophoropsis membranacea (Hofman Bang ex C. Agardh) Børgesen: El Salvador (5, 45, 77, 80), Panama (32, 86)

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Cladophoropsis sundanensis Reinbold: El Salvador (5, 23, 45, 77), Costa Rica (6, 19, 35), Central America (25)

Codium edule P.C. Silva: El Salvador (45, 77, 80)

Codium foveolatum M. Howe: Panama (56a)

Codium geppiorum O.C. Schmidt: El Salvador (5, 23, 45, 77, 80), Nicaragua (24), Costa Rica (6a, 84), Central America (25)

Codium isabelae W.R. Taylor: Costa Rica (6a, 35), Panama (56a, 86)

Codium picturatum F.F. Pedroche et P.C. Silva: Costa Rica (34, 35), Panama (86)

Codium setchellii N.L. Gardner: Panama (20, 32, 75)

Derbesia attenuata E.Y. Dawson: El Salvador (5, 45, 77), Panama (21, 22, 32, 86), Central America (25)

Derbesia fastigiata W.R. Taylor: Panama (86)

Derbesia hollenbergii W.R. Taylor: Panama (86)

Derbesia marina (Lyngbye) Solier: Costa Rica (34), Panama (86)

Derbesia turbinata M.A. Howe et Hoyt: Panama (86)

Enteromorpha clathrata (Roth) Greville [= *Ulva clathrata* (Roth) C. Agardh, Hayden et al. 2003]: Central America (25)

Enteromorpha kylini Bliding [= *Ulva kylini* (Bliding) Hayden, Blomster, Maggs, P.C. Silva, M.J. Stanhope et J.R. Waaland, Hayden et al. 2003]: El Salvador (5, 23, 45, 77) Central America (25)

Enteromorpha plumosa Kützing [= *Ulva flexuosa* subsp. *paradoxa* (C. Agardh) M.J. Wynne, Hayden et al. 2003]: El Salvador (45, 77)

Halimeda discoidea Decaisne: El Salvador (5, 23, 45, 77, 80) Nicaragua (24), Costa Rica (6, 11, 19, 22, 35, 70, 72, 73, 74, 75, 84), Panama (46, 47, 86), Central America (12, 25)

Monostroma ecuadorenum W.R. Taylor: Nicaragua (24), Costa Rica (1, 6, 19, 22, 24, 35), Central America (25)

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Parvocaulis parvulus (Solms-Laubach) S. Berger et al.: El Salvador (23, 45, 77, as *Acetabularia moebii* Solms-Laubach, Berger et al. 2003), Costa Rica (35) (34 as *Acetabularia parvula* Solms-Laubach, Berger et al. 2003), Panama (56a) (86 as *Acetabularia parvula*), Central America (25 as *Acetabularia moebii*)

Polyphysa clavata (Yamada) Schnetter et Bula-Meyer [= *Parvocaulis clavatus* (Yamada) Schnetter et Bula-Meyer, Berger et al. 2003]: Costa Rica (38)

Phaeophila dendroides (P.L. Crouan et H.M. Crouan) Batters: Panama (86) (32, 75 as *Phaeophila engleri* Reinke, Burrows 1991), Central America (25 as *Phaeophila engleri*)

Phyllocladon anastomosans (Harvey) Kraft et M.J. Wynne: El Salvador (80) (5, 23, 45, 77 as *Struvea anastomosans* (Harvey) Piccone et Grunow ex Piccone, Kraft and Wynne 1996), Costa Rica (6, 35) (11, 19, 22 as *Struvea anastomosans*), Nicaragua (24 as *Struvea anastomosans*), Panama (56a, 86), Central America (25)

Phyllocladon robustum (Setchell et N.L. Gardner) Leliaert et Wysor: El Salvador (23, 45, 77 as *Cladophoropsis robusta* Setchell et N.L. Gardner, Leliaert et al. 2008), Costa Rica (6, 19, 35 as *Willella mexicana* E.Y. Dawson, Leliaert et al. 2008), Panama (56a) (86 as *Struveopsis robusta* (Setchell et N.L. Gardner) Rhyne et H. Robinson, Leliaert et al. 2008), Central America (25 as *Cladophoropsis robusta*)

Rhizoclonium lubricum Setchell et N.L. Gardner: Costa Rica (19, 75) (22 as *Lola lubrica* (Setchell et N.L. Gardner) A Hamel et G. Hamel, Guiry and Guiry 2010), Central America (25 as *Lola lubrica*)

Rhizoclonium riparium (Roth) Harvey: Guatemala (8), El Salvador (78, 79, 80) (45, 77 as *Rhizoclonium kernerii* Stockmayer, Wynne 2005) (45, 77 as *Rhizoclonium kochianum* Kützing, Silva et al. 1996), Costa Rica (6, 11, 35, 76, 79) (6 as *Rhizoclonium implexum* (Dillwyn) Kützing, Wynne 2005) (24 as *Rhizoclonium kernerii*), Panama (86) (21, 22, 32 as *Rhizoclonium kochianum*), Central America (25 as *Rhizoclonium kochianum*)

Rhizoclonium rhizophilum W.R. Taylor: Costa Rica (6a), Panama (56a, 86)

Rhizoclonium tortuosum (Dillwyn) Kützing [= *Chaetomorpha ligustica* (Kützing) Kützing, Leliaert and Boedeker in Brodie et al. 2007]: Costa Rica (6, 35)

Ulothrix flacca (Dillwyn) Thuret: El Salvador (45, 77)

Ulva compressa Linnaeus: Costa Rica (6, 19, 35) (1, 22 as *Enteromorpha compressa* (Linnaeus) Nees, Hayden et al. 2003, Central America (25) 87 as *Enteromorpha compressa*

Ulva dactylifera, Setchell et N.L. Gardner [= *Ulva nematoidea* Bory, Norris 2010]: Costa Rica (6a)

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Ulva fasciata Delile: Costa Rica (35, 83)

Ulva flexuosa Wulfen: Guatemala (8), El Salvador (45, 77, 80 as *Enteromorpha flexuosa* (Wulfen) J. Agardh, Hayden et al. 2003), Costa Rica (6, 6a, 11, 19, 35) (74, 75 as *Enteromorpha flexuosa*) (6, 19, 74, 75 as *Enteromorpha lingulata* J. Agardh, Hayden et al. 2003) (22 as *Enteromorpha prolifera* var. *flexuosa* (Wulfen) Doty, Wynne 2005), Panama (86 as *Enteromorpha flexuosa*) (32, 75, 86 as *Enteromorpha lingulata*), Central America (1 as *Enteromorpha flexuosa*) (25 as *Enteromorpha lingulata*)

Ulva intestinalis Linnaeus: Costa Rica (34), Panama (39a)

Ulva lactuca Linnaeus: El Salvador (45, 77), Costa Rica (6, 19, 35, 74, 75, 84), Central America (25, 87)

Ulva lobata (Kützing) Harvey: Guatemala (8), El Salvador (45, 77), Costa Rica (6a), Central America (25)

Ulva paradoxa C. Agardh [= *Ulva flexuosa* subsp. *paradoxa* (C. Agardh) M.J. Wynne, Hayden et al. 2003]: Panama (56a)

Ulva prolifera O.F. Müller: Guatemala (8 as *Enteromorpha salina* Kützing Hayden et al. 2003), El Salvador (80 as *Enteromorpha prolifera* (O.F. Müller) J. Agardh, Hayden et al. 2003), Costa Rica (22), Panama (39a, 41, 86 as *Enteromorpha prolifera*), Central America (25) (22, 87 as *Enteromorpha prolifera*)

Ulvella lens P. Crouan et H. Crouan: Panama (56a)

Rhodophyta

Acanthophora spicifera (Vahl) Børgesen: El Salvador (80), Panama (32, 40, 56a)

Acrochaetium infestans M. Howe et Hoyt: Costa Rica (6, 21, 22) Central America (25)

Acrochaetium subseriatum Børgesen: Central America (25)

Acrochaetium vagum (K.M. Drew) C.C. Jao: Costa Rica (6) (19, 22, 75 as *Acrochaetium penetrale* (K.M. Drew) Papenfuss, Garbary 1987), Central America (25 as *Acrochaetium penetrale*)

Acrochaetium variabile (K.M. Drew) G.M. Smith [= *Colaconema pacificum* (Kylin) Woelkerling, Woelkerling 1971]: Nicaragua (24)

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Acrosorium procumbens E.Y. Dawson: El Salvador (23, 45, 77), Central America (25)

Agardhiella tenera (J. Agardh.) F. Schmitz [= *Agardhiella subulata* (C. Agardh) Kraft et M.J. Wynne, Kraft and Wynne 1979]: El Salvador (23, 45, 77), Central America (25)

Ahnfeltiopsis pygmaea (J. Agardh) P.C. Silva et DeCew: Panama (56a)

Amphiroa beauvoisii J.V. Lamouroux: El Salvador (59) (45, 77 as *Amphiroa mexicana* W.R. Taylor, Riosmena-Rodríguez and Sisqueiros-Beltrones 1996) (5, 45, 77 as *Amphiroa zonata* Yendo, Riosmena-Rodríguez and Sisqueiros-Beltrones 1996), Costa Rica (6, 19, 22, 59) (11 as *Amphiroa crosslandii* M. Lemoine, Riosmena-Rodríguez and Sisqueiros-Beltrones 1996) (6a as *Amphiroa zonata*), Panama (39, 59) (17, 32, 56a as *Amphiroa crosslandii*), Central America (25) (25 as *Amphiroa crosslandii*) (25 as *Amphiroa zonata*)

Amphiroa foliacea J.V. Lamouroux: El Salvador (5, 23, 45, 77), Costa Rica (6, 24), Panama (56a), Central America (25)

Amphiroa minutissima W.R. Taylor: Costa Rica (6, 19, 22, 34, 75), Central America (25)

Amphiroa misakiensis Yendo: El Salvador (59) (5, 23, 45, 77 as *Amphiroa dimorpha* M. Lemoine, Riosmena-Rodríguez and Sisqueiros-Beltrones 1996), Costa Rica (59) (6, 19 as *Amphiroa dimorpha*), Panama (56a) (56a as *Amphiroa brevianceps* E.Y. Dawson, Riosmena-Rodríguez and Sisqueiros-Beltrones 1996) (56a as *Amphiroa dimorpha*) (56a as *Amphiroa magdalenensis* E.Y. Dawson, Riosmena-Rodríguez and Sisqueiros-Beltrones 1996), Central America (22, 25 as *Amphiroa dimorpha*)

Amphiroa polymorpha M. Lemoine: Costa Rica (6, 25, 75)

Amphiroa rigida J. V. Lamouroux: Nicaragua (59) (24 as *Amphiroa taylorii* E.Y. Dawson, Riosmena-Rodríguez and Sisqueiros-Beltrones 1996), Costa Rica (6a, 59) (6, 19, 22 as *Amphiroa taylorii*), Central America (25 as *Amphiroa taylorii*)

Amphiroa subcylindrica E.Y. Dawson [= *Amphiroa van-bosseae* Lemoine, Riosmena-Rodríguez and Sisqueiros-Beltrones 1996]: Panama (56a)

Amphiroa valonioides Yendo: El Salvador (59) (5, 23, 45, 77 as *Amphiroa franciscana* W.R. Taylor, Riosmena-Rodríguez and Sisqueiros-Beltrones 1996), Costa Rica (59) (22 as *Amphiroa annulata* M. Lemoine var. *annulata* M. Lemoine, Norris and Johansen 1981) (6, 19, 75 as *Amphiroa annulata* M. Lemoine, Riosmena-Rodríguez and Sisqueiros-Beltrones 1996) (19, 22 as *Amphiroa annulata* var. *pinnata* E.Y. Dawson, Riosmena-Rodríguez and Sisqueiros-Beltrones 1996), Panama (56a, 59) (56a as *Amphiroa franciscana*), Central America (25 as *Amphiroa annulata*) (25 as *Amphiroa franciscana*)

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Antithamnionella breviramosa (E.Y. Dawson) Wollaston: El Salvador (23, 45, 77 as *Antithamnion breviramsum* E.Y. Dawson, Wollaston in Womersley and Bailey 1970), Costa Rica (11, 19) (26 as *Antithamnion breviramsum*) (21 as *Antithamnion breviramsum* var. *breviramsum* E.Y. Dawson), Panama (22 as *Antithamnion breviramsum*) (21, 32 as *Antithamnion breviramsum* var. *breviramsum*), Central America (25 as *Antithamnion breviramsum*)

Antithamnionella elegans (Berthold) J.H. Price et D.M. John: Costa Rica (6)

Archaeolithothamnion howei Lemoine [= *Sporolithon howei* (Lemoine) N. Yamagishi-Tomita ex M. J. Wynne, Wynne 2005]: Panama (22, 32, 55), Central America (25)

Asparagopsis taxiformis (Delile) Trevisan de Saint-Léon: El Salvador (45, 80), Costa Rica (6, 11, 74), Panama (3, 38, 56a)

Bangia fuscopurpurea (Dillwyn) Lyngbye: Costa Rica (19, 75) (6 as *Bangia atropurpurea* (Roth) C. Agardh), Central America (25)

Bostrychia calliptera (Montagne) Montagne: Guatemala (31, 88) (61, 79, 88 as *Bostrychia pinnata* J. Tanaka et M. Chihara, Zuccarello and West 2003), El Salvador (78, 79, 80) (77, 78, 79, 80 as *Bostrychia pinnata*), Costa Rica (6, 24, 76, 62, 79) (6, 76, 79 as *Bostrychia pinnata*), Panama (22, 32, 62, 56a, 75, 88) (88 as *Bostrychia pinnata*), Central America (25)

Bostrychia moritziana (Sonder ex Kützing) J. Agardh: Guatemala (31, 61, 79, 89), El Salvador (77, 78, 80) (62 as *Bostrychia radicans* f. *moniliforme* Post, Kumano 2002), Costa Rica (6, 76, 79), Panama (56a)

Bostrychia pilulifera Montagne: Costa Rica (6, 76, 79)

Bostrychia radicans (Montagne) Montagne: Guatemala (8, 31, 53, 61, 89, 79, 90), El Salvador (22, 23, 45, 77, 78, 80), Costa Rica (6, 11, 19, 22, 76, 79), Panama (56a), Central America (25)

Bostrychia simpliciuscula Harvey ex J. Agardh: Costa Rica (6, 19, 22), Central America (25)

Bostrychia tenella (J.V. Lamouroux) J. Agardh: El Salvador (77, 79, 80) (23, 45, 77 as *Bostrychia binderi* Harvey, Wynne 2005), Costa Rica (6, 24, 74, 75) (6, 11, 19, 22, 62 as *Bostrychia binderi*), Panama (62) (62 as *Bostrychia binderi*), Central America (25 as *Bostrychia binderi*)

Botryocladia beaudettei E.Y. Dawson: Costa Rica (21, 22), Central America (25)

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Botryocladia pyriformis (Børgesen) Kylin: El Salvador (80)

Callithamnion marshallense E.Y. Dawson: Costa Rica (6, 21, 22, 26), Panama (56a), Central America (25)

Callophyllis ligulata W.R. Taylor: Central America (25)

Caloglossa leprieurii (Montagne) G. Martens: Guatemala (8, 31, 61, 79), El Salvador (23, 45, 77, 78, 79, 80), Costa Rica (6, 11, 19, 22, 73, 74, 76, 79), Central America (25)

Caloglossa leprieurii var. *hookeri* Post: Costa Rica (6, 19)

Caloglossa ogasawaraensis Okamura: Guatemala (61)

Caloglossa rotundata Kamiya: Guatemala (52)

Caloglossa stipitata E. Post: Guatemala (31, 79), El Salvador (77, 78, 79, 80), Costa Rica (6, 76, 79)

Catenella caespitosa (Withering) L.M. Irvine: Guatemala (31, 61, 79), El Salvador (79, 80), Costa Rica (6, 24, 62, 76, 79), Panama (62)

Catenella impudica (Montagne) J. Agardh: El Salvador (23, 45, 77, 78, 79, 80), Costa Rica (6, 11, 62, 79), Central America (25)

Caulacanthus ustulatus (Mertens ex Turner) Kützinger: Costa Rica (6) (19, 22 as *Caulacanthus indicus* Weber-van Bosse, West and Calumpong 1990), Central America (25 as *Caulacanthus indicus*)

Centroceras minutum Yamada: Panama (21, 22, 32), Central America (25)

Ceramium avalonae E.Y. Dawson: El Salvador (5, 45, 77), Costa Rica (6, 21, 22), Central America (25)

Ceramium equisetoides E.Y. Dawson: Costa Rica (6, 19, 22), Central America (25)

Ceramium marshallense E.Y. Dawson: Costa Rica (6, 19, 22), Central America (25)

Ceramium mazatlanense E.Y. Dawson [= *Ceramium macilentum* J. Agardh, Abbott et al. 1999]: El Salvador (23, 45, 77), Costa Rica (6, 19, 22), Central America (25)

Ceramium nakamurae E.Y. Dawson: Costa Rica (6, 19, 22) Central America (25)

Ceramium paniculatum Okamura: El Salvador (80)

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Ceramium personatum Setchell et N.L. Gardner: Costa Rica (6, 19, 22, 75), Central America (25)

Ceramium procumbens Setchell et N.L. Gardner: El Salvador (5, 23, 45, 77), Costa Rica (6, 21, 22), Central America (25)

Ceramium serpens Setchell et N.L. Gardner: Central America (25)

Ceramium taylorii E.Y. Dawson [=*Gayliella taylorii* (E.Y. Dawson) T.O. Cho et S.M. Boo, Cho et al. 2008]: El Salvador (23, 45, 77), Costa Rica (19, 22), Central America (25)

Ceramium vagabundum E.Y. Dawson nom. illeg. [=*Ceramium vagans* P.C. Silva, Silva et al 1987]: El Salvador (5, 23, 45, 77), Costa Rica (6, 19, 22), Central America (25)

Champia parvula (C. Agardh) Harvey: El Salvador (5, 77), Costa Rica (1, 6, 19, 22), Central America (25)

Chondria californica (Collins) Kylin [=*Chondria acrorhizophora* Setchell et N.L. Gardner, Silva 1991]: Costa Rica (6, 19, 22, 75), Panama (1), Central America (25)

Chondria concrescens E.Y. Dawson: El Salvador (23, 45, 77, 80), Costa Rica (23)

Chondria dangeardii E.Y. Dawson: Panama (21, 22), Central America (25)

Chondria lancifolia Okamura: Costa Rica (6, 19, 22)

Chondria platyclada W.R. Taylor: Costa Rica (6, 22, 28, 75), Panama (56a), Central America (25)

Chondria repens Børgesen: El Salvador (5, 45, 77), Costa Rica (6, 19, 22), Central America (25)

Choreonema thuretii (Bornet) F. Schmitz: Costa Rica (1, 22), Central America (25)

Cruoriella dubyi (P.L. Crouan et H.M. Crouan) F. Schmitz [=*Peyssonnelia dubyi* P.L. Crouan et H.M. Crouan, Denizot 1968]: Panama (21, 22, 32), Central America (25)

Cruoriella fissurata E.Y. Dawson: Costa Rica (6, 19, 21), Panama (21, 22, 32), Central America (25)

Cruoriella mexicana (E.Y. Dawson) Denizot: Costa Rica (6) (19, 21, 22 as *Cruoriopsis mexicana* E.Y. Dawson, Denizot 1968), Central America (25 as *Cruoriopsis mexicana*)

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Cryptonemia angustata (Setchell et N.L. Gardner) E.Y. Dawson: El Salvador (23, 45, 77), Costa Rica (6, 21, 22), Central America (25)

Cryptonemia limensis (Kützing) J.A. Lewis: Costa Rica (6) (21, 22 as *Cryptonemia guaymasensis* (E.Y. Dawson) E.Y. Dawson, Lewis 1990) (25 as *Cryptonemia guaymasensis*)

**Dermatolithon pustulatum* (J.V. Lamouroux) Foslie [= *Titanoderma pustulatum* J.V. Lamouroux) Nägeli, Babbini and Versan 1997, = *Lithophyllum pustulatum* (J.V. Lamouroux) Foslie, Woelkerling et al 1985]: Central America (25)

**Dermatolithon saxicolum* (M. Lemoine) Setchell et N.L. Mason: Costa Rica (18, 22, 34, 55, 69, 82), Central America (25)

Dermonema frappierii (Montagne et Millardet) Børgesen [= *Dermonema virens* (J. Agardh) Pedroche et Ávila-Ortíz, Pedroche and Ávila-Ortíz 1996]: El Salvador (5, 23, 45, 77, 80), Central America (25)

Dichotomaria marginata (Ellis et Solander) J.V. Lamouroux: Costa Rica (6, 74 as *Galaxaura marginata* (J. Ellis et Solander) J.V. Lamouroux, Huisman et al. 2004) (75 as *Galaxaura stupocaulon* Kjellman, Huisman et al. 2004) (10, 19, 22, 75 as *Galaxaura veprecula* Kjellman, Huisman et al. 2004), Panama (56a), Central America (25 as *Galaxaura veprecula*)

Dicranema rosaliae Setchell et N.L. Gardner: Costa Rica (22), Central America (25)

Digenea simplex (Wulfen) C. Agardh: Costa Rica (6, 12, 19, 22, 74, 75), Central America (25)

Dudresnaya colombiana W.R. Taylor: Central America (25)

Erythrotrichia bangioides Levring: Guatemala (8), El Salvador (23,45, 77), Central America (25)

Erythrotrichia carnea (Dillwyn) J. Agardh: Costa Rica (1, 6, 19), Central America (25)

Eucheuma isiforme (C. Agardh) J. Agardh: El Salvador (5, 77)

**Fosliella fertilis* (M. Lemoine) Segonzac: Panama (56) (22, 69 as *Litholepis fertilis* (M. Lemoine) Setchell et Manson, Guiry and Guiry 2010) (32, 55, 82 as *Melobesia fertilis* M. Lemoine, Silva et al. 1996), Central America (25 as *Litholepis fertilis*)

**Fosliella minuta* W.R. Taylor: Panama (22, 32, 75), Central America (25)

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**Fosliella paschalis* (M. Lemoine) Setchell et N.L. Gardner: Central America (25)

Galaxaura arborea Kjellman [= *Dichotomaria spathulata* (Kjellman) A. Karihara et Huisman, Huisman and Kurihara 2006]: Costa Rica (24)

Galaxaura filamentosa R. Chou: Costa Rica (6, 11, 17, 19, 22, 34, 74, 75), Panama (56a), Central America (25)

Galaxaura rugosa (J. Ellis et Solander) J.V. Lamouroux: Costa Rica (6a) (6, 19, 22 as *Galaxaura ramulosa* Kjellman, Wynne 2005), Panama (56a, 86) (19, 32, 75 as *Galaxaura ramulosa*) (10, 22, 75 as *Galaxaura squalida* Kjellman, Papenfuss et al. 1982), Central America (25 as *Galaxaura ramulosa*) (25 as *Galaxaura squalida*)

Galaxaura spathulata Kjellman [= *Dichotomaria spathulata* (Kjellman) A. Karihara et Huisman, Kurihara and Huisman 2006]: Nicaragua (24)

Galaxaura stupocaula Kjellman: Costa Rica (19, 22), Central America (25)

Gayliella flaccida (Harvey ex Kützing) T.O. Cho et L.J. McIvor: El Salvador (5, 45, 77 as *Ceramium gracillimum* (Harvey et Mazoyer) Gobi Kützing et Zanardini, Cho et al. 2008) (23 as *Ceramium gracillimum* var. *byssoides* (Harvey) Mazoyer, Abbott et al. 1999), Costa Rica (6, 11 as *Ceramium flaccidum* (Harvey ex Kützing) Ardissonne, Cho et al. 2008) (19, 22 as *Ceramium gracillimum* var. *byssoides*), Panama (56a), Central America (25 as *Ceramium gracillimum* var. *byssoides*)

Gelidiella acerosa (Forsskål) Feldmann et G. Hamel: Central America (22, 25)

Gelidiella hancockii E.Y. Dawson: Costa Rica (6, 21, 22), Panama (21, 22), Central America (25)

Gelidiella machrisiana E.Y. Dawson: Costa Rica (6, 19, 22, 27, 67), Central America (25)

Gelidiella trinitatensis W.R. Taylor: Panama (56a)

Gelidiopsis intricata (C. Agardh) Vickers: Costa Rica (6, 24), Panama (56a, 39)

Gelidiopsis planicaulis (W.R. Taylor) W.R. Taylor: Panama (56a)

Gelidiopsis repens (Kützing) Weber-van Bosse: El Salvador (23, 45, 77), Central America (25)

Gelidiopsis variabilis (J. Agardh) F. Schmitz: El Salvador (5, 23, 45, 77 as *Gelidiopsis tenuis* Setchell et N.L. Gardner, Dawes and Mathieson 2008), Nicaragua (24), Costa Rica (6, 19, 22 as *Gelidiopsis tenuis*), Panama (56a), Central America (25 as *Gelidiopsis tenuis*)

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Gelidium galapagense W.R. Taylor: El Salvador (23, 45, 63, 64, 77), Central America (25)

Gelidium isabelae W.R. Taylor: Central America (25)

Gelidium microdentatum E.Y. Dawson: Central America (25)

Gelidium pusillum (Stackhouse) Le Jolis: El Salvador (5, 23, 45, 77, 80), Costa Rica (6, 11, 12, 19, 75), Panama (22, 32, 63, 56a, 75), Central America (25, 87)

Gelidium pusillum (Stackhouse) Le Jolis var. *pusillum*: El Salvador (5, 77)

Gelidium pusillum (Stackhouse) Le Jolis var. *pacificum* W.R. Taylor: El Salvador (5, 45), Panama (56a)

Gelidium sclerophyllum W.R. Taylor: El Salvador (5, 23, 45, 77), Nicaragua (24), Costa Rica (6, 19, 22, 63, 75), Central America (25)

Gigartina intermedia Suringar [= *Chondracanthus intermedius* (Suringar) Hommersand, Hugley and Hommersand 2008]: El Salvador (23, 45, 77), Central America (25)

Goniolithon tessellatum (M. Lemoine) Setchell et L.R. Mason [= *Lithophyllum prototypum* (Lemoine) Littler, Woelkerling and Campbell 1992]: Panama (21, 22, 32), Central America (25)

Gracilaria brevis W.R. Taylor: Panama (56a)

Gracilaria crispata Setchell et N.L. Gardner: El Salvador (5, 23, 45, 57, 77), Costa Rica (6, 19, 22), Central America (25, 87)

Gracilaria ecuadoreanus (W.R. Taylor) E.Y. Dawson: El Salvador (5, 45, 23), Central America (25)

Gracilaria mammillaris (Montagne) M. Howe: El Salvador (80)

Gracilaria spinigera E.Y. Dawson: Costa Rica (6a)

Gracilaria symmetrica E.Y. Dawson: Costa Rica (13, 21, 22), Central America (25)

Gracilaria tepocensis (E.Y. Dawson) E.Y. Dawson: El Salvador (23, 45, 57), Costa Rica (6, 22, 57, 58) (6, 13, 19 as *Gracilaria crockeri* E.Y. Dawson, Norris 1985), Central America (25)

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Gracilariopsis costaricensis E.Y. Dawson: Costa Rica (6, 13, 19, 22, 43, 44), Central America (25)

Gracilariopsis lemaneiformis (Bory) E.Y. Dawson, Acleto *et* Foldvik: Guatemala (31), Costa Rica (57 as *Gracilaria lemaneiformis* (Bory) Greville, Gurdel *et al.* 2003), Central America (87 as *Gracilaria lemaneiformis*)

Gracilariopsis panamensis (W.R. Taylor) E.Y. Dawson: Costa Rica (6, 19, 22, 44) (75 as *Gracilaria panamensis* W.R. Taylor, Guiry and Guiry 2010), Panama (22, 32), Central America (25) (75 as *Gracilaria panamensis*)

Gracilariopsis sjoestedtii (Kylin) E.Y. Dawson [= *Gracilariopsis andersonii* (Grunow) E.Y. Dawson, Gurdel *et al.* 2003]: El Salvador (23, 45, 77), Costa Rica (1, 22, 28), Central America (25)

Grateloupia filicina (J.V. Lamouroux) C. Agardh: El Salvador (5, 23, 45, 77), Central America (25)

Grateloupia schizophylla Kützing: El Salvador (5, 45, 77)

Grateloupia versicolor (J. Agardh) J. Agardh: El Salvador (23, 45, 77), Central America (25)

Griffithsia barbata C. Agardh [= *Anotrichium barbatum* (C. Agardh) Nägeli, Guiry 1997]: El Salvador (80)

Griffithsia binderiana Sonder [= *Bornetia binderiana* (Sonder) Zanardini, Zanardini 1866]: El Salvador (23, 45, 77), Central America (25)

Griffithsia ovalis Harvey: Costa Rica (6, 24)

Grinnellia lanceolata E.Y. Dawson: Panama (56a)

Gymnogongrus hancockii E.Y. Dawson: Costa Rica (28)

Gymnogongrus johnstonii (Setchell *et* N.L Gardner) E.Y. Dawson: El Salvador (23, 45, 77), Costa Rica (6, 21, 22), Central America (25)

Haloplegma mexicanum W.R. Taylor: Panama (56a)

Halymenia abyssicola E.Y. Dawson: Panama (56a)

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Halymenia actinophysa M. Howe: Costa Rica (21, 22), Panama (56a as *Sebdenia actinophysa* (MA Howe) E Soler-Onís in De Yong nom. inval., Hernández-Kantun et al. 2009), Central America (25)

Halymenia porphyroides Børgesen: Panama (56a)

Halymenia refugiensis E.Y. Dawson: Panama (56a)

Halymenia utriana W.R. Taylor: Central America (25)

Herposiphonia littoralis Hollenberg: El Salvador (45, 45, 77)

Herposiphonia secunda (C. Agardh) Ambronn: El Salvador (23), Costa Rica (6, 19), Panama (32, 41, 75)(1 as *Herposiphonia tenella* f. *secunda* (Agardh) Hollenberg, Schneider and Searls 1997), Central America (25)

Herposiphonia subdisticha Okamura: El Salvador (5, 23, 45, 77), Costa Rica (6, 19, 21, 22), Central America (25)

Herposiphonia tenella (C. Agardh) Ambronn: El Salvador (5, 23, 45, 77), Costa Rica (11, 19, 22) (6 as *Herposiphonia secunda* f. *tenella* (C. Agardh) M.J. Wynne, Schneider et Searles 1997), Central America (25)

Heteroderma minutulum (Foslie) Foslie [= *Pneophyllum confervicola* (Kützinger) Y.M. Chamberlain, Wynne 2005]: El Salvador (23, 45), Panama (22, 75), Central America (25)

**Heteroderma subtilissimum* (Foslie) Foslie: El Salvador (23, 45), Central America (25)

Heterosiphonia crispella (C. Agardh) M.J. Wynne var. *laxa* (Børgesen) M.J. Wynne: Costa Rica (6) (19, 22 as *Heterosiphonia wurdemannii* var. *laxa* Børgesen, Wynne 1985), Panama (56a), Central America (25 as *Heterosiphonia wurdemannii* var. *laxa*)

Hildenbrandia rubra (Sommerfelt) Meneghini: Guatemala (8 as *Hildenbrandia prototypus* Nardo, Wynne 2005), El Salvador (23, 45, 77 as *Hildenbrandia prototypus*), Costa Rica (6, 74) (11, 19, 75 as *Hildenbrandia prototypus*), Panama (22, 32, 75 as *Hildenbrandia prototypus*), Central America (25 as *Hildenbrandia prototypus*)

Hydrolithon onkodes (Heydrich) D. Penrose et Woelkerling: Costa Rica (6) (21, 22 as *Porolithon onkodes* (Heydrich) Foslie, Penrose and Woelkerling 1992), Central America (25 as *Porolithon onkodes*)

Hydrolithon reinboldii (Weber-van Bosse et Foslie) Foslie: El Salvador (2, 23, 45, 77), Central America (25)

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Hypnea boergesenii T. Tanaka: Central America (25)

Hypnea esperi Bory: Costa Rica (6, 19)

Hypnea marchantae Setchell et N.L. Gardner: Central America (25)

Hypnea nidifica J. Agardh: Costa Rica (12)

Hypnea nidulans Setchell: Panama (56a)

Hypnea pannosa J. Agardh: El Salvador (5, 23, 45, 77, 80), Nicaragua (24), Costa Rica (6, 11, 19, 74), Panama (32, 39, 56a, 75), Central America (25, 87)

Hypnea spinella (C. Agardh) Kützing: El Salvador (23, 45, 77) (5, 23, 45, 77 as *Hypnea cervicornis* J. Agardh, Yoshida 1998), Costa Rica (6) (24 as *Hypnea cervicornis*), Panama (56a), Central America (25) (25 as *Hypnea cervicornis*)

Hypnea valentiae (Turner) Montagne: Costa Rica (6a), Central America (25, 87)

Hypoglossum abyssicola W.R. Taylor [=*Hypoglossum attenuatum* var. *abyssicola* (W.R. Taylor) E.Y. Dawson, Dawson 1962c]: Costa Rica (6, 19, 22, 75)

Hypoglossum attenuatum N.L. Gardner: Panama (56a), Central America (25)

Jania adherens J.V. Lamouroux: Central America (87)

Jania capillacea Harvey: El Salvador (23, 45, 77), Costa Rica (6, 11, 19), Panama (56a), Central America (25)

Jania longiarthra E.Y. Dawson: Costa Rica (6, 19, 22), Central America (25)

Jania tenella (Kützing) Grunow: El Salvador (5, 23, 45, 77), Costa Rica (1, 6, 17, 19) (22 as *Jania tenella* var. *tenella*), Central America (25)

Jania tenella var. *zaca* E.Y. Dawson: Nicaragua (24), Costa Rica (6, 19, 17, 22)

Jania ungulata (Yendo) Yendo: Costa Rica (83)

Kallymenia latiloba W.R. Taylor: Panama (56a)

Laurencia decidua E.Y. Dawson: El Salvador (45, 77)

Laurencia lajolla E.Y. Dawson: El Salvador (45, 77)

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Laurencia paniculata (C. Agardh) J. Agardh [= *Chondrophycus thuyoides* (Kützing) G. Furnari, Furnari et al. 2001]: El Salvador (23, 45, 77), Central America (25)

Laurencia papillosa (C. Agardh) Greville [= *Palisada perforata* (Bory) K.W. Nam, Cassano et al. 2009]: El Salvador (45, 77, 80)

Laurencia richardsii E.Y. Dawson: El Salvador (23, 45, 77), Central America (25)

Laurencia subdisticha E.Y. Dawson, Neushul et Wildman: Panama (1, 22, 29), Central America (25)

Lejolisia colombiana W.R. Taylor: Panama (56a), Central America (25)

Liagora ceranoides J.V. Lamouroux: Costa Rica (6, 19, 22, 75), Central America (25)

Lithophyllum alternans M. Lemoine: Panama (56)

Lithophyllum brachiatum (Heydrich) Me. Lemoine: Panama (32, 55, 75)

Lithophyllum canescens (Foslie) Foslie: El Salvador (23, 45, 77 as *Dermatolithon canescens* (Foslie) Foslie, Guiry and Guiry 2010), Costa Rica (6, 19) (24, 22 as *Dermatolithon canescens*), Central America (25 as *Dermatolithon canescens*)

Lithophyllum coibense M. Lemoine: Panama (22, 32, 55, 82), Central America (25)

Lithophyllum divaricatum M. Lemoine: Panama (32, 56, 75)

Lithophyllum fetum Foslie: Costa Rica (22, 55, 82), Panama (32), Central America (25)

Lithophyllum imitans Foslie: El Salvador (23, 45, 77), Central America (25)

Lithophyllum kotshchyanum Unger: Costa Rica (6a)

Lithophyllum lividum M. Lemoine: Costa Rica (22, 55, 82), Panama (32), Central America (25)

Lithophyllum pallescens (Foslie) Foslie: Panama (2, 22), Central America (25)

Lithophyllum propinquum (Foslie) M. Lemoine var. *cocosicum* M. Lemoine: Costa Rica (22, 55), Panama (32), Central America (25)

Lithothamnion australe Foslie: Panama (2, 32, 56, 75)

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Lithothamnion australe f. *americanum* Foslie: Panama (75) (32, 55 as *Mesophyllum australe* var. *minutula* (Foslie) M. Lemoine, Adey et al. 1982)

Lithothamnion australe f. *tualense* Foslie: Panama (75) (32, 55 as *Mesophyllum australe* var. *tualense* (Foslie) M. Lemoine, Adey et al. 1982)

Lithothamnion californicum Foslie: Nicaragua (24)

Lithothamnion crassiusculum (Foslie) L.R. Mason [= *Mesophyllum crassiusculum* (Foslie) P. A. Lebednik, Guiry and Guiry 2010]: Costa Rica (6a)

Lithothamnion fruticulosum (Kützinger) Foslie [= *Spongites fruticulosus* Kützinger, Penrose 1996]: Costa Rica (22), Central America (25)

Lithothamnion giganteum L.R. Mason [= *Lithophyllum frondosum* (Dufour) Furnari, Cormaci et Alongi, Babbini and Bressan 1997]: Central America (25)

Lithothamnion heteromorphum (Foslie) Foslie: Costa Rica (6, 19, 22), Central America (25)

Lithothamnion indicum Foslie: Panama (32, 56, 75)

Lithothamnion lenormandii (J.E. Areschoug) Foslie [= *Phymatolithon lenormandii* (Areschoug) W.H. Adey, Adey 1966]: El Salvador (23, 45, 77), Central America (25)

**Lithothamnion microsporum* (Foslie) Foslie [= *Leptophytum microsporum* (Foslie) Athanasiadis et Adey, Athanasiadis and Adey 2006]: Central America (1)

Lithothamnion validum Foslie: Costa Rica (6, 19, 25, 75)

Lomentaria baileyana (Harvey) Farlow: Costa Rica (6, 16, 22, 75), Central America (25)

Lomentaria hakodatensis Yendo: Costa Rica (6, 21, 22), Central America (25)

Lophosiphonia reptabunda (Suhr) Kylin: El Salvador (5, 23, 45, 77), Costa Rica (6, 19, 22), Central America (25)

Melobesia marginata Setchell et Foslie: El Salvador (23, 45, 77), Costa Rica (22), Central America (25)

Melobesia polystromatica E.Y. Dawson: El Salvador (23, 45, 77), Central America (25)

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Neogoniolithon fosliei (Heydrich) Setchell et L.R. Mason: Costa Rica (6a) (82 as *Paragoniolithon solubile* (Foslie et M. Howe) W.H. Adey, Townsend et Boykins, Wynne 2005)

Neogoniolithon trichotomum (Heydrich) Setchell et L.R. Mason: Costa Rica (6), Panama (22 as *Lithophyllum trichotomum* (Heydrich) M. Lemoine, Wynne 2005), Central America (25 as *Lithophyllum trichotomum*)

Neosiphonia tongatensis (Harvey ex Kützing) M.S. Kim et I.K. Lee: Panama (56a)

Osmundea sinicola (Setchell et N.L. Gardner) K.W. Nam: Panama (56a)

Osmundea splendens (Hollenberg) K.W. Nam: Panama (56a)

Parviphycus tenuissimus (Feldmann et Hamel) B. Santelices: El Salvador (66) (23, 45, 77, 80 as *Gelidiella pannosa* Feldmann et G. Hamel, Santelices 2004), Costa Rica (6, 19, 22 as *Gelidiella pannosa*), Central America (25 as *Gelidiella pannosa*)

Peyssonnelia conchicola Piccone et Grunow: Costa Rica (6, 19, 22), Central America (25)

Peyssonnelia rubra (Greville) J. Agardh: Costa Rica (34)

Platoma fanii E.Y. Dawson: Panama (56a)

Pleonosporium globuliferum Levring: El Salvador (5, 23, 77), Costa Rica (6, 19, 21, 22), Central America (25)

Pleonosporium mexicanum E.Y. Dawson: El Salvador (80), Panama (56a)

Pleonosporium squarrulosum (Harvey) I.A. Abbott: El Salvador (45, 77)

Plocamium cartilagineum subsp. *pacificum* (Kyllin) P.C. Silva: Panama (56a)

Plocamium violaceum Farlow: Panama (56a)

Polyopes clarionensis Setchell et N.L. Gardner [= *Grateloupia clarionensis* (Setchell et N.L. Gardner) S. Kawaguchi et H.W. Wang, Wang et al 2001]: Nicaragua (24)

Polysiphonia bajacali Hollenberg: El Salvador (5, 45, 77)

Polysiphonia beaudettei Hollenberg: Costa Rica (6, 22, 48), Central America (25)

Polysiphonia bifurcata Hollenberg: El Salvador (80), Costa Rica (6, 19, 22, 27, 75), Panama (56a), Central America (25)

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Polysiphonia ferulacea Suhr ex J. Agardh [= *Neosiphonia ferulacea* (Suhr ex J. Agardh) S.M. Guimarães et M.T. Fujii, Guimarães et al. 2004]: Costa Rica (6, 24) Central America (25)

Polysiphonia flaccidissima Hollenberg [= *Neosiphonia flaccidissima* (Hollenberg) M.S. Kim et I.K. Lee, Kim and Lee 1999]: El Salvador (5, 45, 77), Costa Rica (48, 49), Panama (22, 49), Central America (25)

Polysiphonia homoia Setchell et N.L. Gardner: Panama (56a)

Polysiphonia howei Hollenberg [= *Neosiphonia howei* (Hollenberg) Skelton et G.R. South, Skelton and South 2007]: Costa Rica (6, 24), Panama (22, 32, 75), Central America (25)

Polysiphonia mollis J.D. Hooker et Harvey: Costa Rica (6, 19, 34)

Polysiphonia pacifica Hollenberg: El Salvador (5, 45, 77)

Polysiphonia scopulorum Harvey: Costa Rica (6, 19)

Polysiphonia scopulorum var. *villum* (J. Agardh) Hollenberg: Costa Rica (49)(75 as *Lophosiphonia villum* (J. Agardh) Setchell et N.L. Gardner, Hollenberg and Norris 1977)

Polysiphonia sertularioides (Grateloup) J. Agardh: Costa Rica (6)

Polysiphonia simplex Hollenberg [= *Neosiphonia simplex* (Hollenberg) Y.P. Lee, Lee 2008]: Costa Rica (6, 22, 48, 49), Central America (25)

Polysiphonia subtilissima Montagne: El Salvador (5, 23, 45, 77), Costa Rica (6, 19, 22), Central America (25)

Polystrata dura Heydrich: Costa Rica (6a)

**Porolithon castellum* Dawson: Costa Rica (6, 21, 22), Central America (25)

**Porolithon cocosicum* Lemoine: Costa Rica (22, 55, 82), Panama (32), Central America (25)

Porphyra thuretii Setchell et E.Y. Dawson: Costa Rica (1, 22)

Predaea laciniosa Kraft: Panama (56a)

Prionitis subdichotoma E.Y. Dawson: El Salvador (45, 77), Central America (25)

Pterocladia caerulea (Kützinger) Santelices et Hommersand: Panama (56a)

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Pterocladia mcnabbiana E.Y. Dawson: El Salvador (23, 45, 77), Costa Rica (6, 19, 22, 65), Central America (25)

Pterocladia musciformis W.R. Taylor [= *Gelidium musciforme* (W.R. Taylor) Santelices]: El Salvador (5, 23, 45, 65, 77), Costa Rica (6, 19, 22, 63, 65, 75), Central America (25)

Pterocladia pinnata (Hudson) Papenfuss [= *Pterocradiella capillacea* (S.G. Gmelin) Santelices et Hommersand, Santelices 1999b]: El Salvador (23, 45, 77)

Sahlingia subintegra (Rosenvinge) Kornmann: El Salvador (23, 77 as *Erythrocladia subintegra* Rosenvinge, Kornmann 1989), Costa Rica (11), Central America (25 as *Erythrocladia subintegra*)

Sarcodiotheca ecuadoreana W.R. Taylor: Costa Rica (6, 19, 75)

Sarcodiotheca furcata (Setchell et N.L. Gardner) Kylin: Costa Rica (1, 22), Central America (25)

Scinaia complanata (F.S. Collins) A.D. Cotton: Costa Rica (6, 19, 22, 75), Central America (25)

Scinaia confusa (Setchell) Huisman: Costa Rica (6) (21, 22 as *Gloiophloea confusa* Setchell, Huisman 1985), Central America (25 as *Gloiophloea confusa*)

Scinaia johnstoniae Setchell: Costa Rica (6, 19, 75), Central America (25)

Scinaia latifrons M. Howe: Costa Rica (6a), Central America (25)

Scinaia minima E.Y. Dawson: Panama (56a)

Sebdenia flabellata (J. Agardh) P.G. Parkinson: Panama (56a)

Sebdenia rubra W.R. Taylor: Panama (56a)

Smithora naiadum (C.L. Anderson) Hollenberg: Costa Rica (6) (75 as *Porphyra naiadum* C.L. Anderson, Hollenberg 1959)

Spermothamnion speluncarum (Collins et Hervey) M. Howe [= *Ptilothamnion speluncarum* (Collins et Hervey) D.L. Ballantine et M.J. Wynne, Ballantine and Wynne 1998]: El Salvador (23, 45, 77), Central America (25)

Spongites decipiens (Foslie) Y.M. Chamberlain: Costa Rica (6) (19 as *Lithophyllum decipiens* (Foslie) Foslie, Chamberlain 1993), Panama (22 as *Lithophyllum decipiens*), Central America (25 as *Lithophyllum decipiens*)

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Sporolithon pacificum E.Y. Dawson: Costa Rica (6, 21, 22) (27 as *Archaeolithothamnion pacificum* Lemoine, Dawson 1960), Central America (25)

Spyridia filamentosa (Wulfen) Harvey: El Salvador (5, 23, 45, 77), Nicaragua (24), Costa Rica (6, 11, 19, 74), Panama (32, 22, 56a, 75), Central America (25)

Stylonema alsidii (Zanardini) K.M. Drew: El Salvador (5, 45, 77 as *Goniotrichum elegans* (Chauvin) Zanardini, Silva et al. 1996), Costa Rica (6, 19), Panama (56a) (41 as *Goniotrichum alsidii* (Zanardini) M. Howe, Silva et al. 1996), Central America (25 as *Goniotrichum elegans*)

Taenioma perpusillum (J. Agardh) J. Agardh: El Salvador (23, 45, 77), Panama (21, 22, 32), Central America (25)

Tayloriella dictyurus (J. Agardh) Kylin: El Salvador (5, 23, 45, 77), Central America

Tenarea tessellata (Lemoine) M.M. Littler ex Adey et al. [= *Lithophyllum prototypum* (Foslie) Foslie, Guiry and Guiry 2010]: Panama (2)

Titanophycus validus (Harvey) Huisman, G.W. Saunders et A.R. Sherwood: Costa Rica (6, 19, 22, 74, 75 as *Liagora valida* Harvey, Huisman et al. 2006), Panama (56a), Central America (25 as *Liagora valida*)

Trichogloeopsis pedicellata (M. Howe) I.A. Abbott et Doty: Costa Rica (6a)

Tricleocarpa cylindrica (J. Ellis et Solander) Huisman et Borowitzka: El Salvador (45, 77 as *Galaxaura fastigiata* Decaisne, Huisman and Borowitzka 1990), Nicaragua (24 as *Galaxaura fastigiata*), Costa Rica (6a)

Tricleocarpa fragilis (Linnaeus) Huisman et R.A. Townsend: El Salvador (5, 45, 77, 80 as *Galaxaura oblongata* (J. Ellis et Solander) J.V. Lamouroux, Huisman and Townsend 1993), Panama (56a)

Wrangelia argus (Montagne) Montagne: Panama (21, 32, 22), Central America (25)

Wrangelia bicuspidata Børgesen: Panama (56a)

Wrangelia dumontii (E.Y. Dawson) I.A. Abbott: Costa Rica (6, 11) (22 as *Antithamnion dumontii* E.Y. Dawson, Abbott 1979), Panama (21, 22, 32 as *Antithamnion dumontii*) Central America (25 as *Antithamnion dumontii*)

Wurdemannia miniata (Sprengel) Feldman et G. Hamel: El Salvador (5, 23, 45, 77), Nicaragua (24), Costa Rica (6, 19, 22), Panama (32, 56a, 75), Central America (25, 75)

Unconfirmed records

1. *Dictyota adnata* Zanardini: Costa Rica (38)
2. *Dictyota dichotoma* (Hudson) J.V. Lamouroux: El Salvador (80), Central America (22, 25). **Note:** According to Tronholm et al. 2010 this species is geographically distributed only in the NE Atlantic Ocean and Mediterranean Sea.
3. *Dictyota divaricata* J.V. Lamouroux: El Salvador (9, 23, 45, 77, 80), Costa Rica (6, 11, 19), Central America (25). **Note:** According to De Clerck this is a synonymy of *Dictyota dichotoma* var. *intricata*. Recently Tronholm et al. 2010 studied that *Dictyota dichotoma* var. *intricata* is *D. dichotoma* and that this species is geographically distributed only in the NE Atlantic Ocean and Mediterranean Sea
4. *Sargassum fluitans* (Børgesen) Børgesen: El Salvador (80) **Note:** The distribution of this species is restricted to Atlantic and Indian Oceans.
5. *Anotrichium tenue* (C. Agardh) Nägeli: Costa Rica (11)
6. *Antithamnion antillanum* Børgesen: Costa Rica (11)
7. *Callithamnion rupicola* Anderson: Costa Rica (11)
8. *Centroceras clavulatum* (C. Agardh) Montagne: El Salvador (5, 23, 45, 77, 80), Costa Rica (6, 11, 19), Panama (22, 32, 75), Central America (25, 87). **Note:** The occurrence of this species must be clarified according to the study of Won et al. 2009.
9. *Ceramium clarionense* Setchell et N.L. Gardner: Costa Rica (11)
10. *Ceramium hamatispinum* E.Y. Dawson: Costa Rica (11)
11. *Ceramium sinicola* Setchell et N.L. Gardner: Costa Rica (11)
12. *Ceramium tenuicorne* (Kützing) Waern: Costa Rica (11)
13. *Gracilaria verrucosa* (Hudson) Papenfuss: Costa Rica (25), Central America (25).
14. *Griffithsia globulifera* Harvey ex Kützing: Costa Rica (74)
15. *Laurencia obtusa* var. *densa* Yamada: El Salvador (45)
16. *Scinaia setchellii* W.R. Taylor: Costa Rica (11)

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Discussion

The present checklist of the marine macroalgae of the Pacific of Central America includes 379 species (46 brown algae, 81 green algae, and 252 red algae) regarded as currently valid names and 16 unconfirmed records. The total is 144 more species than the list published by E.Y. Dawson (1962b). Costa Rica is the country with the greatest number of species of marine macroalgae with 216 species (18 species present at Isla del Coco), followed by Panama with 174, El Salvador (146), Nicaragua (24) and Guatemala (16). At this moment there are no records published for the Pacific coast of Honduras (Nelson 1990) (Table 1.1). From the total of unconfirmed records, 11 were listed only in unpublished literature (theses and government reports) and 5 (*Dictyota dichotoma*, *D. divaricata*, *Sargassum fluitans*, *Centroceras clavulatum*, *Gracilaria verrucosa*) required further taxonomic clarification to establish distribution in Central American Pacific coast.

Table 1.1. Number of marine macroalgae species on the Pacific coast of Central American, by country.

	Guatemala	El Salvador	Nicaragua	Costa Rica	Panama
Ochrophyta- Phaeophyceae	0	14	6	26	25
Chlorophyta	5	36	6	44	52
Rhodophyta	11	96	12	146	97
Total	16	146	24	216	174

Patterns of species number vary along the Pacific coast of Central America (Fig. 1.3). Los Cóbanos reef and La Libertad intertidal rocky shores and cliffs (C4), Gulf of Fonseca (C6), inner Nicoya Gulf and central Pacific coast of Costa Rica (C11), and south Pacific of Costa Rica including Golfo Dulce (C13) have the highest number of species (>80). While the quadrants with the lowest species number (< 20) are: the Guatemala coast (C1, 2, 3), the north Pacific of Nicaragua (C7), outside the Nicoya Peninsula in Costa Rica

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(C10), the coastal zone of Gulf of Chiriqui in Panama (C14), Azuero Peninsula, Panama (C16) and Parita Bay, Panama (C17).

Differences in species number among the countries and local sites may be explained by differences in research effort and habitat heterogeneity. The greatest number of species has been reported for sites in Costa Rica, Panama and El Salvador visited by E.Y. Dawson in the 1950s and 1960s, and subsequently, by local and international experts since the 1980s. Currently there are no phycological researchers in Guatemala or Honduras. Most of the collections in Guatemala were made by foreign experts. The sites with the highest number of species have extensively sampled. In contrast, there are many sites (Fig. 1.3, C1, 2, 3, 7, 14, 16, 17) that have not been explored in detail and need further examination. Indeed, in a recent study of niche evolution and biogeography Verbruggen et al. (2009) predicted, on the basis of habitat preferences, that since the Pliocene rise of the Central American Isthmus the CAP is likely to harbor species of *Halimeda* that have not been reported previously for the region.

The second explanation for the differences in species number is the variety of ecosystems and habitats linked with geomorphological and oceanographic characteristic (coastal upwellings) (Cortés 2007). Guatemala's coast is the least heterogeneous (Fig. 1.3, C1, 2, 3), among the countries. It consists mainly of sandy beaches, with extensive mangrove forests landward of the sand bars (Jiménez 1984, Cortés 2007). Sampling efforts in Guatemala have focused almost exclusively on the mangrove-associated marine flora (Pedroche et al. 1995, Dreckmann and Gamboa-Contreras 1998, Karsten et al. 2000, Zuccarello and West 2002, 2003, 2006, Kamiya et al. 2003, Tejada 2007a), resulting in the apparent absence of marine macroalgae, especially brown algae. The coast of El Salvador (Fig. 1.3, C4, 5, 6) has a diverse geomorphology and habitat structure. The northern part that borders with Guatemala is composed mainly of sandy beaches and mangroves. At Los Cóbano (Fig. 1.3, C4) and La Libertad (Fig. 1.3, C5), there are rocky outcrops, intertidal rocky shores platforms (Fig 1.4 B) and cliffs (Cortés 2007). There are also isolated coral reefs and rocky reef formations (Reyes Bonilla and Barraza 2003), which provide a high diversity of habitats where marine macroalgae can grow. Southward to the Gulf of Fonseca

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(Fig. 1.3, C6), the coast consists of high-energy sandy beaches. This gulf is shared by El Salvador, Honduras and Nicaragua, but the marine flora reported is from El Salvador's coasts and islands. The gulf is surrounded by rocky outcrops, islands, and the most extensive mangrove forests along the Pacific coast of these three countries (Cortés 2007).

The Pacific coast of southern Nicaragua (Fig. 1.3, C7, 8), all of Costa Rica (Fig. 1.3, C9, 10, 11, 12, 13) and most of Panama (Fig. 1.3, C14, 15, 16, 17, 18, 19) consist of a combination of rocky points, sandy beaches, cobble beaches, deltas and several gulfs (Cortés 2007). There are diverse and productive areas, which are essential to the local artisanal fisheries (Vargas and Mata 2004), mangrove habitats with high sediments inputs (Fig. 1.3, C7, 11, 12, 13, 16, 19) (Voorhis et al. 1983, Jiménez 1984, Hebbeln and Cortés 2001), well developed coral and rocky reefs (Fig. 1.3, C8, 9, 10, 12, 13, 15, 18, 19) (Glynn and Maté 1997, Jimenez 2001, Cortés and Jiménez 2003, Maté 2003, Alvarado et al. 2005, Alvarado 2010) and many islands and islets ranging from a few square meters to several square kilometers (Cortés 1997).

In combination with this geomorphological complexity, the oceanographic effects of coastal upwellings further increase the heterogeneity of the CAP so that temperature and the nutrients vary significantly by season (dry and rainy) (Glynn 1988, Cortés 1997). Because of this high variety of habitats we expect that the marine algal species number, especially in Nicaragua and Guatemala, will be increased with new collections and sampling efforts.

According to the taxonomic distinctiveness indices (Δ^+) (Fig. 1.5), the composition of the macroalgae varies along the countries of CAP coast. Nicaragua and Guatemala are the countries with the lowest taxonomic distinctiveness (Fig. 1.5), but Guatemala has the highest variation, with few species in few taxonomic groups. Although there are only four published papers that record marine macroalgae in Nicaragua (Dawson and Beudette 1959, Dawson 1962a, Norris and Johansen 1981, De Clerk 2003), the few species reported belong to all higher taxonomic groups (red, green, and brown algae), while in Guatemala the majority of the collections were focused on algae associated with mangrove prop roots and so most of the species reported from that country are red algae (Dreckmann and Gamboa-

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Contreras 1998, Pedroche et al. 1995, Karsten et al. 2000, Zuccarello and West 2002, 2003, 2006, Kamiya et al. 2003, Tejada 2007a).

Costa Rica, Panama and El Salvador are the countries with the greatest taxonomic distinctiveness (Fig. 1.5). Although El Salvador is less diverse (Table 1.1), all countries are well represented by the majority of taxa and there is a good representation of most of the orders, families and genera.

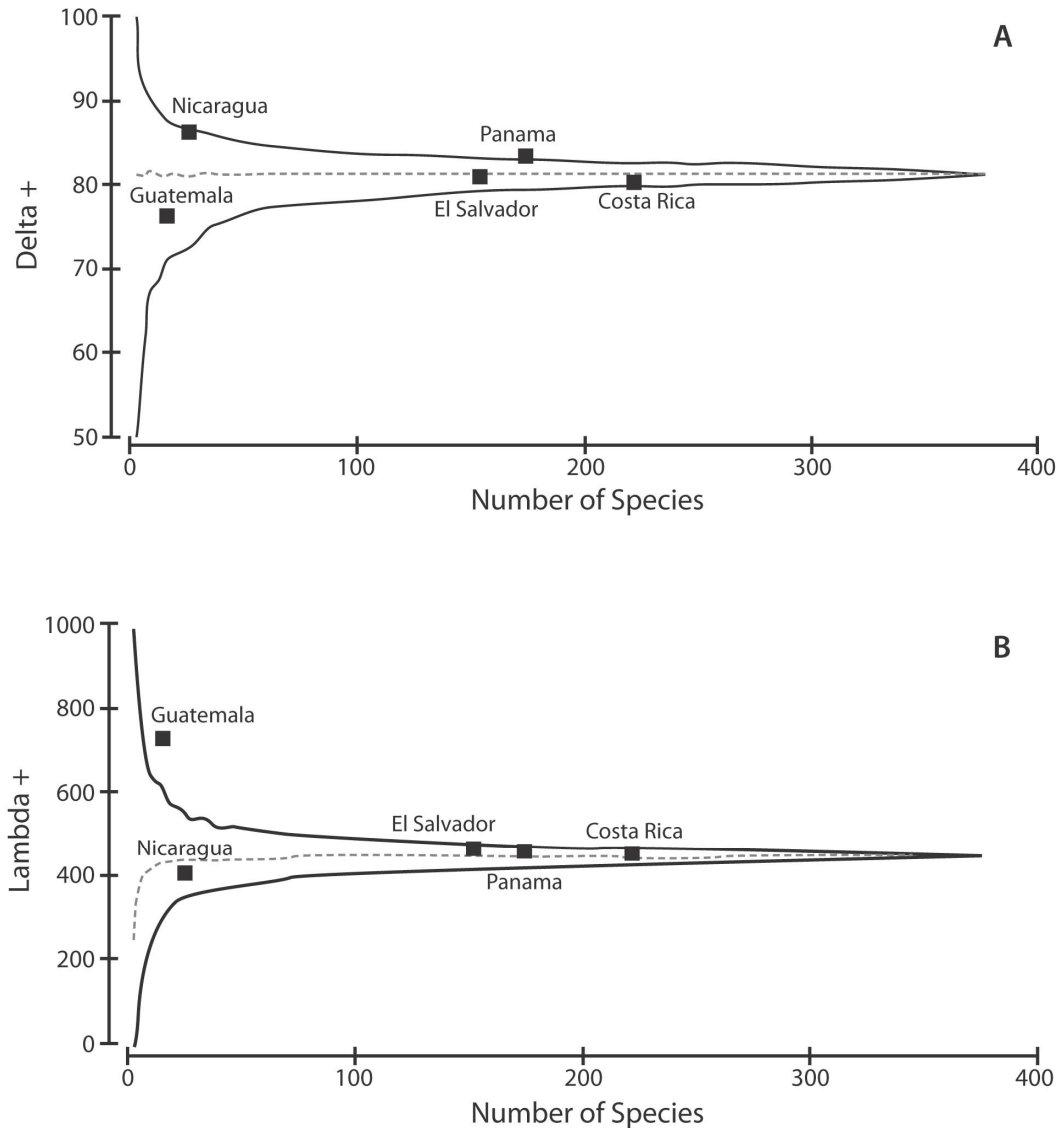


Fig. 1.5. Taxonomic distinctness indexes: A) average (delta: Δ^+), and B) their variation (lambda: Λ^+) on the Central America Pacific marine macroalgae. Solid line: 95% confidence limit; dotted line: Δ^+ average value.

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According to the cumulative curves (Fig. 1.6) and the Chao species estimator, the total species number would probably increase with future samplings efforts. The estimator shows that the number of Phaeophyceae could increase from the 49 species reported here to 85.1 ± 3.5 species; Chlorophyta could increase from 81 to 111.3 ± 1.9 species and Rhodophyta from 257 to 398.2 ± 2.4 species. Although the marine flora of CAP has not been extensively studied, when compared to that of neighboring regions in the eastern tropical Pacific such as southern Mexico, Galápagos and Colombia, algal species number is nevertheless high (Table 1.1). However, in contrast with more distant sites such as the Gulf of California (sub-tropical region), number of species in the CAP, is considerably lower. The Pacific coast of Colombia appears to be most similar to the CAP in species composition, with 71% shared species, while Mexican Tropical Pacific and Galapagos Islands share fewer (58% and 37% respectively) (Table 1.2).

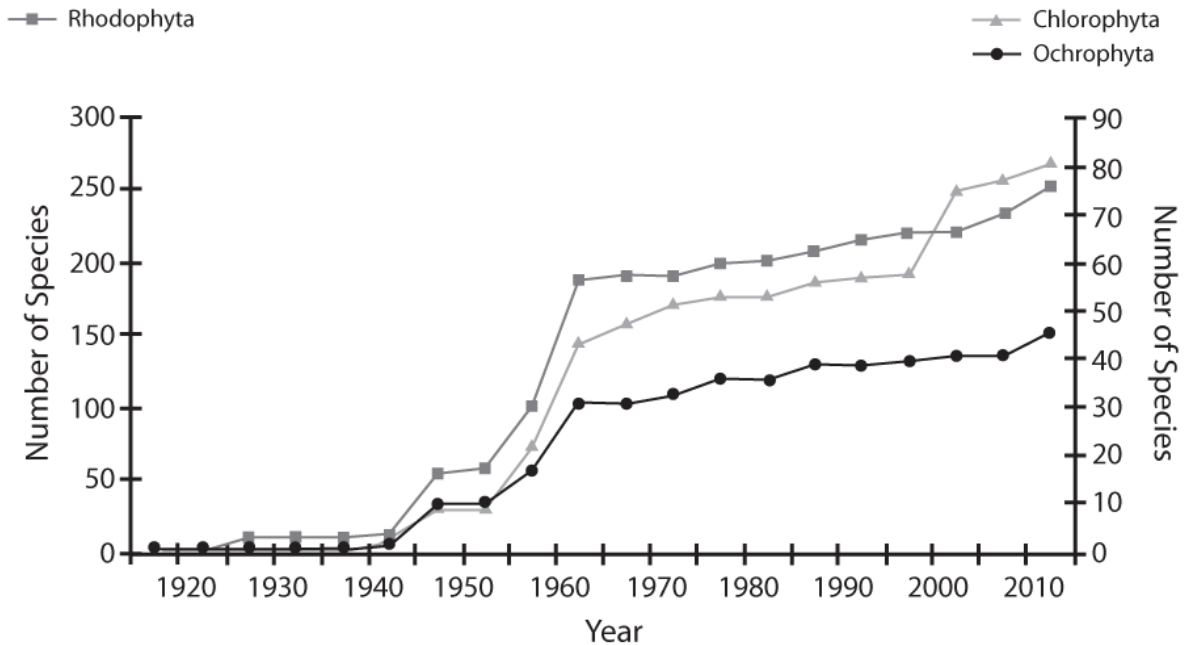


Fig. 1.6. Cumulative curves of new species reported per year of Rhodophyta, Chlorophyta and Ochrophyta-Phaeophyceae for Pacific Central America.

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Table 1.2. Marine macroalgal species number per phylum in some regions and countries in the Eastern Tropical Pacific and the Gulf of California. Numbers in parentheses refer to the species that overlap with Pacific of Central America. References: 1= González-González et al. 1996, 2= Riosmena-Rodríguez 2005, 3= González-González 1993 (Nayarit to Chiapas), 4= Schnetter and Bula-Meyer 1982, Bula-Meyer 1995, Peña-Salamanca 2008, 5= Garske 2002.

	Entire Mexican Pacific¹	Gulf of California²	México Tropical Pacific³	Pacific Central America (this study)	Colombian Pacific⁴	Galápagos Islands⁵
Ochrophyta-Phaeophyceae	209	148	22 (13)	46	20 (14)	46 (16)
Chlorophyta	140	160	38 (25)	81	28 (18)	42 (30)
Rhodophyta	998	690	78 (40)	252	79 (50)	228 (69)
Total	1347	998	138	379	119	316

Red algae (Rhodophyta) were the most speciose group (Table 1.2), as in other eastern Pacific regions (Schnetter and Bula 1982, Bula-Meyer 1995, González-González et al. 1996, Garske 2002, Riosmena-Rodríguez 2005, Peña-Salamanca 2008). However, the green and brown algae do not reflect patterns in other regions. In the CAP, Colombia, south México and the Gulf of California, green algae are more speciose than brown algae. The species of Fucales and Laminariales in the Galapagos Islands and the northern Mexican Pacific are not present in tropical eastern Pacific waters.

Apparent species number measures for the CAP arise from a combination of geomorphological configuration and habitat structure (sandy and muddy bottoms, mangroves, coral and rocky reefs, rhodolith beds and intertidal habitats). Also the floristic differences are related with the differential sampling effort and facilities in the area. To further explore effects of these on macroalgal species distributions, greater collection efforts in unexplored and remote areas will be required.

**IDENTIFICACIÓN ASISTIDA POR ADN DEL GÉNERO *CAULERPA*
(CAULERPACEAE, CHLOROPHYTA), REDUCCIÓN DE LA RIQUEZA DE
ESPECIES EN EL PACÍFICO TROPICAL ORIENTAL**

DNA- assisted identification of *Caulerpa* (Caulerpacae, Chlorophyta) reduces species richness estimates for the Eastern Tropical Pacific

Resumen: La taxonomía y riqueza de especies del género *Caulerpa* ha sido problemática debido a la dificultad de que una especie puede presentar varias morfologías y no existe uniformidad en definir estas especies. Es por esto que el presente trabajo evalúa la taxonomía y distribución de las especies de este género en el Pacífico Tropical Oriental (PTO), basado en un análisis morfológico y de secuencias génicas (gen *tufA*). Los análisis moleculares revelan la presencia de seis clados a nivel de especie: *C. verticillata*, *C. sertularioides*, *C. cupressoides*, *C. serrulata*, *C. racemosa* var. *mucronata* y *C. racemosa laetevirens/peltata/turbinata*. Estos resultados muestran una reducción del estimado de riqueza de especies en 50 % (de 13 a 6). En concordancia con otros trabajos recientes, nuestros datos morfológicos y moleculares garantizan el reconocimiento a nivel de especie del complejo *C. laetevirens/turbinata/peltata*, siendo *C. chemnitzia*, el nombre más antiguo aplicado a este grupo de especies, así mismo se propone el uso de ecadas como una solución práctica para la identificación de la diversidad morfológica de esta especie en el PTO. Aunado a esto se reconoce la sinonimia de *C. racemosa* var. *mucronata* con *C. racemosa* var. *macrophysa*. Las seis especies de *Caulerpa* encontradas en este estudio presentan distribución pantropical. Dentro del PTO; cuatro de estas tienen una distribución restringida, mientras que dos especies muestran una amplia distribución latitudinal (*C. chemnitzia* y *C. sertularioides*).

Abstract: The taxonomy and species richness estimates of the genus *Caulerpa*, has proven to be problematic due to the difficulty of assessing the various morphologies that are known to occur to modern species-level entities and well-defined species concepts. In the present study we evaluate the taxonomy of the genus and we assess species distributions within the Eastern Tropical Pacific (ETP), based on morphology and gene sequence data (*tufA*). Molecular analyses revealed the presence of six species-level clades: *C. verticillata*, *C. sertularioides*, *C. cupressoides*, *C. serrulata*, *C. racemosa* var. *mucronata* and *C. racemosa laetevirens/peltata/turbinata*. Our results reduce species richness estimates throughout the ETP by over 50% (from 13 to 6). In accordance with other recent studies, our morphological and DNA results warrant the recognition of the *C. laetevirens/turbinata/peltata* complex at species level, being *C. chemnitzia* the earliest legitimate name, we propose the use of ecads as a practical identification tool for morphological diversity below the species level present at the ETP, in addition we recognize the synonymy of *C. racemosa* var. *mucronata* with *C. racemosa* var. *macrophysa*. The six species of *Caulerpa* found in this study are pantropical in distribution. Within the ETP region; four species have restricted distributions, while two show a wide latitudinal distribution (*C. chemnitzia* and *C. sertularioides*).

Key Words: Bryopsidales, Central America, Colombia, DNA-assisted identification, Mexico, phenotypic plasticity, taxonomy, *tufA*

Introduction

The genus *Caulerpa* Lamouroux (Caulerpaceae, Bryopsidales, Chlorophyta) is a group of siphonous green algae described by Lamouroux, for those green algae consisting of a creeping tubular stolon (Greek: *caulos* = stem, *erpo* = I creep) with erect structures, known as assimilators and/or fronds (Lamouroux 1809, Weber-van Bosse 1898, Lee 2008). The coenocytic thallus consists of a single, large multinucleate cell, which is reinforced by invaginations of the cell wall known as trabeculae (Silva 2003, Lee 2008). Fibrous colorless rhizoids emerge from the basal stolon to secure the thallus in loosely consolidated sediments. *Caulerpa* is distributed throughout the tropical and warm temperate waters worldwide (Smith and Walters 1999, Senerpont Domis et al. 2003, Silva 2003). Its predominant clonal spreading and its phenotypic plasticity result in a flexible adaptative response to different environments (Børgesen 1907, Ohba and Enomoto 1987, Ohba et al. 1992, Collado-Vides and Robledo 1999, Senerpont Domis et al. 2003, Fernández-García et al. 2012), which often challenges accurate species identifications.

The biology, ecology and species diversity of *Caulerpa* have been extensively studied, in part due to the highly invasive nature of some species, primarily *C. taxifolia* (M.Vahl) C.Agardh (Meinesz and Hesse 1991, Ceccherelli et al. 2000), *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman and Boudouresque (Piazzi et al. 1994, Piazzi 1997), *C. ollivieri* Dostál (Lapointe et al. 2005) and *C. sertularioides* (S.G.Gmelin) M.A.Howe (Fernández and Cortés 2005, Fernández 2007), and as part of recent efforts to regulate the movement of such species around the world (Stam et al. 2006, Walters et al. 2006). Regions impacted by *Caulerpa* invasions have suffered dramatic ecological impacts, including biodiversity loss (e.g., Bellan-Santini et al. 1996, Ceccherelli et al. 2000, Piazzi et al. 2001, Fernández 2007, Smith et al. 2010) that can lead to severe economic impacts (Francour et al. 1995, Baskin 1996).

Currently, 86 species of *Caulerpa* are recognized (Guiry and Guiry 2012). Species discrimination lies primarily in morphological variation of the assimilators, but recent systematic investigations have relied upon molecular markers to elucidate biodiversity

(Senerpont Domis et al. 2003, Famà et al. 2002, Stam et al. 2006). These studies have revealed that characters that were thought to constitute well-defined morphological boundaries among species are actually quite plastic. In fact, two or more morphotypes can sometimes be found on the same thallus, suggesting that there is no genetic basis for the recognition of certain morphological forms (Ohba and Enomoto 1987, Ohba et al. 1992, Senerpont Domis et al. 2003, this study). It remains unclear how ecological factors (e.g., substratum, water motion, temperature, light intensity or other factors) trigger the expression of variable morphologies (Eubank 1946, Coppejans 1992, Coppejans and Prud'homme van Reine 1992, Senerpont Domis et al. 2003), but it is abundantly clear that ongoing efforts to document algal diversity throughout the world must rely on morphology-independent species assessments. For example, if phenotypic plasticity is triggered by an increase in temperature (as might be predicted under scenarios of global climate change, Solomon et al. 2007), then biodiversity assessments would report the presence of different species as a consequence of global warming when, in fact, there was no change at all.

As part of a series of studies to establish algal diversity foundations throughout the poorly studied marine floras of Central America (see Fernández-García et al. 2011) we undertook the investigation of *Caulerpa* diversity in the Eastern Tropical Pacific. This region extends from the south of the Baja California Peninsula, in Mexico, to Ecuador (Fig. S1) (Pennington et al. 2006, Spalding et al. 2007), including the oceanic islands: Clipperton (France), Revillagigedo (Mexico), Cocos (Costa Rica), Malpelo (Colombia), and Galapagos (Ecuador). The main natural disturbances affecting the ETP are El Niño-Southern Oscillation (ENSO) warming events and three coastal upwellings during the dry season (December-April). These events cause drastic alterations in the ETP associated with important biological changes (Amador et al. 2006, Wang and Fiedler 2006) that may influence algal distribution and species composition.

Recent studies of *Caulerpa* have sampled across broad geographic scales, however, representatives from the Eastern Tropical Pacific (ETP) have only been scarcely investigated, with only two specimens sequenced by Famà et al. (2002) (AJ417946 and AJ417949). *Caulerpa* species are an important component in the marine flora of the ETP.

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Some species (*C. sertularioides* and *C. racemosa*) have bloomed recently, raising concerns for environmental impacts reported elsewhere (see above). *Caulerpa* bloom events in the ETP have been ephemeral such as in Panamá (*C. racemosa*, *C. sertularioides*, Glynn and Maté 1997) and in the south Gulf of California (*C. sertularioides*, Scrosati 2001), while in Costa Rica (*C. sertularioides*, Fernández and Cortés 2005, Fernández-García et al. 2012) and other regions of Panama (Smith et al. 2010) the alga has maintained high densities for several years.

Thirteen *Caulerpa* species have been previously reported for the ETP (Table 2.1). The first report of *Caulerpa* in the ETP was made by E.Y. Dawson (in 1957) for the Pacific coast of Costa Rica (Golfo de Nicoya and Golfo Dulce); since then three more species of the genus has been reported for this country (Table 2.1) (Fernández-García et al. 2011). In later floristic surveys Dawson reported *C. racemosa* var. *peltata* for El Salvador (Dawson 1961) and *C. sertularioides* for Nicaragua (Dawson 1962a); Alvarado et al. (2011) recently reported from Nicaragua *C. racemosa*. Schnetter and Bula-Meyer (1982), in their book of marine algae of the Pacific coast of Colombia found a total of four species of this genus (Table 2.1).

For the Galapagos Islands, Garske (2002) reported *C. racemosa* with three varieties (*peltata*, *occidentalis* and *uvifera*). Later, Wysor (2004) presented five species of *Caulerpa* on the Pacific coast of Panama. Litter and Littler (2009) included another two new species (*C. macrophysa* and *C. nummularia*), bringing the total for Pacific Panama to seven species. In the Mexican tropical Pacific, Pedroche et al. (2005), reported six species of *Caulerpa*, including 2 varieties (Table 2.1). Finally, for the oceanic islands, a single species was documented for Clipperton (Payri et al. 2008) and two for Revillagigedo (Serviere-Zaragoza et al. 2007) (Table 2.1). At the moment there are no records of this genus for the coasts of Guatemala, Honduras, Ecuador, and Malpelo Island.

Thus, the aims of the present study are: 1) to evaluate the taxonomy of the genus *Caulerpa* in the Eastern Tropical Pacific using morphological variables and chloroplast encoded *tufA* gene sequences, and 2) to assess species distribution within the region.

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Table 2.1. Species of the genus *Caulerpa* reported for the Eastern Tropical Pacific. MEX=Mexico, ES= El Salvador, NIC= Nicaragua, CR=Costa Rica, PAN=Panama, CA= Central America, COL= Colombia, ECU= Ecuador, CLI= Clipperton island, RI= Revillagigedo island, CI= Cocos island, GL= Galápagos Islands.

Species	Current name (this study)	MEX	ES	NIC	CR	PAN	CA	COL	ECU	CLI	Reference
<i>C. cupressoides</i> var. <i>cupressoides</i>	<i>C. cupressoides</i>	x									Pedroche et al. 2005
<i>C. cupressoides</i> var. <i>lycopodium</i> Weber-van Bosse	<i>C. cupressoides</i>	x					x	x			Dawson 1962b, Schnetter and Bula-Meyer 1982, Pedroche et al. 2005
<i>C. mexicana</i> Sonder ex Kützing	<i>C. cupressoides</i>	x									Pedroche et al. 2005
<i>C. macrophysa</i> (Sonder ex Kützing) G Murray	<i>C. racemosa</i> var. <i>macrophysa</i>					x					Littler and Littler 2009
<i>C. microphysa</i> (Weber van Bosse) Feldmann	<i>C. microphysa</i> Requires revision					x					Earle 1972, Wysor 2004
<i>C. nummularia</i> Harvey ex J Agardh	<i>C. chemnitzia</i>					x					Littler and Littler 2009
<i>Caulerpa fastigiata</i> Montagne	<i>C. chemnitzia</i> ecad <i>vanbossea</i>	x (RI)									Serviere-Zaragoza et al. 2007
<i>C. racemosa</i> (Forsskål) J. Agardh	<i>C. chemnitzia</i>	x	x	x	x	x		x	x (GL)	x	Earle 1972, Avilés and Canjura 1979, Schnetter and Bula-Meyer 1982, Gutiérrez 1985, Glynn 1990, González-González et al. 1996, Glynn and Maté 1997, Garske 2002,

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Species	Current name (this study)	MEX	ES	NIC	CR	PAN	CA	COL	ECU	CLI	Reference
											Tejada 2003, Wysor 2004, Pedroche et al. 2005, Serviere-Zaragoza et al. 2007, Fernández and Alvarado 2008, Payri et al. 2008, Bernecker and Wehrtmann 2009, Alvarado et al. 2011
											As <i>C. racemosa</i> var. <i>uvifera</i> : Gutiérrez 1985, González-González et al. 1996, Garske 2002, Tejada 2003, Tejada 2001
<i>C. racemosa</i> var. <i>peltata</i> (J.V. Lamouroux) Eubank	<i>C. chemnitzia</i> <i>ecad peltata, ecad</i> <i>laetevirens</i>	x	x	x	x	x		x	x	(GL)	Dawson 1957, Dawson 1961b, Dawson 1962b, Avilés and Canjura 1979, Gutiérrez 1985, González- González et al. 1996, Tejada 2003, Wysor 2004, Tejada 2007, Bernecker 2009, Alvarado et al. 2011
											As <i>Caulerpa peltata</i> : Earle 1972, Schnetter and Bula-Meyer 1982, Soto and Bermúdez 1990, González- González et al. 1996, Glynn and Maté 1997, Garske 2002, Tejada 2003, Pedroche et al. 2005, Serviere- Zaragoza et al. 2007, Fernández and Alvarado 2008
											As <i>C. racemosa</i> var. <i>laetevirens</i> : Dawson 1962b, González-González et al. 1996

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Species	Current name (this study)	MEX	ES	NIC	CR	PAN	CA	COL	ECU	CLI	Reference
<i>C. racemosa</i> var. <i>occidentalis</i> (J. Agardh) Børgesen	<i>C. chemnitzia</i> <i>ecad laetevirens</i>	x (RI)							x (GL)		Garske 2002, Serviere-Zaragoza et al. 2007
<i>C. serrulata</i> (Forsskål) J. Agardh	<i>C. serrulata</i>				x (CI)	x					Fernández 2008, Fernández and Alvarado 2008, Wysor 2004, Littler and Littler 2009
<i>C. sertularioides</i> (S.G. Gmelin) M. Howe	<i>C. sertularioides</i>	x		x	x	x		x			Dawson 1962a, Dawson 1962b, Earle 1972, Schnetter and Bula-Meyer 1982, Soto 1983, González-González et al. 1996, Glynn and Maté 1997, Wysor 2004, Fernández and Cortés 2005, Pedroche et al. 2005, Bezy et al. 2006, Fernández 2007, Fernández and Alvarado 2008, Fernández and Cortés 2009, Littler and Littler 2009
<i>Caulerpa verticillata</i> J. Agardh	<i>C. verticillata</i>	x				x					Pedroche et al. 2005, Wysor and Fernandez, pers. obs.
Number of current species		4	2	2	3	5	-	4	4	1	This study

Materials and Methods

Sample collection

A total of 139 samples of *Caulerpa* specimens were collected from 69 field locations throughout the ETP between 2008 and 2010. Detailed specimen information including specimen identification numbers, morphological and DNA identification, collecting site and date, and collectors, can be found in the supplementary material (Table S1). All specimens were collected manually by SCUBA diving or snorkeling, and were preserved in silica gel, formalin and as herbarium vouchers for molecular and morphological examinations. Voucher specimens are deposited in the USJ herbarium (Escuela de Biología, Universidad de Costa Rica), HBCS herbarium (Universidad Autónoma de Baja California Sur, Mexico), CUVC herbarium (Universidad del Valle, Cali, Colombia) and GENT herbarium (Ghent University, Belgium).

Morphological and ecological characteristics

For each specimen, the depth, substratum and wave exposure to wave energy were recorded. In the laboratory all specimens were analyzed for morphological characters, from both vegetative and reproductive thalli. We also recorded detailed locality information and geographic coordinates, which were plotted on maps with ArcGIS 9.2

Preliminary species identifications were made on the basis of morphology with reference to the following sources for the Eastern Pacific: Taylor (1945), Schnetter and Bula-Meyer (1982), Wysor (2004), Littler and Littler (2009) and Norris (2010). Measurements of morphometric characters were carried out on formalin-preserved specimens with a Nikon Coolpix 4300 camera and image processing with the UTHSCSA software Image Tool version 3.0. Following Senerpont Domis et al. (2003) and Ortuño-Aguirre and Riosmena-Rodríguez (2007) and, we used five qualitative and quantitative characters to delimit species: form of the frond, branching, length and width of the fronds and stolon diameter. For each character, minimum and maximum sizes and the 95 percentile were determined, represented as (Min-) 95% Range (-Max).

DNA extraction, amplification and sequencing

Dried algal biomass was ground for 60s at maximum speed ($6.5 \text{ m}\cdot\text{s}^{-1}$) using the FastPrep-24 automated homogenizer system with Lysing Matrix A (garnet) and ceramic ball in 2 ml microcentrifuge tube (MP Biomedical, Solon, OH), or ground by hand with sterile silica gel using a mortar and pestle. DNA was extracted from ground biomass using the Plant DNEasy Mini-Kit (Qiagen, Valencia, CA) following manufacturer instructions, and separating final elutions in PCR-water. Frequently, DNA extractions prepared with the FastPrep-24 instrument required gel purification prior to successful amplification, which was accomplished as described below. We attribute this result to the co-extraction of PCR inhibitors from efficient cell lysis using the FastPrep-24 instrument. Initial amplification success was higher with hand grinding. Amplification of the plastid encoded *tufA* gene (Famà et al. 2002) was performed in a total volume of 20 μl in a Bio-Rad C1000 thermocycler. Each reaction consisted of 1x BioMix Red (Bioline, Taughton, MA), 0.5 μM each primer (Table 2.5), 1 M Betaine and 1.0 μl of undiluted or diluted (1:10 and 1:100) genomic DNA extract. Amplification profiles consisted of an initial denaturation at 94°C for 3 minutes followed by 35 cycles of 94°C for 1 minute, 42°C for 2 minutes and 65°C for 3 minutes, a final extension at 65°C for 7 minutes for *tufA*. Amplicons were visualized on a DarkReader (Clare Chemical, Dolores, CO) and excised from 1.2% ultrapure low-melting point (Invitrogen, Carlsbad, CA) TAE (MP Biomedical, Solon, OH) agarose and stained with 50 $\mu\text{l/l}$ GelGreen (Biotium, Hayward, CA). Excised products were cleaned using the Qiagen Gel Extraction kit (Qiagen, Valencia, CA) following manufacturer instructions. The DNA concentration of cleaned amplicons was estimated using a Nanodrop 1000 spectrophotometer (Thermo Scientific, Wilmington, DE). Cycle sequencing reactions, prepared in 20 μl total volume with 2.5-5.0 ng/100 bp of amplicon, and subsequent automated sequencing on an ABI 3130xl was performed by the Rhode Island Genomics and Sequencing Center.

Analysis

Forward and reverse sequences were edited and aligned using Sequencher v. 4.10.1 (Gene Codes, Ann Arbor, MI) and aligned with published sequence data (Table S2).

The *tufA* alignment used for delimitation of species was 820 bp long. Due to missing data at the 3' and 5'-ends, only 820 of the original 903 bp alignment were analyzed. In order to delimit species clades we conducted an UPGMA analysis using MEGA 5.0 (Tamura et al. 2011).

To elucidate a possible association between morphological types and haplotype structure in specimens belonging to the *Caulerpa racemosa laetevirens/turbinata/peltata* complex, we generated a detailed haplotype tree for this species. We used BEAST v.1.5.4 to infer a haplotype tree based on a coalescent model (Drummond and Rambaut 2007). Fifty-three sequences belonging to the complex as well as 12 sequences of related species were included in the analysis. These additional sequences included *C. integerrima*, *C. mexicana*, *C. racemosa* var. *mucronata*, *C. scalpelliformis* and *C. racemosa racemosal/corynophora/lamourouxii*. The BEAST analysis used a HKY+G4 model of sequence evolution with the three codon positions completely unlinked and an uncorrelated lognormal clock model. The MCMC chain was started from a UPGMA tree and run for 10 million generations, sampling every 1,000th generation. A constant population size coalescent prior was used as tree prior. All other priors and operators were kept at their default values. We used Tracer v.1.5 to assess convergence and applied an automated method (Beiko et al. 2006) to determine a suitable burn-in value (116,000 generations). The post-burn-in trees were summarized with TreeAnnotator v.1.5.4

Results

Following the traditional morphological taxonomic classification, and the keys available for the ETP, seven different morphotypes were identified for this region: *C. cupressoides*, *C. macrophysa*, *C. nummularia*, *C. racemosa* (var. *peltata*, var. *laetevirens* and intermediate forms), *C. serrulata*, *C. sertularioides* and *C. verticillata*.

However, according to the molecular analysis of the *tufA* gene, Eastern Tropical Pacific *Caulerpa* specimens clustered in six species-level clades, which are highlighted in figure 2.1. These clades are labeled *C. verticillata*, *C. sertularioides*, *C. racemosa* var. *mucronata*, *C. cupressoides*, *C. serrulata*, and *C. racemosa laetevirens/peltata/turbinata*. These clade names were applied based on correspondence with morphology-based identifications of specimens belonging to the clusters or previous work in case of the two *C. racemosa* clades (Senerpont Domis et al. 2003). Our specimens from the ETP that fell in the *C. racemosa* var. *mucronata* cluster were identified as *C. macrophysa* according to Littler and Littler (2009). The *C. racemosa laetevirens/peltata/turbinata* cluster contained ETP samples conforming to the morphological descriptions of *C. nummularia* as well as *C. racemosa* (varieties *peltata*, *laetevirens* and intermediate forms).

In many cases, morphological species are monophyletic lineages, e.g. *C. sertularioides*, *C. verticillata*, *C. cupressoides* and *C. serrulata*. However, in correspondence with previous work, *Caulerpa racemosa* (in the traditional morpho-species sense) is a polyphyletic taxon, with at least three widely divergent genetic lineages (Figs. 2.1 and 2.2) (Senerpont Domis et al. 2003, Stam et al. 2006, Wynne et al. 2009). The DNA sequences show that all Eastern Pacific specimens clustered in the *mucronata* and the *laetevirens/turbinata/peltata* genetic lineages (Figs. 2.1 and 2.2). The latter clade includes the disc-like forms typical of *C. peltata* and *C. nummularia* as well as the more typical compact pyriforms and clavate forms (Fig. 2.2). While the group is well-supported (PP 1.0) at the species level, there is no resolution within that could help define sub-specific taxa (Fig. 2.2).

From the 13 species reported for the ETP (Table 2.1), we found that *C. mexicana* Sonder ex Kützing (Pedroche et al. 2005) is a misidentification of the species *C. cupressoides*, these two species can be easily confused due to the wider branchlets exhibited by some specimens of *C. cupressoides* in the ETP, and we were not able to confirm the presence of *C. microphysa* (Weber van Bosse) Feldmann reported originally by Earle (1972) and reinterated by Wysor (2004).

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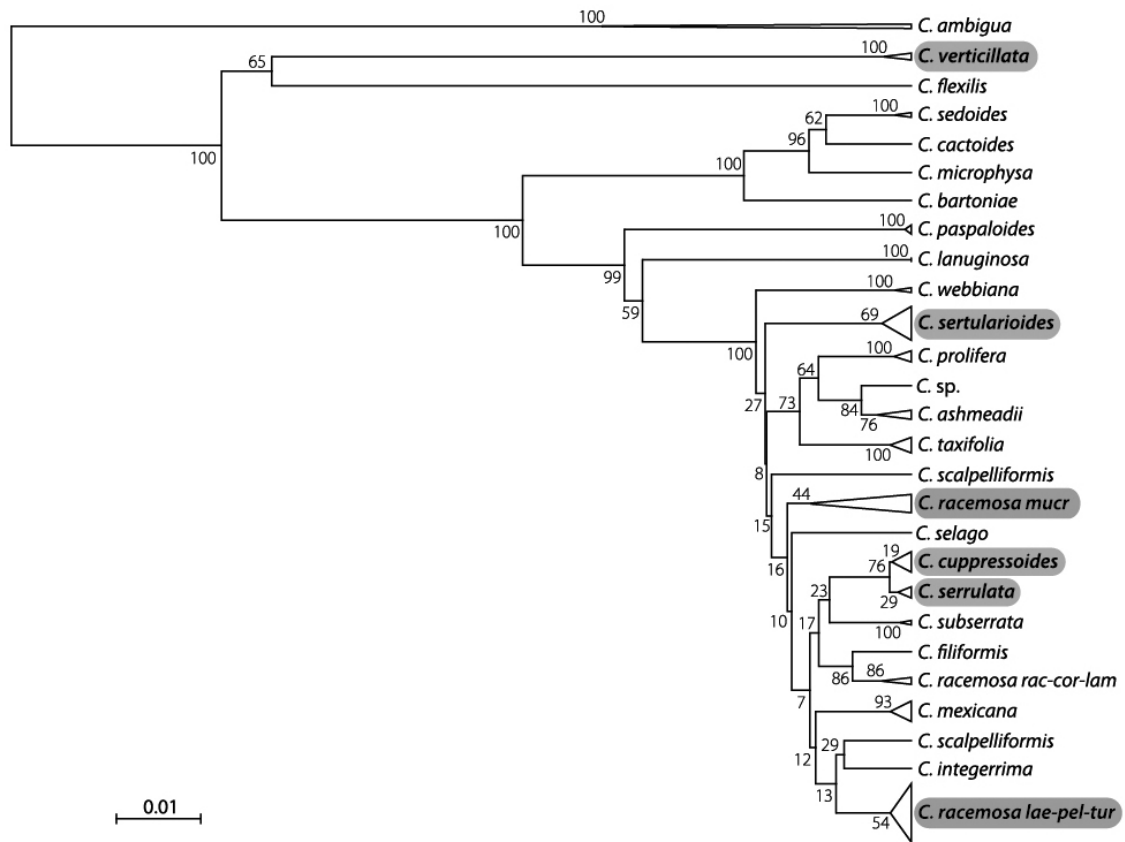


Fig. 2.1. UPGMA cluster analysis of *Caulerpa* species based on the *tufA* chloroplast sequences. Support values are next to the branches. Gray shadow indicates species clades that have Eastern Tropical Pacific sequences.

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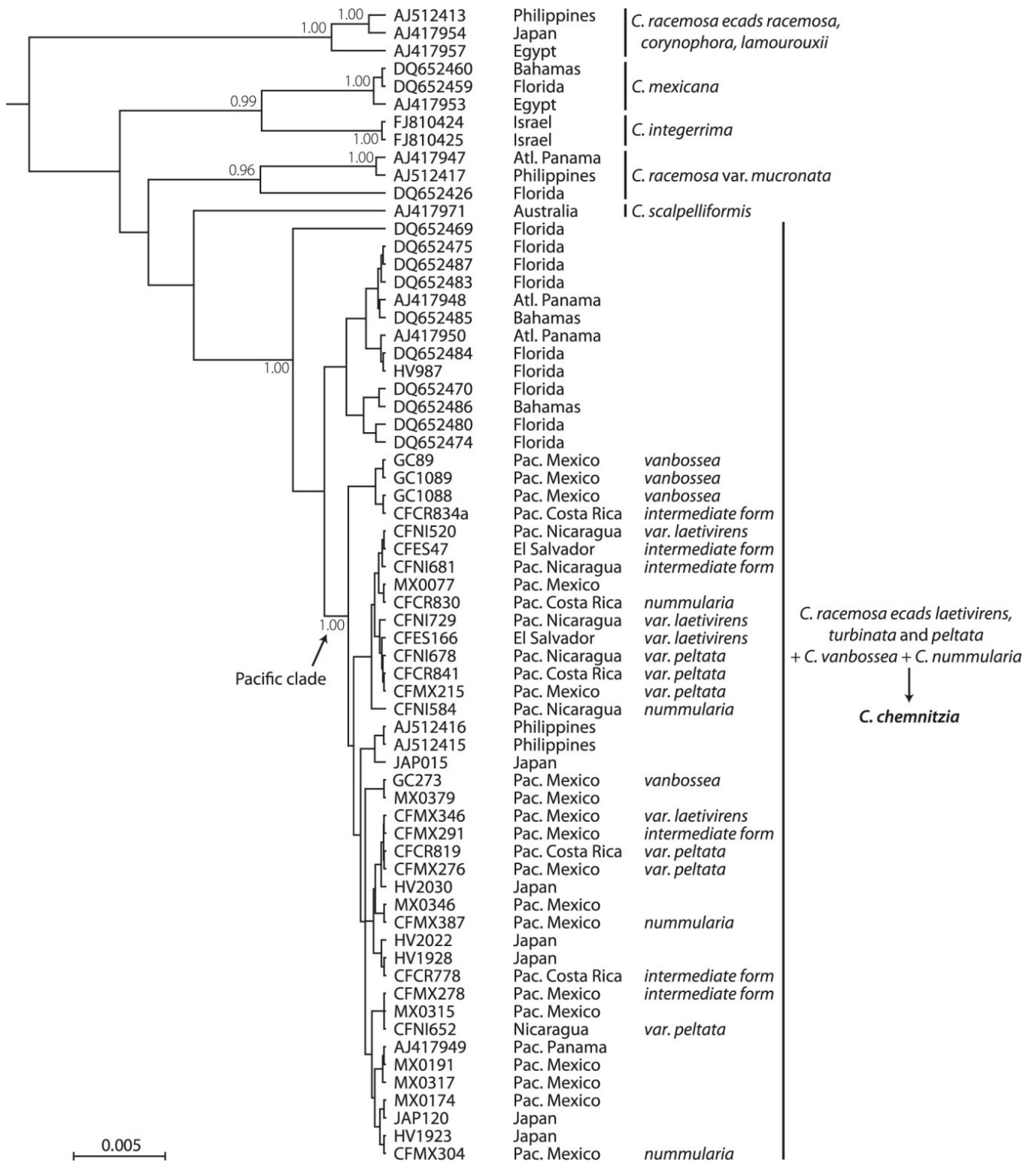


Fig. 2.2. Haplotype tree of *Caulerpa racemosa* lineages. Bootstrap values are next to the branches. See text for explanation of clade designations

Discussion

The *tufA*-inferred phylogeny presented here is consistent with previous studies (Famà et al. 2002, Stam et al. 2006), in which the *tufA* gene has sufficient variation to distinguish species, but provides no meaningful resolution of sub-specific taxa. In this study we document a total of six species for the ETP (Figs. 2.2, 2.3). These six species, in combination with *C. webbiana* from Chile (Ramírez and Santelices 1991) and *C. filiformis* from Peru (Acleto 1973, Ramírez and Santelices 1991), make up the entire list of *Caulerpa* native species from the Eastern Pacific. *Caulerpa taxifolia* was accidentally introduced in California (Jousson et al. 2000) but since eradicated.

Traditionally, the morphology of the fronds has been used to delineate species within the genus *Caulerpa*. Our results, however, show that morphological identifications of species have inflated previous assessments of species richness, because some phenotypically plastic species have been recognized by several names. This is why sequenced-based species delimitation is a valuable tool in organisms in which morphological discrimination is difficult or impossible, such as in many algal groups (Verbruggen et al. 2005, Leliaert et al. 2009). Evidently, it can be especially useful in taxa with phenotypic plasticity, such as *Caulerpa* and several other taxa (Saunders 2005, Leliaert et al. 2009, Mattio and Payri 2011). The *tufA* gene has shown to be a fairly good marker at species taxonomic level in this genus, showing well-supported species-level clusters, but does not yield much useful information when trying to delineate entities below the specie level (e.g. subspecies), which could possibly emerge with other genetic markers.

Our analysis of 139 specimens of *Caulerpa* reduces species number estimates from throughout the ETP region by over 50%, from 13 to 6. We did not encounter, nor have we been able to obtain, material conforming to *C. microphysa*, which has been documented previously from the region (Earle 1972), so the actual number of species could be seven instead of six species. Regardless, an improved estimate of species richness for eastern Pacific *Caulerpa* has resulted from a systematic effort to reconcile morphological diversity and a *tufA*-inferred phylogeny. This pattern in species richness reduction has also been reported for other taxa, such as *Sargassum* spp. (Mattio and Payri 2011) and *Macrocystis pyrifera* (Demes et al. 2009, Macaya and Zuccarello 2010). A consensus has emerged that

morphology of a given species may vary in time, at intra- or inter-individual levels, depending on environmental conditions, and spatial distribution. The absence of a stable morphological foundation has been an obstacle in taxonomy to delimit some species.

The notion of phenotypic plasticity among species in *Caulerpa* has a long history. Since 1809, when the genus *Caulerpa* was established, Lamouroux had commented on the presence of intermediate forms, and he wondered whether some new species might be variants of species described before (Silva 2003). One well recognized example of this taxonomic problem is *Caulerpa racemosa* (Weber-van Bosse 1898, Coppejans and Prud'homme van Reine 1992), a pan-tropical to temperate-warm water species widely distributed throughout the world. This species was described as *Fucus racemosus* Forsskål, (1775), and during the last century, researchers have described all clavate-spherical forms under *C. racemosa* with several varieties, forms and ecads (a form expressed in response to a particular environment). Eubank (1946) considered the disc like shape fronds of *C. peltata* Lamouroux, as a variety of *C. racemosa* because of the presence of transitional clavate forms observed in Hawaiian material. Kraft (2007), in his book of benthic algae of Lord Howe Island and the Southern Great Barrier Reef, distinguished *Caulerpa peltata* as always having simple peltate assimilators and consistently thinner stolons (350-600 µm diameter), while “*C. racemosa* var. *peltata* Eubank-type” has assimilators bearing multiple peltate ramuli and coarser stolons (1000 -3000 µm diameter). However, according to Wynne (2011), the problem is that Lamouroux’s description of *C. peltata* (1809, pl. III, Fig. 2.2) conforms to the “Eubank-type” rather than Kraft’s interpretation of *C. peltata*. So it is the latter form that should retain (*C. peltata*) and Kraft’s concept of “peltata” did not agree with what Lamouroux depicted (1809 Pl. III, Fig. 2.2). Also the measurements, of the stolon diameter in our study, do not agree with the description of Kraft’s (2007) *C. peltata*, as we found that specimens with simple peltate assimilators can have stolons of more than 600 µm in diameter (see below for details).

Benzie et al. (1997) and Verlaque et al. (2000) were the first to demonstrate that, different specimens attributed to *C. racemosa* may belong to distinct species. Moreover, recent molecular studies, have demonstrated that *C. racemosa* is polyphyletic (Benzie et al. 1997, Famà et al. 2002, Senerpont Domis et al. 2003, Stam et al. 2006), and constitutes a

complex of at least three lineages, each exhibiting phenotypic plasticity. The taxonomy complex has recently been revised based on DNA data from the *tufA* and UCP3 regions, leading to the recognition of the distinct lineages at the species level and the assignment of previously described species names to the species-level lineages (Belton et al. in review). Our *Caulerpa* specimens from the ETP fall in two of these lineages, as proposed by Senerpont Domis et al. (2003): *C. racemosa* var. *mucronata* and *C. racemosa* ecads *laetevirens/turbinata/peltata*. Based on the distinctiveness of these lineages, and following the conclusions of Belton et al. (in review), we recognize these two lineages at the species level.

The complex *C. racemosa laetevirens/turbinata/peltata* has the widest distribution around the tropical and subtropical regions of the marine environments and has been the focus of numerous studies of morphological variability (Ohba and Enomoto 1987). Laboratory and field studies have revealed that there are transitional forms between morphotypes and morphological differentiation in specimens within this lineage is correlated with environmental factors, such as light intensity and temperature (Børgesen 1907, Børgesen 1925, Calvert 1976, Ohba and Enomoto 1987 and Ohba et al. 1992, Silva 2003).

Following the ICN rule of priority and analyzing all epithets used to name the species within this clade (see Belton et al., in review), the earliest legitimate name would be “*chemnitzia*”. This description was first proposed by Esper (1800) for *Fucus chemnitzia*, which Lamouroux (1809) transferred to *Caulerpa chemnitzia* and later synonymized with *C. racemosa* var. *turbinata*. Weber-van Bosse (1898) discusses the opinion of several early phycologists who thought of conspecificity between *C. peltata* and *C. chemnitzia*, and she considered, that *C. chemnitzia* is a transitory form of *C. racemosa* to *C. peltata*, and those tightly linked to the f. *turbinata*. As Weber-van Bosse (1898) and Belton et al. (in review) opinions, in this study we found that *C. chemnitzia* is defined as a monophyletic *tufA*-inferred phylogenetic group, with several morphotypes that conform to the species: *C. vanbossea*, *C. nummularia*, and *C. racemosa* var. *laetevirens*, *C. racemosa* var. *turbinata*, *C. racemosa* var. *peltata*.

Since our DNA results show no indication that morphology is associated with subspecific molecular clusters (Fig. 2.3), we propose to recognize the morphological variants occurring in the ETP as ecads as a practical solution, following Coppejans (1992) and Coppejans and Prud'homme van Reine (1992). An ecad is a form expressed in response to a particular environment rather than based on a genotypic difference (Silva et al. 1996), and in situations like the one here it can be an alternative to avoid nomenclatural problems while enhancing the morphological meaningfulness of identifications while still conforming to the DNA-based species concept. Thus we choose to recognize this clade as the single species *Caulerpa chemnitzia* with the following ecads, as described below: *peltata*, *intermedia* and *laetevirens*. Also, it is important to note that in the *C. chemnitzia* clade (Fig. 2.3), there are sequences from specimens of the Gulf of California (Table S1, Fig. 2.3 under GC 89, 273, 1088, 1089), which had been identified as *C. vanbossea*, according to the description of Setchell and Gardner (1924). This species forms dense pulvinate masses, with erect fronds, cylindrical, slightly clavate apices, with irregular branching, and shows to be another morphological variant of the species *C. chemnitzia*. We therefore propose that *C. vanbossea* be subsumed into *C. chemnitzia* as an ecad.

Senerpont Domis et al. (2003) recognized the species-level lineage *C. racemosa* var. *mucronata*, however in the Hawaiian and ETP marine floras the species is regarded as *C. macrophysa* (Abbott and Huisman 2004, Littler and Littler 2009 and Fernández-García et al. 2011) and *C. racemosa* var. *macrophysa* in the Western Atlantic (Wynne 2011). Originally, *Chauvinia macrophysa* Sonder ex Kützinger was described from Tropical Central America. However, it is unclear whether the type material was obtained from the Pacific or the Atlantic side. Furthermore, the type has been lost and cannot be checked for further collection information (W. Prudhomme van Reine, I. Price, J. Milne-MEL Herbarium, pers. com.). Our analysis reveals that the clade harboring the ETP *C. racemosa* var. *macrophysa* is also found in the Atlantic, and was identified as such by Famá et al. (2002) (accession AJ417947 and AJ417956, Table S2). Hence, regardless of its geographical origin in the region, it seems that the subspecific rank can be applied with confidence.

Draisma and Prud'homme van Reine (2009) consider this clade as 'true' *C. racemosa* based on a picture of the type of *Fucus racemosus* from Suez, Red Sea. However,

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no sufficient molecular data accompanied by morphological observations is currently available from this location to ascertain so. Also, according to Belton et al. (in review), the lineage in question should retain the name *C. racemosa*. Based on our results, we synonymize the variety *mucronata* with *macrophysa* which is an earlier epithet (Sonder ex Kützing, 1857). Hence, the name *Caulerpa racemosa* var. *macrophysa* is tentatively applied to the ETP entity, but the clade in question requires further morphological and DNA studies based on worldwide collections and further clarification on the molecular identity of the latter in the Red Sea.

In the light of the synonymies proposed here, based on the morphological characters correlated with the species groups resulting from our DNA-assisted reevaluation of species concepts, we present here a dichotomous key (Table 2.2) and an annotated list of *Caulerpa* spp from the Eastern Tropical Pacific.

Table 2.2. Key to the species of *Caulerpa* species in the Eastern Tropical Pacific

1 a Assimilators filamentous, branchlets forming distinct whorls.....	<i>C. verticillata</i>
1b Assimilators not filamentous, branchlets not as above.....	2
2a Assimilators feather like, generally unbranched.....	<i>C. sertularioides</i>
2b Assimilators not as above.....	3
3a Assimilators with marginal teeth or spines.....	4
3b Assimilators without teeth or spines, branchlets spherical, mushroom or/and disc like shaped.....	5
4a Erect assimilators branchlets spine like.....	<i>C. cupressoides</i>
4b Assimilators compressed, twisted or spiral with marginal teeth.....	<i>C. serrulata</i>
5a Thallus upright cylindrical with end of the branchlets spherical or vesicle-like, vesicle 1.7-3.4 mm diam and stolons 1.6-1.9 mm diam	<i>C. racemosa</i> var. <i>macrophysa</i>
5b Thallus with disc like assimilators or/and with upright mushroom like assimilators, stolons 1.1-1.3 mm diam, when mushroom like branchlets crowded and gradually clavate.....	<i>C. chemnitzia</i>

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Annotated list of Caulerpa species from the ETP

***Caulerpa cupressoides* (West) C. Agardh 1817 (Fig. 2.3 a,b)**

Description: Light green erect cylindrical assimilators. Branching pinnate opposite, with fusiform ramuli placed in several longitudinal rows along a cylindrical main axis. The specimens found in Mexico are (0.5-) 0.6-0.8 (-1.1) cm high and (1.1-) 1.4-1.9 (-2.3) mm wide. Stolons creeping, (0.7-) 0.7- 0.9 (-1.0) mm diameter. However, Schnetter and Bula-Meyer (1982) documented specimens in Colombia that reached 20 cm high with stolons of 3 mm diameter.

Type Locality: St Croix, Virgin Islands.

Missapplied names: *C. mexicana* Sonder ex Kützing *sensu* Pedroche et al. 2005

Habitat: attached to rocky substratum, to 2 m deep.

Distribution in the ETP: Mexico: Nayarit, Jalisco, Central America, Colombia: Isla Gorgona.

References: Dawson 1962b, Schnetter and Bula-Meyer 1982, Pedroche et al. 2005, Fernández-García et al. 2011.

Other remarks: New collections of this species were found from the Tropical Mexican Pacific but not Central America. Although Dawson (1962b) reported it for that region, there is no specific locality where he collected the specimen.

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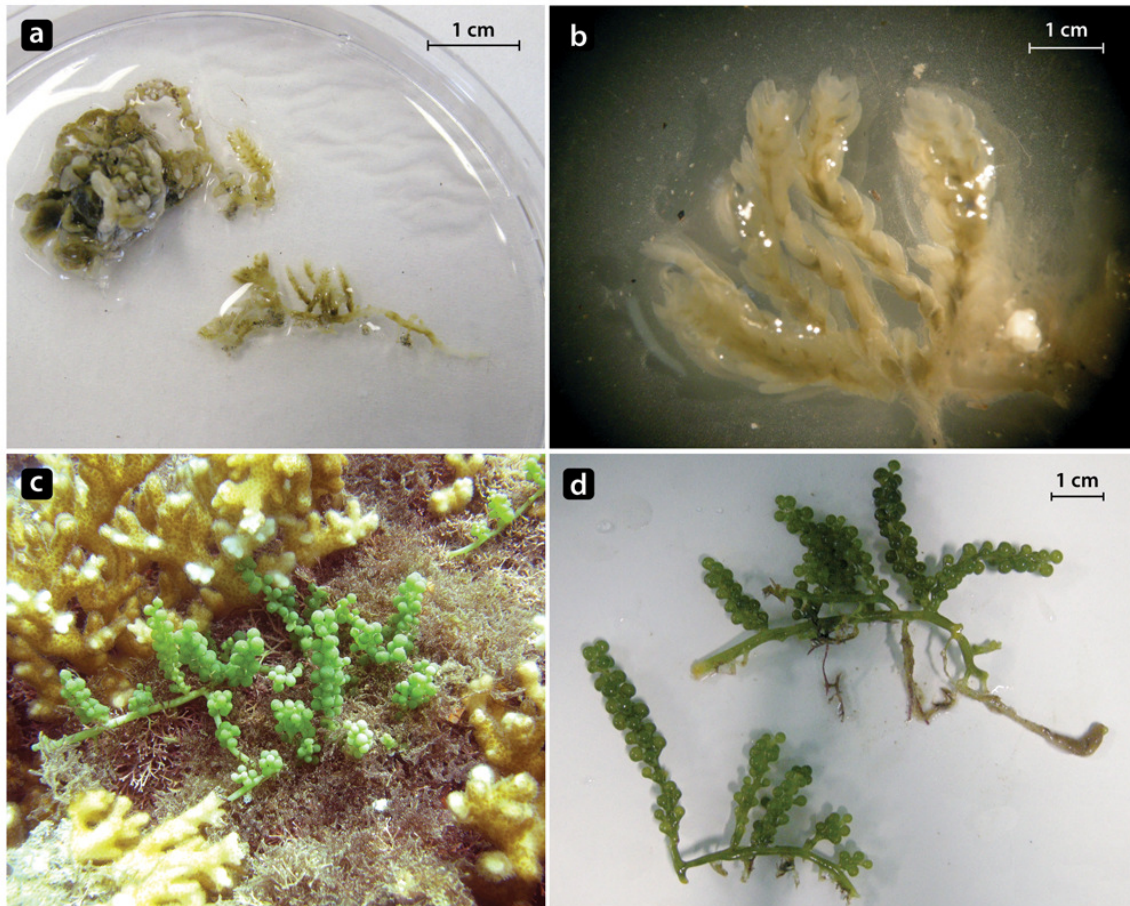


Fig. 2.3. Habit and frond morphology: (a,b) *C. cupressoides*, (c,d) *C. racemosa* var. *macrophysa*

***Caulerpa chemnitzia* Esper 1800 (Figs. 2.4, 2.5)**

Description: This is the most common and widespread *Caulerpa* species along the ETP (Fig. 2.7) Assimilators can be disc-like (single or branched), clavate, pyriform and thread-like, varying from (0.1-) 0.7-0.8 (-2.4) cm height and (1.1-) 3.0-3.2 (-6.9) mm wide. Stolons are (0.3-) 1.1-1.3 (-3.3) mm in diameter.

Type Locality: Malabar Coast, India.

Heterotypic synonyms: *Caulerpa peltata* Lamouroux, *Caulerpa laetevirens* Montagne, *Caulerpa nummularia* Harvey ex J.Agardh, *Caulerpa racemosa* var. *laetevirens* (Montagne) Weber-van Bosse, *Caulerpa vanbossea* Setchell and N.L.Gardner, *Caulerpa racemosa* var. *peltata* (J.V. Lamouroux) Eubank in Stephenson, *Caulerpa racemosa* var. *turbinata* (J.Agardh) Eubank; *Caulerpa racemosa* (Forsskål) J. Agardh 1873 *sensu* Earle 1972, Avilés and Canjura (1979), Schnetter and Bula-Meyer (1982), Gutiérrez (1985), Glynn (1990), González-González et al. (1996), Glynn and Maté (1997), Garske (2002), Tejada (2003), Wysor (2004), Pedroche et al. (2005), Serviere-Zaragoza et al. (2007), Fernández and Alvarado (2008), Payri et al. (2008), Bernecker and Wehrtmann (2009); *Caulerpa racemosa* var. *occidentalis* (J.Agardh) Børgesen, *sensu* Garske (2002), Serviere-Zaragoza (2007); *Caulerpa racemosa* var. *uvifera* (C.Agardh) J.Agardh *sensu* Gutiérrez (1985), González-González et al. (1996), Garske (2002), Tejada (2003, 2007).

Distribution in the ETP: Mexico: Nayarit, Jalisco, Colima, Michoacán, Guerrero, Oaxaca, Isla Revillagigedo, El Salvador: Sonsonate, La Libertad, La Unión, Nicaragua: León, Rivas, Costa Rica: Guanacaste, Puntarenas, Isla del Coco, Panamá: Golfo de Chiriquí, Golfo de Panamá, Colombia: Bahía Málaga (Chocó), Isla Gorgona, Ecuador: Esmeraldas, Islas Galápagos, France: Clipperton Island.

References: Earle 1972, Avilés and Canjura 1979, Gutiérrez 1985, Glynn 1990, Glynn and Maté 1997, Tejada, 2003, 2007, Wysor 2004, Pedroche et al. 2005, Fernández and Alvarado 2008, Bernecker and Wehrtmann 2009.

Nomenclature: The *tufA*-inferred phylogeny presented here is consistent with previous studies (Famà et al. 2002, Stam et al. 2006), in which the *tufA* gene has sufficient variation to distinguish species, but provides no meaningful resolution of sub-specific taxa. We describe the morphological attributes of each ecad, because of this, and because

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morphological plasticity has been documented for *C. chemnitzia* we adopt the “ecad” concept to recognize different morphologies within *C. chemnitzia*, which are elaborated below and in the taxonomic key in Table 2.3. This category is not recognized by the ICN, but that is not a problem since it has no taxonomical meaning and has as its purpose that the morphological variants of the species can be specified.

Other remarks: The morphology of the fronds is highly variable and seems under strong control of the environmental conditions. According to Senerpont Domis et al. (2003), light intensity and water motion are significant factors that explain the variance in assimilator form in this species.

Table 2.3. Key to the ecads of *Caulerpa peltata* J.V. Lamouroux

1a	Assimilators filamentous, tread-like with clavate or pyriform apices.....	<i>C. chemnitzia</i> ecad <i>vanbossea</i>
1b	Non filamentous assimilators.....	2
2a	Assimilators in an upright axis, mushroom like, end of the branchlets rounded and clavate, without disc like structures.....	<i>C. chemnitzia</i> ecad <i>laetevirens</i>
2b	Assimilators disc like in complete thallus or in part of it.....	3
3a	Complete thallus with disc like assimilators, sometimes blades showing proliferating stalks, creeping,	<i>C. chemnitzia</i> ecad <i>peltata</i>
3b	Partial thallus with disc like assimilators, mixed with upright mushroom like assimilators, end of the branchlets disc-like or rounded.....	<i>C. chemnitzia</i> ecad <i>intermedia</i>

***Caulerpa chemnitzia* ecad *intermedia* (Fig. 2.4 a,b)**

Description: Transitional form between *C. chemnitzia* ecad *peltata* and ecad *laetevirens*. Fronds branched, not flat but somewhat convex and the stipe is not broadly conical making a transition to the disc-like fronds. Often crowded, creeping, forming dense mats and covering a large surface of the substratum. Fronds (0.1-) 0.6-0.7 (-1.7) cm high, (1.1-) 2.7-2.9 (-5.1) mm wide. Stolons creeping, (0.6-) 1.2-1.3 (-2.0) mm diameter.

Habitat: attached to rocky and dead coral substratum, intertidal to 10 m.

Other remarks: very common throughout the ETP.

***Caulerpa chemnitzia* ecad *laetevirens* (Fig. 2.4 c,d)**

Description: Thallus erect or creeping, crowded, often forming dense mats. Fronds clavate or pyriform with regularly rounded apices, occasionally mushroom-shaped, (0.1-) 1.06-1.10 (-2.5) cm high, (1.1-) 3.4-3.5 (-6.9) mm wide. Stolons creeping (0.7-) 1.4-1.6 (-3.0) mm diameter.

Habitat: attached to rock and dead coral, mainly intertidal but occurs subtidally to 3 m deep

Other remarks: Especially adapted to live in shallow waters, with high light intensity (Ohba and Enomoto 1987, Ohba et al. 1992).

***Caulerpa chemnitzia* ecad *peltata* (Fig. 2.5 a,b,c,d)**

Description: Thallus prostrate, solitary or clustered, frequently forming dense mats. Complete thallus with flattened disc-like assimilators, (0.1-) 0.4-0.5 (-2.2) cm high, (1.1-) 2.9-3.0 (-5.9) mm wide. When branched (Fig. 2.5 c,d), branches are placed up along the main axis, turning flat discs upwards, sometimes lower discs show proliferating stalks. Stolons creeping, (0.3-) 0.9-1.1 (-3.3) mm diameter.

Habitat: attached to rocky and dead coral substratum, between 2 and 13 m deep, more common between 3-6 m deep, rarely intertidal.

Other remarks: Sometimes forming dense patches on rocks or dead coral. According to experimental studies the *peltata* type assimilators are formed at low light intensity (Ohba and Enomoto 1992), this is why this morphology was mainly found in subtidal environments. This is the most common ecad that can be found in the ETP. *Caulerpa nummularia* specimens were differentiated from *C. peltata* because of proliferating stalks from lower discs and scalloped margins of the discs, however intermediate thalli show both characteristics and also specimens having these characteristics appear to be in the same *C. chemnitzia* clade (Fig 2.4b).

***Caulerpa chemnitzia* ecad *vanbossea* (Fig. 2.5 e,f)**

Description: Forming dense masses. Cylindrical thread-like fronds, pinnula filiform (Fig. 2.5f) up to 2 cm high, branching subdichotomous, pinnula with short branches spine-like horizontal stolons of more or less similar diameter, 0.4-1 mm diameter.

Habitat: attached to rocky and dead coral substratum.

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Other remarks: *Caulerpa vanbossea* was described by Setchell and Gardner (1924), and is only known from the Gulf of California. According to our results this species is part of the *C. chemnitzia* complex (Fig. 2.2). It seems that the typical disc-like or clavate fronds are reduced; this can be the effect of particular environmental conditions of Gulf of California, such as seasonal temperature variation (temperatures can drop to 8-12°C during the winter and rise to 30°C during the summer, Lluch-Cota et al. 2007) and/or light intensity. We find it interesting that this ecad is not more common at the ETP, considering that it survives large seasonal variations in temperature.

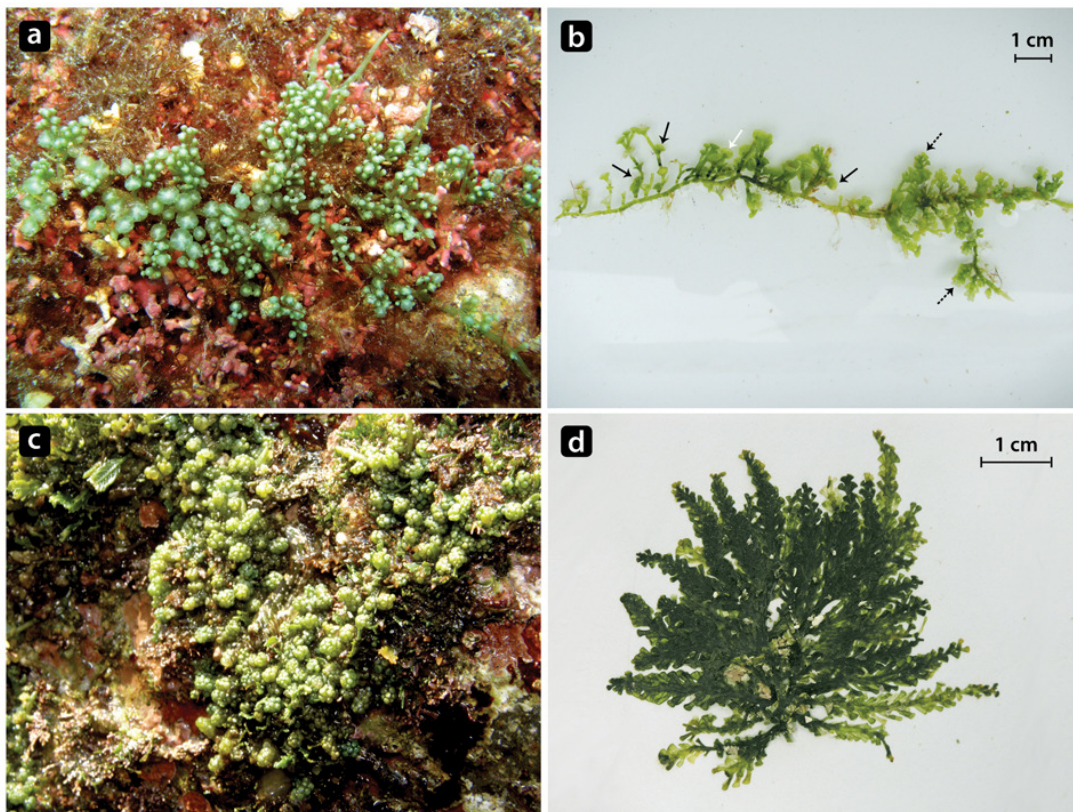


Fig. 2.4. Habit and frond morphology of *Caulerpa chemnitzia* clade: (a,b) *C. chemnitzia* ecad *intermedia*, black arrows points *nummularia* type fronds, white arrow *peltata* type fronds, discontinuous black arrow *laetevirens* type fronds, (c,d) *C. chemnitzia* ecad *laetevirens*

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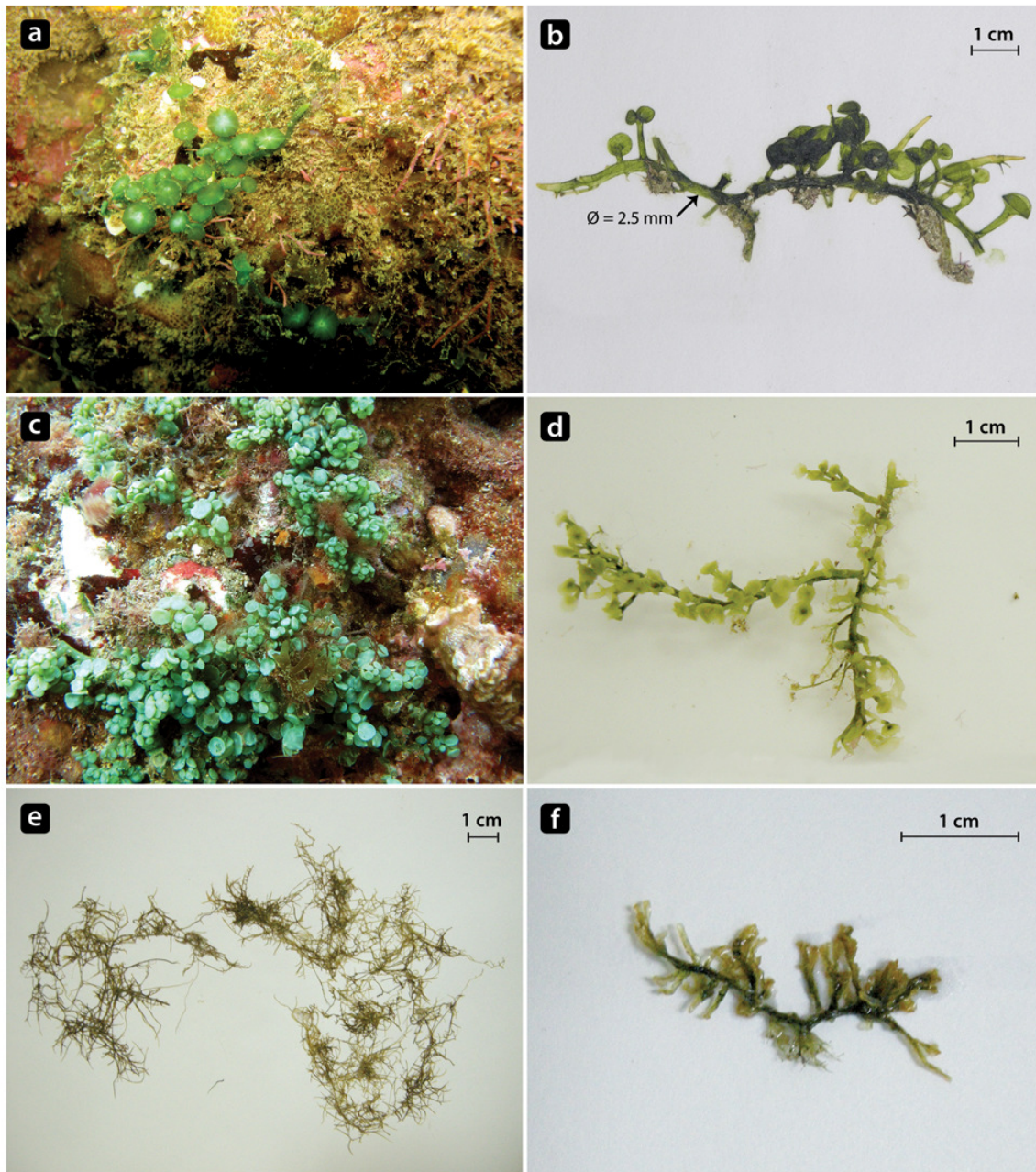


Fig. 2.5. Habit and frond morphology of of *Caulerpa chemnitzia* clade: (a,b) Non branched *C. chemnitzia* ecad *peltata*, (c,d) Branched *C. chemnitzia* ecad *peltata*, (e,f) *C. chemnitzia* ecad *vanbossea*

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***Caulerpa racemosa* var *macrophysa* (Sonder ex Kützing) W.R. Taylor 1928**

(Fig. 2.3 c,d)

Description: Erect, light green thallus. Fronds (1.2-) 2.2-2.6 (-4.9) cm high and (3.7-) 5.8-6.2 (-8.1) mm wide. Stalked branchlets vesicle-like, 1.7-3.4 mm diameter, often arranged in four vertical planes. Stolons spreading, creeping, (0.9-) 1.6-1.9(-2.9) mm diameter, often in massive pale yellow clumps.

Type Locality: Central America, possibly Atlantic according to Murray (1887)

Heterotypic synonyms: *Caulerpa racemosa* var. *mucronata* De Senerpont Domis (Senerpont Domis et al. 2003), *Caulerpa macrophysa sensu* Littler and Littler (2009) and Fernández-García et. al (2011).

Habitat: attached to rocky substratum, dead coral and rubble, between 4-8 m deep

Distribution in the ETP: Panama: Golfo de Chiriquí, Colombia: Isla Gorgona, Ecuador: Esmeraldas.

References: Littler and Littler 2009 (identified as *C. macrophysa*).

Other remarks: First report for Colombia and Ecuador Pacific coasts.

***Caulerpa serrulata* (Forsskål) J. Agardh 1837 (Fig. 2.6 a,b)**

Description: Erect to prostrate thallus. Compressed assimilators, with white spotted in the field, twisted in random directions, with marginal serrations, (1.2-) 2.2-2.6 (-4.5) cm high, (1.7-) 2.7-3.1 (-4.9) mm wide. Dichotomous branching. Stolons creeping, (0.5-) 0.7-0.8 (-1.1) mm diameter.

Type Locality: Mokha, Yemen.

Habitat: Rocky and dead coral, between 5-15 m deep.

Distribution in the ETP: Costa Rica: Isla del Coco, Panama: Golfo de Chiriquí.

References: Wysor 2004, Fernández 2008, Fernández and Alvarado 2008, Littler and Littler 2009, Fernández-García et al. 2011.

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***Caulerpa sertularioides* (S.G. Gmelin) M. Howe 1905 (Fig. 2.6 c,d)**

Description: Erect, light green thallus. Feather like assimilators, with a central rachis, generally unbranched, (0.2-) 1.5-1.6 (-5.8) cm high, (1.2-) 4.9-5.2 (-11.0) mm wide, but showing a reduction of the frond size in intertidal environments. Distichous subopposite rows of filiform ramuli that arise at acute angles and curve toward the apices. Stolons spreading, creeping (0.3-) 0.8-0.9 (-3.0) mm diameter, with highly branched rhizoids in sandy bottoms.

Type Locality: “in coralliis americanis”, possibly tropical Atlantic America.

Habitat: attached to rock and other hard substrata such as, dead and alive coral and coral rubble, sandy bottoms, intertidal to 23 m deep, more common between 4-7 m. In intertidal, can be growing on rocks with medium energy wave action. Patches of this species have been found in estuaries.

Distribution in the ETP: Mexico: Nayarit, Colima, Guerrero, Oaxaca, Nicaragua: Chinandega, Costa Rica: Guanacaste, Isla del Caño, Panama: Golfo de Chiriquí, Golfo de Panamá, Colombia: Bahía Málaga (Chocó), Nariño.

References: Dawson 1962a, Dawson 1962b, Earle 1972, Soto 1983 Glynn and Maté 1997, Wysor 2004, Fernández and Cortés 2005, Bezy et al. 2006, Fernández 2007, Fernández and Alvarado 2008, Fernández and Cortés 2009, Littler and Littler 2009, Smith et al. 2010, Fernández-García et al. 2011.

Other remarks: In Costa Rica (Fernández and Cortés 2005) and Panama (Glynn and Maté 1997, Smith et al. 2010) this species has exhibited seasonal bloom patterns. The alga has maintained high densities for periods of several years, covering up to 90% of the benthos in some regions (Fernandez-García et al. 2012). In the Mexican tropical Pacific, Pedroche et al. (2005) have reported the forms: *C. sertularioides* f. *brevipes* (Colima and Oaxaca states) and *C. sertularioides* f. *longiseta* (Oaxaca state), which according to Fernandez-García et al. (2012) may represent morphological adaptations to variable substrata and/or depth ranges. On shallow and rocky depths assimilators tended to be smaller and or even absent and the stolons were thicker. At greater depths and in finer sediments, assimilators are longer and stolons were thinner with more branched rhizoids (Fernández-García et al. 2012).

***Caulerpa verticillata* J. Agardh 1847 (Fig. 2.6 e,f)**

Type Locality: not specified. According to Skelton and South (2004:301) the type locality is probably West Indies.

Description: Forming dense small patches on rocks, generally covered by fine sediments, that are collected between the ramifications. Dark green filament fronds, tubular, (0.3-) 0.6-0.7 (-1.2) cm high, (0.8-) 1.4-1.6 (-3.0) mm wide. Whorled branchlets with dichotomous branching, apices forked. Fine creeping stolons, (0.1-) 0.2-0.3 (-0.5) mm diameter.

Habitat: attached to rocky substratum with fine sediments, in turbid waters, intertidal (tide pools) to 2 m deep.

Distribution in the ETP: Mexico: Colima, El Salvador: Golfo de Fonseca, Panama: Golfo de Chiriquí.

References: Pedroche et al. 2005.

Other remarks: First report for the Central American Pacific coast. Uncommon species, found on shores, but where encountered often forming dense turfs.

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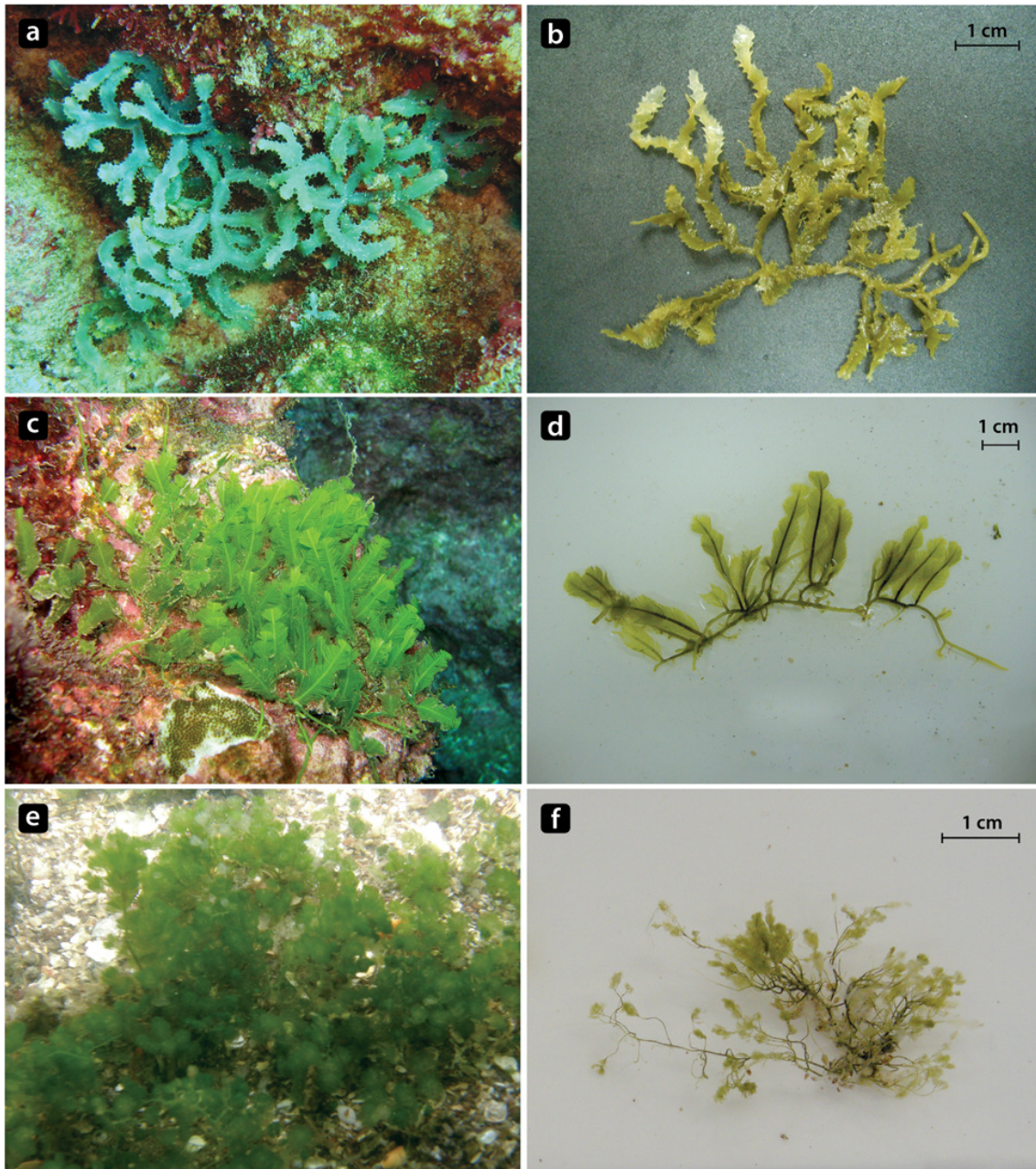


Fig. 2.6. Habit and frond morphology: (a,b) *C. serrulata*, (c,d) *C. sertularioides*, (e,f) *C. verticillata*

Biogeography

The six species of *Caulerpa* from the ETP found in this study are pantropical. However, within the ETP, certain species appear to have restricted distributions. For example *C. serrulata* (Fig. 2.7a) and *C. macrophysa* (Fig. 2.7b) are found only at low latitudes.

Caulerpa cupressoides shows a very limited distribution, in our recent collections we found one specimen along the Mexican coast (Nayarit) (Fig. 2.7c), but the species has been recorded in other parts of the ETP. Dawson (1962b) reported the species for Central America (no specific locality), while Schenetter and Bula-Meyer (1982) reported it for Colombia, and Pedroche et al. (2005) for other sites along the Mexican coast.

Caulerpa verticillata was found in El Salvador and Panama and is the first record for those countries; this species was also reported by Pedroche et al. (2005) for the tropical coast of Mexico (Colima) (Fig. 2.7d). It seems that this species is restricted to estuaries, and probably with more extensive sampling in these habitats the distribution of this species may increase.

This study confirmed the wide latitudinal distribution of *C. chemnitzia* (Fig. 2.7e) and *C. sertularioides* (Fig. 2.7f) not only along the ETP, but also inside the Gulf of California, Mexico. These two species show considerable morphological plasticity, which might enhanced their potential to colonize different habitats (Calvert 1976, Ohba and Enomoto 1987, Ohba et al. 1992, Fernandez-García et al. 2012). They were found in most of the intertidal and subtidal sites sampled during this study. According to Scheiner (1993) plasticity is strongly favored in species growing in heterogeneous environments, which applies to the ETP with its various habitats (e.g. rocky intertidals, sandy beaches, mangroves, coral and rocky reefs) and oceanographic conditions (e.g. temperature, sedimentation, light intensity, nutrients, wave action, tides, upwelling). It is possible that these factors favor the wide distribution of *C. chemnitzia* in the ETP and its different morphologies, which vary from tread-like fronds (i.e. *C. chemnitzia* ecad *vanbossea*), to clavate (i.e. *C. chemnitzia* ecad *laetevirens*) and disc-like (i.e. *C. chemnitzia* ecad *peltata*) fronds. These morphological variations might be an important determinant for enhancing the distribution of algal species (Collado-Vides and Robledo 1999, Leliaert et al. 2009).

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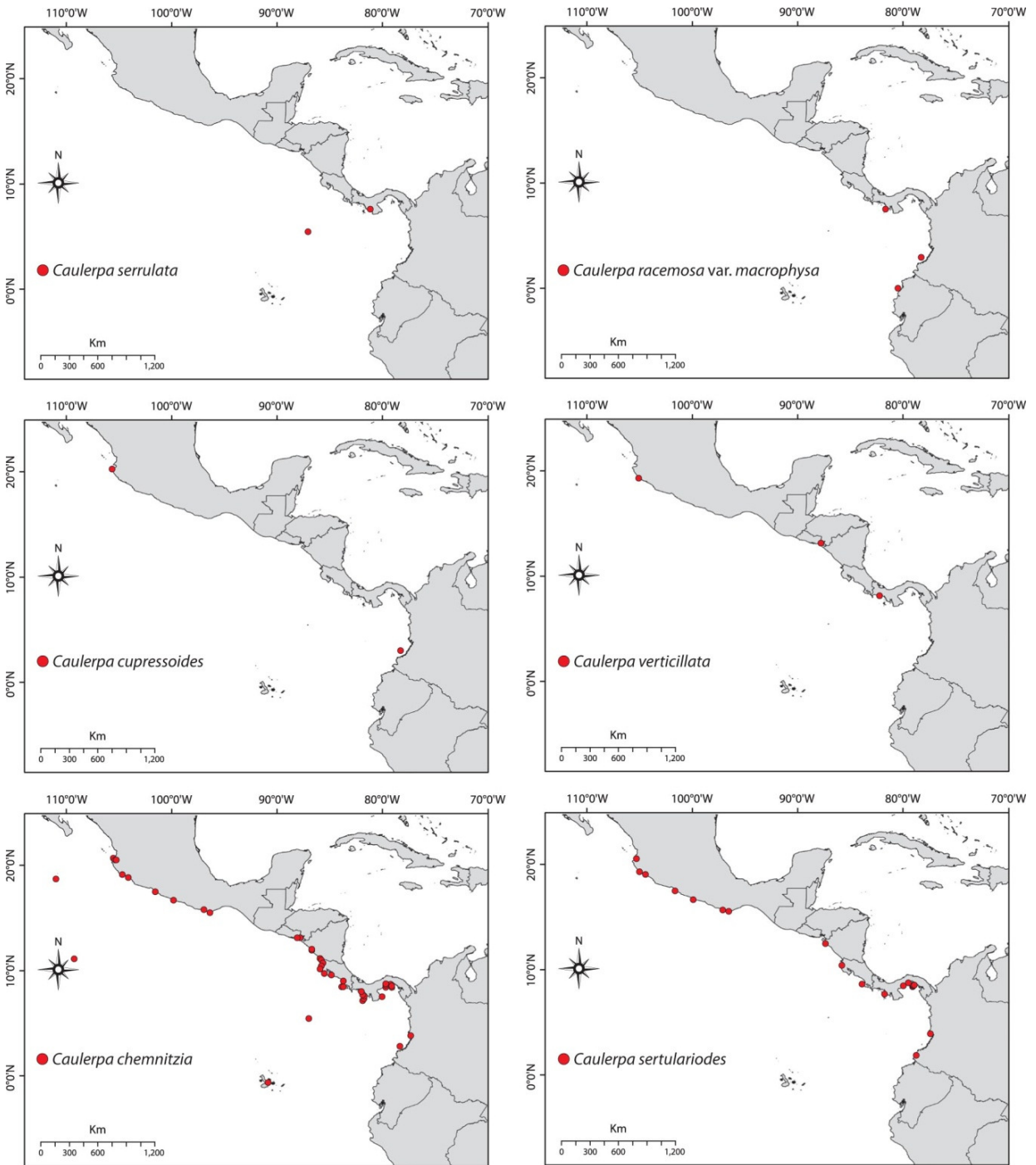


Fig. 2.7. Distribution of *Caulerpa* species in the Eastern Tropical Pacific

At the same time it is interesting to point out that although Caribbean and Pacific sequenced specimens of *C. chemnitzia* are nested, Pacific lineage receives maximal support (1.0) (Fig. 2.2). Specimens from both coasts of Panama, which was one of the last sections of the Central America Isthmus to emerge, separate into different groups. This might be suggesting a recent subdivision of populations of this species between the ocean basins; however, additional sampling is needed to verify these results.

The number of *Caulerpa* species reported for the ETP (six) is markedly lower in contrast to those of other tropical regions such as the Caribbean Sea (18, Littler and Littler 2000), Australia (16, Price 2010), Florida (15, Dawes and Mathieson 2008) and Hawaii (12, Sauvage 2010). Though this comparison maybe somewhat problematic because the above regions have not been subjected to the same molecular scrutiny. Even so, we expect that the actual number of species in the ETP is low rather than being a sampling artefact. In fact, species in western Atlantic and central and western Pacific marine floras have been subjected to molecular systematic treatment which has validated many of the species concepts. For example, Famà et al. (2002) included 18 specimens from the Western Atlantic and divergence was sufficient to recognize these entities as 14 distinct species. The low diversity of the Eastern Tropical Pacific could result from several factors, including the impossibility of some species to survive environmental changes associated with the emergence of the Central American Isthmus (Lessios et al. 2001, Wysor 2004). Also cooler waters associated with seasonal upwellings and overall change in current patterns (Glynn 1972, Cortés 2011) causing local extinction of species that were part of a homogeneous regional flora prior to the final closure of the Central America Seaway (Wysor 2004). Other factors include the absence of the right habitats that favor the presence of *Caulerpa* species, for instance the Caribbean and the Indo-Pacific show extensive carbonate platforms, seagrass beds and well developed coral reefs environments, in comparison to the ETP (Cortés 2011). Finally, another factor that should be explored in the future is the effect of herbivorous fishes in the presence or absence of marine macroalgae along the ETP. In a recent study, Edgar et al. (2011) found that overfishing of predatory fishes within the ETP has led to increased densities of habitat modifying macroinvertebrates and herbivorous fishes, which has contributed to regional declines in coral cover, which could enhance

opportunities for algal colonization. When this is coupled with eutrophication or other types of natural (e.g., ENSO events) and/or anthropogenic disturbances, predominance of fewer species, rather than sustenance of many may result to have direct impact on macroalgae communities (Glynn and Maté 1997, Smith et al. 2010).

Conclusions

In this study we have found the presence of six pantropical species of the genus *Caulerpa* at the Eastern Tropical Pacific. Our molecular assessment showed a reduction in species number in this region due to morphological plasticity that was previously mistaken for species diversity. In accordance with recent molecular studies, we also demonstrated that *C. racemosa* constitutes a complex of several lineages that exhibit phenotypic plasticity. ETP *C. racemosa* specimens were recovered in two of those clades. The first is *C. racemosa* var. *mucronata*, which we proposed to be a synonym of *C. racemosa* var. *macrophysa*. The second includes several names (*C. nummularia*, *C. racemosa* var. *laetevirens*, *C. vanbossea*, *C. racemosa* var. *peltata*, *C. peltata*), but a recent study indicates that the oldest epithet applicable to this clade is *C. chemnitzia*, which is the most dominant and widespread species in tropical and subtropical marine environments of the world.

RE-EVALUACIÓN TAXONÓMICA DEL GÉNERO *PADINA* (PHAEOPHYCEAE, OCHROPHYTA) DEL PACÍFICO TROPICAL ORIENTAL, CON EL RESTABLECIMIENTO DE *PADINA CAULESCENS*

Taxonomic re-assessment of the genus *Padina* (Phaeophyceae, Ochrophyta) from the Eastern Tropical Pacific, with the reinstatement of *Padina caulescens*

Resumen: Estudios taxonómicos del género *Padina* asistidos por análisis molecular han demostrado un incremento en el número de especies reportadas. En este trabajo se evalúa la taxonomía de este género, así como la distribución de la especie en el Pacífico Tropical Oriental, basado en un análisis morfológico y molecular (gen *cox3*). Se encontró que la identificación morfológica debe realizarse en talos adultos, ya que los estadios jóvenes comparten características que pueden llevar a una identificación errónea de las especies. El análisis molecular y morfológico revelaron la presencia de cuatro clados a nivel específico: *P. caulescens*, *P. concrescens*, *P. durvillei* y *P. mexicana*. Aunado a esto se confirma la presencia de un complejo de especies, que se encuentran exclusivamente dentro y fuera de la Península de Baja California, compuesto por cuatro especies adicionales que requieren futuros análisis. De acuerdo a otros trabajos recientes, los datos morfológicos y moleculares de este trabajo garantizan el reconocimiento de *P. caulescens* como un nombre válido, y no como sinónimo de *P. durvillei* como fue propuesto. Así mismo se reconoce que *P. crispata* es un sinónimo de *P. mexicana*. Las cuatro especies encontradas en el Pacífico Tropical Oriental se encontraron exclusivamente en esta región y muestran una amplia distribución latitudinal dentro de esta.

Abstract: DNA-assisted taxonomic studies of the genus *Padina* has resulted in an increase of the number of species. In the present study we evaluate the taxonomy of the genus and we assess species distributions within the Eastern Tropical Pacific (ETP), based on morphology and gene sequence data (*cox3*). Morphological identification of *Padina* species must be done in well-developed adult thalluses. Young specimens show many characteristics shared between species and this can lead to a misidentification of the species. Molecular analyses revealed the presence of four species-level clades: *P. caulescens*, *P. concrescens*, *P. durvillei* and *P. mexicana*. In addition we confirmed the presence of a complex of species exclusively found inside and outside the Peninsula of Baja California; *P. arborescens*, composed of four morphological closely allied species, which required future analysis. In accordance with other recent studies, our morphological and DNA results warrant the recognition of *P. caulescens* as a current valid name and not a synonym of *P. durvillei* as proposed before. Also we recognized *P. crispata* as a synonym of *P. mexicana*. The four species found at the ETP, appear to be exclusively distributed in this region, and show wide latitudinal distribution along the region.

Key Words: algae, Dictyotales, Central America, Colombia, Mexico, *Padina*, taxonomy

Introduction

The brown algal genus *Padina* (Dictyotales) is a common component of shallow to deepwater coastal ecosystems in tropical and warm temperate regions. Several recent studies have addressed species-level diversity and phylogenetic relationships of *Padina* using gene sequence data (Ni-Ni-Win et al. 2008, 2010, 2011a,b), making it one of the better studied seaweed genera with tropical to warm temperate affinities. The DNA-assisted taxonomic studies resulted in an increase of the number of species, with the description of 10 new species, mainly from the Western Pacific Ocean and the Mediterranean Sea. Recently, Silberfeld et al. (in review), compared morphology with algorithmic sequence-based species delimitation approaches and discussed their mutual taxonomic and biogeographical relevance. The analysis of Silberfeld and co-authors relied on a significant global sampling effort, including numerous collections from previously under-represented areas, such as the Eastern Tropical Pacific (ETP). Diversity estimates range from 39 to 61 species (Silberfeld et al. in review), depending on the species delineation method and the information content of the molecular marker, many of them with poorly morphological descriptions. In their work they included for the Eastern Tropical Pacific (ETP) and Gulf of California 12 specimens, which clustered in 3 species. The ETP diversity, however, is in need of critical morphological and taxonomic reassessment to link the names which have traditionally been used to the clades revealed in recent molecular studies.

Ten species have been reported from the ETP (Table 3.1), of which, six have their type locality in the region. The first report of *Padina* in the ETP was made by E.Y. Dawson in 1944, when he described *Padina mexicana*. Later, F. Thivy (1945), in her Ph. D. dissertation, described three new species for the region (*P. caulescens*, *P. concrescens* and *P. crispata*), that were formally published by W.R. Taylor (1945) in his book of Pacific marine algae of the Allan Hancock expeditions to the Eastern Pacific. Thivy's descriptions were based on the following anatomical features: sorus distribution, number of cell layers, the presence of an indusium covering the sporangia, the distribution of piliferous and glabrous zones, primary hairs, distal margin, size of cortical cells, diameter of the

sporangia, length of antheridia, sporelings, distribution of sexes and incrustations. Thivy also recognized *P. mexicana* as a valid species. Later, Ávila-Ortiz and Pedroche (2005) reviewed the taxonomy of this genus in the tropical Pacific of Mexico, where they recognized the presence of six species (Table 3.1). They also proposed a new species, *P. ramonribae*, but a Latin diagnosis was not provided at the time making this name invalid.

Riosmena-Rodríguez et al. (2009), evaluating recent collections from the Gulf of California against historical collections and type material, concluded that only three species (*P. durvillei*, *P. conrescens* and *P. mexicana*) should be recognized for the area, based on four discriminating characters: 1)- presence of calcium carbonate in the cell wall; 2)- number of medullary cell layers in the basal area; 3)- number of medullary cell layers in the middle part and 4)- presence/absence of cortical cells. They therefore proposed the synonymy of *P. caulescens* with *P. durvillei* and *P. crispata* with *P. mexicana*. In addition to these studies, three other species were recorded from the area: *P. vickersiae* (El Salvador, Tejada 2003, 2007), *P. pavonica* (El Salvador, Tejada 2003, 2007) and *P. fraseri* (Panamá, Littler and Littler 2009) (Table 3.1).

All previous taxonomic studies of *Padina* at the ETP and the Gulf of California were based only on morphological characteristics (Thivy 1945, Taylor 1945, Schnetter and Bula-Meyer 1982, Garske 2002, Ávila-Ortiz and Pedroche 2005, Pedroche et al. 2008, Riosmena-Rodríguez et al 2009, Norris 2010), and there are many inconsistencies between the descriptions (Ávila-Ortiz and Pedroche 2005). This is why we consider it necessary to combine the molecular results resulting from gene sequence analyses with morphological investigations to clarify the taxonomy of the genus in this region. There to, we expanded the taxon sampling from Silberfeld et al. (in review) from 12 to 83 specimens, sampling *cox3* genes, reassessed the morphology of the various clades and linked these to the type specimens. In addition our taxon sampling also enables us to thoroughly assess species distributions along the Pacific side of Central America, Colombia and Mexico.

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Table 3.1. Species of the genus *Padina* reported for the Eastern Tropical Pacific. MEX=Mexico, ES= El Salvador, NIC= Nicaragua, CR=Costa Rica, PAN=Panama, CA= Central America, COL= Colombia, ECU= Ecuador, RI= Revillagigedo island, CI= Cocos island, GL= Galápagos islands. TL= Type locality. In bold species which type locality is in the Eastern Pacific.

Species reported	Current name this study	MEX	ES	NIC	CR	PAN	CA	COL	ECU	Reference
<i>Padina caulescens</i> Thivy in Taylor TL: Nayarit, Pacific México	<i>Padina caulescens</i> Thivy in Taylor 1945	x		x	x		x			Dawson 1957, Dawson 1961a, Dawson 1962a,b, Avila-Ortiz and Pedroche 2005, Pedroche et al. 2008, Bernecker 2009
<i>Padina conrescens</i> Thivy in Taylor TL: Galapagos I., Ecuador	<i>Padina conrescens</i> Thivy in Taylor 1945	x (RI)				x			x (GL)	Garske 2002, Serviere-Zaragoza et al. 2007, Pedroche et al. 2008, Littler and Littler 2009, Norris 2010, Fernández-García et al 2011
<i>P. crispata</i> Thivy in Taylor TL: Golfo Dulce, Pacific Costa Rica	<i>Padina mexicana</i> E.Y Dawson 1944, proposed by Riosmena Rodríguez et al. 2009 and this study	x (RI)	x		x (CI)	x		x		Taylor 1945, Dawson 1957, Dawson 1961a,b, Dawson 1962a,b, Schnetter and Bula-Meyer 1982, Gutiérrez 1985, Ávila-Ortiz and Pedroche 1999, Tejada 2003, 2007, Ávila-Ortiz and Pedroche 2005, Serviere-Zaragoza et al. 2007, Fernández 2008, Pedroche et al. 2008, Bernecker 2009, Littler and Littler 2009, Norris 2010, Fernández-García et al 2011

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Species reported	Current name this study	MEX	ES	NIC	CR	PAN	CA	COL	ECU	Reference
<i>Padina durvillei</i> Bory de Saint-Vincent TL: La Concepción, Chile	<i>Padina durvillei</i> Bory de Saint-Vincent 1887	x (RI)			x	x	x	x	x (GL)	Dawson 1944, Taylor 1945, Dawson 1957, Dawson 1962 a,b, Schnetter and Bula-Meyer 1982, Garske 2002, Avila-Ortiz and Pedroche 2005, Serviere-Zaragoza et al. 2007, Pedroche et al. 2008 Bernecker 2009, Littler and Littler 2009, Norris 2010, Fernández-García et al 2011
<i>Padina gymnospora</i> (Kützing) Sonder TL: Virgin Islands, Caribbean	<i>Padina caulescens</i> Require further study	x								Norris 2010
<i>Padina mexicana</i> E.Y Dawson TL: Baja California, Mexico	<i>Padina mexicana</i> E.Y Dawson 1944	x								Avila-Ortiz and Pedroche 2005, Pedroche et al. 2008, Norris 2010
<i>Padina fraseri</i> (Greville) Greville TL: New South Wales	Required further study					x				Littler and Littler 2009, Fernández-García et al 2011
<i>Padina pavonica</i> (Linnaeus) Thivy TL: In mari Europae australis	<i>Padina caulescens</i> Thivy in Taylor 1945, this study		x					x		Tejada 2003, 2007, Schnetter and Bula-Meyer 1982, Fernández-García et al 2011

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Species reported	Current name this study	MEX	ES	NIC	CR	PAN	CA	COL	ECU	Reference
<i>Padina ramonribae</i> Avila-Ortiz and Pedroche ined. TL: Pacific Mexico	<i>Padina caulescens</i> Thivy in Taylor 1945, this study	x								Avila-Ortiz and Pedroche 2005, Pedroche et al. 2008
<i>Padina vickersiae</i> Hoyt TL: North Carolina, USA	<i>Padina mexicana</i> E.Y Dawson 1944, this study		x							Gutiérrez 1985, Tejada 2003, 2007, Fernández- García et al 2011

Materials and Methods

Sample collection

A total of 83 samples of *Padina* specimens were collected from 71 field locations throughout the Eastern Pacific (Gulf of California, Mexican Tropical Pacific, Central America, Colombia) between 2008 and 2011. Detailed specimen information including specimen identification numbers, morphological and DNA identification, collecting site and date, collectors, can be found in the supplementary material (Table S3). Specimens were collected by SCUBA diving and preserved in silica gel, formalin and as herbarium vouchers for molecular and morphological examination. Vouchers are deposited in USJ herbarium (Escuela de Biología, Universidad de Costa Rica), HBCS herbarium (Universidad Autónoma de Baja California Sur), CUVC herbarium (Universidad del Valle, Cali, Colombia) and GENT herbarium (University of Ghent).

Morphological and ecological characteristics

For each specimen the depth, substratum and habit (erect or prostrate) were recorded. Detailed locality information was integrated in a Geographic Information System (ArcGIS 9.2), used to plot the distributions of the various species. Preliminary species identifications were based on morphological comparisons with the original descriptions, type specimens (Fig. 3.1) and regional floras (Dawson 1944, Taylor 1945, Schnetter and Bula-Meyer 1982, Littler and Littler 2009, Riosmena-Rodríguez et al. 2009).

Specimens were analyzed morphologically, scoring a list of 22 qualitative and quantitative characters from vegetative and reproductive thalli (Fig. 3.2 a,b): color of the thallus, branching, presence/absence of calcium carbonate, thallus length, thallus width (margin, central, basal), and number of medullary cells layer (margin, central, basal) were measured. Heights and widths of cortical and medullary cells were measured in transverse section in marginal, central, and basal sections of the thallus (Fig. 3.2b). Mature parts of each individual were selected for reproductive features. Soral width was measured in surface view. Height and diameter of antheridia, oogonia and sporangia were measured in transverse section. For each character, minimum and maximum sizes and the 95 percentile were determined. Measurements were carried out on formalin-preserved specimens with a

Nikon Coolpix 4300 camera and image processing with the UTHSCSA software Image Tool version 3.0. Transverse sections were made by hand using a razor blade. In cases where only herbarium specimens were available, thallus fragments were rehydrated in a detergent solution with formalin (4%) in sea water for one month.

DNA Extraction, Amplification and Sequencing

Total genomic DNA was extracted using a standard CTAB-extraction method and subsequent purification with a Wizard[®] DNA Clean-Up System (Promega Inc., Madison, WI, USA) as outlined in De Clerck et al. (2006). The mitochondrial *cox3* gene was amplified and sequenced according to De Clerck et al. (2006) and Tronholm et al. (2010). The protein coding sequences were aligned manually using MEGA 4 (Kumar et al. 2008). A complete list of specimens used in the molecular analyses is detailed in Table S3.

Analysis

Forward sequences were edited and aligned using MEGA 5.0 (Tamura et al. 2011). The *cox3* sequences were aligned with those obtained from the Phycological Laboratory of Ghent University and Silberfeld et al. (in review) and the final alignment was done manually. Bayesian phylogenetic inference (BI) was carried out with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) using the same partitions and models, and default priors. Heated chains were run for three million generations, sampling every 1000th generation. A burnin sample of 500 trees was removed before constructing the majority rule consensus tree.

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Fig. 3.1. Type specimens of *Padina* species reported for the Eastern Tropical Pacific. (a) *P. mexicana*-UC, (b) *P. crispata*-UC, (c) *P. crispata*-MICH, (d) *P. conrescens*-MICH, (e) *P. caulescens*-UC, (F) *P. durvillei*.

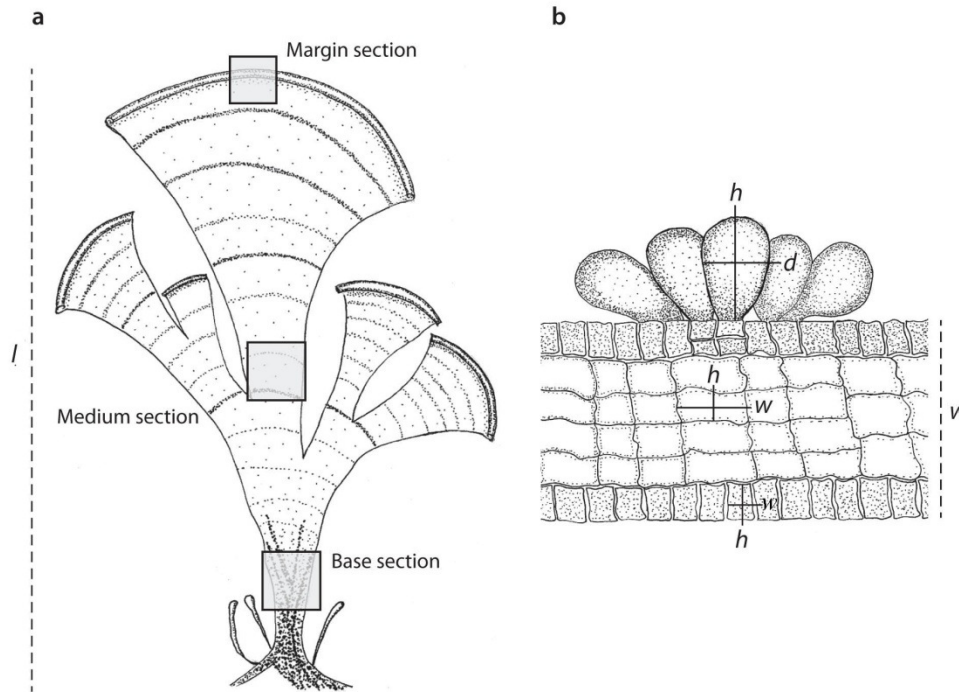


Fig 3.2. Morphometric measurements. (a) Thallus measurements, and parts of the thallus where transversal sections were done, (b) Transversal section measurements. w =width, l =length, d =diameter, h =height.

Results

Morphological identification of *Padina* species must be done in well-developed adult thalluses. Young specimens show many characteristics shared between species and this can lead to a misidentification of the species (Table 3.2).

From the molecular analysis of the gene *cox3* we distinguish 7 clades that include sequences exclusively from the ETP and Gulf of California (Fig. 3.3). We also found one separate clade with sequences from the Gulf of California clustered with sequences of Japan that belong to *P. arborescens* (Fig. 3.3). Species names were assigned to the genotypic clusters on the basis of correspondence with morphology-based identifications and according to type specimens analysis. Clusters correspond to the species descriptions of: *P. caulescens* (interpretation of Thivy 1945, Fig. 3.5), *P. conrescens* (Thivy, 1945, Fig. 3.6), *P. durvillei* (interpretation of Thivy 1945 from the type of Bory Saint-Vincent, 1827,

Fig. 3.7) and *P. mexicana* (Dawson 1944, Fig. 3.8) and three new species (Table 3.2). In all cases species are well supported monophyletic lineages (Fig. 3.3).

We agreed that the synonymy of *P. crispata* with *P. mexicana*, proposed by Riomena-Rodríguez et al. (2009), was very pertinent. Thus, when Thivy (1945) was describing *P. crispata*, she pointed that this two species are not very different between each other (same number of medullary cells at the margin and relative agreement in the length of cortical and sub-cortical cells). She proposed that the difference lies in their habit, *P. mexicana* with an undivided, broadly flabellate frond, while *P. crispata* a little larger usually with profuse lobes. However, our morphologic and molecular data shows that both habits belong to one clade.

According to the morphological approach of Riomena-Rodríguez et al. (2009), *P. caulescens* was synonymized with *P. durvillei*, because the analysis of the holotype of *P. caulescens* showed the same features as the isoelectotype of *P. durvillei*. Our molecular data show that there are two clades that validate both species (Fig. 3.3). The main difficulty in identifying these species has been the plastic morphology that presents *P. caulescens*, which shows similar morphological characteristics with other ETP *Padina* species, including *P. durvillei*. Indeed, our morphological analysis confirms that the number of medullary cells of these species can overlap (Table 3.2). In order to delimit both species is necessary to include other morphological features such as width of the thallus (thinner in *P. caulescens* at the margin) and measurements of medullar and cortical cells (Table 3.2).

Padina arborescens, was not reported before for the Eastern Pacific and have been confused with *P. conrescens* along the Baja California Peninsula, which is the northern limit of the genus *Padina* at the ETP. The misidentification is due to similarities in the morphology of the thallus and that are not calcified, but we have found differences in the number of medullary cell layers and width of the thallus (Table 3.2).

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Table 3.2. Morphological comparison of *Padina* species from the Eastern Tropical Pacific and Gulf of California. Values are: (Minimum-)(95% Range)(-Maximum).

	<i>Padina arborescens</i> ccomplex	<i>Padina caulescens</i>	<i>Padina concrescens</i>	<i>Padina durvillei</i>	<i>Padina mexicana</i>
Calcium carbonate	Lightly or not calcified	Lightly or not calcified	Not calcified	Lightly or not calcified	Heavily calcified
Thallus length (cm)	(2.8-)5.8-6.7(-20.5) 15-30*	(0.4-)3.5-4.4(-10.6) 16*	(1.8-)3.9-4.6(-9.4) 5-11*	(1.7-)4.1-4.6(-8.9) 5-40*, 10-15**	(0.4-)1.2-1.5(-4.0) 1.5-4⁺, 0.5-1.5**
Thallus width (µm)	Base (242.6-)248.5-253.2(-260.1)	(117.4-)214.5-235.7(-323.1) 220-250*	(201.7-)283.7-307.0(-425.8) 400-500*	(201.2-)334.2-365.0(-518.6) 250-500*	(82.0-)112.1-127.8(-162.8)
	Central (232.0-)246.6-268.2(-352.2)	(80.8-)165.9-185.3(-285.3)	(128.7-)178.2-199.1(-331.9)	(147.6-)247.5-272.8(-406.3)	(92.9-)103.9-108.4(-116.3)
	Margin (151.5-)180.5-194.9(-234.7)	(77.9-)118.3-128.8(-178.1)	(98.4-)128.1-136.7(-163.9) 200*	(125.8-)202.9-225.4(-358.9) 75-130*	(76.4-)84.3-88.5(-96.9)
Medullary cells					
	Base (3-)8-10(-13)	(2-)6-7(-9) 9-12*	(6-)8-9(-11) 10-20*	(5-)8-10(-14) 9-18*, 8-9**	(2-)2-3(-4) 2⁺
Number of layers	Central (6-)8-10(-14) 6⁺⁺	(2-)5-6(-10) 9-12*	(2-)5-6(-9)	(4-)7-8(-14) 1-4**	(2-)2-3(-4) 4-6⁺
	Margin (4-)7-8(-11)	(1-)3-4(-6)	(2-)3-4(-5) 6*	(2-)5-6(-10) 3-6*	(2-)2-3(-3)
Height (µm)	Base (19.3-)24.5-25.4(-34.1)	(9.5-)30.2-31.6(-50.3)	(15.0-)31.2-32.3(-47.6)	(17.2-)37.2-38.8(-67.1)	(16.6-)27.6-29.1(-42.1)
	Central (18.0-)25.8-26.8(-41.1)	(15.6-)25.8-26.9(-39.1)	(15.5-)27.8-29.2(-49.3)	(16.6-)28.4-29.6(-52.1) 40-45**	(17.4-)23.2-24.4(-33.0) 30-35**
	Margin (15.4-)24.3-25.4(-37.6)	(13.4-)25.2-26.2(-41.7)	(14.5-)26.2-27.2(-42.7)	(17.3-)30.0-31.3(-54.0)	(13.3-)21.6-22.9(-35.6)
Width (µm)	Base (15.8-)33.3-35.2(-54.8)	(21.2-)41.2-43.5(-84.9)	(14.6-)39.1-41.8(-98.7)	(21.8-)38.7-40.2(-65.8)	(27.1-)38.0-40.6(-73.2)
	Central (23.5-)33.0-34.3(-51.0)	(12.9-)33.4-34.9(-55.9)	(17.1-)34.6-36.4(-81.6)	(17.4-)32.4-33.8(-66.0) 15-20**	(16.8-)30.7-32.8(-52.0) 10-15**
	Margin (16.2-)32.2-33.6(-49.0)	(19.2-)30.9-31.9(-44.5)	(13.1-)29.6-30.9(-52.9)	(13.8-)32.5-33.7(-52.7)	(15.1-)25.0-26.7(-41.2)

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	<i>Padina arborescens</i> ccomplex	<i>Padina caulescens</i>	<i>Padina conrescens</i>	<i>Padina durvillei</i>	<i>Padina mexicana</i>	
Cortical cells						
	Base	(14.7-)19.9-20.6(-28.8)	(14.8-)23.0-23.7(-34.1)	(10.5-)24.1-25.1(-39.3)	(18.7-)28.5-29.6(-48.3)	(15.7-)21.2-22.0(-27.5)
Height (µm)	Central	(15.1-)21.3-22.1(-32.6) 12-38*	(12.2-)21.3-22.0(-29.7) 20-25*	(12.6-)23.1-24.0(-37.9) 15-45*	(13.5-)23.5-24.3(-36.6) 15-35*, 15-20**	(12.4-)19.6-21.0(-32.4) 30-35**
	Margin	(12.9-)20.3-21.2(-30.1)	(12.4-)19.6-20.3(-33.7)	(14.9-)22.0-22.6(-28.6)	(11.5-)24.3-25.2(-40.1)	(15.1-)20.4-21.3(-29.5)
	Base	(11.5-)18.0-18.9(-29.4)	(13.6-)21.8-22.7(-40.0)	(11.0-)33.2-35.1(-79.5)	(14.2-)25.0-26.3(-50.1)	(12.2-)27.5-29.5(-41.9)
Width (µm)	Central	(11.4-)18.6-19.4(-26.4) 12-30*	(10.0-)19.7-20.4(-32.1)	(15.2-)27.5-28.6(-44.5) 12-30*	(14.0-)20.6-21.4(-32.6) 10-20*, 15-20**	(14.5-)24.0-25.7(-39.4) 20-25**
	Margin	(12.8-)17.5-18.4(-31.3)	(11.6-)19.1-19.8(-30.4)	(13.7-)24.8-25.7(-41.8)	(11.8-)21.0-21.9(-36.9)	(17.1-)25.2-26.5(-39.9)
Sporangia						
Height (µm)	no data	(74.0-)88.0-90.5(-104.6)	(85.7-)119.9-125.7(-151.9) <130*	(82.3-)118.8-122.9(-184.9) 60-65**	(46.2-)72.3-80.2(-117.1) 55-60**	
Diameter (µm)	no data	(45.3-)56.5-59.0(-82.5)	(56.0-)77.5-82.4(-113.5) 100-120*	(38.3-)73.9-76.9(-104.6) 80-125*	(33.4-)61.1-66.4(-85.7) 40-45**	
Male gametophytes						
Sori width (µm)	237.6	(230.3-)297.2-332.3(-374.6)	no data	500-1000*	no data	
Antheridia height (µm)	(36.3-)46.2-50.4(-56.9)	(56.3-)62.3-65.1(-70.2)	no data	40-50*	no data	
Antheridia diameter (µm)	(13.8-)16.7-17.7(-19.1)	(23.8-)28.1-29.5(-32.2)	no data	no data	no data	
Female gametophytes						
Sori width (µm)	no data	(163.6-)274.7-355.7(-478.2)	(50.9-)56.6-63.3(-73.5)	200-500*, 170-175**	220**	
Oogonia height (µm)	no data	(41.2-)51.2-55.6(-70.9)	(67.8-)82.9-86.8(-103.7)	85-105*, 55-60**	50-55**	
Oogonia diameter (µm)	no data	(22.9-)29.0-30.7(-37.3)	(31.3-)37.2-38.8(-44.7)	30-60*, 25-30**	40-55**	

[†]Dawson (1944) from type description, ^{††}Holmes (1896) from type description, *Thivy (1945) from type description, **Riosmena-Rodríguez et al (2009)

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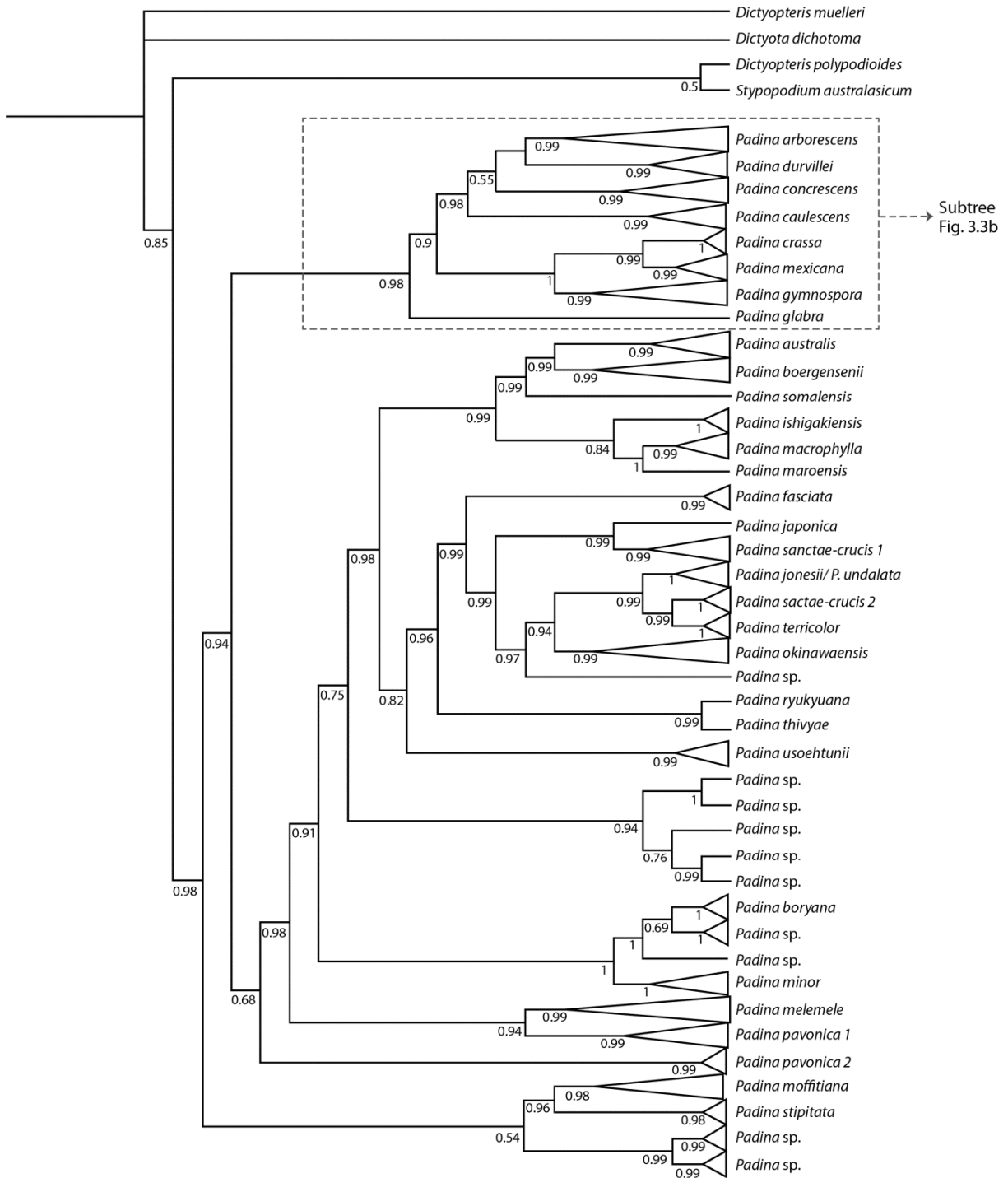


Fig. 3.3a. Consensus tree resulting from the Bayesian Inference analysis of *cox3* sequences of *Padina*. In square ETP species.

Discussion

Padina species are common in the littoral flora on the tropical and subtropical waters of the Pacific American coast, which can be found forming dense patches in the intertidal and subtidal marine environments (Taylor 1945, Dawson 1957, Dawson and Beudette 1959, pers. obs.). As found worldwide (Ni-Ni-Win et al. 2011b), *Padina* species diversity in this region, has been underestimated. This study confirms the presence of *P. durvillei*, *P. conrescens* and *P. mexicana* and the reinstatement of *P. caulescens* as a valid species name. We also found the already described species *P. arborescens* and 3 new species, for a total of 8 species. From the ten species reported for this region three misapplied names were found: *P. pavonica*, *P. ramonribae* and *P. vickersiae*. The first two correspond with misidentifications of *P. caulescens* and the last with *P. mexicana*.

We were not able to confirm the presence of *Padina fraseri*, reported by Littler and Littler (2009). This species has its type locality in Western Australia, and has been reported mainly for the Indo-Pacific region. This report is based on a young specimen and its distribution at the ETP seems to be doubtful.

Padina durvillei, *P. conrescens* and *P. mexicana* have been the species with most taxonomic consistency throughout the region; however *P. durvillei* has been confused with *P. caulescens*, mainly because they have in common a branched morphology and an overlap in the number of medullary cells.

Padina caulescens, consist of specimens with a very plastic morphology, which has generated a misidentification of this species along the ETP and Gulf of California. An example of this problem, is in the paper Dawson (1957), of marine algae from the Pacific Costa Rican gulfs, where he reported the presence of *P. crispata* and commented on the apparently difference between his samples with the type specimen, due to its ill development nature. In a revision of the three specimens he cited, we concluded that there is one that match with the type (D16848/UC1834351) of *P. crispata* (now *P. mexicana*), however the other two specimens (D16723/UC1834349, D16783/UC1834350) match with our new molecular-morphological interpretation of *P. caulescens*. We consider that this has happened with the other specimens of *Padina*, because *P. caulescens* shares many

morphological characteristics with the other species from the ETP (see other remarks in *P. caulescens*).

Padina mexicana is a wide spread species along the ETP and inside the Gulf of California, and a common inhabitant of intertidal environments, with a patchy habit. As Riosmena-Rodríguez et al. (2009), proposed we agree that the holotype of *P. crispata* (Fig. 3.1 b,c) have same diagnostic features as in the type material of *P. mexicana* (Fig. 3.1a) and concluded that they are heterotypic synonyms due to the number of medullary cells, measurements of medullar and cortical cells and presence of heavily calcified thallus.

We have found that several specimens from the Eastern Pacific were either erroneously transferred or assigned to the species *Padina crispata* (Taylor 1945, Dawson 1957, 1961 a,b, 1962 a,b, Schnetter and Bula-Meyer 1982, Gutiérrez 1985, Ávila-Ortiz and Pedroche 1999, Tejada 2003, 2007, Ávila-Ortiz and Pedroche 2005, Serviere-Zaragoza et al. 2007, Fernández 2008, Pedroche et al. 2008, Bernecker 2009, Littler and Littler 2009, Norris 2010) and most of those specimens seem to belong to either *P. mexicana* or *P. caulescens*. Although, *P. crispata* is a synonym of *P. mexicana*, a revision is needed of all the specimens named under *P. crispata*, before transferring the labels of the herbariums specimens directly to *P. mexicana*.

Most of the *Padina* species found have distribution along the ETP and inside the Gulf of California. However, there is a complex of species exclusively found inside and outside the Peninsula of Baja California (Fig. 3.3). This complex was found also by Silberfeld et al. (in review), and was named *Padina arborescens*. Our molecular data shows that this complex consists of four morphological closely allied species; three confined to the Peninsula of Baja California, Mexico and one containing Japanese as well as Mexican samples (Fig. 3.3b) and includes species having a thallus between 8-10 layers of medullar cells at the base.

The 95 percentile range of our data set of morphological characters show no overlap of most characters, however the minimum and maximum values do overlap between species (Table 3.2). This is why we determined that there are no specific morphological characters that can be used in the identification of species of *Padina* in the ETP and Gulf of California, but a combination of several characters do. Morphological plasticity identification based exclusively on morphological features is often problematic and this has

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been a problem in determining marine macroalgae species diversity at the Eastern Pacific (Lopez-Vivas et al. 2012, Fernández-García et al in prep., Andrade-Sorcía et al in prep.). This is another example on how the use of molecular tools is necessary to elucidate the taxonomy in this region (Fernandez-García et al. in prep).

Here we present a dichotomous key to the Eastern Tropical Pacific *Padina* species based on the molecular-assisted re-evaluation of the morphological species concept (Table 3.3).

Table 3.3. Key to the species of *Padina* at the Eastern Tropical Pacific and Gulf of California

1a Blades heavily calcified, light chalky brown color, 2-3 medullar cells near margin and the central part of the thallus.....	<i>P. mexicana</i>
1b Blades lightly calcified or not calcified, more than 3 medullar cells near margin and central part of the thallus.....	2
2a Thallus highly stipose for considerable distance above the base and branched, complete thallus arising from a well-developed disc-like holdfast, blades can be lightly calcified.....	3
2b Blades arising directly from the holdfast or attached directly to the substratum with filamentous hairs, generally a bunch of complete blades not branched, not calcified.....	4
3a Thallus leathery, generally dark brown, with 8-10 layers of medullary cells near base and 5-6 near margin, thallus width between 334-365 μm near base and between 203-225 μm near margin.....	<i>P. durvillei</i>
3b Thallus not leathery, generally reddish or olive brown, with 6-7 layers of medullary cells near base and 3-4 near margin, thallus width between 214-236 μm near base and between 118-129 μm near margin.....	<i>P. caulescens</i>
4a Thallus light brown, blades attached to each other or to the substratum, with 8-9 layers of medullary cells near base and 3-4 near margin, thallus width between 284-307 μm near base and between 128-136 μm near margin	<i>P. conrescens</i>
4b Thallus dark brown, blades not attached to each other or to the substratum, with 8-10 layers of medullary cells near base and 7-8 near margin, thallus width between 348-253 μm near base and between 180-195 μm near margin	<i>P. arborescens</i>

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Annotated list of Padina species from the ETP and Gulf of California

A morphometric comparison of the species lineages identified in this study can be found in Table 3.2. Taxonomic, ecological and nomenclatural implications are detailed below.

***Padina arborescens* complex Holmes 1896 (Fig. 3.4)**

Description: Thallus composed of several layers of medullary cells with not variable number from the basal area to the tips (Table 3.2). Not conspicuous basal stupose stipe. Tetrasporangia in the apical and central part of both sides of the blade, more abundant on the inner part.

Type Locality: Enoshima, Japan

Etymology: Tree like

Habitat: On rocky substrate. Intertidal to 7 m deep.

Distribution in EP: México: Sonora, Baja California, Baja California Sur

Other Remarks: First report to the Eastern Pacific. In the Gulf of California, this complex consists of four species; three confined to the Peninsula of Baja California, Mexico and one containing Japanese as well as Mexican samples that is the real *P. arborescens*. These species have been confused with *P. concrescens* because both species have blades that grow gregarious (Riosmena-Rodríguez et al. 2009) and also have been confused with *P. durvillei* (Norris 2010), because its stupose base, no calcification on some of the specimens and morphology of the frond. The difference, in both cases lies in the number of medullary cells. This species require further study to elucidate its morphology, seasonal variation and distribution along the Baja California Peninsula.

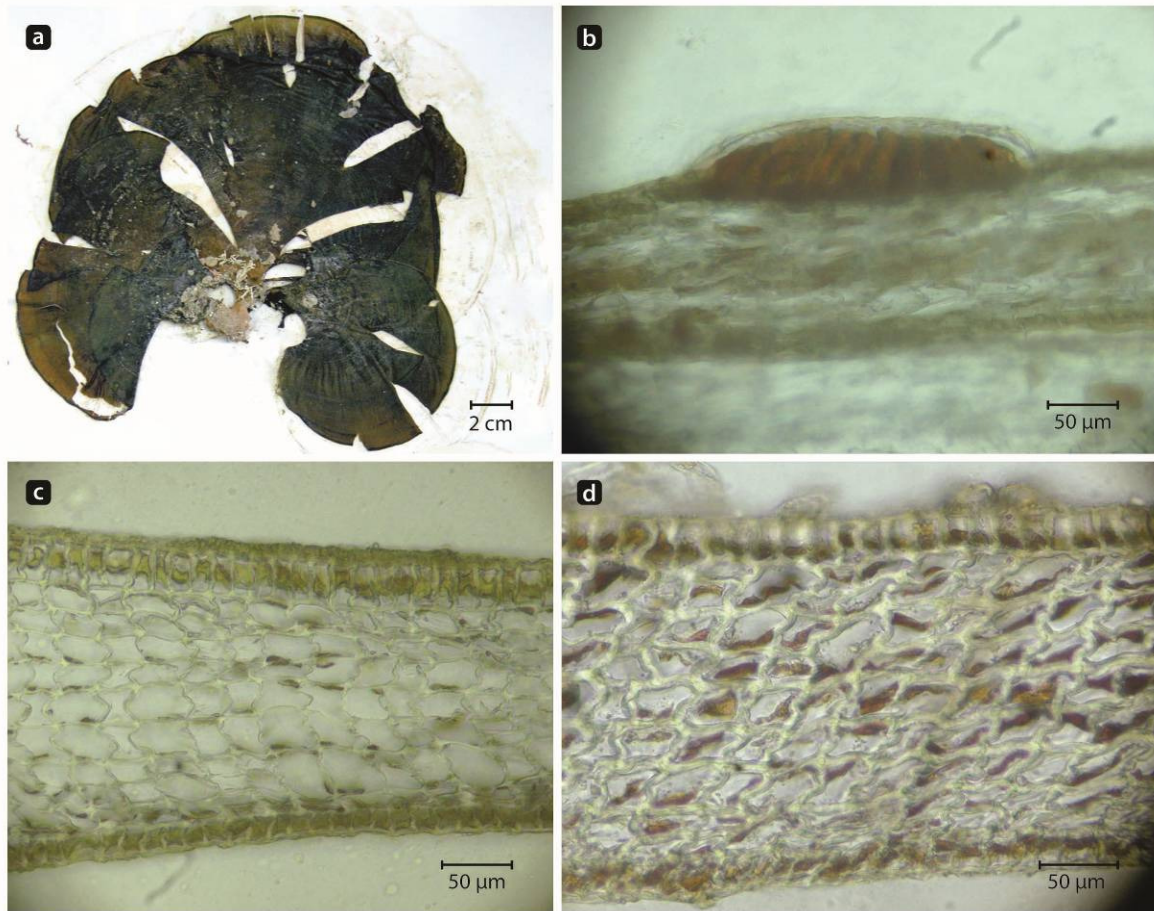


Fig. 3.4. *Padina arborescens*. (a) Habit pressed specimen, (b) Transverse section of the blade with masculine sori, (c) Transverse section of the blade near margin, (d) Transverse section of the blade near base.

***Padina caulescens* Thivy in Taylor 1945 (Fig. 3.5)**

Description: Thallus erect, blades flabellate narrowed toward a conspicuous thinner stipe, with a strong primary stipe. Lightly or not calcified. Blades often divided by repeated splitting. Stupose rhizoidal holdfast. Composed of several layers of medullary cells reducing in number from the basal parts to the tips. Lines of phaeophyceyan hairs very distinctive. Ovoid sporangia in continuous and/or discontinuous bands between hair lines, on upper and midportion of the thallus. Ovoid oogonia in sori. Antheridia in sori with indusium, linear.

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Synonyms: *Padina ramonribae* Ávila-Ortiz and Pedroche 2005

Missapplied names: *Padina pavonica* (Linnaeus) Thivy *sensu* Tejada (2003, 2007) and, Schnetter and Bula-Meyer (1982)

Type Locality: Isla María Magdalena, Las Tres Marías, Nayarit, Mexico. WR. Taylor 39-669/UC-694714 (Fig. 3.1e)

Etymology: A latin word meaning having a stem or with a visible stem

Habitat: On rocky, dead coral and rubble substrate. Intertidal to 12 m deep.

Distribution in ETP: Mexico: Nayarit, Oaxaca, Colima, El Salvador: La Libertad, Nicaragua: León, Rivas, Managua, Costa Rica: Guanacaste, Puntarenas, Panama: Chiriquí

Other Remarks: First report for El Salvador and Panama. *Padina caulescens* shows a very plastic morphology and this has been the problem with the recognition of this species along the Eastern Pacific coast. The thallus can vary from isolated blades to very flabellate and branched, can be heavily calcified to lightly calcified or even no calcification on its blades. When dried in herbarium sheets it can be of a very distinctive reddish color to a dark brown color. This species has been confused with all the species known in the ETP. With *P. mexicana* shares the flabellate form of the thallus; calcification and both can be found in the intertidal zone forming extensive patches. With *P. concrescens* shares the number of layers of medullary cells. With *P. durvillei* has in common its branched morphology. Riosmena-Rodríguez et al. (2009) proposed the synonymy of *P. caulescens* and *P. durvillei* based on the analysis of the holotype of *P. caulescens* that showed the same features as the isolectotype of *P. durvillei*, however they addressed that the differences between the lectotype of *P. durvillei* and its isolectotype still need to be addressed when new collections from the type locality with reproductive structures and the possibility to explore molecular relationships become available. The description proposed by Ávila-Ortiz and Pedroche (2005) of *P. ramonribae* match with the morphological measurement of the reddish specimens of *P. caulescens* clade as described in this study.

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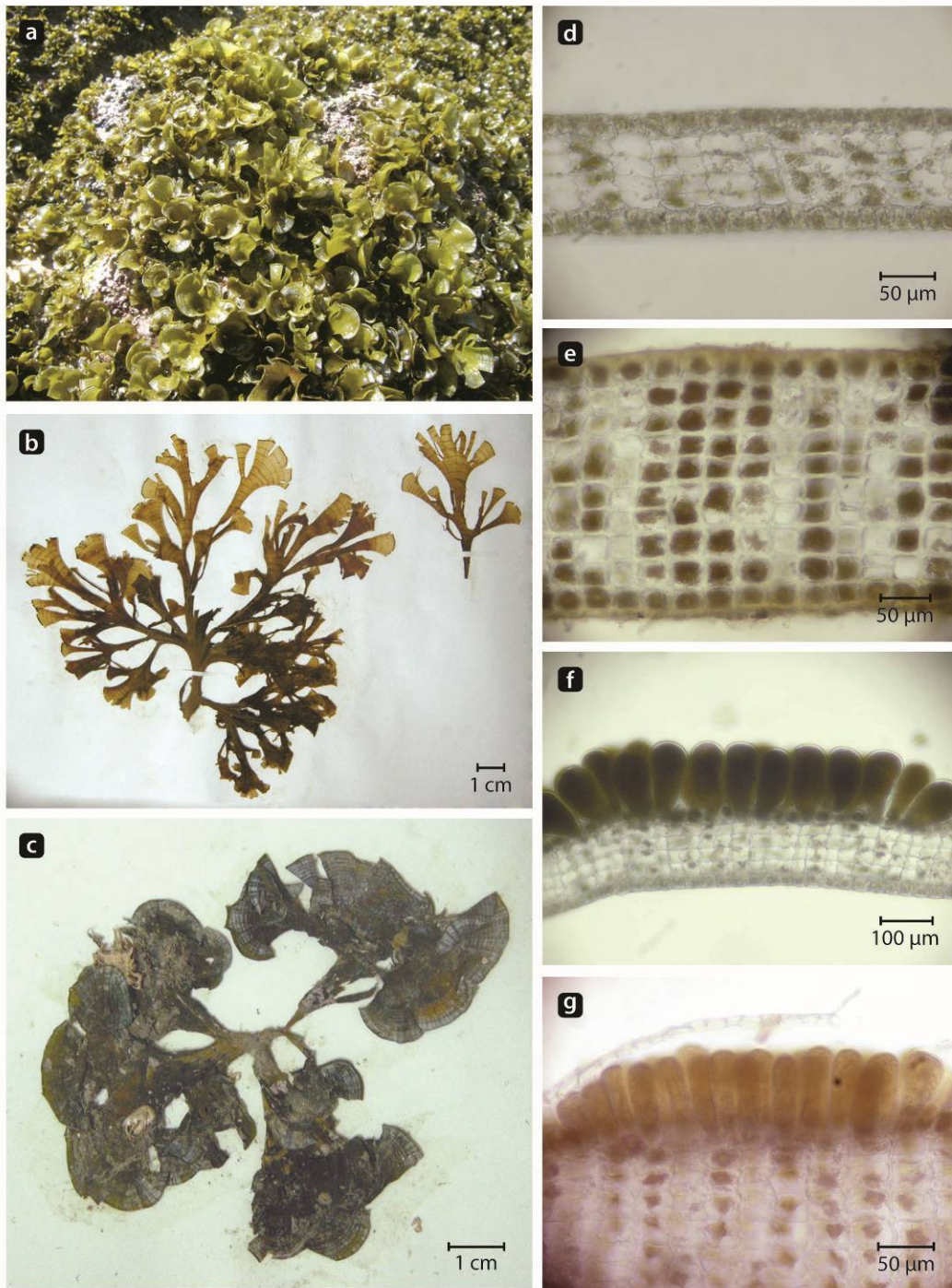


Fig. 3.5. *Padina caulescens* (a) Habit *in situ*, (b) Habit of uncalcified reddish specimens, (c) Habit of calcified olive brown specimens, (d) Transverse section of the blade near margin, (e) Transverse section of the blade near base, (f) Transverse section of the blade with sporangia, (g) Transverse section of the blade with oogonia.

***Padina concrescens* Thivy in Taylor 1945 (Fig. 3.6)**

Description: Thallus light brown, erect (Fig. 3.6a) to prostrate to (Fig. 3.6b) with no defined holdfast. When prostrate, attached to the substrate and to other blades by ventral rhizoidal cushions, when erect basal portion stipelike and stupose, blades also attached by ventral rhizoids. Blades generally, unbranched and frequently found isolated or gregarious. Composed of several layers of medullary cells reducing in number from the basal parts to the apical part. Calcification absent on both sides of the blades. Rounded to ovoid sporangia in the apical and midportion of the thallus, in continuous lines and or patches between hair lines, on both sides of the blade. Rounded oogonia, in patchy sori. Presents *Vaughaniella* stage (CFCR-910, Table S3).

Type Locality: Black Beach Anchorage, Isla Santa María, Galapagos Islands, Ecuador.
Isotype: W.R. Taylor # 166 in MICH (Fig. 3.1d)

Etymology: From the latin word *concrescientia*, that means grown together

Habitat: On rocky and dead coral substrate. Intertidal to 13 m deep, more common between 4-6 m deep.

Distribution in ETP: México: Baja California Sur, Oaxaca, Guerrero, Colima, Jalisco, Nicaragua: Managua, Rivas Costa Rica: Guanacaste, Puntarenas, Ecuador: Galapagos

Other Remarks: First report for Nicaragua and Costa Rica. Confused in the Gulf of California with *P. arborecens*, and this is why Riosmena-Rodríguez et al. (2009) description of this species has more medullary cells than our description of *P. concrescens*, which is the main difference between both species (Table 3.2).

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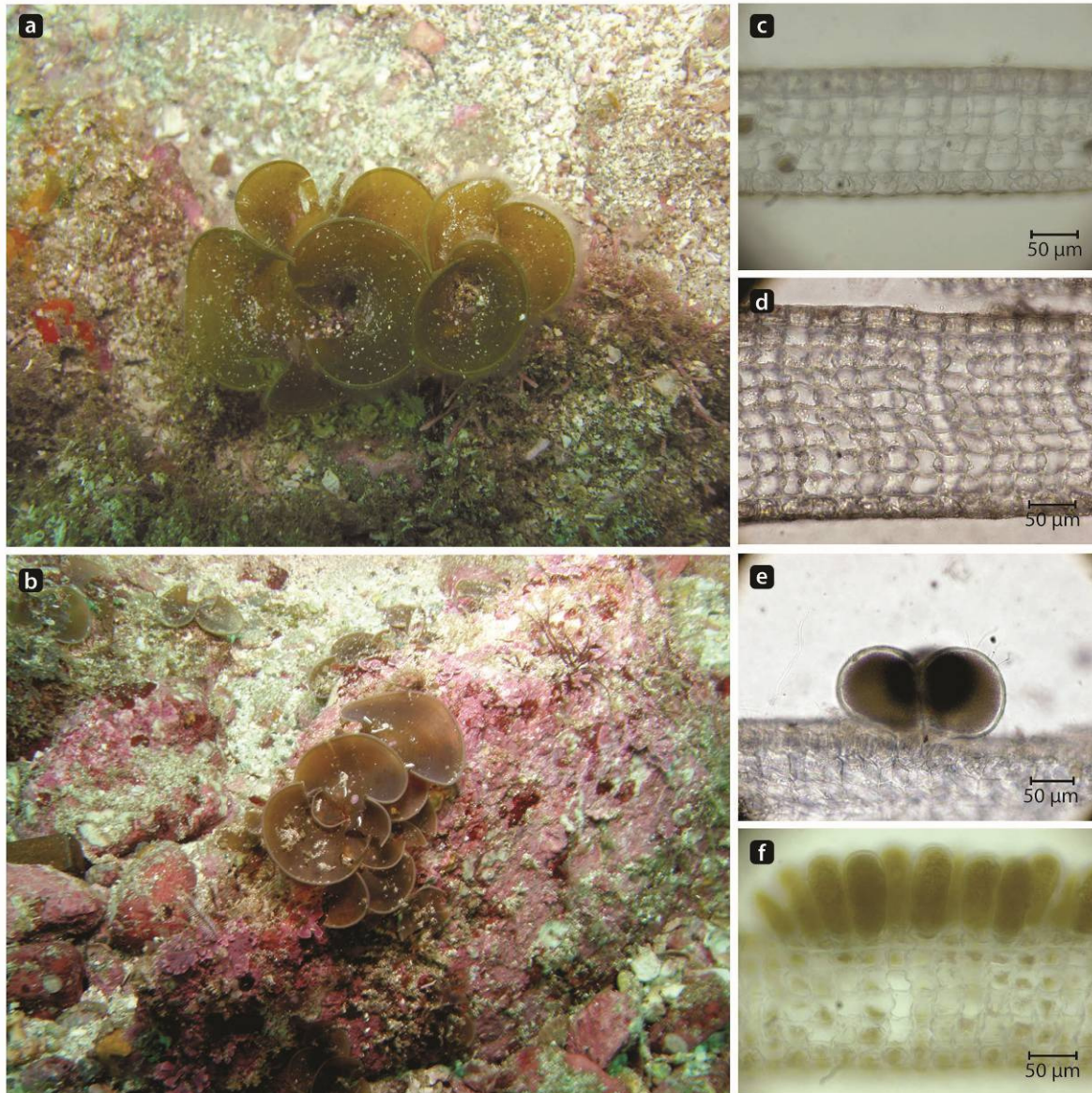


Fig. 3.6. *Padina concrescens* (a) Erect habit *in situ*, (b) Prostrate habit *in situ*, (c) Transverse section of the blade near margin, (d) Transverse section of the blade near base, (e) Transverse section of the blade with sporangia.

***Padina durvillei* Bory Saint-Vincent 1827 (Fig. 3.7)**

Description: Thallus erect, membranous to coriaceous, light or dark brown, or black, densely stupose stipe, composed of several layers of medullary cells reducing in number from the basal parts to the tips. Blades splitting into segments basally narrow. Disc-like or cone-like holdfast formed by rhizoids. In most specimens calcification is absent, however some samples show very light calcification in concentric lines on the lower surfaces, this was also observed by E.Y. Dawson (1957) in samples that he collected in Golfo de Nicoya, Costa Rica (UC1834405, D16704). Ovoid sporangia, in continuous lines or patches scattered in the upper and midportion of the thallus, on both sides of the blade.

Type Locality: Concepción, Chile (Fig. 3.1f)

Etymology: Named for Jules Sébastien César Dumont d'Urville (1790-1842), French naval officer and explorer.

Habitat: On rocky and dead coral substrate. Intertidal to 10 m. More common between 2-4 m deep.

Distribution in ETP: Mexico: Baja California Sur, Oaxaca, Guerrero, Jalisco, El Salvador: La Unión, Nicaragua: Rivas, Managua, León, Costa Rica: Guanacaste, Puntarenas, Panama: Bahía Panamá, Colombia: Isla Gorgona, Ecuador: Galapagos

Other Remarks: First report for El Salvador and Nicaragua. Also reported by Dawson et al. (1964) from Peruvian coast (Talara). This species showed that it is abundant and widely distributed in the lower littoral and upper sublittoral belts throughout the Eastern Pacific (from Baja California Peninsula to Chile). This species is sporadic and pseudo-perennial depending on the locality and is adaptable to great variations of water temperature known to exist in its habitats (Dawson 1944, Riosmena-Rodríguez et al. 2009). Commonly lacerated because of herbivory and covered with other organisms (red and green algae, bryozoans). Our morphological measurements match with the ones that Riosmena-Rodríguez et al. (2009) took from the type material (Table 3.2).

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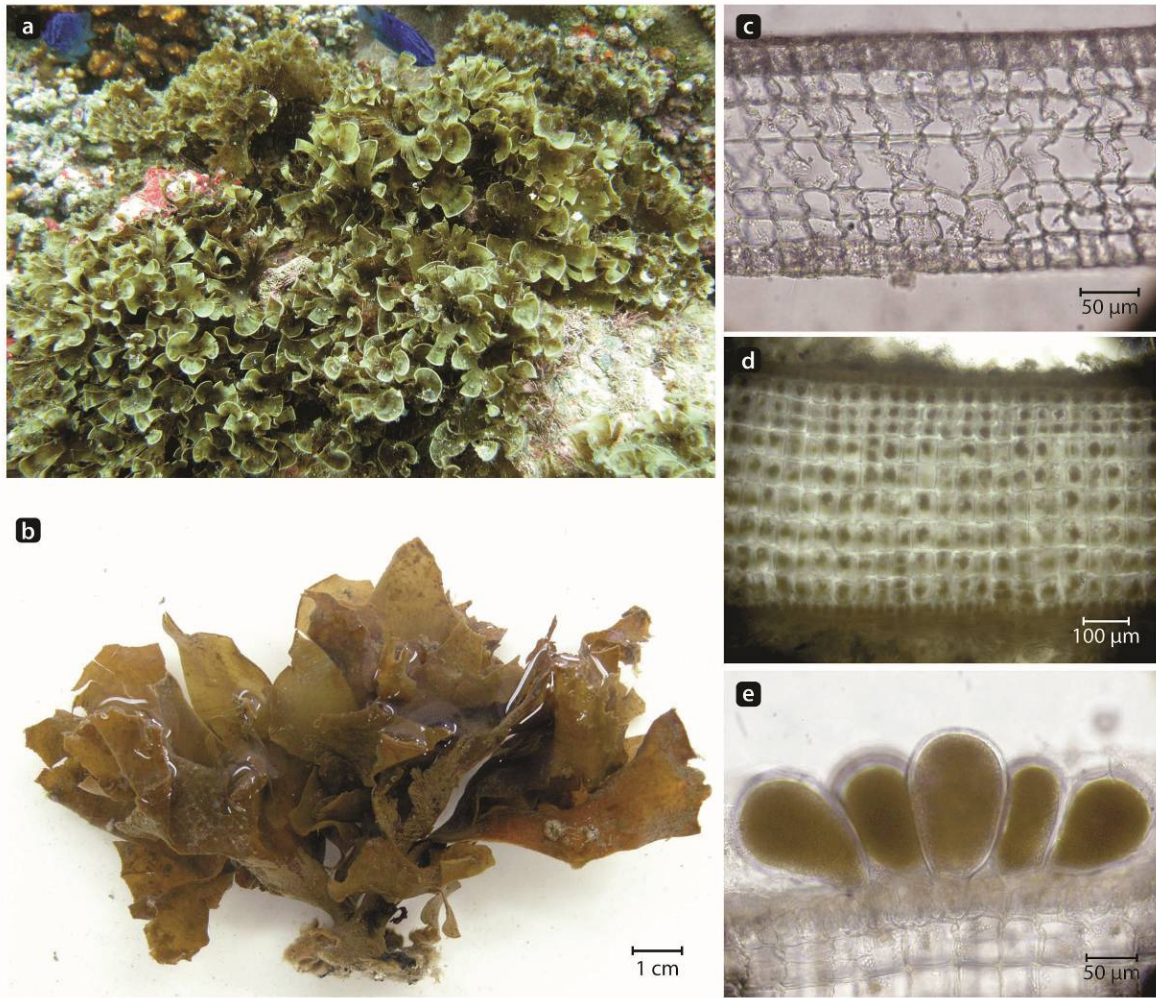


Fig. 3.7. *Padina durvillei* (a) Habit *in situ*, (b) Habit of the blades, (c) Transverse section of the blade near margin, (d) Transverse section of the blade near base, (e) Transverse section of the blade with sporangia.

***Padina mexicana* E.Y. Dawson 1944 (Fig. 3.8)**

Description: Thallus erect to prostrate, flat, expanded, resuspinate, broadly flabellate, 1.5-4 cm. broad, entire, without a recognizable basal stipe, attached at base and throughout by numerous rhizoids from the under surface. Heavily calcified, of a light chalky, gray-brown color, zonate, but noncalcified piliferous lines parallel with the margins. Composed of up to 4 layers of medullary cells which a less variable number from the basal parts to the apical. Hairs on upper side only. Rounded to ovoid sporangia in continuous, discontinuous bands and patches between hair lines, on upper and midportion of the thallus, more common in the inner part of the blade. Male gametophytes unknown.

Synonyms: *Padina crispata* Thivy in Taylor 1945. W.R Taylor 39-100/ UC694715 (Fig. 3.1b), W.R Taylor 39-100/MICH 1306527 (Fig. 3.1c)

Missapplied names: *Padina vickersiae* Hoyt *sensu* Guitierrez (1985), Tejada (2003, 2007)

Type Locality: Isla Turner Reef, off Isla Tiburón, Golfo de California, Mexico (D-725, UC-700866) (Fig 3.1a).

Etymology: pertaining to Mexico

Habitat: On rocky substrate and coral rubble. Very common in the intertidal zone, however it can reach to 8 m deep.

Distribution in ETP: Mexico: Baja California Sur (southeast of the Golfo de California), Nayarit, Oaxaca, Guerrero, Jalisco, El Salvador: La Libertad, Nicaragua: Managua Costa Rica: Guanacaste, Puntarenas, Panama: Chiriquí

Other Remarks: Only reported for the coast of México. In the rest of the countries this species has been reported as *P. crispata*, however specimens should be reviewed because of misidentification with *P. caulescens*. Ávila-Ortíz and Pedroche (2005) have recognized two varieties for *P. mexicana* based on the prostrate and erect growth forms of the plants. However our molecular data do not support genetic differences of the two growth forms.

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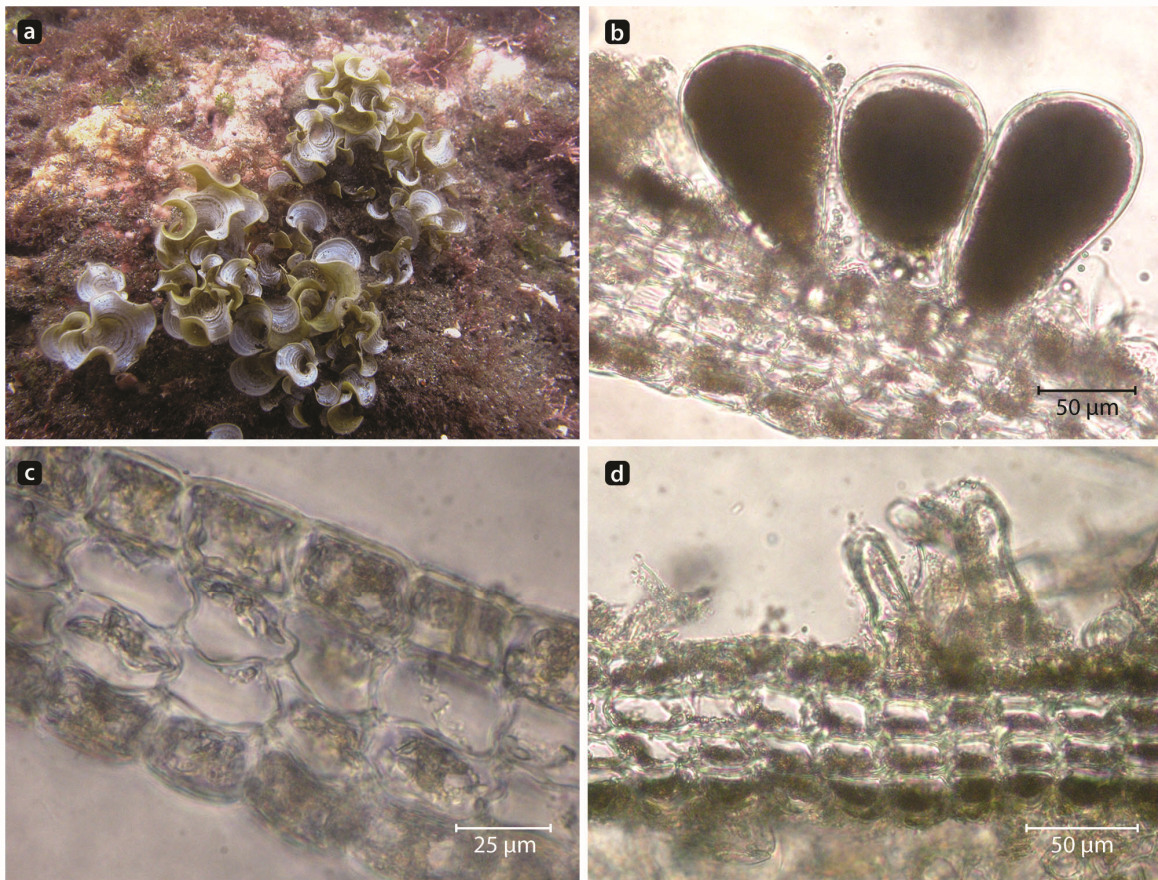


Fig. 3.8. *Padina mexicana* (a) Habit *in situ*, (b) Transverse section of the blade with sporangia, (c) Transverse section of the blade near margin, (d) Transverse section of the blade near base.

Biogeography

From the five species of *Padina* discussed in this paper, four species were only found at the Eastern Pacific: *Padina durvillei*, *P. concrescens*, *P. caulescens* and *P. mexicana* and have a wide latitudinal distribution at the ETP (Fig. 3.9). The fifth species *P. arborecenes* has a Gulf of California and Japan distribution.

It seems that the species of *Padina* are endemic to the Eastern Pacific (Fig. 3.3), with exception of *P. arborecenes* that is distributed along the Baja California Peninsula and

Japan (Fig. 3.9). These findings may indicate relationships between the Japanese and Baja California Peninsula floras.

All ETP *Padina* species lineages are very related between each other and grouped together in a well-supported clade (PP 0.98) (Fig. 3.3), suggesting that this genus has probably speciated after the closure of the Central American Isthmus; however this must be confirmed with future comparisons with specimens from other biogeographic regions.

Despite that the Eastern Pacific is a large region, with several biogeographic ecoregions (Spalding 2007), the total number of *Padina* species reported (8) is similar as other regions such as the Hawaii (7 species, Abbott and Huisman 2004), Philippines (8 species, Geraldino et al. 2005), Japan (8 species, Ni-Ni-Win et al. 2010), Indian Ocean (17 species, Silva et al. 1996), Caribbean Sea (7 species, Littler and Littler 2000). This was also recently observed with *Caulerpa* (Fernández-García et al. in prep) and *Dictyota* species (Fernández-García et al. in prep).

Conclusions

In this study we have found the presence of four endemic species of the genus *Padina* at the Eastern Tropical Pacific (*P. caulescens*, *P. concrescens*, *P. durvillei* and *P. mexicana*), which show a wide latitudinal distribution along the region. The molecular and morphological assessment showed a decrease in species number (from 10 to 4) in this region. This reduction in species number is due to species misidentification with similar species not present at the ETP, morphological plasticity of some species and overlap of morphological measurements within different species. Our morphological and DNA results warrant the recognition of *P. caulescens* as a current valid name and not a synonym of *P. durvillei* as proposed before. Also we recognized *P. crispata* as a synonym of *P. mexicana*. We found the presence of a complex of species exclusively found inside and outside the Peninsula of Baja California; *P. arborescens*, composed of four morphological closely allied species, which required future analysis.

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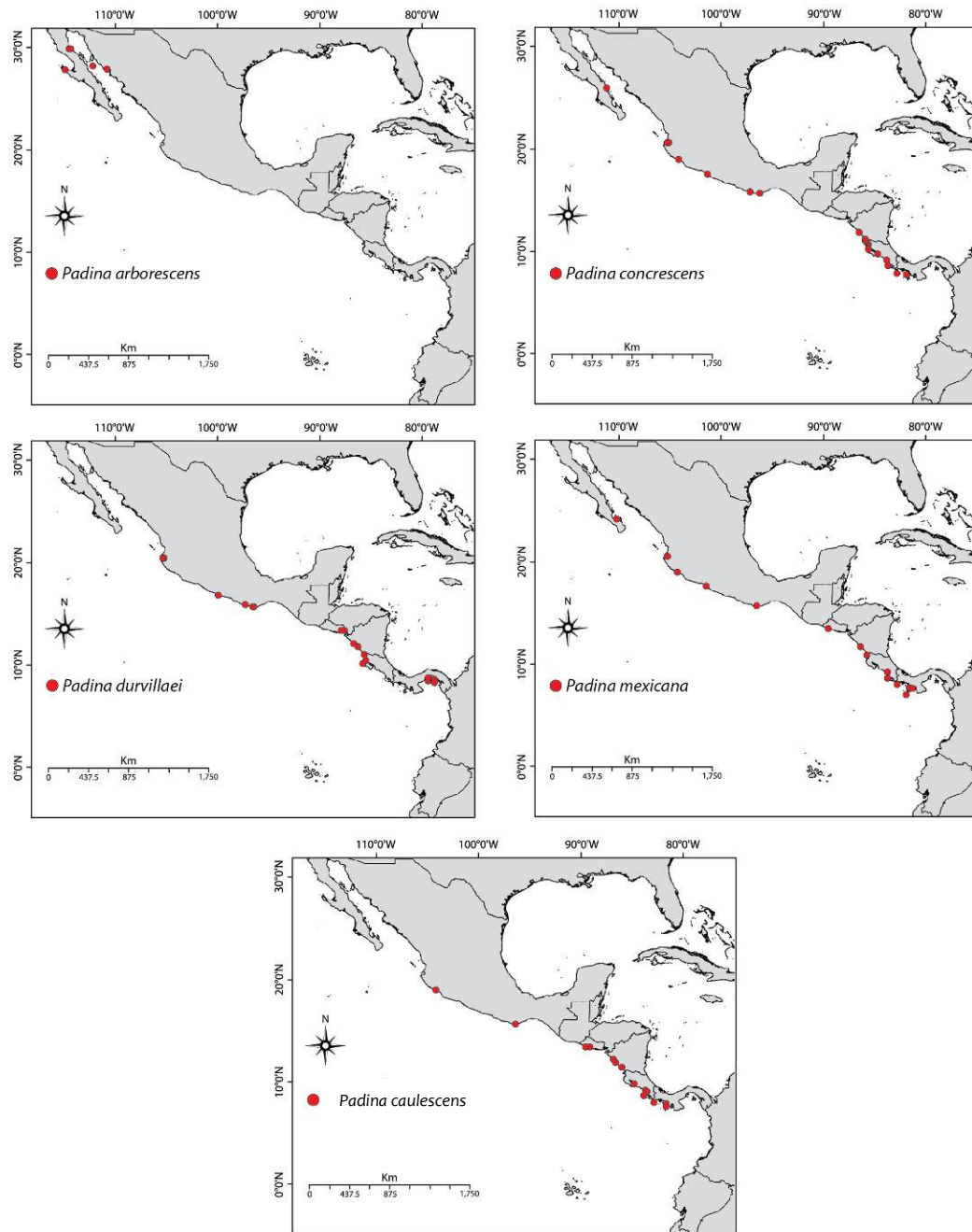


Fig. 3.9. Distribution of new collections of *Padina* species in the Eastern Tropical Pacific.

**TAXONOMÍA Y BIOGEOGRAFÍA DEL GÉNERO *DICTYOTA*
(DICTYOTACEAE) EN EL PACÍFICO TROPICAL ORIENTAL**

Taxonomy and Biogeography of the genus *Dictyota* (Dictyotaceae) in the Eastern Tropical Pacific

Resumen: Los estudios taxonómicos del género *Dictyota* asistidos por análisis molecular han demostrado un descenso en el número de especies (16 a 7) documentadas para el Pacífico Tropical Oriental (PTO). En este trabajo se evalúa la morfología y la filogenia inferida con el gen *cox3* de este género y una reevaluación de la distribución mundial a la luz de una nueva definición de las especies. Los resultados muestran que la identificación de *Dictyota* basada en la morfología ha fallado debido a: la plasticidad fenotípica intrínseca del género, vaga definición en los caracteres de las especies descritas y mala identificación por el uso de claves taxonómicas no acordes con la región. De las 13 especies reportadas para el PTO, se encontraron 3 nombres válidos (*D. crenulata*, *D. humifusa*, *D. stolonifera*), 10 identificaciones erróneas (*D. adnata*, *D. baytaresiana*, *D. ciliolata*, *D. concrescens*, *D. dichotoma*, *D. divaricata*, *D. flabellata*, *D. friabilis*, *D. linearis*, *D. pinnata*) y 3 reportes no confirmados (*D. binghamiae*, *D. major*, *D. masonii*). Aunado se encontraron dos especies polifiléticas, una no reportada antes para la región (*D. ceylanica*) y *D. stolonifera*, la cuál fue descrita originalmente para el PTO. Asimismo, se propone el reconocimiento de tres especies nuevas para el PTO. La mayoría de las especies de *Dictyota* (5 de 7) consideradas en este estudio muestran un ámbito de distribución restringido en la región, mientras que dos especies (*D. humifusa* and *D. ceylanica*) están presentes en muchas provincias biogeográficas de latitudes tropicales.

Abstract: Molecular-characterization of *Dictyota* spp. has resulted in a decrease in the number of species (16 to 7) documented for the Eastern Tropical Pacific (ETP). Here we evaluate the morphology and *cox3*-inferred phylogeny of the genus, and re-assess the world-wide distribution in the light of refined species concepts. The results reveal that morphological identifications of *Dictyota* spp. have failed due to: intrinsic phenotypic plasticity of many species, poorly defined characters in available descriptions, and mis-identification resulting from the use of taxonomic keys from regions geographically distinct from the ETP. From the 16 species reported for the ETP, we encountered 3 valid names (*D. crenulata*, *D. humifusa*, *D. stolonifera*), 10 misidentifications (*D. adnata*, *D. baytaresiana*, *D. ciliolata*, *D. concrescens*, *D. dichotoma*, *D. divaricata*, *D. flabellata*, *D. friabilis*, *D. linearis*, *D. pinnata*) and 3 un-confirmed records (*D. binghamiae*, *D. major*, *D. masonii*). In addition, we reveal polyphyly for one species not reported for the region (*D. ceylanica*) previously, and for *D. stolonifera*, which was originally described from the ETP. We propose the recognition of three new species for the ETP. The majority of *Dictyota* spp. (5 of 7) considered in this study appear to be range restricted within the region, while two (*D. humifusa* and *D. ceylanica*) are present in many oceanographic provinces of tropical latitudes.

Key Words: Central America, *Dictyota*, Dictyotales, Eastern Tropical Pacific, marine floristics Mexico, taxonomy

Introduction

Dictyota Lamouroux is a tropical to subtropical genus of erect or prostrate brown algae, composed of flat ribbon-like fronds that are clumped or bushy in appearance. The genus is characterized by a monostromatic cortex and medulla throughout, except for stolons that could have a multilayered medulla (De Clerck et al. 2006). Branching may be regularly or irregularly dichotomous or alternate throughout, while blades exhibit smooth, dentate, crenulate, or ciliate margins. Most species are attached by a single, or several rhizoidal holdfasts, although a few species are attached by stoloniferous holdfasts (De Clerck 2003, Kraft 2009, Norris 2010). There is a single meristematic apical cell that contributes to development of the surface as well as the internal tissues of the medulla; cells below the apical region do not undergo further division, apart from the development of reproductive structures and the formation of vegetative proliferations (De Clerck 2003, Graham et al. 2009).

Among brown algae, *Dictyota* is second only to *Sargassum* in species richness (Kraft 2009). Presently 316 species (and infraspecific) names are listed in AlgaeBase (Guiry and Guiry 2012), of which 76 have been flagged as currently accepted taxonomically. The proliferation of names is a function of the high degree of morphological variability exhibited by species in the genus and the lack of easily defined characters (De Clerck and Coppejans 1999, De Clerck et al. 2001, De Clerck 2003, Tronholm et al. 2008). In addition, most tropical representatives of *Dictyota* have nearly identical reproductive structures and thallus anatomies (De Clerck et al. 2001). These problems generally inflate species richness estimates (De Clerck et al. 2001, De Clerck 2003, Norris 2010), while obscuring patterns of distribution – problems that are only now being clarified by molecular analyses and rigorous comparisons with the type material (De Clerck 2003, Tronholm et al. 2008, 2010a, b, 2012, in review).

For the Eastern Tropical Pacific (ETP), defined here as the region extending from the South Baja California Peninsula to Ecuador, 16 species are reported (Table 1), of which, 8 have type localities from within this range. Of the total of species reported, three

have been reported for this region but according to Fernández-García et al. (2011), their distribution within the ETP seems doubtful: *D. adnata* (Schnetter and Bula-Meyer 1982, Fernández-García et al. 2011), *D. dichotoma* (Garske 2002, Pedroche et al. 2008, Fernández-García et al. 2011), and *D. divaricata* (Schnetter and Bula-Meyer 1982, Garske 2002, Serviere-Zaragoza et al. 2007, Pedroche et al. 2008, Fernández-García et al. 2011). *D. dichotoma* and *D. divaricata*, according to recent studies of De Clerck (2003) and Tronholm et al. (2010) are limited geographically to the Northeast Atlantic Ocean and Mediterranean Sea.

To date, all taxonomic studies of *Dictyota* in the ETP have been based strictly on interpretations of morphology (Taylor 1945, Dawson 1950, Schnetter and Bula-Meyer 1982, Norris 2010). Here we attempt to reconcile morphological and molecular phylogenetic species concepts of *Dictyota* spp. from throughout the ETP. This analysis informs ongoing efforts to elucidate the diversity of tropical marine floras throughout Central America, and promotes a re-assessment of algal biogeography.

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Table 4.1. Species of the genus *Dictyota* reported for the Eastern Tropical Pacific. MEX=Mexico, ES= El Salvador, NIC= Nicaragua, CR=Costa Rica, PAN=Panama, CA= Central America, COL= Colombia, ECU= Ecuador, RI= Revillagigedo Island, France, GL= Galápagos Islands, Ecuador, TL= Type locality. In bold species which type locality is in the Eastern Pacific.

Species reported	Current status at the ETP (this study)	MEX	ES	NIC	CR	PAN	CA	COL	ECU	Reference
<i>Dictyota adnata</i> Zanardini TL: Kepulauan Kai, Indonesia	Not present at the ETP				x			x		Fonseca 1999, Schnetter and Bula-Meyer 1982
<i>Dictyota bartayresiana</i> J.V. Lamouroux TL: Antilles, West Indies	Not present at the ETP	x								Pedroche et al. 2008
<i>Dictyota binghamiae</i> J. Agardh TL: Santa Barbara, California, USA	Unconfirmed record	x			x	x		x (GL)		Taylor 1945, Garske 2002, Bernecker 2009, Littler and Littler 2009, Pedroche et al. 2008
<i>Dictyota ciliolata</i> Sonder ex Kützing TL: La Guaira, Venezuela	<i>Dictyota crenulata</i>	x								Pedroche et al. 2008
<i>Dictyota conrescens</i> W.R. Taylor TL: Cabo San Lázaro, Point Hughes, Baja California, Mexico	Not present at the ETP	x				x				Pedroche et al. 2008, Littler and Littler 2009

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Species reported	Current status at the ETP (this study)	MEX	ES	NIC	CR	PAN	CA	COL	ECU	Reference
<i>Dictyota crenulata</i> J. Agardh TL: San Agustín, Oaxaca, Mexico	<i>Dictyota crenulata</i>	<i>x</i> (RI)			<i>x</i>		<i>x</i>			Dawson 1950, 1957, 1961b, 1962b, Soto and Bermúdez 1990, Taylor 1945, Dawson, Serviere-Zaragoza et al. 2007, Pedroche et al. 2008, Bernecker 2009
<i>Dictyota dichotoma</i> (Hudson) J.V Lamouroux TL: Walney Island, Lancashire, England	Not present at the ETP	<i>x</i>	<i>x</i>				<i>x</i>		<i>x</i> (GL)	Garske 2002, Pedroche et al. 2008, Fernández-García et al. 2011
<i>Dictyota divaricata</i> J.V Lamouroux TL: Mediterranean coast of France	Not present at the ETP	<i>x</i>	<i>x</i>		<i>x</i>		<i>x</i>	<i>x</i>	<i>x</i> (GL)	Schnetter and Bula-Meyer 1982, Garske 2002, Serviere-Zaragoza et al. 2007, Pedroche et al. 2008, Fernández-García et al. 2011
<i>Dictyota flabellata</i> (Collins) Setchell et N.L. Gardner TL: La Jolla, California, U.S.A.	Not present at the ETP	<i>x</i>			<i>x</i>	<i>x</i>	<i>x</i>			Taylor 1945, Dawson 1950, 1957, Earle 1972, Abbott and Hollenberg 1976, Zertuche González et al. 1995, Sibaja-Cordero 2005, Sibaja-Cordero and Vargas-Zamora 2006, Pedroche et al. 2008, Littler and Littler 2009

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Species reported	Current status at the ETP (this study)	MEX	ES	NIC	CR	PAN	CA	COL	ECU	Reference
<i>Dictyota friabilis</i> Setchell TL: Tafaa Point, Tahiti	<i>Dictyota humifusa</i>	x	x		x		x			Dawson 1957, Dawson 1961b, Dawson 1962b, Tejada 2003, Pedroche et al. 2008, Bernecker 2009
<i>Dictyota humifusa</i> Hörnig, Schnetter et Coppejans TL: Punta Chengue, Santa Marta, Depto del Magdalena, Caribbean, Colombia	<i>Dictyota humifusa</i>					x				Little and Little 2009
<i>Dictyota linearis</i> (C. Agardh) Greville TL: Cádiz, Spain	<i>Dictyota ceylanica</i>	x								Pedroche et al. 2008
<i>Dictyota masonii</i> Setchell et N.L. Gardner TL: Isla Clarión, Baja California, Mexico	Unconfirmed record	x (RI)			x		x			Dawson 1960, 1961b, 1962b, Serviere-Zaragoza et al. 2007, Pedroche et al. 2008, Bernecker 2009
<i>Dictyota major</i> W.R. Taylor TL: Post Office Bay, Isla Santa Maria, Galapagos	Unconfirmed record					x			x (GL)	Garske 2002, Little and Little 2009

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Species reported	Current status at the ETP (this study)	MEX	ES	NIC	CR	PAN	CA	COL	ECU	Reference
<i>Dictyota stolonifera</i> E.Y Dawson TL: Masachapa, Nicaragua, Pacific Ocean	<i>Dictyota stolonifera</i>			x	x	x		x		Dawson 1962a, Schnetter and Bula-Meyer 1982, De Clerk, O. 2003, Fernández 2008, Bernecker 2009, Littler and Littler 2009
<i>Dictyota pinnata</i> (E.Y. Dawson) Hörnig Schnetter et Prud'homme van Reine TL: Miramar, Nayarit, Mexico	<i>Padina</i> sp.	x	x					x		Pedroche et al. 2008. <i>As Dilophus pinnatus:</i> Schnetter and Bula-Meyer 1982, Gutiérrez 1985, Tejada 2003

Materials and Methods

Sample collection

A total of 143 samples of *Dictyota* specimens were collected from 61 field locations throughout the ETP (Mexican Tropical Pacific, Central America, Colombia) between 2008 and 2011 (Table S4). Detailed specimen information including specimen identification numbers, morphological and DNA identification, collection site and date, and collectors, is summarized in the supplementary material (Table S4). All specimens were collected manually by SCUBA diving and were preserved in silica gel, 4 % formalin/seawater and pressed on herbarium sheets for molecular and morphological examination. Voucher of the specimens are deposited in USJ herbarium (Universidad de Costa Rica, San José, Costa Rica), HBCS herbarium (Universidad Autónoma de Baja California Sur, La Paz, Mexico), CUVC herbarium (Universidad del Valle, Cali, Colombia) and GENT herbarium (University of Ghent, Ghent, Belgium).

Morphological and ecological characteristics

For each specimen, the depth, substratum and habit were recorded, along with geographic coordinates, from which distribution maps were plotted using ArcGIS 9.2 (Esri Redlands, CA, USA). In the laboratory all specimens were analyzed for morphology, morphometric and anatomical characters, from both vegetative and reproductive thalli.

Preliminary species determinations were made on the basis of morphological comparisons with original descriptions, type herbarium specimens (Fig. 4.1) and with reference to the following sources for the Eastern Pacific: Dawson (1950), Taylor (1945), Schnetter and Bula-Meyer (1982), Littler and Littler (2009), Norris (2010). Additional data was obtained from historically valuable collections of the region that are housed in the following herbaria: MICH, UC, NY, COL and USJ.

Measurements of morphometric characters were carried out on formaline-preserved specimens with a Nikon Coolpix 4300 camera and image processing in the UTHSCSA software Image Tool version 3.0. Some vegetative and reproductive measurements were done using handmade transverse sections with a razor blade.

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Following De Clerck and Coppejans (1999), De Clerck (2003) and Tronholm et al. (2010), we used 8 qualitative and 20 quantitative characters to delimit species (representing 19 vegetative, 9 reproductive features) (Fig. 4.2a, b). Habit, color and texture of the thallus, iridescence color, presence/absence of stolons, shape and position of dentation, and sporangia aggregation were determined. Thallus height and width (transversase section), number of branches from main axis, length and width of interdichotomies, apex width, branching angles (apical and middle-basal), were measured (Fig. 4.2a). Heights and widths of cortical and medullary cells were measured in transverse sections (Fig. 4.2b). Mature parts of each individual were selected for reproductive features. Diameters of sporangia were measured in surface view and height in transverse sections. Sori maximum width was measured in surface view. Height and diameter of antheridia and oogonia were measured in transverse section. From each morphometric character, minimum and maximum sizes and the 95 percentile were determined (Table 4.2).

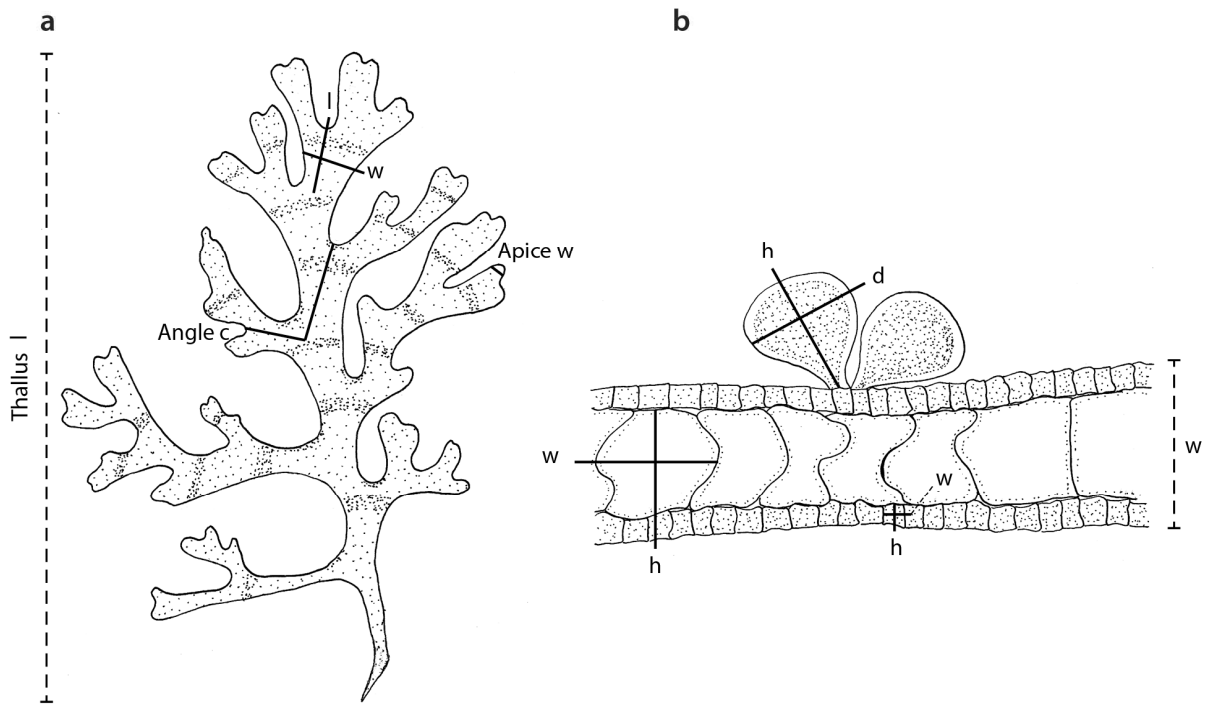


Fig 4.2. Morphometric measurements. (a) Thallus measurements: interdichotomies, angle and apical portion (b) Transversal section measurements. w =width, l =length, d =diameter, h =height.

DNA Extraction, Amplification and Sequencing

Total genomic DNA was extracted using a standard CTAB-extraction method and subsequent purification with a Wizard[®] DNA Clean-Up System (Promega Inc., Madison, WI, USA) as outlined in De Clerck et al. (2006). The mitochondrial *cox3* gene was amplified and sequenced using primers and thermal cycling parameters as outlined in De Clerck et al. (2006) and Tronholm et al. (2010). The protein coding sequences were aligned manually using MEGA 4 (Kumar et al. 2008). A complete list of specimens used in the molecular analyses is detailed in Table S4.

Results

Type material analysis

When evaluating the type collections of the 16 *Dictyota* species reported for the ETP (Table 4.1, Fig. 4.1), we determined that the holotype of *D. pinnata* do not exhibit the diagnostic characters of the genus. *Dictyota pinnata*, was first described as *Dilophus pinnatus* (Fig. 4.1b) by Dawson (1950) growing on mats of small algae on a rocky shore at Miramar, Nayarit, Mexico. The species was later transferred to the genus *Dictyota* by Hörnig et al. (1993) on the basis of the examination of several *Dictyota* species, with respect to the character multilayered medulla, that did not result in a separation or grouping of species within both genera. Our analysis of the type material shows that this specimen exhibits features consistent with the *Vaughaniella*-stage of the closely related genus *Padina*. Holotype material has pinnate branching, the spores occur in transverse bands and the medulla is composed of 3-5 cell layer. Also Riosmena-Rodríguez et al. (in prep) noticed the presence of inrolled margin in one of the specimens of the holotype. According to Fernández-García et al. (Chapter 3) *Vaughaniella*-stage is common in the area, and the morphology of specimens (CFCR-910, Table S3) found in that study, is similar to what Dawson (1950) described as *Dilophus pinnatus*.

Dictyota concrescens, was described by Taylor (1945) from specimens collected at Point Hughes, Cabo San Lázaro, Baja California (AHFH 144 in UC-Fig. 4.1a). According to Dawson (1950b), Norris (2010) and Riosmena-Rodríguez et al. (in prep) the type specimen of *D. concrescens* may be inadequate for clear interpretation. Riosmena-Rodríguez et al. (in prep) considered that this species is a synonymy of *D. friabilis*.

However further analyses that include the type locality are needed to clarify its taxonomic status (Norris 2010). Specimens reported for the Mexican Tropical Pacific (Michoacán) under this name by Stout and Dreckmann (1993) and considered in Pedroche et al. (2008) catalogue, required further study to elucidate the real identity.

Littler and Littler (2009) applied the name *D. concrescens* to Pacific Panamanian specimens, which exhibited creeping, dark yellow-brown; often becoming attached to each other or overlapping, and completely lying flat. Blades strap-shaped, to 140(-500) μm thick, to 5(-15) mm wide; margins smooth; apices blunt or rounded. These traits do not correspond to Taylor's original description in which plants are crowded, light brown thallus, the blades commonly becoming attached to each other but with erect portions, the segments short and relatively broad, tapering downward, lower segments commonly to 2-3 cm long, narrow below and to 15 mm wide at the top, where they branch so closely as to appear subpalmate, the upper segments 2-3 mm broad, rounded truncate. Littler and Littler (2009) specimens does match with recent collections made in this study (see “Remarks” in *D. sp. 1*).

Species delimitation

Comparisons of morphological measurements of species found in this study are presented in Table 4.2. According to the molecular analysis of the *cox3* gene and the morphological assessment, Eastern Tropical Pacific *Dictyota* specimens clustered in seven species-level clades (Fig. 4.3a,b)

Of the 13 species reported from the ETP, we found 3 valid names (*D. crenulata*, *D. humifusa*, *D. stolonifera*), 7 misidentifications (*D. baytaresiana*, *D. ciliolata*, *D. concrescens*, *D. flabellata*, *D. friabilis*, *D. linearis*, *D. pinnata*) and 3 un-confirmed records (*D. binghamiae*, *D. major*, *D. masonii*). In addition we found 1 species not reported before for the region (*D. ceylanica*) and 3 new species. As well, we confirmed that the species *D. divaricata*, *D. dichotoma* and *D. adnata* are not distributed at the ETP. Specimens under these names have been misidentified with other species present in the region.

In many cases, morphological species are monophyletic lineages, (e.g. *D. humifusa*, *D. crenulata*, *D. sp. 1*, *D. sp. 2* and *D. sp. 3*). However, *D. stolonifera* and *D. ceylanica* are polyphyletic taxa, with at least two and five widely divergent genetic lineages, respectively (Fig. 4.3).

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Table 4.2. Morphological comparison of *Dictyota* species from the Eastern Tropical Pacific. Values are: (Minimum-)(95% Range)(-Maximum).

		<i>D. sp. 1</i>	<i>D. sp. 2</i>	<i>D. sp. 3</i>	<i>D. crenulata</i>
Thallus	Texture	smooth	smooth	smooth-gelatinous	crisp
	Habit	postrate	erect	erect and postrate	erect
	Iridescence	absent	dark blue	yellow to greenish	yellow to greenish
	Stolon	absent	absent	absent	absent
	Length (cm)	postrate	(5.4-)5.8-7.6(-8)	(1.2-)3.2-3.8(-7.3)	(2.9-)3.3-4.5(-6.5)
	Width (µm)	95.9	82.5	(44.77-)101.7-115.5(-160.12)	(78.1-)82.1-95.1(-107.6)
Dentation		absent	absent	absent	crenulate, triangular teeth
	Shape				
Branches from main axes	Number	not determined	(6-)6(-7)	(2-)4-5(-8)	(5-)5-7(-8)
Interdichotomies	Length (mm)	(2.7-)2.9-3.4(-4.5)	(4.4-)7.7-9.2(-13.4)	(2.3-)5.9-6.3(-14.6)	(2.4-)4.9-5.6(-9.1)
	Width (mm)	(2.0-)2.4-2.8(-3.3)	(1.7-)2.1-2.4(-2.8)	(1.2-)2.61-2.9(-9.8)	(1.7-)2.3-2.5(-3.5)
Apices	Width (mm)	(1.6-)1.8-2.6(-2.7)	(1.0-)1.2-1.5(-1.9)	(0.6-)1.2-1.3(-2.4)	(1.5-)1.9-2.1(-2.8)
Branching angle	Apical (°)	(61.6-)81.0-92.1(-107.5)	(33.1-)41.8-47.0(-73.7)	(34.5-)62.5-65.2(-103.0)	(44.1-)66.9-72.1(-98.0)
	Middle- basal (°)	(67.4-)75.7-82.8(-98.1)	(32.1-)45.3-49.1(-57.6)	(27.1-)74.5-79.1(-129.9)	(44.7-)74.9-80.3(-112.0)
Medullary cells	Height (µm)	(38.1-)42.5-46.3(-52.9)	(56.8-)60.1-62.4(-66.4)	(27.9-)70.1-75.1(-133.7)	(40.6-)50.5-54.0(-72.7)
	Width (µm)	(42.9-)53.2-61.2(-74.0)	(36.7-)44.0-47.1(-48.6)	(49.9-)77.5-81.5(-149.0)	(29.3-)53.6-59.0(-80.4)
Cortical cells	Height (µm)	(14.4-)15.8-16.9(-18.2)	(8.7-)9.4-10.0(-11.0)	(7.2-)14.8-15.6(-27.7)	(11.0-)15.0-16.1(-20.5)
	Width (µm)	(13.1-)17.3-20.8(-25.3)	(9.1-)12.0-14.0(-17.3)	(9.9-)19.3-20.3(-30.7)	(7.9-)12.6-14.0(-19.6)
Sporangia	Diameter (µm)	no data	no data	(59.0-)78.9-81.8(-105.2)	(68.3-)81.3-89.5(-97.3)
	Height (µm)	no data	no data	(46.5-)68.6-72.8(-109.0)	(84.6-)91.3-95.2(-98.8)
	Sorus Max Width (µm)	no data	no data	(369.4-)404.0-427.6(-477.5)	no data
Male gametophyte	Antheridia diameter (µm)	no data	no data	(19.5-)26.0-29.2(-31.5)	no data
	Antheridia height (µm)	no data	no data	(62.9-)72.6-79.2(-89.8)	no data
	Sorus Width (µm)	no data	no data	(200.0-)253.8-283.7(-360.7)	no data
Female gametophyte	Oogonia diameter (µm)	no data	no data	(19.7-)32.0-36.1(-50.7)	no data
	Oogonia height (µm)	no data	no data	(44.9-)62.0-67.8(-83.2)	no data

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Cont. Table 4.2. Morphological comparison of *Dictyota* species from the Eastern Tropical Pacific. Values are: (Minimum-)(95% Range)(-Maximum).

		<i>D. ceylanica</i>	<i>D. humifusa</i>	<i>D. stolonifera</i>
Thallus	Texture	smooth	smooth	smooth
	Habit	erect, forming mats	prostrate, forming mats	erect
	Iridescence	green to bluish or absent	blue to greenish in bands	pink or bluish
	Stolon	absent	absent	present
	Length (cm)	(1.1-)1.9-2.3(-3.3)	(0.9-)1.4-1.6(-2.3)	(1.0-)3.3-3.7(-9.2)
	Width (µm)	(107.6-)130.2-140.3(-167.1)	(58.9-)70.9-76.5(-109.6)	(55.4-)100.4-104.1(-139.8)
Dentation	Shape	absent	absent	absent
Branches from main axes	Number	(4-)5-6(-7)	(2-)3(-4)	(2-)5-6(-11)
Interdichotomies	Length (mm)	(1.9-)3.6-4.0(-8.6)	(2.4-)3.7-4.0(-6.3)	(1.9-)5.8-6.4(-16.7)
	Width (mm)	(0.3-)1.1-1.3(-2.1)	(1.0-)2.1-2.4(-3.5)	(1.1-)3.3-3.5(-11.9)
Apices	Width (mm)	(0.3-)0.5-0.7(-1.9)	(0.6-)1.3-1.5(-2.5)	(0.7-)1.6-1.7(-3.5)
Branching angle	Apical (°)	(48.0-)82.6-86.6(-123.0)	(34.1-)82.0-86.0(-127.7)	(35.5-)65.9-68.2(-174.4)
	Middle- basal (°)	(65.6-)92.3-95.5(-137.5)	(65.9-)88.8-92.8(-124.5)	(28.5-)78.5-80.9(-140.6)
Medullary cells	Height (µm)	(55.2-)84.4-89.1(-131.6)	(26.7-)43.7-45.9(-75.5)	(37.0-)67.5-69.0(-105.5)
	Width (µm)	(64.4-)102.1-107.4(-153.78)	(27.0-)46.5-48.6(-85.4)	(33.7-)71.3-73.1(-130.3)
Cortical cells	Height (µm)	(11.3-)17.1-18.0(-26.8)	(9.1-)15.8-16.4(-22.1)	(7.7-)(15.2-15.6(-26.2)
	Width (µm)	(12.0-)22.2-23.4(-39.5)	(12.8-)21.4-22.3(-33.8)	(9.5-)18.5-19.1(-40.3)
Sporangia	Diameter (µm)	no data	(68.9-)83.0-87.1(-108.3)	(54.1-)73.3-74.8(-92.7)
	Height (µm)	no data	(48.0-)70.8-74.9(-85.6)	(49.6-)59.9-93.5(-107.9)
	Sorus Max Width (µm)	no data	no data	(263.7-)413.9-465.8(-673.7)
Male gametophyte	Antheridia diameter (µm)	no data	no data	(15.0-)19.5-21.0(-27.4)
	Antheridia height (µm)	no data	no data	(35.4-)61.4-66.5(-83.8)
	Sorus Width (µm)	no data	no data	(135.8-)270.5-292.6(-501.9)
Female gametophyte	Oogonia diameter (µm)	no data	no data	(22.6-)36.1-37.8(-48.9)
	Oogonia height (µm)	no data	no data	(45.6-)80.2-83.4(-117.3)

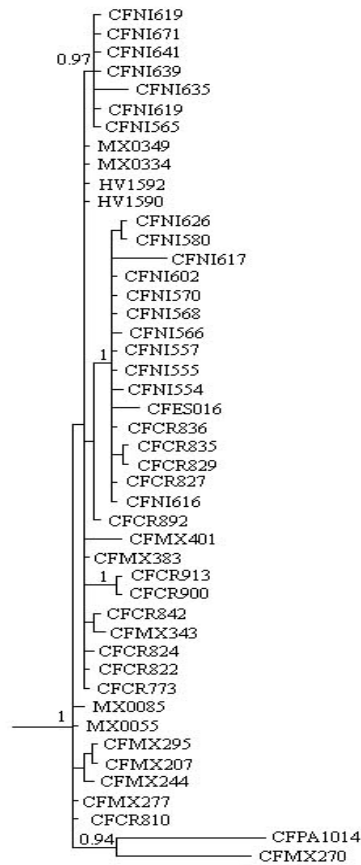
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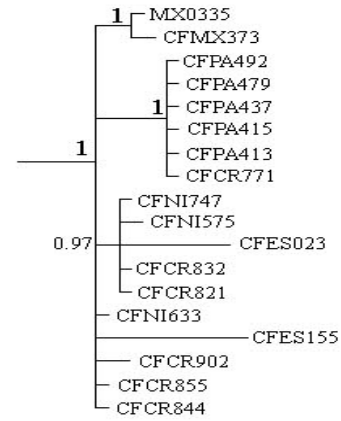
Fig. 4.3a. Consensus tree resulting from the Bayesian Inference analysis of *cox3* sequences showing seven species of *Dictyota* from the ETP. In squares polyphyletic clades of *D. ceylanica* and *D. stolonifera*.

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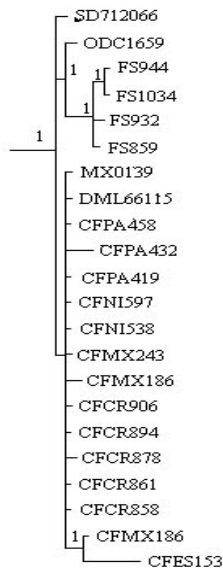
a *Dictyota stolonifera*



b *Dictyota sp. 3*



c *Dictyota humifusa*



d *Dictyota ceylanica*

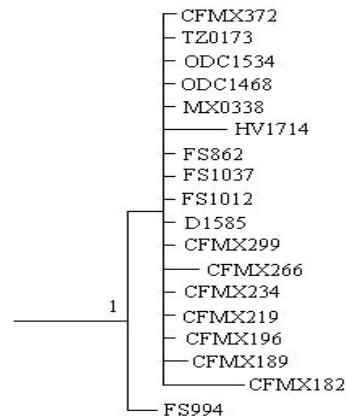


Fig. 4.3b. Consensus tree resulting from the Bayesian Inference analysis of *cox3* sequences of *Dictyota*. (a) *D. stolonifera* ETP clade, (b) *D. sp. 3*, (c) *D. humifusa*, (d) *D. ceylanica* ETP + IndoPacific clade.

Discussion

Dictyota species are a conspicuous or even dominant component of the marine algal flora in the Eastern Tropical Pacific; however we found that many specimens in the herbariums (USJ, CR, UC, MICH, ITIC) lie unidentified or incorrectly identified. This state of affairs is likely a result of intrinsic phenotypic plasticity among species in the genus, poorly defined characters in available descriptions and misidentification resulting from the use of taxonomic keys designed for other geographic regions (e.g., *D. bartayresiana* and *D. ciliolata*). Below we elucidate these problems with reference to the 7 phylogenetic species now recognized for the ETP and identified in the *cox3*-inferred phylogeny (Fig. 4.3).

Dictyota pfaffii has been reported in most of the Mexican Pacific coast, however according to Wysor and De Clerck (2003) this species is a synonym of *D. friabilis*, and Pedroche et al. (2008), recall this synonymy when reporting the species *D. pfaffii*. Our results demonstrated that this two species has been a misidentification of *D. humifusa* which is a very common species along the ETP and easily confused because of its branch shape. According to Bula-Meyer 1994 and this study the same has happened with the report of *D. adnata* from Costa Rica (Fonseca 1999) and Colombia (Schnetter and Bula-Meyer 1982), which are also misidentifications of *D. humifusa*. The molecular data provided here allow us to reject the possibility that there are many diminutive, mat-forming *Dictyota* spp. in the ETP, since all specimens exhibiting this habit constitute a monophyletic group that are distinct from other such species, such as *D. friabilis* and *D. adnata* known from the Caribbean Sea and/or other geographically distinct locals.

In this study we found the two polyphyletic species *D. stolonifera* and *D. ceylanica*. One of the two *D. stolonifera* clades (Fig. 4.3a,b) is exclusively constituted of sequences from specimens from the ETP and the other with specimens from the Indo-Pacific region. Since *D. stolonifera*, was described by Dawson (1962a) from Nicaragua's Pacific coast, the ETP clade should retain the ephithet *stolonifera*, while specimens from the other clade will require further study in order to determine an appropriate species designation.

Similarly as *D. stolonifera*, *D. ceylanica* constituted various polyphyletic cryptic clades (Fig 4.3a,b) that require further analysis to elucidate species classification. Our

results show that all specimens under *D. divaricata* (Taylor 1945, Dawson 1957, Dawson 1961a, Schnetter y Bula-Meyer 1982) have been misidentified, and the real identity is *D. ceylanica*. When Taylor (1945) reported *D. divaricata*, said that these specimens leave much to desire for records of this species, but found some similarities in branching and form of the branch. Also the report of Pedroche et al. 2008 of *D. linearis* from the Mexican Tropical Pacific coast possibly is a misidentification of *D. ceylanica*, as described in this study, but require further confirmation. According to De Clerck (2003) *D. ceylanica* has been considered a synonym of *D. linearis*, currently; this species is a synonym of *D. dichotoma* var. *intricata*. *Dictyota ceylanica* is a new record for the marine flora of the ETP, however this species require further study to elucidate the specific classification.

Dictyota dichotoma has been reported in the Atlantic, Indian and Pacific Oceans (Guiry and Guiry 2012), however several authors have questioned the presence of this species in the Indian and Pacific (De Clerck 2003, South and Skelton 2003, Tsuda 2004), suggesting that the distribution of this species is restricted to European, Mediterranean and Canary Islands (Schnetter et. al. 1987, Tronholm et al. 2008). Our data reveal that a revision of all the specimens under this name is needed, in order to elucidate their real identity.

We have found that several specimens from the Eastern Pacific were either erroneously transferred or assigned to the species *D. friabilis* (Dawson 1957, 1961b, 1962b, Tejada 2003, Pedroche et al. 2008, Bernecker 2009), *D. adnata* (Schnetter and Bula-Meyer 1982, Fernández-García et al. 2011), *D. dichotoma* (Pedroche et al. 2008, Fernández-García et al. 2011), *D. divaricata* (Pedroche et al. 2008, Fernández-García et al. 2011) and *D. linearis* (Pedroche et al. 2008). In this study we confirmed the absence of these five species in the ETP.

Based on the morphological characters correlated with the species groups resulting from our DNA-assessment of species concepts, we present here a dichotomous key (Table 4.3) and an annotated list of species of *Dictyota* from the Eastern Tropical Pacific.

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Table 4.3. Key to the species of *Dictyota* at the Eastern Tropical Pacific

1a Attached by means of conspicuous stoloniferous holdfast, that consist of multicellular medulla.....	<i>D. stolonifera</i>
1b Attached either in a single point or in several places, but always lacking stoloniferous holdfasts.....	2
2a Margins toothed.....	<i>D. crenulata</i>
2b Margins not toothed.....	3
3a Thalli lying flat in the substratum with no erect portions, forming a sprawling crust in the substratum, in situ dark brown.....	<i>D. sp. 1</i>
3b Thalli pseudo-erect, erect or prostrate with erect portions.....	4
4a Width of the interdichotomies often extremely variable from the base to the apex; between 1.1-1.3 mm, in some cases <0.9 mm, in situ can present greenish iridescence.....	<i>D. ceylanica</i>
4b Width of the interdichotomies not variable from the base to the apex, generally >2 mm, never less <0.9mm.....	5
5a Thalli erect, with a single point of attachment at the base.....	<i>D. sp. 2</i>
5b Thalli prostrate or pseudo-erect, with several points of attachments.....	6
6a Medullary cells 70.1-75.1 μm high and 77.5-81.5 μm wide. In situ banding vivid bluish-green iridescent and extremely supple; often prostrate forming dense turf mats.....	<i>D. humifusa</i>
6b Medullary cells 43.7-45.9 μm high and 46.5-48.6 μm wide. In situ not banded bluish-green iridescence, prostrate to erect.....	<i>D. sp. 3</i>

Annotated list of Dictyota species from the ETP

***Dictyota* sp. 1 (Fig. 4.4)**

Description: Thallus procumbent, completely lying flat in the substrate, attached by patches of rhizoids occurring over the complete length of the thallus, 95.9 µm thick. Color in situ dark brown with no iridescence. Interdichotomies (2.7-) 2.9-3.4 (-4.5) mm long and (2.0-) 2.4-2.8 (-3.3) mm wide. Blunt or rounded apices attached to each other or overlapping, (1.6-) 1.8-2.6 (-2.7) mm wide. Branching dichotomous to irregular. Angles broader toward apical segments (61.6-) 81.0-92.1 (-107.5)°, and narrower in middle and basal segments, (67.4-) 75.7-82.8 (-98.1)°. Smooth margins. Cortex unilayered, cells (13.1-) 17.3-20.8 (-25.3) µm wide, and (14.4-) 15.8-16.9 (-18.2) µm high. Medulla unilayered, (42.9-) 53.2-61.2 (-74.0) µm wide, and (38.1) 42.5-46.3 (-52.9) µm high. Reproductive structures not found.

Holotype: Playa La Audiencia, Manzanillo, Colima, Mexico, 23-02-09, CFMX-318,

Misapplied names at the ETP: *Dictyota conrescens sensu* Littler and Littler (2009)

Habitat: Growing on rock and coralline substrate, in intertidal environments.

Distribution in ETP: Mexico: Colima

Other Remarks: Specimens reported by Littler and Littler (2009) do not correspond in morphology to the type specimen of *D. conrescens* (Fig. 4.1a), however they document features that compare well to the features of the new species described here revealing a monostromatic medulla and the presence of an attachment rhizoid. At this moment, molecular data on *D. conrescens* is not available; however we project that this species would be phylogenetically distinct with *D. sp. 1*, given the morphological comparisons we document here.

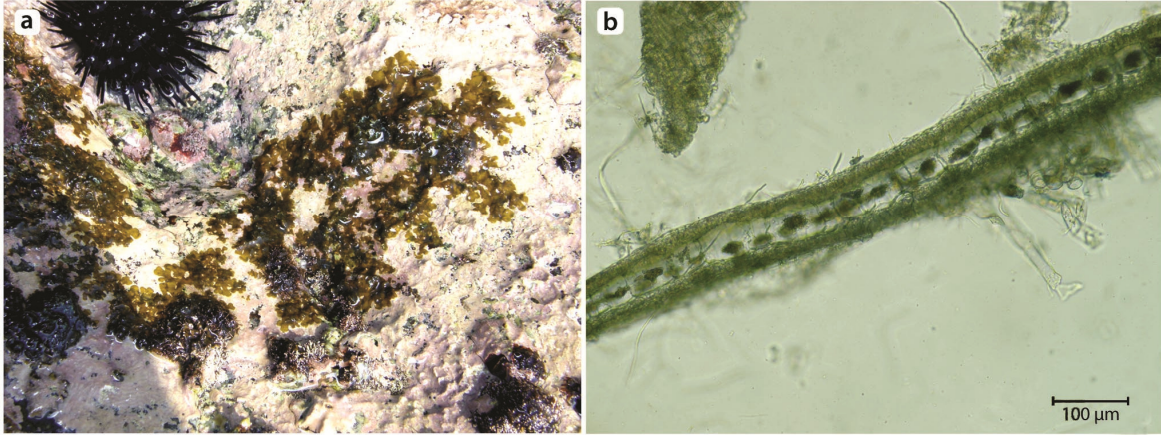


Fig. 4.4. *Dictyota* sp. 1. (a) Habit *in situ*, (b) Transverse section of the mid blade.

***Dictyota* sp. 2 (Fig. 4.5)**

Description: Thallus erect, (5.4-) 5.8-7.6 (-8) cm long and 82.5 μm thick. Color *in situ* dark brown with entirely blue iridescence. Interdichotomies (4.4-) 7.7-9.2 (-13.4) mm long and (1.7-) 2.1-2.4 (-2.8) mm wide. Apices rounded, (1.0-) 1.2-1.5 (-1.9) mm wide. Branching dichotomous, 6 (-7) times branched. Angles acute toward apical segments, (33.1-) 41.8-47.0 (-73.7) $^{\circ}$ and similar in middle and basal segments, (32.1-) 45.3-49.1 (-57.6) $^{\circ}$. Smooth margins. Cortex unilayered, cells (9.1-) 12.0-14.0 (-17.3) μm wide, and (8.7-) 9.4-10.0 (-11.0) μm high. Monostromatic medulla, cells (36.7-) 44.0-47.1 (-48.6) μm wide, and (56.8-) 60.1-62.4 (-66.4) μm high. Reproductive structures not found.

Holotype: Caletas, Puerto Vallarta, Jalisco, Mexico, 28-02-09, CFMX-389

Isotypes: CFMX-389 duplicate

Habitat: Growing on rocky substratum, 5-9 m.

Distribution in ETP: Mexico: Jalisco

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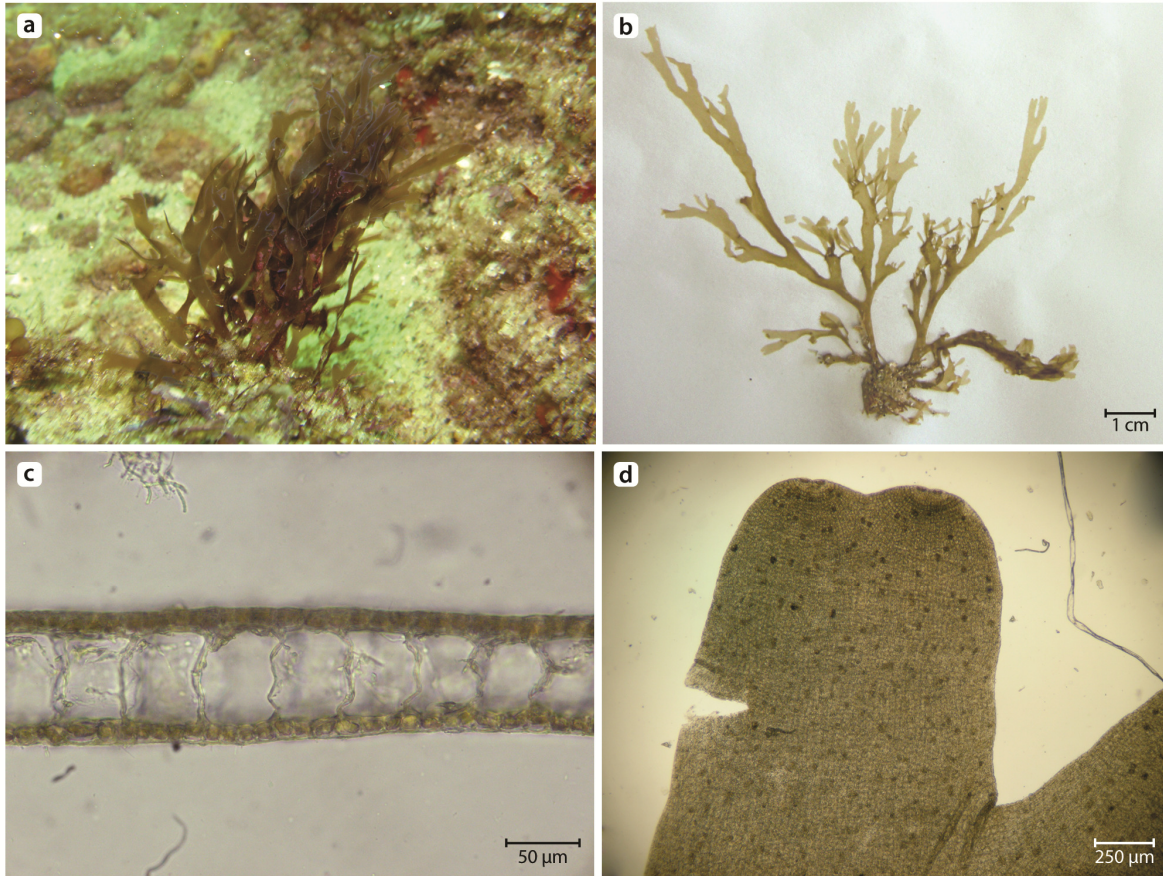


Fig. 4.5. *Dictyota* sp. 2 (a) Habit *in situ*, (b) Habit of the blades, holotype CFMX-389, (c) Transverse section of the mid blade, (d) Surface view of blunt-shaped thallus apex, showing early dichotomy and two apical cells.

***Dictyota* sp. 3 (Fig. 4.6)**

Description: Thallus (1.2-) 3.2-3.8 (-7.3) cm long and (44.77-) 101.7-115.5 (-160.12) thick, prostrate to pseudo-erect with slippery texture. Color in situ light brown with yellow to greenish iridescence, square shaped dark patches consecutively in the middle of the entire thallus especially visible *in vivo*, usually fading upon preservation. Interdichotomies (2.3-) 5.9-6.3 (-14.6) mm long and (1.2-) 2.61-2.9 (-9.8) mm wide. Apices acute to rounded, (0.6-) 1.2-1.3 (-2.4) mm wide. Branching dichotomous, (2-) 4-5 (-8) times branched. Angles acute toward apical segments, (34.5-) 62.5-65.2 (-103.0)°, and similar size in middle and basal segments, (27.1-) 74.5-79.1 (-129.9)°. Smooth margins, occasionally with small teeth that become leaflike proliferations. Cortex monostromatic, cells (9.9-) 19.3-20.3 (-30.7) µm wide, and (7.2-) 14.8-15.6 (-27.7) µm high. Medulla monostromatic, cells (49.9-) 77.5-81.5 (-149.0) µm wide, and (27.9-) 70.1-75.1 (-133.7) µm high. Sporangia scattered across entire thallus surface (i.e. not restricted to bands/zones) singly or in groups (Fig. 6f,g) (59.0-)78.9-81.8(-105.2) µm in diameter and (46.5-) 68.6-72.8 (-109.0) µm high. Oogonia grouped in rounded to oval sori (Fig 6h), with maximum sori length of (200.0-) 253.8-283.7 (-360.7) µm. Mature oogonia (19.7-) 32.0-36.1 (-50.7) µm in diameter and (44.9-) 62.0-67.8 (-83.2) µm high. Antheridia grouped in ellipsoidal sori (Fig. 6j,k), with maximum sori length of (369.4-) 404.0-427.6 (-477.5) µm. Mature antheridia (19.5-) 26.0-29.2 (-31.5) µm in diameter and (62.9-) 72.6-79.2 (-89.8) µm high.

Type Locality: La Cueva del Tiburón, Isla del Caño, Costa Rica, 20-07-09, CFCR-821 (Fig. 4.5d)

Isotypes: CFCR-821 duplicate.

Habitat: Growing on dead coral and rocky substratum. Intertidal to 13 m deep

Distribution in ETP: Mexico: Jalisco, El Salvador: La Libertad, La Unión, Nicaragua: Rivas, Costa Rica: Guanacaste, Puntarenas, Panama: Perlas Archipelago (Panama Bay)

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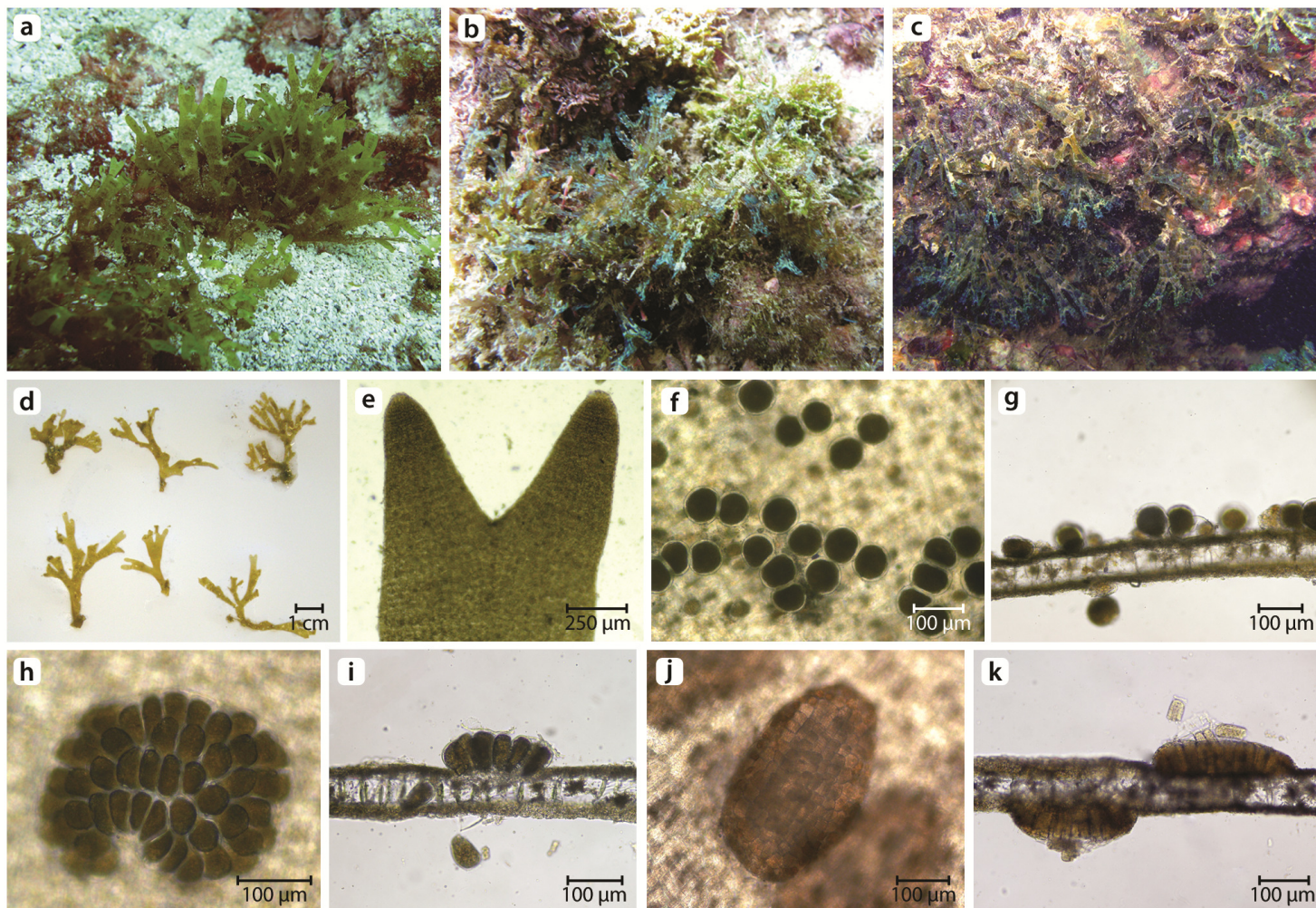


Fig. 4.6. *Dictyota* sp. 3 (a) Erect habit *in situ*, (b) Repent habit *in situ*, (c) Prostrate habit *in situ*, (d) Habit of the blades, holotype CFCR-821, (e) Acute apical section of the thalli, showing early dichotomous branching (f) Surface view of the blade with single and grouped sporangia, (g) Transverse section of the blade with sporangia, (h) Surface view of the oval oogonial sori, (i) Transverse section of oogonial sori, (j) Surface view of the ellipsoidal antheridial sori, (k) Transverse section of antheridial sori.

***Dictyota ceylanica* Kützing, 1859 (Fig. 4.7)**

Description: In situ bright green to bluish iridescence, sometimes showing a faint banding pattern, or non-iridescent pale brown. Pseudo-erect or cushion-like habit, without a conspicuous base (Fig 4.7 a,b). Acute apical segment. Width of the interdichotomies can vary considerably, Abrupt tapering of fronds, from wide to very narrow towards the apical section. Some thalli appear nearly filamentous with interdichotomies rarely exceeding 0.3 mm width, whereas other specimens possess straps up to 2.1 mm wide. It is common to find this range of variation within a single specimen, which is a distinctive characteristic of the species. No reproductive structures observed in analyzed specimens.

Type Locality: Ceylon Island, Sri Lanka (Kützing 1859, Fig. 4.1c)

Misapplied names at the ETP: *D. divaricata sensu* Schnetter and Bula-Meyer (1982), Dawson (1957, UC-1830976, D-16857), Dawson (1961a).

Etymology: pertaining to Ceylon, an island in the Indian Ocean off southern India

Habitat: Growing on rocks, dead coral and corallines substrate, 1-10 m, more common between 2-5 m deep.

Distribution in ETP: Mexico: Jalisco, Colima, Guerrero, Oaxaca, El Salvador: La Unión (Dawson 1961a), Costa Rica: Puntarenas (Dawson 1957), Colombia: Valle del Cauca, Isla Gorgona (Schnetter and Bula-Meyer 1982).

Other Remarks: Worldwide distribution in the tropics and subtropics, our analysis shows that ETP specimens are in the same clade as specimens distributed in Kenya, Queensland-Australia, Phillipines, Baja California Sur (La Concha), Tanzania, Micronesia (Fig 4.3). What Schnetter and Bula-Meyer (in Colombia, 1982) and Dawson (in Costa Rica, 1957) described as *D. divaricata* are likely *D. ceylanica* and the epithet *divaricata* is mis-applied, in this sense De Clerck (2003) indicated that tropical representatives of this species have often been named *D. divaricata*. *D. ceylanica* in the ETP resembles *D. pulchella* in the Caribbean, however further molecular and morphology studies should be needed in order to establish taxonomic status.

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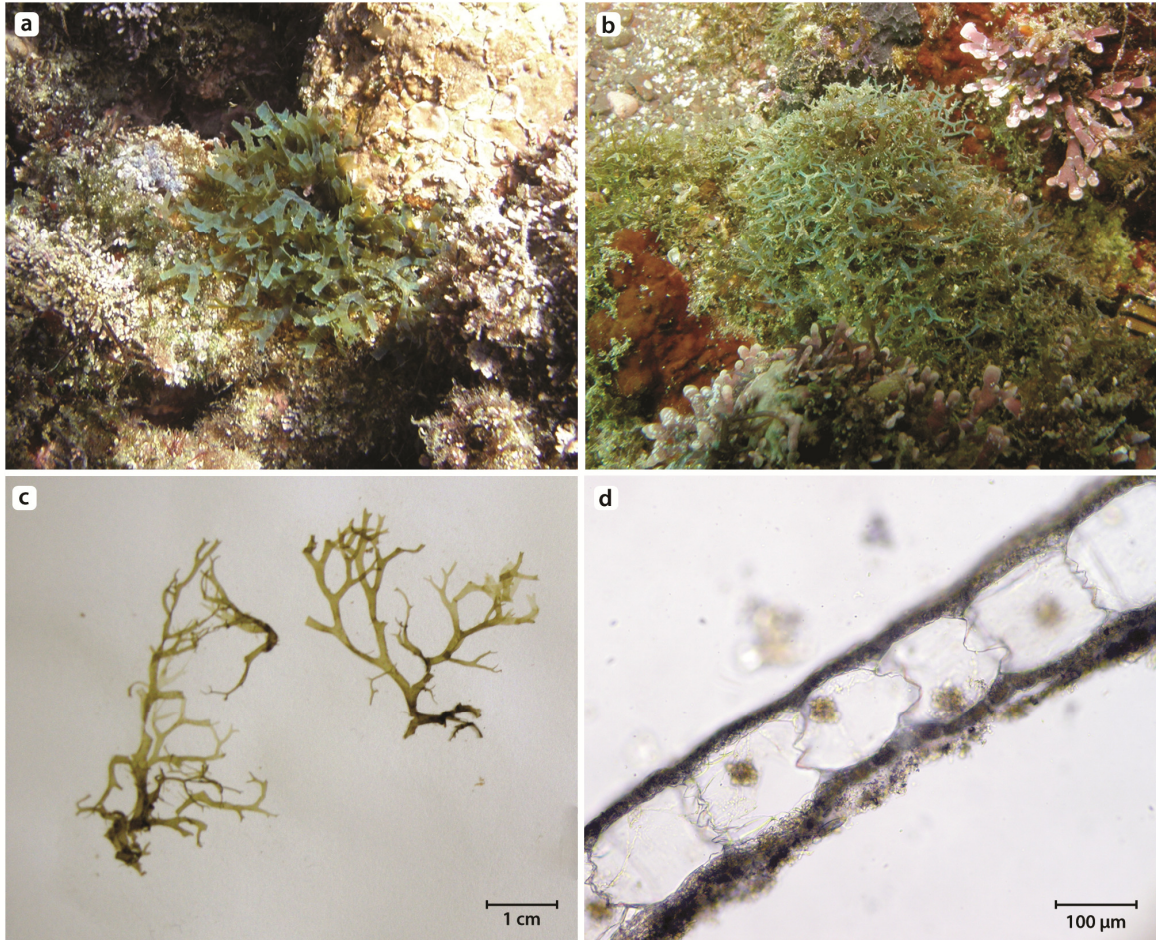


Fig. 4.7. *Dictyota ceylanica* (a) Repent habit *in situ*, (b) Cushion habit in the field, (c) Habit of the blades, (d) Transverse section of the blade showing monostromatic cortex and medullary layers.

***Dictyota crenulata* J. Agardh, 1847 (Fig. 4.8)**

Description: Thallus erect with dichotomous branching. Stupose base. Conspicuous crenulate margin composed of triangular teeth, rounded to obtuse. Yellow-greenish iridescence. Apices broad and pale transverse banding pattern and square shaped dark patches scattered over the entire thallus especially visible *in vivo*, and fading on preservation. Sporangia are scattered over both surfaces of the thallus, singly or grouped in small sori (Tronholm *et al.* 2012). Nizamuddin and Gerloff (1980) observed a multi-layered medulla in the lower parts of the fronds of their (insert geographic location) specimens, and therefore transferred this species to the genus *Dilophus*. The specimens studied here exhibited a monostromatic medulla, as was the case for Mexican specimens study by Pedroche *et al.* (2005).

Type Locality: San Agustín, Oaxaca, Mexico (LD 49049a, Nizamuddin & Gerloff 1979) (Fig. 4.1d)

Misapplied names at the ETP: *D. ciliolata sensu* Pedroche *et al.* (2008).

Etymology: notched or somewhat scalloped, in reference to the marginal teeth in the margins of the blades

Habitat: Growing on rocky substrate. Intertidal to 9 m deep.

Distribution in ETP: Mexico: Jalisco, Colima, Oaxaca, Costa Rica: Guanacaste (Taylor 1945, Dawson 1957, Soto and Bermúdez 1990, Bernecker 2009, Fernández-García *et al.* 2011), Central America: Dawson (1962b).

Other Remarks: Tronholm *et al.* (2012) found that genuine *D. crenulata* is restricted to the Pacific Central America coasts. According to De Clerck (2003) lectotypification was established by Nizamuddin & Gerloff (1979), who erroneously cited the specimen as LD 49042a. Actually the specimen bears the number LD 49049a.

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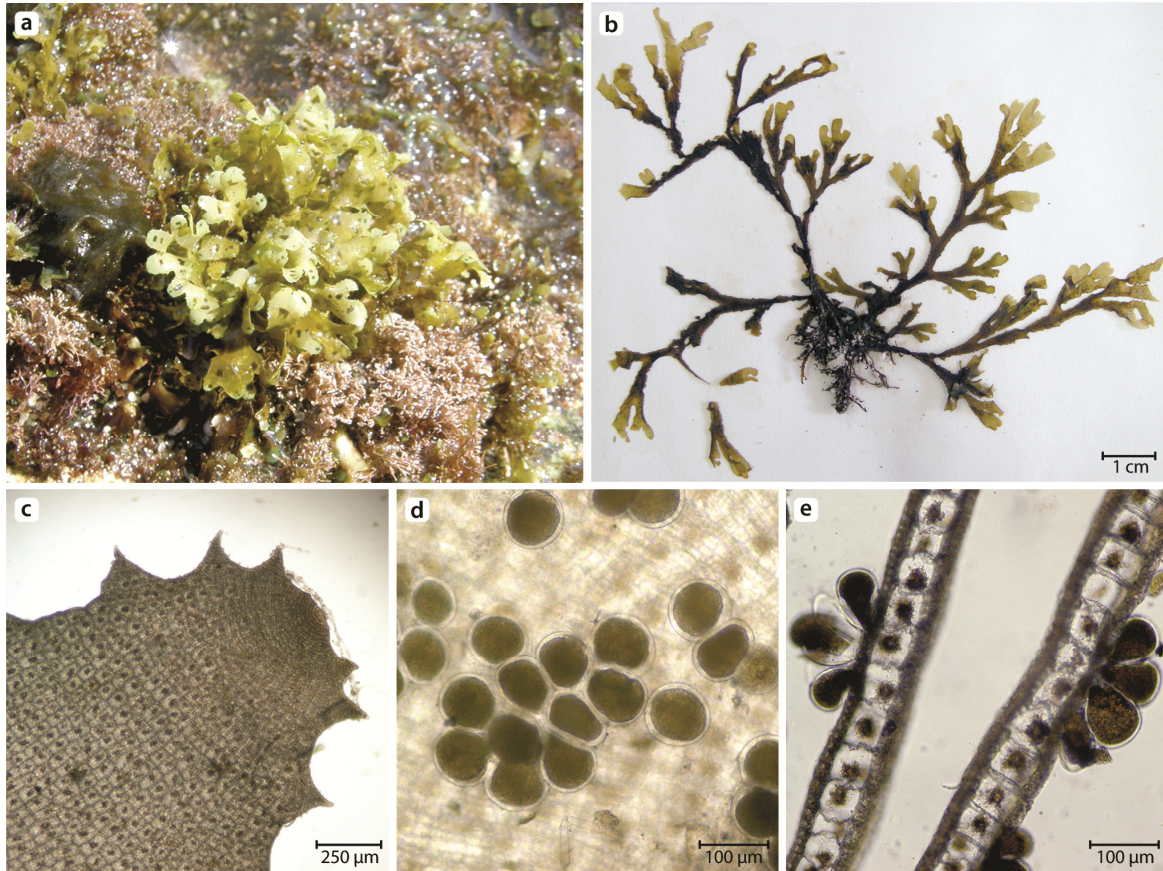


Fig. 4.8. *Dictyota crenulata* (a) Habit of intertidal specimen *in situ*, (b) Habit of pressed specimen, (c) Apical section of the thallus showing triangular teeth along the blade margin, (d) Surface view of the blade with sporangia, (e) Transverse section of the blade with sporangia.

***Dictyota humifusa* Hörnig, Schnetter et Coppejans, 1992 (Fig. 4.9)**

Description: Prostrate to repent thalli, margins smooth, occasionally forming marginal proliferations after mechanical damage (grazing) (Fig. 4.9c). Attached to the substrate by multicellular rhizoids occurring over the thallus (Fig. 4.9d). The whole thallus of similar width or some branches conspicuously narrower. Branching dichotomous. Apices rounded to truncate. *In situ* presents bluegreen iridescence in banding transverse pattern with non-iridescence bands. Individuals densely pack together; due to its delicate texture it is difficult to separate the thalli from each other.

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Type Locality: Punta Chengue, Santa Marta, Depto del Magdalena, Caribbean, Colombia, (COL-A-4287, Fig. 4.1e)

Missapplied names at the ETP: *D. friabilis* sensu Pedroche (2008), *D. adnata* sensu Schnetter and Bula-Meyer (1982)

Etymology: sprawling on the ground, or spread out over the ground.

Habitat: Very common forming turf mats on rocks, dead coral, coralline and sunken ship substrata. Between 1-17 m deep, more common between 2-7m deep.

Distribution in ETP: Mexico: Colima, Guerrero, Oaxaca, El Salvador: La Libertad, La Unión, Nicaragua: Rivas, Costa Rica: Guanacaste, Puntarenas, Isla del Coco, Panama: Chiriquí, Perlas Archipelago (Panama Bay).

Other Remarks: Worldwide distribution in the tropics, our analysis shows that this species is distributed in the Caribbean Sea, Indonesia and Kenya. Specimens reported under *D. adnata*, are misidentifications of this species. Wide latitudinal distribution at the ETP.

Dictyota pfaffii Schnetter (1972) was considered synonymous with *D. humifusa* by Bula-Meyer (1994). However, according to De Clerck 2003 both species are clearly distinct. Furthermore, *D. pfaffii* has recently been considered a synonym of *D. friabilis* (Wysor & De Clerck 2003). According to De Clerck (2003), *D. humifusa* may bear some resemblance with *D. friabilis*, by their procumbent growth form, dichotomous branching and the rounded sinuses. However, in situ *D. friabilis* is never as brightly iridescent and the thalli are more brittle (friable).

The long standing confusion between *D. humifusa* and *D. adnata* Auct. has been thoroughly explained and solved by Coppejans (1990) and Hörnig et al. (1992). In short *D. adnata* is a non-iridescent species from the supralittoral fringe often associated with mangroves, and is characterized by marginal sporangial sori and hence easily distinguishable from *D. humifusa* with sporangia scattered over the blade surface.

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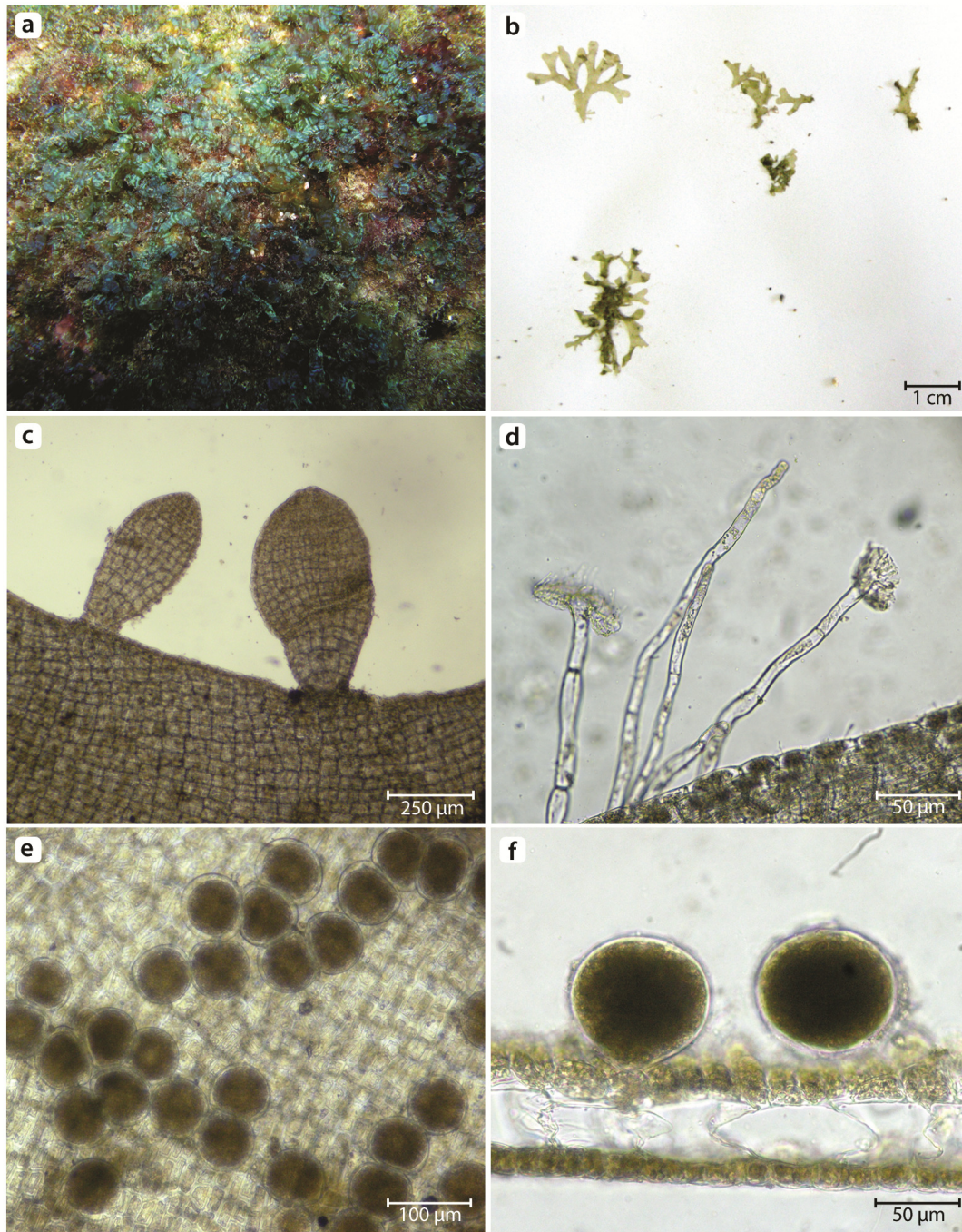


Fig. 4.9. *Dictyota humifusa* (a) Habit *in situ*, (b) Habit of the blades, (c) Marginal proliferations, (d) Hyaline multicellular rhizoids, (e) Surface view of the blade with sporangia, (f) Transverse section of the blade with sporangia.

***Dictyota stolonifera* E.Y. Dawson, 1962a (Fig. 4.10)**

Description: Thalli repent to erect, consisting of one to several blades from primary discoid holdfasts, stipe and blade bases stipose. Blades irregularly dichotomous, brown banded and blue or pink iridescence *in vivo*, fading on preservation, margins smooth. Apices broad and rounded. Very plastic morphology (Fig. 4.10a,b,c,d), but all specimens provided with several or many terete to somewhat compressed stoloniferous holdfast fibres in the lower most segment of the thallus, that can be simple or occasionally pinnate, spreading and composed of 4-6 (-8) medullary cells with one layer of cortex cells on transverse section (Fig. 4.10f).

Type Locality: Masachapa, Pacific Nicaragua (EYD No 22767 in UC, Fig. 4.1f)

Misapplied names at the ETP: *D. flabellata sensu* Taylor (1945)

Etymology: provided with stolons.

Habitat: Very common as turf on rocks, dead coral and coralline substrate. Between 1-17 m deep, more common between 2-6 m deep.

Distribution in ETP: Mexico: Jalisco, Colima, Guerrero, Oaxaca, El Salvador: La Unión, Nicaragua: Rivas, Costa Rica: Guanacaste, Puntarenas, Panama: Chiriquí (Coiba National Park Islands)

Other Remarks: The morphology of this species is very plastic. It has been confused with *D. flabellata* from the Gulf of California. In fact, when, Dawson (1962a) first described this species, he noticed that it resembles *D. flabellata*, but he distinguished them by the consistent production of linear stolons from the slender stipe and primary blade, and by the banded blades somewhat iridescence in life. According to Abbott and Huisman (2004), Hawaiian population of this species are not robust in their branching pattern as the Nicaraguan type specimens. Our molecular analysis reveals two clades named under *D. stolonifera* (Fig. 4.3). Since the type locality of *D. stolonifera* is at the ETP (Masachapa, Nicaragua), specimens reported as *D. stolonifera* from the Indian Ocean by De Clerck (2003), should be considered a new species.

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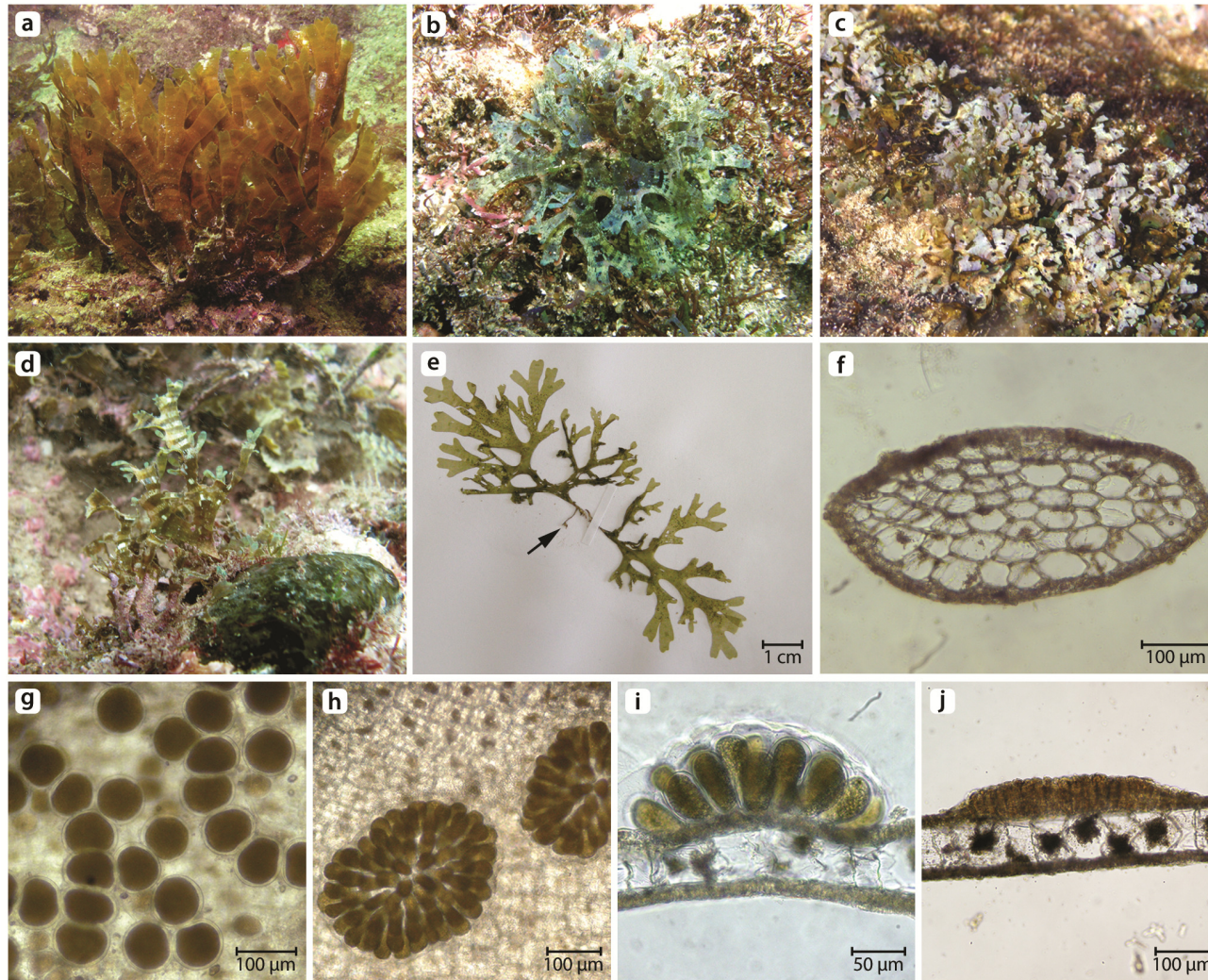


Fig. 4.10. *Dictyota stolonifera* (a, b, c, d) Plastic morphology habit *in situ*, (e) Habit of pressed specimen showing stolon, (f) Stolon with one layer of cortical cells and polystromatic medulla, (g) Surface view of the blade with sporangia, (h) Surface view of the oogonial sori, (i) Transverse section of oogonial sori, (j) Transverse section of antheridial sori.

Notes on other records of the ETP not found in this study

***Dictyota binghamiae* J. Agardh, 1894**

Type Locality: Santa Barbara, California, USA (AHFH 54037 in UC, UC-1878257, Fig. 4.1g)

Remarks: The type material is not a complete thallus and is damaged. Specimens cited by Taylor (1945) from Islas Secas, Panama (456C-3 in MICH) and Cabo San Lázaro, Mexico (599 in MICH) do not have the same morphology as the type, this was also observed by Dawson (1950). The specimen from Panama seems to correspond in morphology with *D. stolonifera*, as characterized in this study. Given the uncertain and apparent discrepant determinations with regard to this species, we suggest that specimens designated as *D. binghamiae* in other studies (Garske 2002, Littler and Littler 2009, Pedroche et al. 2008) should be re-evaluated with reference to type material. We therefore regard the distribution of *D. binghamiae* in the ETP as uncertain.

***Dictyota flabellata* (Collins) Setchell and Gardner, 1924**

Type locality: La Jolla, California, U.S.A. (UC- NY00780707, Fig. 4.1h)

Remarks: Our molecular and morphological analysis demonstrate that *D. flabellata* is an endemic species from the Pacific coast of northern America (Baja California Peninsula, Mexico and California, USA), as already proposed by De Clerck (2003) (Fig. 4.3).

Dawson (1950) proposed the synonymy of *D. flabellata* with *D. hesperia*, however, McEnroe et al. (1977) considered that both species should be considered two different species because of the presence of different diterpenoids. Taylor (1945) reported this species for the Pacific of Costa Rica and Panama. He noted, however, that the specimens seemed rather thin for *D. flabellata*, an observation that he attributed to the possibility that his specimens were deep-water and/or juvenile forms. Morphological examination of the specimens cited by Taylor (1945) from Islas Secas, Panama (456B-35 in MICH) and Port Culebra, Costa Rica (528 in MICH, cited erroneously by Taylor as 258) show that they correspond in morphology to our clade of *D. stolonifera*, a finding that seems to support the uncertainty with which Dawson (1950) regarded Taylor's (1945) determinations of the same specimens.

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Other reports of this species should require further study in order to establish possible misidentifications (Dawson 1957, Earle 1972, Abbott and Hollenberg 1976, Zertuche González et al. 1995, Sibaja-Cordero 2005, Sibaja-Cordero and Vargas-Zamora 2006, Pedroche et al. 2008, Littler and Littler 2009)

***Dictyota major* Taylor, 1945**

Type Locality: Post Office Bay, Isla Santa Maria, Galapagos Islands (AHFH 145 in UC, UC- 1884211, Fig. 4.1i)

Remarks: Specimens cited by Littler and Littler (2009) from Panama, does not fit with the type specimen, the last is larger and thinner, and tapering towards the base. The specimens documented in Littler and Littler (2009, <http://biogeodb.stri.si.edu/pacificalgae/specie/47>) corresponds in morphology to our *D. stolonifera* complex. *D. major* remains a poorly known species, rarely reported outside its type locality.

***Dictyota masonii* Setchell et N.L. Gardner, 1930**

Type locality: Isla Clarion, Revillagigedo Archipelago, Nayarit, Mexico (UC-1967939, S1j)

Remarks: A single specimen attributed to this species was reported by Dawson 1960 (D.21075), but he remarked that this specimen required further study.

Biogeography

Dictyota species found at the Eastern Tropical Pacific follow two worldwide distributional patterns. First, some species appear to be present in many oceanographic provinces mainly in the tropical zone (e.g. *D. ceylanica*, *D. humifusa*). Second, many species appear to be restricted to the ETP (e.g. *D. stolonifera*, *D. sp. 1*, *D. sp. 2*, *D. sp. 3* and *D. crenulata*).

Within the Eastern Tropical Pacific certain species appear to have restricted latitudinal distributions: *D. ceylanica*, *D. crenulata*, *D. sp. 1* and *D. sp. 2* (Fig. 4.11). In this study, these four species were only found along the Mexican coast. *D. ceylanica* was not known to be distributed at the ETP, however this tropical clade requires further study. Historically *D. crenulata* was reported to occur also in the Atlantic (as *D. jamaicensis*), recent molecular data has shown that this species have much more restricted geographic

ranges (Tronholm et al. 2012, Tronholm et al. in review), being exclusively confined to the ETP. Although, *D. crenulata* is also reported for Central American Pacific coast (Taylor 1945, Dawson 1957, Soto and Bermúdez 1990), there are no recent collections of this species out of Mexican Pacific coasts. *D. crenulata* is a good example on how misconceptions about species boundaries impact on our understanding of distributions and historical biogeography of tropical seaweeds (Tronholm et al. 2012). *D. sp. 1* and *D. sp. 2*, were only found in one locality, however specimens described by Littler and Littler (2009), from Panama) seems to fit with the description of *D. sp. 1* in this study.

On the other hand, this study confirmed the wide latitudinal distribution of *D. sp. 3*, *D. stolonifera* and *D. humifusa* throughout the ETP (Fig. 4.11). *Dictyota sp. 3* was mostly found along the Central American Pacific coast; however there is one report in Mexico. *D. stolonifera* and *D. humifusa*, are the most abundant and widely distributed species of *Dictyota* in the ETP.

Conclusions

In this study we have found the presence of seven species of the genus *Dictyota* at the Eastern Tropical Pacific: three already reported by other authors *D. crenulata*, *D. humifusa*, *D. stolonifera*, one new record *D. ceylanica* and three new species. Our molecular analysis we reveal polyphyly of *D. ceylanica* (with at least 5 clades) and for *D. stolonifera* (in two clades), which was originally described from the ETP. The molecular and morphological assessment showed a decrease in species number (from 16 to 7) in this region. Morphological identifications of *Dictyota* spp. have failed due to: intrinsic phenotypic plasticity of many species, poorly defined characters in available descriptions, and mis-identification resulting from the use of taxonomic keys from regions geographically distinct from the ETP. In total we encountered 10 misidentifications (*D. adnata*, *D. baytaresiana*, *D. ciliolata*, *D. concrescens*, *D. dichotoma*, *D. divaricata*, *D. flabellata*, *D. friabilis*, *D. linearis*, *D. pinnata*) and 3 un-confirmed records (*D. binghamiae*, *D. major*, *D. masonii*). Specimens under these names have been misidentified with other species present in the region. Most of *Dictyota* spp. (5 of 7) considered in this study appear to be range restricted within the region, while two (*D. humifusa* and *D. ceylanica*) are present in many oceanographic provinces of tropical latitudes.

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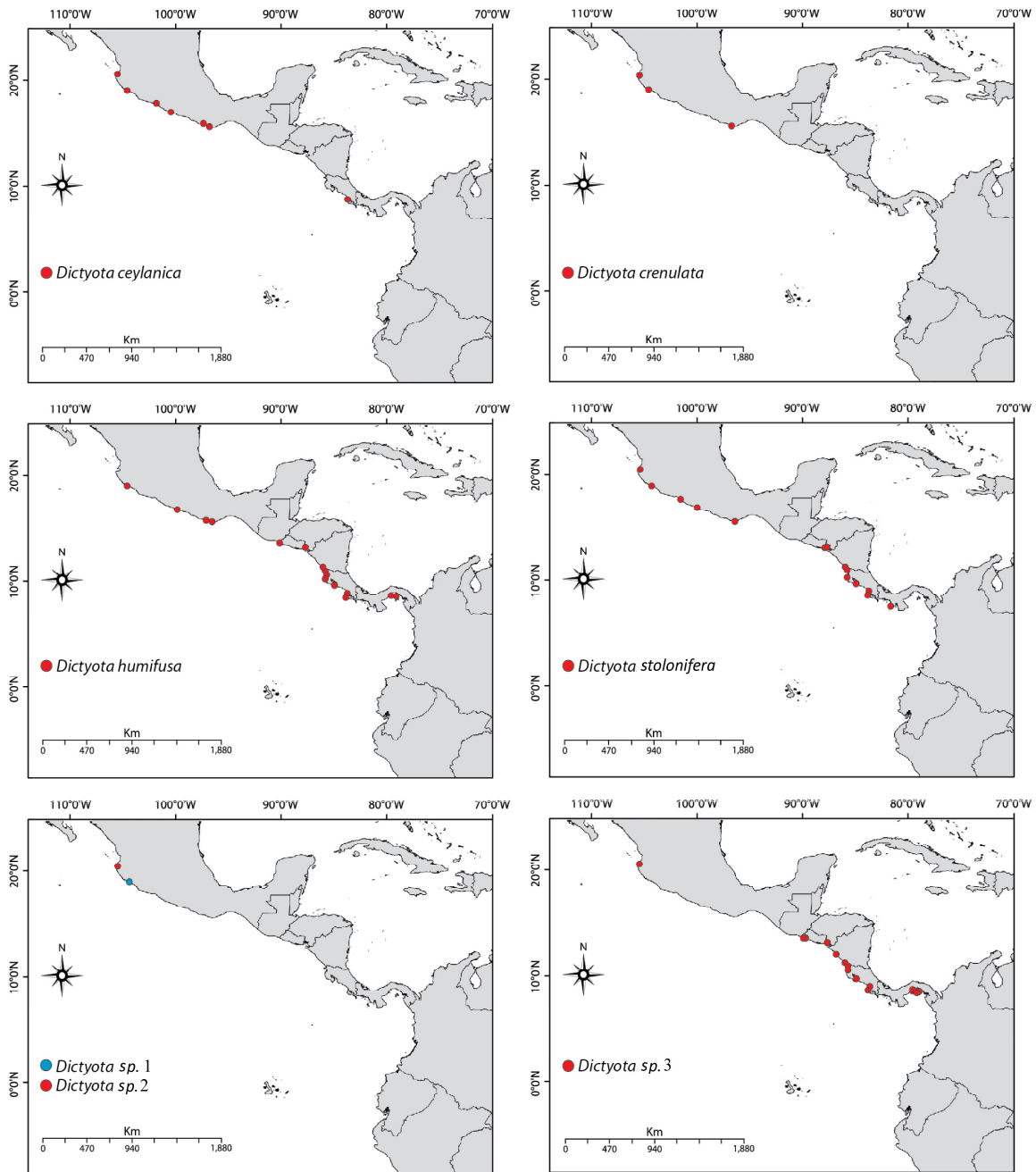


Fig. 4.11. Distribution of new collections of *Dictyota* species in the Eastern Tropical Pacific.

ANÁLISIS GENÉTICO DE CÓDIGO DE BARRAS REVELA DIVERSIDAD DEL GÉNERO *AMPHIROA* (CORALLINACEAE, RHODOPHYTA) EN EL PACÍFICO TROPICAL ORIENTAL**DNA Barcoding reveals *Amphiroa* (Corallinaeae, Rhodophyta) diversity from the Eastern Tropical Pacific**

Resumen: En total se han usado 24 nombres de especies para caracterizar la diversidad del género *Amphiroa* en el Pacífico Tropical Oriental (PTO). A partir de 1996 ese número bajó considerablemente con la propuesta de varias sinonimias y en la actualidad se consideran 13 especies válidas reportadas del género *Amphiroa* para esta región. Sin embargo a la luz de la revisión taxonómica de otros géneros de algas en el PTO, donde el número de especies ha disminuido con una evaluación molecular y debido a que el género *Amphiroa* presenta amplia variabilidad morfológica, aún quedan mucho trabajo por realizar para una buena delimitación de la especies. Por lo que este trabajo busca reevaluar la taxonomía del género *Amphiroa*, desde el punto de vista molecular, por medio del código de barras (gen mitocondrial COI-5P). Después del análisis de 61 especímenes de 42 localidades de la región, se obtuvo la presencia de 11 especies. Debido a la falta de comparación con otros especímenes (secuencias) del mundo, para este estudio se definieron cinco complejos de especies: Complejo A con una especie; Complejo B con tres especies; Complejo C con dos especies; Complejo D con dos especies y Complejo E con cuatro especies. La mayoría de los grupos de especies mostraron consistencia morfológica, sin embargo se requieren estudios adicionales, colecta de especies nuevas y comparación con el material tipo para definir algunas de estas. Asimismo se encontraron dos clados con secuencias exclusivas del Golfo de California, México.

Abstract: Twenty four species names have been used to characterize the diversity of the genus *Amphiroa* in the Eastern Tropical Pacific (ETP). Since 1996 that number dropped considerably because many species were proposed as synonymies of others. At the moment there are 13 valid species names for the region. However, in the light of recent taxonomic revisions of other algae genera at the ETP, in where the species number has decrease after a molecular reassessment and also because the genus *Amphiroa* shows extensive morphological variability, still is work remain to carry out in order to establish a good delimitation of the species. Thus, the aim of this work is to reassess the taxonomy of the genus *Amphiroa* in the ETP, from a molecular point of view, through a barcode evaluation (mitochondrial encoded COI-5P gene). After the analysis of 61 specimens from 42 field locations throughout the region, we concluded that 11 species are present. Because of the lack of comparison with other specimens (sequences) around the world, for this study we defined five morphological complexes of species: Complex A, one species; Complex B, three species; Complex C, two species; Complex D, two species and Complex E four species. Most species groups are well defined morphologically; however some require further study, addition of new specimens and comparison with type material in order to define some species. Also we also found two clades exclusively with sequences from the Gulf of California, Mexico.

Key Words: *Amphiroa*, COI-5P, Central America, diversity, Mexico

Introduction

Amphiroa is a large widespread genus in tropical and subtropical regions with a variety of morphological types from a few millimeters high to as much as 30 cm. The genus is primarily characterized by the anatomy of the branching fronds, which are made up of numerous jointed branches consisting of calcified segments called intergenicula. The intergenicula are separated from one another by uncalcified nodes, or genicula. Extending through a branch is a core of medullary filaments with the cells in tiers, which is surrounded by a cortex and epithallus (Norris and Johansen 1982, Dolan 2001). Fronds are composed of compressed or subterete intergenicula separated from one another by uncalcified genicula, each intergeniculum containing tiers of medullary cells of differing heights, surrounding cortex and a layer of epithallial cells. Intergenicula may be terete or flat, and sometimes have midribs and wings (Abbott 1999).

Present-day taxonomy of corallines, establish that the genus *Amphiroa* belongs to the subfamily Lithophylloideae (Aguirre et al. 2010). Weber-van Bosse (1904) and Yendo (1904) considered the number of tiers in genicula to be useful in recognizing the genus, and more recently Riosmena-Rodríguez and Sisqueiros-Beltrones (1996) and Dolan (2001) considered the arrangement of tiers as a useful character to distinguish the genera of articulated corallines. Recently with the lectotypification and epitypification of the type species of *Amphiroa*, *A. tribulus* Ellis & Solander, Woelkerling and Harvey (2012) states that *Amphiroa* is characterized by uniporate tetrasporangial conceptacles, secondary pit connections between cells of adjacent vegetative filaments and genicula consisting of one or more tiers of cells but without dimerous flangelike branches. These diagnostic characters are evident in the epitype (but not the lectotype) of the type species, *A. tribulus*. Characters mentioned/illustrated in the protologue of *A. tribulus* (Ellis and Solander 1786) are evident in both the lectotype and the epitype.

In *Amphiroa* the long- and short-celled tiers are separated by transverse lines, termed “zonation” (Yendo, 1902, Dorlan 2011), and the pattern, number and length of

medullary tiers have been used as species level taxonomic criteria (Riosmena-Rodríguez and Sisqueros-Beltrones 1996, Dolan 2001).

According to Guiry and Guiry (2012), there are 226 species (and infraspecific) names in their database at present, of which 47 have been flagged as currently accepted taxonomically. A total of 24 names have been used to delimit species at the Eastern Tropical Pacific (ETP), of which, the 80% were reported by Lemoine (1929), Taylor (1945) and Dawson (1953, 1963). In those studies, the authors described 16 species that have their type locality in the region (Table 5.1).

Later, Norris and Johansen (1981), in their revision of *Amphiroa* from the Gulf of California, evaluated the taxonomy of many species occurring at the ETP, reducing the species number from 16 to 7 and considered that many species described by Lemoine (1929), Taylor (1945) and Dawson (1953) were synonyms. Riosmena-Rodríguez and Sisqueros-Beltrones (1996), after the analysis of 800 specimens from the Gulf of California found that morphotypic variation among the species has obscure the real number of species and proposed that only five species are present for that region. According to the synonymies proposed by these two studies currently there are thirteen species of *Amphiroa* in the ETP (Table 5.1). However, according to Harvey et al. (2009), the diagnostic value of many characters and character states currently used to separate species of *Amphiroa* need critical reassessment to determine their variability within and across populations of individuals.

In the light of recent taxonomic revisions of other algae genera (*Caulerpa*, *Padina* and *Dictyota*) at the ETP, in where the species number has decrease after a molecular reassessment and also because the genus *Amphiroa* shows extensive morphological variability, still is work remain to carry out in order to establish a good delimitation of the species of this genus. Thus, the aim of the present study is to determine species number of the genus *Amphiroa* in the Eastern Tropical Pacific using morphological variables and mainly mitochondrial encoded COI-5P barcode gene sequences.

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Table 5.1. Species of the genus *Amphiroa* reported for the Eastern Tropical Pacific. MEX=Mexico, ES= El Salvador, NIC= Nicaragua, CR=Costa Rica, PAN=Panama, COL= Colombia, ECU= Ecuador, CL= Clipperton Islands, France, CI= Coco Island, Costa Rica, GL= Galápagos Islands, Ecuador. L= Type locality. In bold species which type locality is in the Eastern Pacific.

Species reported	Synonyms	MEX	ES	NIC	CR	PAN	COL	ECU	Reference
<i>Amphiroa beauvoisii</i> J.V. Lamouroux TL: Coast of Portugal	<i>A. mexicana</i> W.R. Taylor* TL: Bahía Petatlán, Guerrero, Mexico	x	x		x	x	x	x	Lemoine 1929, Taylor 1945, Dawson 1953, Dawson 1957, Dawson 1961b, Dawson 1962b, Earle 1972, Avilés and Canjura 1979, Norris and Johansen 1981, Schnetter and Bula-Meyer 1982, Gutiérrez 1985, Glynn 1990, González-González 1993, Garske 2002, Tejada 2003, Serviere-Zaragoza et al. 2007, Bernecker 2009, Bernecker and I. Wehrtmann 2009, Littler and Littler 2009
	<i>A. zonata</i> Yendo ⁺ *								
	<i>A. crosslandii</i> M. Lemoine ⁺ *								
	<i>A. peninsularis</i> W.R. Taylor ⁺								
<i>Amphiroa compressa</i> M. Lemoine TL: Galapagos Islands								x	Lemoine 1929, Taylor 1945, Garske 2002
<i>Amphiroa crustiformis</i> E.Y. Dawson TL: Galapagos Islands								x	Dawson 1963, Garske 2002

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Species reported	Synonyms	MEX	ES	NIC	CR	PAN	COL	ECU	Reference
<i>Amphiroa dilatata</i> Lamouroux TL: Australasie								x (GL)	Garske 2002
<i>Amphiroa foliacea</i> J.V. Lamouroux TL: Mariana Islands, Micronesia			x		x	x			Taylor 1945, Dawson 1961a, Dawson 1962a, b, Avilés and Canjura 1979, Gutiérrez 1985, Tejada 2003, Bernecker 2009, Littler and Littler 2009
<i>Amphiroa galapagensis</i> W.R. Taylor TL:Galapagos Islands								x (GL)	Taylor 1945, Garske 2002
<i>Amphiroa minutissima</i> W.R. Taylor TL: Golfo Dulce, Costa Rica					x (CI)				Taylor 1945, Dawson 1957, Dawson 1961b, Dawson 1962b, Fernández 2008, Bernecker 2009

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Species reported	Synonyms	MEX	ES	NIC	CR	PAN	COL	ECU	Reference
<i>Amphiroa misakiensis</i> Yendo TL: Misaki, Japan	<i>A. dimorpha</i> M. Lemoine* TL: Galapagos Islands <i>A. brevianceps</i> E.Y. Dawson* TL: Salina Cruz, Oaxaca, Mexico <i>A. magdalenensis</i> E.Y. Dawson* TL: Isla Magdalena, Baja California, Mexico	x (CL)	x		x	x		x (GL)	Lemoine 1929, Taylor 1945, Dawson 1957, Dawson 1961a, b, Dawson 1962b, Avilés and Canjura 1979, Norris and Johansen 1981, Gutiérrez 1985, González-González 1993, Garske 2002, Tejada 2003, Serviere-Zaragoza et al. 2007, Bernecker 2009, Littler and Littler 2009
<i>Amphiroa peruana</i> Areschoug TL: Galapagos Islands								x (GL)	Taylor 1945, Garske 2002
<i>Amphiroa polymorpha</i> M. Lemoine TL: Galapagos Islands					x			x (GL)	Lemoine 1929, Taylor 1945, Dawson 1962b, Garske 2002, Bernecker 2009
<i>Amphiroa rigida</i> J. V. Lamouroux TL: Mediterranean Sea	<i>A. taylorii</i> E.Y Dawson* TL: Bahía Braithwaite, Isla Socorro, Revillagigedo Archipelago, Mexico	x (CL)		x	x				Dawson 1957, Dawson 1961b, Dawson 1962a,b, Norris and Johansen 1981, Serviere-Zaragoza et al. 2007, Bernecker 2009, Bernecker and I. Wehrtmann 2009

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Species reported	Synonyms	MEX	ES	NIC	CR	PAN	COL	ECU	Reference
<i>Amphiroa van-bosseae</i> M. Lemoine TL: Galapagos Islands	<i>A. subcylindrica</i> E.Y. Dawson* TL: Sonora, Mexico					x		x (GL)	Lemoine 1929, Taylor 1945, Garske 2002, Littler and Littler 2009
<i>Amphiroa valonioides</i> Yendo TL: Japan	<i>A. francicana</i> W.R. Taylor* TL: Esmeraldas, Ecuador <i>A. annulata</i> M. Lemoine* TL: Galapagos Islands	x (CL)	x		x	x		x (GL)	Lemoine 1929, Taylor 1945, Dawson 1957, Dawson 1961a,b, Dawson 1962b, Avilés and Canjura 1979, Norris and Johansen 1981, Gutiérrez 1985, González- González 1993, Garske 2002, Tejada 2003, Serviere- Zaragoza et al. 2007, Bernecker 2009, Littler and Littler 2009

Synonymies proposed by: †Norris and Johansen 1981, *Riosmena-Rodríguez and Sisqueiros-Beltrones 1996

Materials and Methods

Sample collection

A total of 61 samples of *Amphiroa* specimens were collected from 42 locations throughout the ETP (Mexican Tropical Pacific and Central America) between 2008 and 2011 (Table S5). Detailed specimen information including specimen identification numbers, morphological and DNA identification, collecting site and date and collectors, can be found in the supplementary material (Table S5). All specimens were collected manually by SCUBA diving and were preserved in silica gel, 4 % formalin/seawater and pressed on herbarium sheets for molecular and morphological examination. Voucher of the specimens are deposited in the USJ herbarium (Escuela de Biología, Universidad de Costa Rica) and HBCS herbarium (Universidad Autónoma de Baja California Sur).

Morphological and ecological characteristics

For each specimen, the depth, substratum and habit were recorded. In the laboratory all specimens were analyzed for morphology, morphometric and anatomical characters, from both vegetative and reproductive thalli.

Preliminary species determinations were made on the basis of morphological comparisons with the original descriptions, type herbarium specimens, when available, and with reference to the following sources for the Eastern Pacific: Taylor (1945), Dawson (1953), Norris and Johansen (1981), Schnetter and Bula-Meyer (1982), Riosmena-Rodríguez and Siqueiros-Beltrones (1996), Littler and Littler (2009).

Measurements of morphometric characters were carried out on formaline-preserved specimens with a Nikon Coolpix 4300 camera and image processing in the UTHSCSA software Image Tool version 3.0.

Following Taylor (1945), Dawson (1953), Norris and Johansen (1981), Riosmena-Rodríguez and Siqueiros-Beltrones (1996), we used 6 qualitative and 5 quantitative characters for each specimen to delimit species (9 vegetative, 2 reproductive) (Fig. 5.1). Habit, color of the thallus, branch plane and form, intergenicula shape and position of the conceptacle in the surface of the thallus were determined. Thallus height, intergenicula length and width, and apical portion width were measured (Fig. 5.1). Diameters of

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conceptacles were measured in surface view. From each character, minimum and maximum sizes and the 95 percentile were determined (Table 5.2).

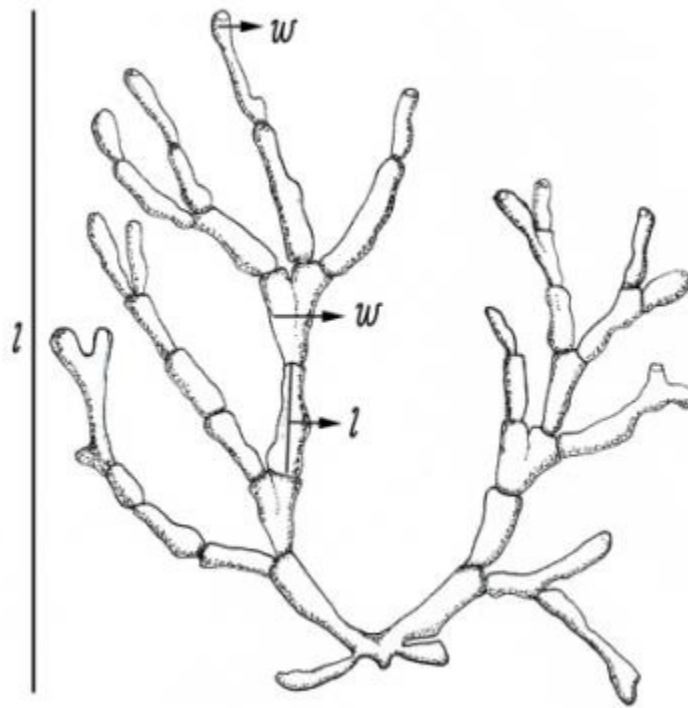


Fig 5.1. Thallus morphological measurements. w =width, l =length

Molecular analysis

In this study we use the COI-5P gene to explore the genetic diversity of *Amphiroa* species from the ETP. Total DNA extraction, amplification and sequencing followed Saunders and McDevit (2012).

Forward sequences were edited and aligned with published sequence data using MEGA 5.0 (Tamura et al. 2011), and the final alignment (602 bp long) was done manually. Bayesian phylogenetic inference (BI) was carried out with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) using the same partitions and models, and default priors. Chains were run for six million generations, sampling every 1000th generation. A burnin sample of 200 trees was removed before constructing the majority rule consensus tree.

Results and Discussion

Amphiroa is the most common and prominent articulate coralline in intertidal and subtidal environments of the Eastern Tropical Pacific. In accordance with Hernández-Kantún et al. (in review) relationships among species of the subfamily Lithophylloideae: *Lithophyllum* (polyphyletic), *Amphiroa*, and *Titanoderma* were unclear in the present reconstruction (Fig. 5.2).

According to the molecular analysis of the COI-5P gene, we proposed that *Amphiroa* specimens of this region clustered in 11 species-level clades (Fig. 5.2). With the morphological data obtained in this study, we validate the species clades proposed. However species B1, B2 and C3 (Fig. 5.2) require additional samples in order clarify if they represent a complex of species (B1: 2 sp., B2: 2 sp., C3: 3 sp.), or if the specimens represent haplotypes of different localities. We also found two clades exclusively with sequences from the Gulf of California (Fig. 5.2, in squares), that possibly represent new species, to be described. A comparison of morphological measurements of complexes can be found in this study (Table 5.2).

Because of the lack of comparison with other specimens (sequences) around the world, for this study we define five morphological complexes of species, supported on similarities of the intergenicula shape, length and width. All complexes and species clades proposed are well-supported (PP > 0.99) (Fig. 5.2). Each complex is composed by one to four species clades: Complex A, one species (A1); Complex B, two species (B1, B2); Complex C, two species (C1, C2); Complex D, two species (D1, D2) and Complex E four species (E1, E2, E3, E4).

Since the type localities of *A. beauvoisii* and *A. rigida* are in Europe and recent studies has shown that the marine flora of this region has no biogeographical relation with the ETP, it is possible that the synonymous species described at the ETP, will be reinstated. These species require further attention in order to validate their status.

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We found that many of species delimited in our molecular analysis does not correspond with any of the species described before (B2, C1, E2). Nevertheless, it is necessary a revision of 24 type specimens of the species reported in the region and a detailed comparison of the morphologies found in is study with the type material.

As recent studies with *Caulerpa*, *Padina* and *Dictyota* (previous chapters), in which old names were reinstated and occurrence of misidentifications with other species names had happened, we considered the analysis of the 24 species names that have been used for *Amphiroa* along the ETP. Taxonomic, ecological and nomenclatural implications of *Amphiroa* complexes are detailed below.

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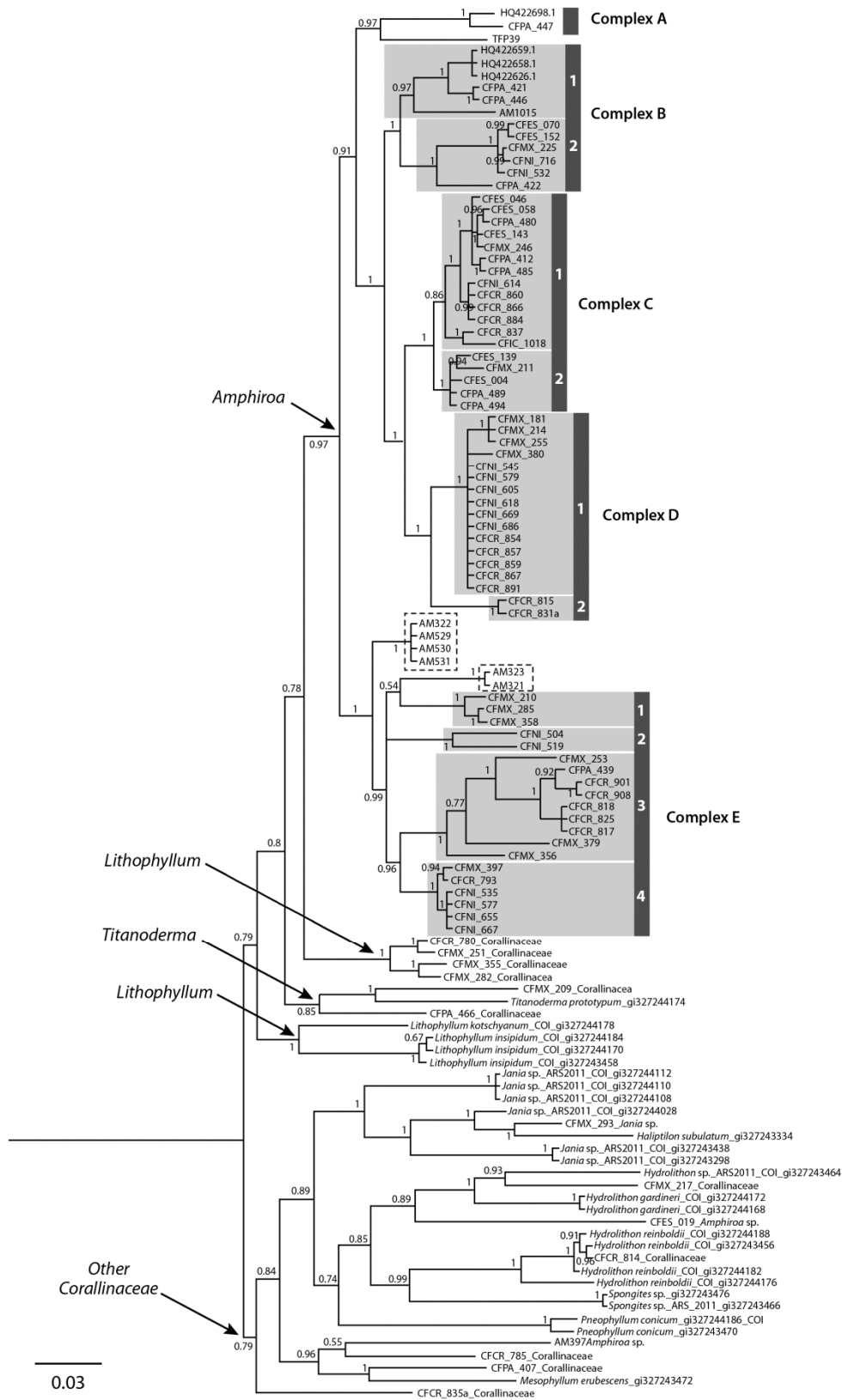


Fig 5.2. Consensus tree resulting from the Bayesian Inference analysis of *cox1* sequences of *Amphiroa*. Showing five species complexes of the ETP, and including two clades with sequences exclusively from the Gulf of California, Mexico (in squares).

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Table 5.2. Morphological comparison of *Amphiroa* complexes from the Eastern Tropical Pacific. Values are: (Minimum-)(95% Range)(-Maximum).

	Complex A	Complex B	Complex C	Complex D	Complex E
Color <i>in situ</i>	Bright pink with white tips	Red to pinkish	Light pink, with purple sections	Purple to pinkish, Mexican specimens completely purple	Bright pink with purple sections
Branch shape	Cylindrical	Cylindrical to subcylindrical	Flattened to subcylindrical, rarely cylindrical	Flattened to subcylindrical	Cylindrical to subcylindrical, some flattened
Thallus length (cm)	0.6	(0.7-)1.1-1.6(-2.3)	(0.5-)1.1-1.4(-2.2)	(2.2-)2.5-2.9(-3.5)	(0.9-)2.3-3.1(-4.6)
Apice width (mm)	(0,1-)0.2-0.3(-0.4)	(0.3-)0.4-0.6(-0.9)	(0.3-)0.6-0.7(-1.2)	(0.7-)1.6-1.8(-2.8)	(0.3-)0.6-0.7(-1.4)
Intedichotomy length (mm)	(0.9-)1.3-1.8(-2.7)	(1.0-)2.7-3.0(-4.8)	(1.4-)2.6-2.9(-5.6)	(2.1-)5.5-6.1(-10.7)	(1.2-)3.0-3.6(-11.9)
Intedichotomy width (mm)	(0,2-)0.2-0.3(-0.4)	(0.3-)0.6-0.8(-1.3)	(0.4-)0.7-0.9(-1.7)	(1.0-)2.9-3.4(-7.6)	(0.4-)0.8-1.0(-2.1)
Conceptacle diameter (µm)	(200-)300-400(400)	(200-)300-400(-500)	(150-)200-400(-450)	(100-)200-300(-400)	(100-)200-400(-600)

***Amphiroa* Complex A (Fig. 5.3)**

Description: Thallus cushion like growing pattern, without a conspicuous base. Intergercula very narrow, with truncate tips. Upper and lower portions of the thallus cylindrical throughout. Branching dichotomous. The conceptacles are relatively large and seem to be chiefly superficial on the branch.

Habitat: Growing in sunken ship, 2-3 m.

Distribution in ETP: Panama

Possible species within this clade:

1. *A. valonioides* Yendo (Type locality: not specifically, Provinces of Hiuga and Misaki, Japan; Yendo 1902)
2. *A. minutissima* W.R. Taylor (Type locality: Golfo Dulce, Costa Rica, Taylor 1945)
3. *A. annulata* M. Lemoine (Type locality: James Bay, Isla James, Galapagos; Lemoine 1929)
4. *A. franciscana* W.R. Taylor (Type locality: Esmeraldas, Bahía de San Francisco, Ecuador; Taylor 1945)

Other Remarks: The sequences from the ETP of this complex of species, clades with specimens from Hawaii available in GenBank identified as *A. valonioides*. The specimens collected in Panama correspond with the description of Yendo (1902) of *A. valonioides* which is the most diminutive plant of *Amphiroa*. Also description of *A. minutissima* by Taylor (1945) seems to correspond with this species, and require further study. According to Norris and Johansen (1981) *A. annulata* and *A. franciscana* are synonyms of *A. valonioides*, however the features on which this synonymy was established are not clear and require further study.

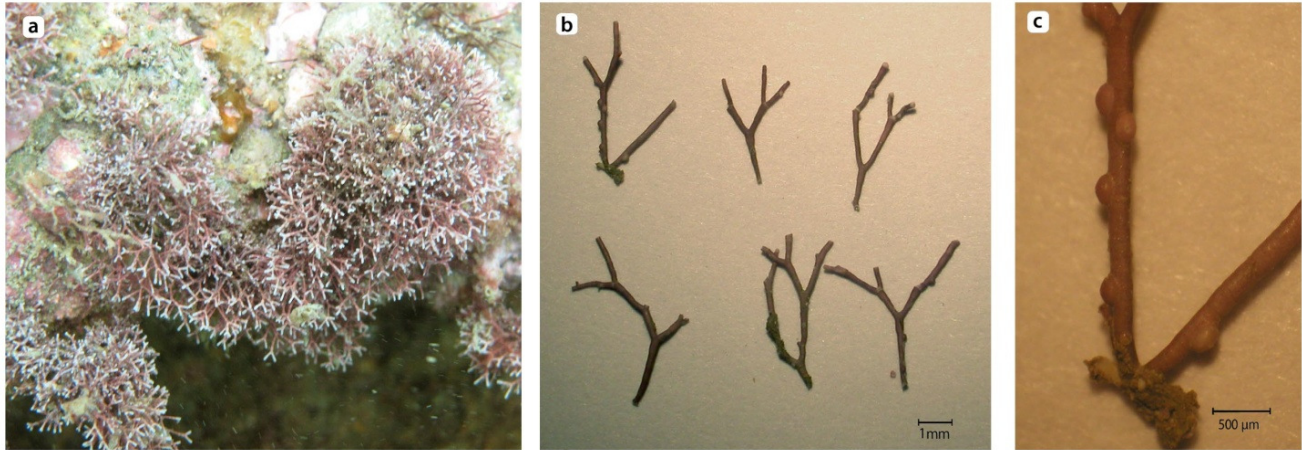


Fig. 5.3. *Amphiroa* Complex A. (a) Habit *in situ*, (b) Habit of pressed specimen, (c) Conceptacles markedly protruding over the intergenicular surface.

Amphiroa Complex B (Fig. 5.4)

Description: Thallus prostrate with some erect portions, in one plane. Upper portions of the thallus cylindrical, rarely subcylindrical. Lower portions subcylindrical to cylindrical. Branching dichotomous, but can present alternate branching. Conspicuous conceptacles scattered and protruding over intergenicular surface.

Habitat: Turfy, more common exposed in the intertidal, but can reach to 6 m deep.

Distribution in ETP:

B1: Gulf of California, Mexico; Panama.

B2: Mexico, El Salvador, Nicaragua, Panama

Possible species within this clade:

1. *A. rigida* J. V. Lamouroux (Type locality: Mediterranean Sea; Lamouroux 1916)
2. *A. taylorii* E.Y Dawson (Type locality: Bahía Braithwaite, Isla Socorro, Revillagigedo, Archipelago, Mexico; Dawson 1953)

Other Remarks: The sequences from the ETP of this complex of species, clades with specimens from Hawaii available in GenBank identified as *A. foliacea*, however none of the specimen found in our study under this complex have flat and winged intergenicula which is a diagnostic characteristic of the species *foliacea*. The species *A. taylorii* seems to correspond with this complex, however according to Riosmena-Rodríguez and Sisqueiros-Beltrones (1996), this species is a synonym of *A. rigida*, synonymy that should be revised, since the type locality of the last is in the Mediterranean.

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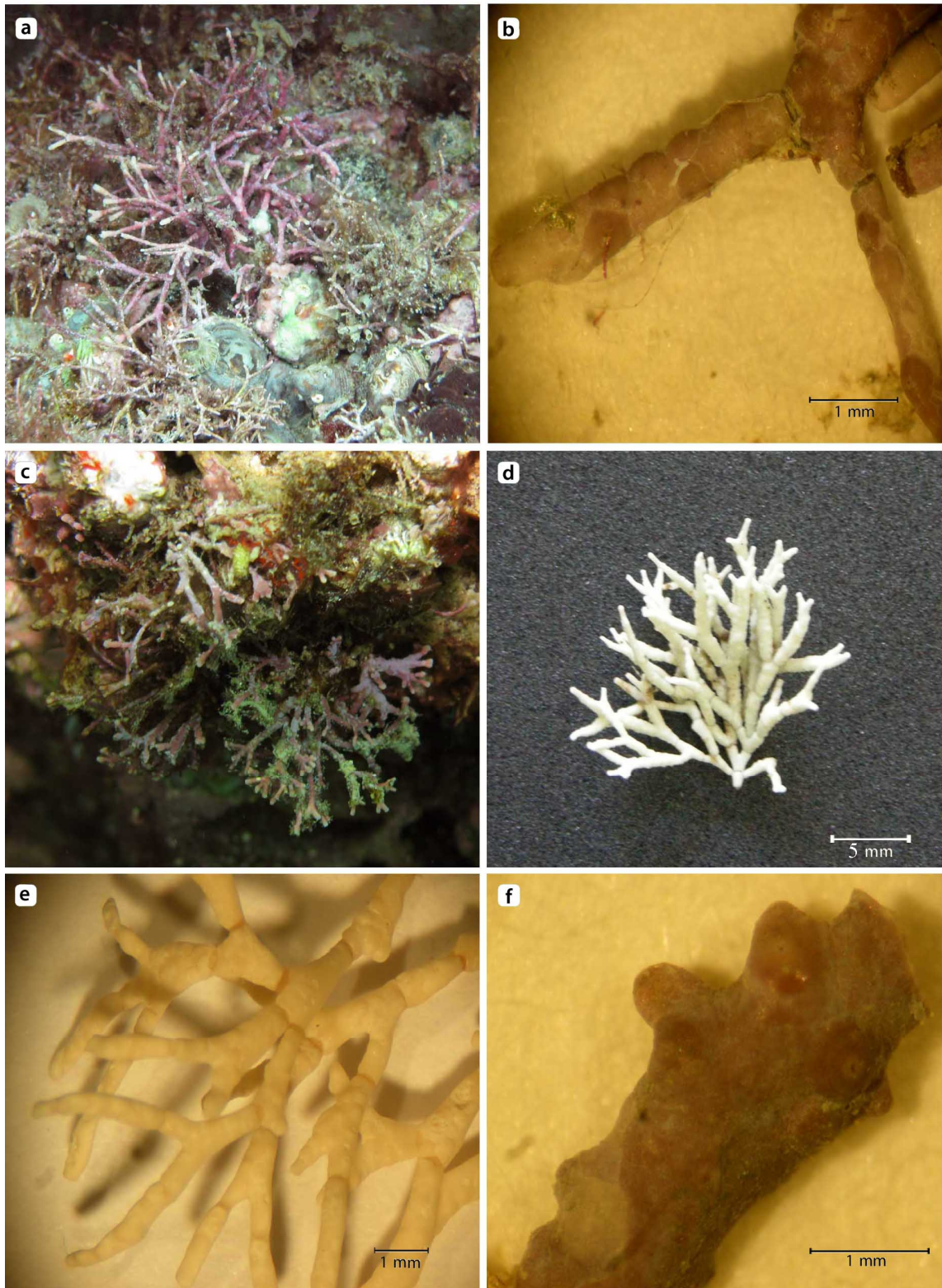


Fig. 5.4. *Amphiroa* Complex B. **B1:** (a) Habit *in situ*, (b) Conceptacles protruding over intergenicular surface, **B2:** (c) Habit *in situ*, (d) Habit of pressed specimen, (e) Protruding conceptacles, showing granulose surface, (f) Closer view of the conceptacles.

***Amphiroa* Complex C (Fig. 5.5)**

Description: Thallus prostrate with some erect portions, in one plane. Upper portions of the thallus flattened to subcylindrical, rarely cylindrical. Lower portions subcylindrical, rarely cylindrical. Branching dichotomous. Conspicuous conceptacles on intergeniculate surface.

Habitat: Turfy, sometimes forming mats. Intertidal to 15 m deep. More common between 3-7 m deep.

Distribution in ETP:

C1: Mexico, El Salvador, Nicaragua, Costa Rica, Panama.

C2: Mexico, El Salvador, Nicaragua, Panama.

Possible species within this clade:

1. *A. van-bosseae* M. Lemoine (Type locality: Post Office Bay, Isla Charles, Galapagos Islands; Lemoine 1929)
2. *A. subcylindrica* E.Y. Dawson (Type locality: Punta Colorado, near Guaymas, Sonora, Mexico; Dawson 1953)

Other Remarks: *A. subcylindrica* seems to correspond with species C2. Its synonymy with the type of *A. van-bosseae* requires further analysis. C1 seems to be a new species to describe.

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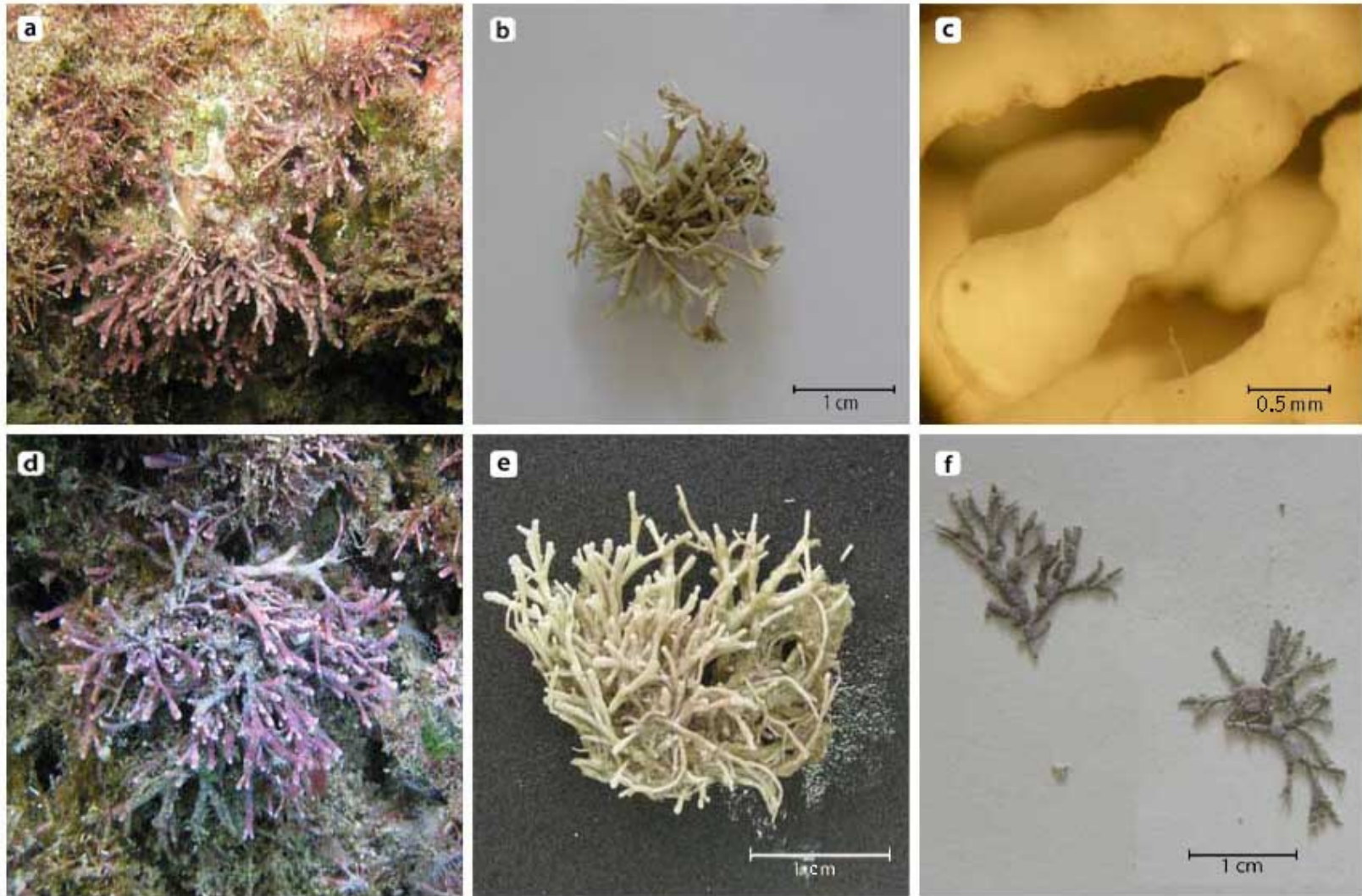


Fig. 5.5. *Amphiroa* Complex C. C1: (a) Habit *in situ*, (b) Habit of pressed specimen, (c) Protruding conceptacles, C2: (d) Habit *in situ*, (e) Habit of pressed specimen, (f) Conceptacles.

***Amphiroa* complex D (Fig. 5.6)**

Description: Thallus prostrate or erect, in one or more planes. Intergenicula irregularly shaped. Upper portions of the thallus flattened. Lower portions flattened, rarely subcylindrical. Intergenic. Branching dichotomous, subdichotomous or alternate, sometimes arising irregularly from intergenicula. Inconspicuous conceptacles, protruding slightly on intergenicular surface.

Habitat: From 1 to 15 m deep. More common between 3-8 m deep.

Distribution in ETP:

D1: Mexico, Nicaragua, Costa Rica.

D2: Costa Rica.

Possible species within this clade:

1. *A. brevianiceps* E.Y. Dawson (Type locality: Salina Cruz, Oaxaca, Mexico; Dawson 1953)
2. *A. compressa* M. Lemoine (Type locality: Tagus Cove, isla Albemarle, Galápagos; Lemoine 1929)
3. *A. crustiformis* E.Y. Dawson (Type locality: Bahía Wreck, Isla San Cristobal, Galapagos; Dawson 1963)
4. *A. dimorpha* M. Lemoine (Type locality: James Bay, Isla James, Galapagos; Lemoine 1929)
5. *A. foliacea* J.V. Lamouroux in Quoy and Gaimard (Type locality: Mariana Islands, Micronesia; Quoy and Gaimard 1824)
6. *A. magdalenensis* E.Y. Dawson (Type locality: Punta Entrada, Isla Magdalena, Baja)
7. *A. misakiensis* Yendo (Type locality: Misaki, Japan, Yendo 1902), California, Mexico; Dawson 1953)
8. *A. polymorpha* M. Lemoine (Type locality: Post Office Bay, Isla Charles, Galápagos; Lemoine 1929)

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Other Remarks: Descriptions of *A. misakiensis* and synonyms proposed by Riosmena-Rodríguez and Sisqueros-Beltrones (1996) seems to fit with species D1. Descriptions of *A. crustiformis* E.Y. Dawson seems to fit with species D2. What Littler and Littler (2009) identified as *A. foliacea*, from Panama, seems to correspond with specimens in this complex.

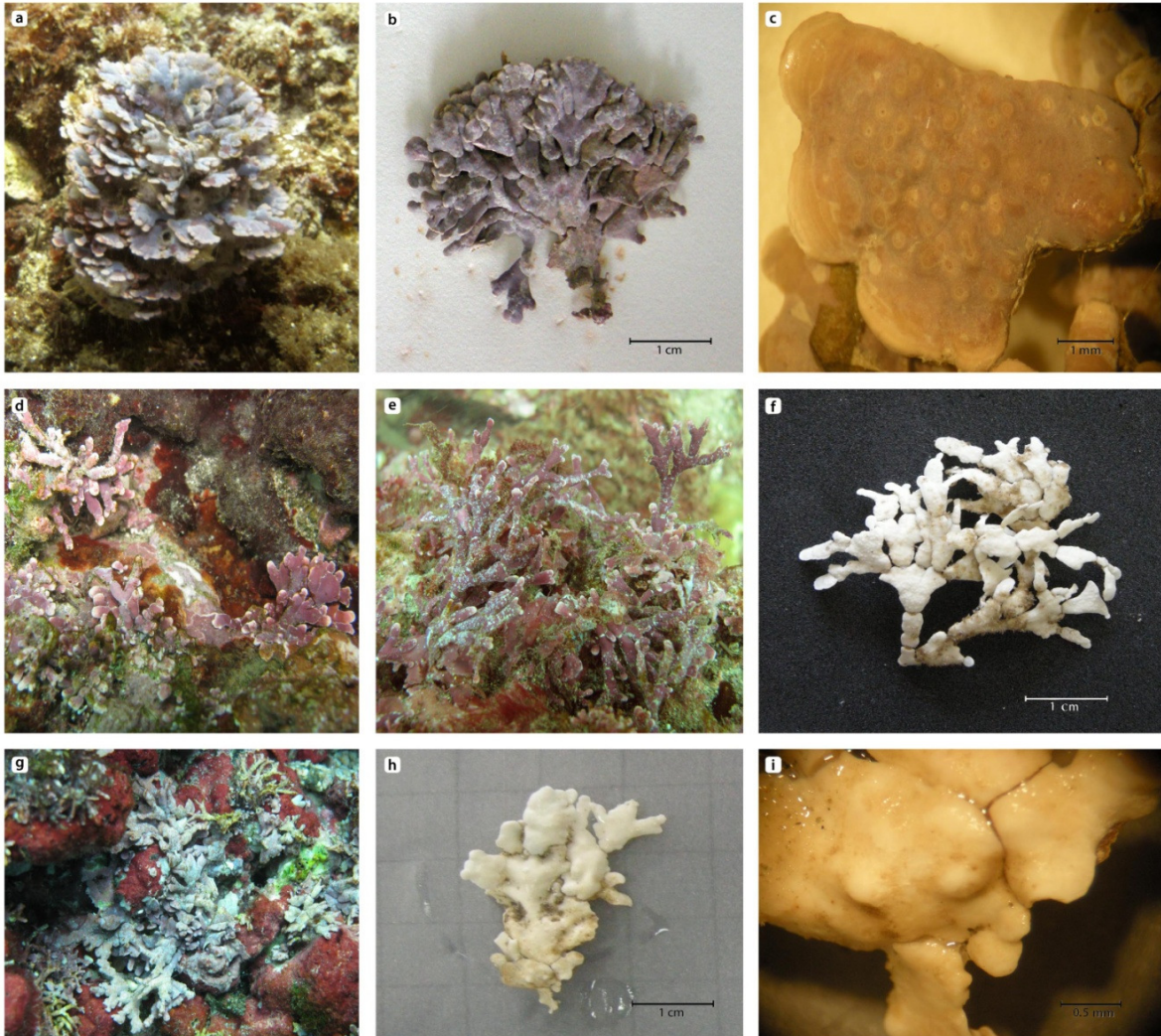


Fig. 5.6. *Amphiroa* Complex D. **D1:** (a) Habit *in situ* of Mexican clade, (b) Habit of pressed specimen of Mexican clade, (c) Conceptacles of Mexican clade, (d, e) Habit *in situ* of Central American specimens, (f) Habit of pressed specimen of Central American specimens, **D2:** (g) Habit *in situ*, (h) Habit of pressed specimen, (i) Conceptacles.

***Amphiroa* Complex E (Fig. 5.7, 5.8)**

Description: Thallus erect, sometimes with some prostrate portions, commonly in various planes, but can be in one plane. Upper portions of the thallus cylindrical to subcylindrical, rarely flattened. Lower portions cylindrical to subcylindrical, rarely flattened. Branching dichotomous. Inconspicuous conceptacles on intergeniculate surface. Some specimens present conspicuous base.

Habitat: Intertidal to 18 m deep.

Distribution in ETP:

E1: Mexico.

E2: Nicaragua.

E3: Mexico, Costa Rica, Panama.

E4: Mexico, Nicaragua, Costa Rica.

Possible species within this clade:

1. *A. beauvoisii* J.V. Lamouroux (Type locality: Coast of Portugal; Lamouroux 1916)
2. *A. crosslandii* M. Lemoine (Type locality: Isla Gorgona, Colombia; Lemoine 1929)
3. *A. mexicana* W.R. Taylor (Type locality: Bahía Petatlán, Guerrero, Mexico; Taylor 1945)
4. *A. peninsularis* W.R. Taylor (Type locality: Isla Cedros, Baja California, Mexico; Taylor 1945)
5. *A. zonata* Yendo (Type locality: not specifically designated but the Japanese localities of Misaki, Shimoda and Sunosaki indicated; Yendo 1902)
6. *A. peruana* Areschoug (Type locality: unknown)

Other Remarks: Since the type locality of *A. beauvoisii* is in Europe and recent studies has shown that the marine flora of this region has no biogeographical relation with the ETP, the synonymy of *A. crosslandii*, *A. mexicana*, *A. peninsularis* and *A. zonata* with *A. beauvoisii* require further attention in order to validate its status.

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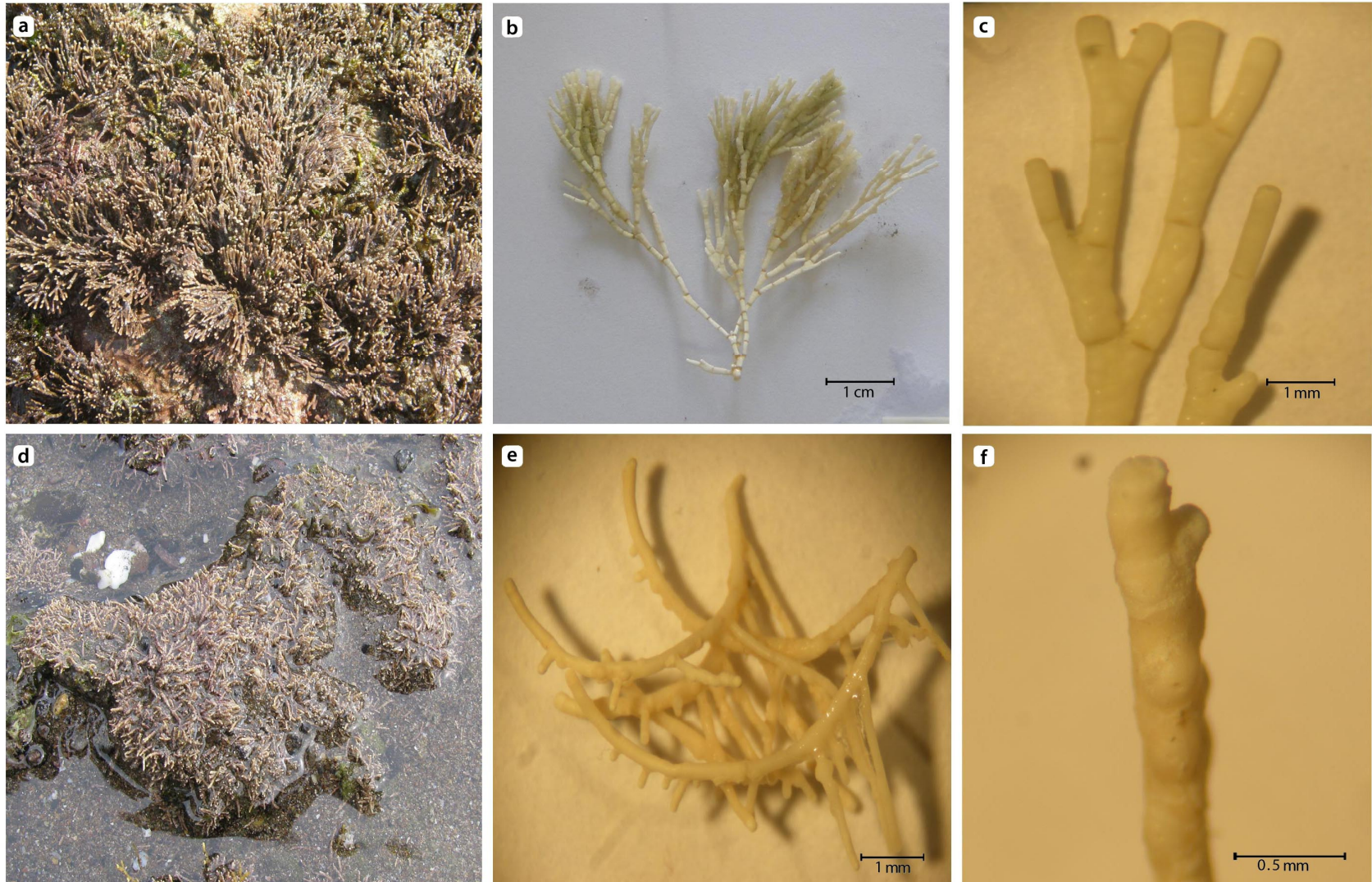


Fig. 5.7. *Amphiroa* Complex E. **E1**: (a) Habit *in situ*, (b) Habit of pressed specimen, (c) Conceptacles, **E2**: (d) Habit *in situ*, (e) Habit of pressed specimen, (f) Conceptacles.

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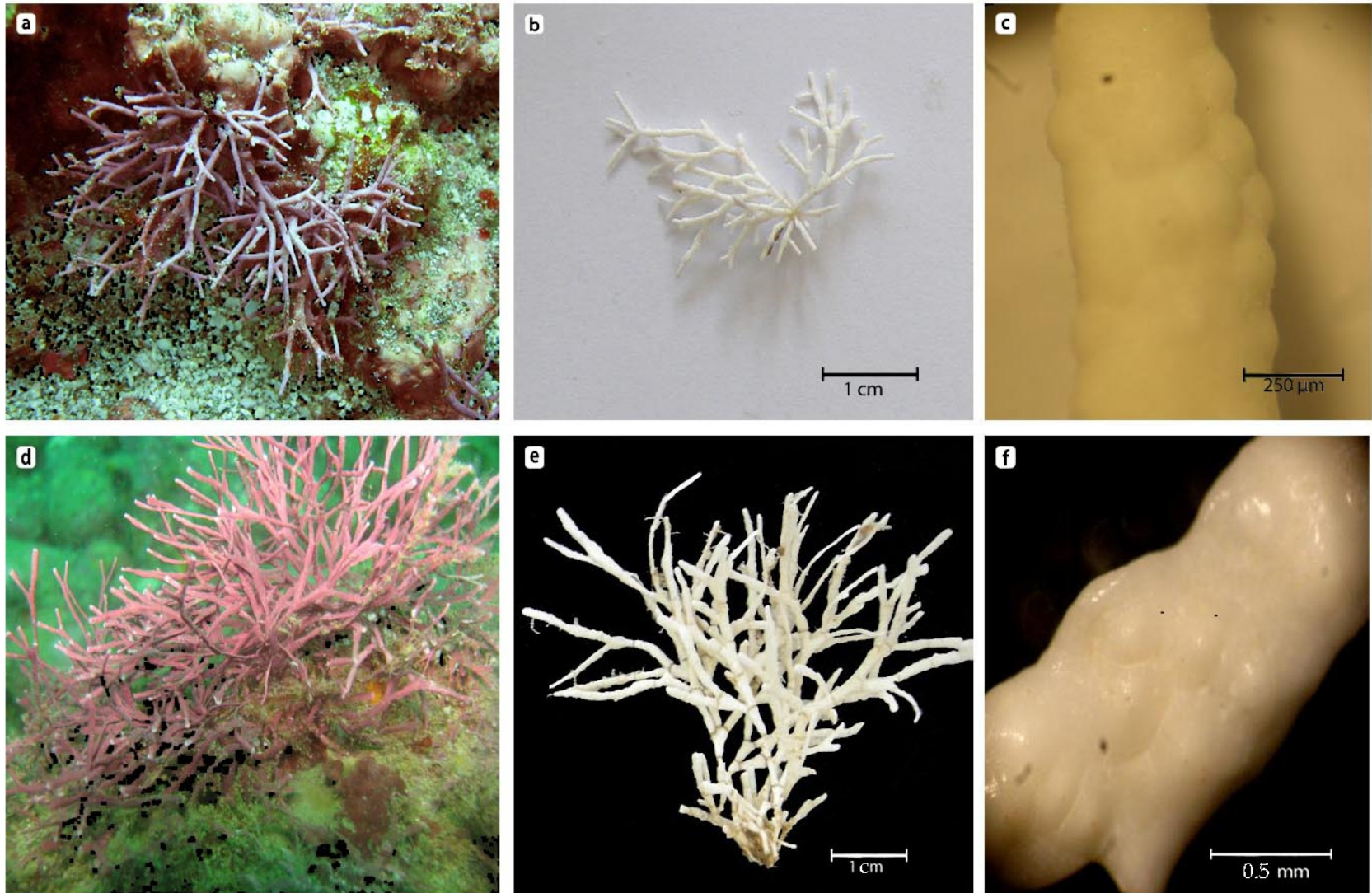


Fig. 5.8. *Amphiroa* Complex E. **E3:** (a) Habit *in situ*, (b) Habit of pressed specimen, (c) Conceptacles, **E4:** (d) Habit *in situ*, (e) Habit of pressed specimen, (f) Conceptacles.

Notes on other species reported at the ETP that require further study:

***A. dilatata* Lamouroux, 1916**

Type locality: Australasie, Lamouroux.

Remarks: This species was reported by Garske (2002), for the Galápagos Islands. There is no description available for this record. Unique report of this species at the ETP. Require further study.

***A. galapagensis* W.R. Taylor, 1945**

Type locality: Tagus Cove, Isla Isabela, Galápagos Islands

Remarks: Turf-like intertidal plant. Described from the Galapagos Islands. Unique report of this species at the ETP. Require further study.

Conclusions

In this study we have found the presence of eleven species level clades (delimited in five complexes in this study) of the genus *Amphiroa* at the Eastern Tropical Pacific. Three of these clades require additional samples in order clarify if they represent a complex of species or if the specimens represent haplotypes of different localities. We also found two clades exclusively with sequences from the Gulf of California that possibly represent new species to be described. We found that many of species delimited in our molecular analysis does not correspond with any of the species described before and also it is possible that some synonymized species will be reinstated as valid species names. However, before describing or reinstate species it is necessary a revision of the 24 type specimens of the species reported in order to validate their status.

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Checklist of the Pacific marine macroalgae of Central America

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Abstract

Our present knowledge of marine macroalgal diversity for the Central American Pacific coast is limited by the short history of investigations (ca. 100 years) and few algal specialists through a large geographical area. While recent checklists have emerged for other regions of the eastern Pacific, there have been virtually no attempts to inventory macroalgal diversity for the Pacific of Central America. This checklist of the marine macroalgae was developed based on published scientific literature and unpublished records in student theses. A total of 379 species records are regarded as current valid names of marine macroalgae. The red algae (Rhodophyta) had the highest species number (252 species), followed by green algae (Chlorophyta: 81 species) and brown algae (Phaeophyceae: 46 species). The country with the greatest diversity of marine macroalgae is Costa Rica with 216 species, followed by Panama with 174, El Salvador with 146, Nicaragua with 24, and Guatemala with 16. At present, there are no published records for the Pacific coast of Honduras. Variation in number of species throughout the Pacific coast of Central America is likely due to differences in geomorphology, habitat heterogeneity among national coastal-marine zones, and unbalanced research efforts.

Keywords: Chlorophyta; eastern tropical Pacific; marine floristics; Phaeophyceae; Rhodophyta.

Introduction

Knowledge of marine macroalgal diversity for the Central American Pacific coast (CAP) is limited by a short history

of investigations (ca. 100 years) and few algal specialists throughout a large geographical area (~3829 km from Guatemala to Panama). While recent checklists have emerged for other regions of the eastern Pacific, to the north (González-González 1993, González-González et al. 1996, Riosmena-Rodríguez 2005, Payri et al. 2008) and south (Schnetter and Bular-Meyer 1982, Bula-Meyer 1995, Garske 2002), there have been virtually no attempts to inventory macroalgal diversity for the CAP. Such inventories are useful starting points for investigations of algal evolution and biogeography and are essential to monitoring efforts that seek to determine the impacts of global climate change or synanthropic transport of species, to name but two. Given the availability of Wynne's (2005) exhaustive catalogue of western Atlantic macroalgal diversity and known or projected disturbances to the Central American landscape (climate change, coastal infrastructure, expansion of the Panama Canal), a checklist Pacific Central American algae is both timely and essential.

The history of algal exploration through CAP can be divided into three stages: 1) regional exploration and documentation, 2) species checklists by country, and 3) sampling for DNA-based diversity assessments.

The first stage commenced in 1909 with Marshall Avery Howe's *Botanical visit to the Isthmus of Panama*. During a one-week visit to the Pacific coast, Howe (1910) collected upwards of 50 species of closely encrusting, minutely filamentous and unicellular forms of marine algae, but he seemed more impressed by the apparent paucity of macroalgae at that latitude than by those that he actually encountered. Numerous later works (Grunow 1915–1916, Lemoine 1929, Setchell 1937, Setchell and Mason 1943), especially those derived from the Allan Hancock Expeditions aboard the *Velero III* (Dawson 1944, 1949, 1950a,b,c, 1953, 1955, 1962c, Taylor 1945, Chou 1947) and those of Dawson (Dawson 1957, 1959, 1960, 1961a,b, 1962a,b, Dawson and Beaudette 1959) would reveal a much more species-rich marine flora. Dawson's (1962b) illustrated taxonomic key documented 235 species of benthic macroalgae (167 Rhodophyta, 46 Chlorophyta and 22 Phaeophyceae) based on observations made in El Salvador, Nicaragua, Costa Rica and Panama. This work remains the only regional account of marine floristic diversity for CAP to date. The untimely death of Dawson in 1966 (Hawkes 1996) marked the end of the first stage of CAP phycology, a time period in which over 50% of the known algal taxa for the CAP were listed in the literature (Figures 1 and 2).

The second stage of algal diversity assessments in the CAP spanned more than three decades from 1965 to 1998. Numerous national marine floristic surveys were undertaken (Guatemala: Bird and McIntosh 1979, Dreckmann and Gamboa-Contreras 1998; El Salvador: Avilés and Canjura 1979, Gutiérrez 1985, Castro-Avilés and Tejada 1993; Costa Rica:

Fig. S1. Primera Página del Artículo Publicado: Fernández-García, C., Riosmena-Rodríguez, R., Wysor, B., Tejada, O. & Cortés, J. 2011. Checklist of the Pacific Marine Macroalgae of Central America. *Bot. Mar.* 54: 53–73

Tabla S1. Listado de especímenes colectados del género *Caulerpa* en el Pacífico Tropical Oriental.* Especímenes utilizados en el análisis molecular.

Table S1. List of *Caulerpa* specimens from the Eastern Tropical Pacific. *Specimens used in the DNA-analysis.

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
Eastern Tropical Pacific							
CFES-005	<i>Caulerpa verticillata</i>	<i>Caulerpa verticillata</i>	Isla Zacatillo, Golfo de Fonseca, La Unión	El Salvador	13°17'29.6" 87°46'05.5"	22-01-09	C. Fernández-A. Planas
CFES-008	<i>Caulerpa verticillata</i>	<i>Caulerpa verticillata</i>	Chiquirin, Golfo de Fonseca	El Salvador	13°17'44.3" 87°46'56.7"	22-01-09	C. Fernández-A. Planas
CFES-009	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Pirigallo Sur, Golfo de Fonseca, La Unión	El Salvador	13°10'00.2" 87°41'08.7"	22-01-09	C. Fernández-A. Planas
CFES-038	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Suroeste Isla Meanguera, Golfo de Fonseca, La Unión	El Salvador	13°10'8.8" 87°43'22.2"	22-01-09	C. Fernández-A. Planas
CFES-047*	<i>Caulerpa intermediae laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Isla Meanguera, Playa Mahaul, Golfo de Fonseca, La Unión	El Salvador	13°10'02.9" 87°42'55.1"	22-01-09	C. Fernández-A. Planas
CFES-158*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa Maculiz, La Unión	El Salvador	13°09'4.2" 87°55'19.6"	07-02-09	C. Fernández-J.J. Alvarado
CFES-160*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa Maculiz, La Unión	El Salvador	13°09'4.2" 87°55'19.6"	07-02-09	C. Fernández-J.J. Alvarado
CFES-162*	<i>Caulerpa intermediae laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Playa Maculiz, La Unión	El Salvador	13°09'4.2" 87°55'19.6"	07-02-09	C. Fernández-J.J. Alvarado
CFES-164	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Playa Maculiz, La Unión	El Salvador	13°09'4.2" 87°55'19.6"	07-02-09	C. Fernández-J.J. Alvarado
CFES-166*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa Maculiz, La Unión	El Salvador	13°09'4.2" 87°55'19.6"	07-02-09	C. Fernández-J.J. Alvarado
CFES-168*	<i>Caulerpa intermediae laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Playa Maculiz, La Unión	El Salvador	13°09'4.2" 87°55'19.6"	07-02-09	C. Fernández-J.J. Alvarado
CFES-170*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa Maculiz, La Unión	El Salvador	13°09'4.2" 87°55'19.6"	07-02-09	C. Fernández-J.J. Alvarado
CFES-171*	<i>Caulerpa intermediae laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Playa Maculiz, La Unión	El Salvador	13°09'4.2" 87°55'19.6"	07-02-09	C. Fernández-J.J. Alvarado

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
CFES-172*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa Maculiz, La Unión	El Salvador	13°09'4.2" 87°55'19.6"	07-02-09	C. Fernández- J.J. Alvarado
CFES-173*	<i>Caulerpa intermedia</i> <i>laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Playa Maculiz, La Unión	El Salvador	13°09'4.2" 87°55'19.6"	07-02-09	C. Fernández- J.J. Alvarado
CFMX-183*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa El Panteon, Puerto Angel, Oaxaca	Mexico	15°39.842 96°29.725	13-02-09	C. Fernández
CFMX-195*	<i>Caulerpa intermedia</i> <i>laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Playa El Panteon, Puerto Angel, Oaxaca	Mexico	15°39.842 96°29.725	13-02-09	C. Fernández
CFMX-197*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Playa El Panteon, Puerto Angel, Oaxaca	Mexico	15°39.842 96°29.725	13-02-09	L.Tyberghein- H. Verbruggen
CFMX-198*	<i>Caulerpa intermedia</i> <i>laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Playa El Panteon, Puerto Angel, Oaxaca	Mexico	15°39.842 96°29.725	13-02-09	L. Tyberghein- H. Verbruggen
CFMX-212	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Mazunte, Oaxaca	Mexico	15°39.705 96°33.365	15-02-09	C. Fernández
CFMX-215*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Mazunte, Oaxaca	Mexico	15°39.705 96°33.365	15-02-09	C. Fernández
CFMX-226*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Mazunte, Oaxaca	Mexico	15°39.705 96°33.365	15-02-09	H. Verbruggen
CFMX-229	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Mazunte, Oaxaca	Mexico	15°39.705 96°33.365	15-02-09	H. Verbruggen
CFMX-232*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Mazunte, Oaxaca	Mexico	15°39.705 96°33.365	15-02-09	H. Verbruggen
CFMX-238a*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Puerto Angelito, Oaxaca	Mexico	15°51.432 97°04.464	16-02-09	C. Fernández
CFMX-239*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Puerto Angelito, Oaxaca	Mexico	15°51.432 97°04.464	16-02-09	C. Fernández
CFMX-249	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Puerto Escondido, Oaxaca	Mexico	15°51.453 97°03.940	17-02-09	C. Fernández
CFMX-258*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	NW de la Isla Roqueta 3, Acapulco, Guerrero	Mexico	16° 49.425 99° 54.859	19-02-09	C. Fernández
CFMX-260*	<i>Caulerpa intermedia</i> <i>laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	NW de la Isla Roqueta 1, Acapulco, Guerrero	Mexico	16°49.504 99°54.668	19-02-09	H. Verbruggen

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
CFMX-263	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	NW de la Isla Roqueta, Acapulco, Guerrero	Mexico	16°49.504 99°54.668	19-02-09	H. Verbruggen
CFMX-267	<i>Caulerpa intermediate laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	NW Isla Roqueta, Acapulco, Guerrero	Mexico	16° 49.430 99° 54.731	20-02-09	H. Verbruggen
CFMX-274*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Isla de la Virgen, Acapulco, Guerrero	Mexico	16°49'26.85" 99°54'01.32"	20-02-09	C. Fernández
CFMX-276*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Isla de la Virgen, Acapulco, Guerrero	Mexico	16°49'26.85" 99°54'01.32"	20-02-09	H. Verbruggen
CFMX-278*	<i>Caulerpa intermediate laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Playa del Palmar, Ixtapa	Mexico	17°39.139 101°36.019	21-02-09	C. Fernández
CFMX-279*	<i>Caulerpa intermediate laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Playa del Palmar, Ixtapa	Mexico	17°39.139 101°36.019	21-02-09	C. Fernández
CFMX-280*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Playa del Palmar, Ixtapa	Mexico	17°39.139 101°36.019	21-02-09	C. Fernández
CFMX-283*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa del Palmar, Ixtapa	Mexico	17°39.139 101°36.019	21-02-09	C. Fernández
CFMX-288*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Playa del Palmar, Ixtapa	Mexico	17°39.139 101°36.019	21-02-09	C. Fernández
CFMX-291*	<i>Caulerpa intermediate laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Playa del Palmar, Ixtapa	Mexico	17°39.139 101°36.019	21-02-09	C. Fernández
CFMX-298*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Manzanillo, Zihuatanejo	Mexico	17°37.260 101°31.300	22-02-09	C. Fernández
CFMX-302*	<i>Caulerpa intermediate laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Caleta de Chon, Zihuatanejo	Mexico	17°36.938 101°33.314	22-02-09	C. Fernández
CFMX-303a*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Caleta de Chon, Zihuatanejo	Mexico	17°36.938 101°33.314	22-02-09	C. Fernández
CFMX-304*	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Caleta de Chon, Zihuatanejo	Mexico	17°36.938 101°33.314	22-02-09	C. Fernández
CFMX-319	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Playa La Audiencia, Manzanillo	Mexico	19°06.300 104°21.122	23-02-09	C. Fernández
CFMX-326*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Playa La Audiencia, Manzanillo	Mexico	19°06.300 104°21.122	23-02-09	L. Tyberghein

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
CFMX-346*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa Tenacatita, Michoacán	Mexico	19°16.894 104°52.348	25-02-09	C. Fernández
CFMX-348*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa Tenacatita, Michoacán	Mexico	19°16.894 104°52.348	25-02-09	C. Fernández
CFMX-349*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Playa Tenacatita, Michoacán	Mexico	19°16.894 104°52.348	25-02-09	C. Fernández
CFMX-350*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Playa Tenacatita, Michoacán	Mexico	19°16.894 104°52.348	25-02-09	C. Fernández
CFMX-367	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Playa Mismaloya, Puerto Vallarta, Jalisco	Mexico	20°31.927 105°17.598	26-02-09	C. Fernández
CFMX-368	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa Mismaloya, Puerto Vallarta, Jalisco	Mexico	20°31.927 105°17.598	26-02-09	L. Tyberghein
CFMX-376*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa Careyero, Pta Mita, Puerto Vallarta, Jalisco	Mexico	20°47.059 105°30.710	27-02-09	L. Tyberghein
CFMX-387*	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Caletas, Puerto Vallarta, Jalisco	Mexico	20°30.299 105°22.480	28-02-09	C. Fernández
CFMX-404*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Bajo del Cristo, cerca de los arcos, Puerto Vallarta, Jalisco	Mexico	20°32.797 105°17.269	28-02-09	C. Fernández
CFMX-406*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Bajo del Cristo, cerca de los arcos, Puerto Vallarta, Jalisco	Mexico	20°32.797 105°17.269	28-02-09	C. Fernández
CFPA-409	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Islotes antes de Saboga, Archipiélago de las Perlas	Panama	8°38.787 79°03.314	04-06-09	C. Fernández
CFPA-410	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Islotes antes de Saboga, Archipiélago de las Perlas	Panama	8°38.787 79°03.314	04-06-09	C. Fernández
CFPA-411*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Islotes antes de Saboga, Archipiélago de las Perlas	Panama	8°38.787 79°03.314	04-06-09	C. Fernández
CFPA-423*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Isla Saboga, Archipiélago de las Perlas	Panama	8°37.732 79°03.309	04-06-09	C. Fernández
CFPA-430*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Isla Pacheca, Archipiélago de las Perlas	Panama	8°39.729 79°03.199	04-06-09	C. Fernández
CFPA-435*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Otoque Sur, Archipiélago de las Perlas	Panama	8°34.059 79°35.454	10-06-09	C. Fernández

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
CFPA-449*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Isla Urabá, Archipiélago de las Perlas	Panama	8°46.933 79°32.178	10-06-09	C. Fernández
CFPA-469*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Isla Mogo-Mogo, Archipiélago de las Perlas	Panama	8°34.692 79°01,698	24-06-09	C. Fernández
CFPA-472*	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Isla Mogo-Mogo, Archipiélago de las Perlas	Panama	8°34.692 79°01,698	24-06-09	C. Fernández
CFPA-474*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Isla Mogo-Mogo, Archipiélago de las Perlas	Panama	8°34.692 79°01,698	24-06-09	C. Fernández
CFPA-475*	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Isla Mogo-Mogo, Archipiélago de las Perlas	Panama	8°34.692 79°01,698	24-06-09	C. Fernández
CFPA-484*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Isla Contadora, Archipiélago de las Perlas	Panama	8°37.681 79°01.628	24-06-09	C. Fernández
CFPA-490*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Islote Trapiche, Isla Pedro González, Archipiélago de las Perlas	Panama	8°25.554 79°06.549	25-06-09	C. Fernández
CFPA-491*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Islote Trapiche, Isla Pedro González	Panama	8°25.554 79°06.549	25-06-09	C. Fernández
CFPA-495*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Islote Trapiche, Isla Pedro González	Panama	8°25.554 79°06.549	25-06-09	C. Fernández
CFPA-498*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Playa Don Bernardo, Isla Pedro Gonzalez	Panama	8°24.025 79°04.769	25-06-09	C. Fernández
CFPA-500*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Isla Bayoneta, Archipiélago de las Perlas	Panama	8°29'15.29 79°04'03.53"	25-06-09	C. Fernández- A. Alvarez, JJ Alvarado, J. Aguirre
CFNI-520*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa El Tránsito, León	Nicaragua	12° 02' 54.2" 86° 42' 17.0"	30-06-09	C. Fernández- A. Alvarez, JJ Alvarado, J. Aguirre
CFNI-537*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	La Flor, San Juan del sur, Rivas	Nicaragua	11°08'09.0" 85°48'04.2"	02-07-09	C. Fernández
CFNI-569*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	La Peña Rota, Rivas	Nicaragua	11°14'00.3" 85°52'01.5"	02-07-09	C. Fernández
CFNI-584*	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	La Peña Rota, Rivas	Nicaragua	11°14'00.3" 85°52'01.5"	02-07-09	C. Fernández

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
CFNI-611	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Gigante, Rivas	Nicaragua	11°23'07.9" 86°02'12.4"	03-07-09	J. Aguirre
CFNI-624	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	La Anciana, Rivas	Nicaragua	11°21'10.6" 86°00'08.0"	03-07-09	J. Aguirre
CFNI-632*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Guacalito, Rivas	Nicaragua	11°21'17.3" 86°00'06.9"	03-07-09	C. Fernández-J. Aguirre
CFNI-652*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Punta El Clavo, Rivas	Nicaragua	11°19'12.6" 85°56'43.0"	04-07-09	C. Fernández
CFNI-659	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Punta El Clavo, Rivas	Nicaragua	11°19'12.6" 85°56'43.0"	04-07-09	J. Aguirre
CFNI-662*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Costa Blanca, Rivas	Nicaragua	11°18'57.20" 85°56'23.90"	04-07-09	C. Fernández
CFNI-670*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Costa Blanca, Rivas	Nicaragua	11°18'57.20" 85°56'23.90"	04-07-09	C. Fernández
CFNI-678*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Marsella, Rivas	Nicaragua	11°16'59.20" 85°54'22.50"	04-07-09	C. Fernández
CFNI-681*	<i>Caulerpa intermediate laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Marsella, Rivas	Nicaragua	11°16'59.20" 85°54'22.50"	04-07-09	C. Fernández
CFNI-723*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Isla El Cardón, Puerto Corinto, Chinandega	Nicaragua	12°28'32.8" 87°11'22.2'	07-07-09	C. Fernández-JJ. Alvarado, J. Aguirre
CFNI-729*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa Hermosa, León	Nicaragua	12°06'21.7" 86°44'09.2	09-07-09	C. Fernández
CFNI-766	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Playa Hermosa, León	Nicaragua	12°06'21.7" 86°44'09.2	09-07-09	C. Fernández
CFCR-778*	<i>Caulerpa intermediate laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Roca Tres Hermanas, Parque Nacional Marino Ballena, Puntarenas	Costa Rica	09°06'14.84" 83°42'28.30"	16-07-09	C. Fernández
CFCR-802	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Catarata 1, Reserva Biológica Isla del Caño, Puntarenas	Costa Rica	08°42'52.7" 83°52'03.0"	18-07-09	C. Fernández
CFCR-809*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Catarata 2, Reserva Biológica Isla del Caño, Puntarenas	Costa Rica	08°42'24.0" 83°51'58.9"	18-07-09	C. Fernández

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
CFCR-813*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Catarata 2, Reserva Biológica Isla del Caño, Puntarenas	Costa Rica	08°42'24.0" 83°51'58.9"	18-07-09	C. Fernández
CFCR-819*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	El Jardín, Reserva Biológica Isla del Caño, Puntarenas	Costa Rica	08°42'55.7" 83°52'28.3"	19-07-09	C. Fernández
CFCR-827a*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	San Josecito, Puntarenas	Costa Rica	8°40'15.4" 83°43'6.5"	21-07-09	C. Fernández
CFCR-830a*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	San Josecito, Puntarenas	Costa Rica	8°40'15.4" 83°43'6.5"	21-07-09	C. Fernández
CFCR-834a*	<i>Caulerpa intermediate laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	San Josecito, Puntarenas	Costa Rica	8°40'15.4" 83°43'6.5"	21-07-09	C. Fernández
CFCR-830*	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Isla Bolaños, Bahía Salinas, Guancaste	Costa Rica	11°02'53.6" 85°42'43.1"	28-07-09	C. Fernández-A. Planas
CFCR-834*	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Isla Bolaños, Bahía Salinas, Guancaste	Costa Rica	11°02'53.6" 85°42'43.1"	28-07-09	C. Fernández-A. Planas
CFCR-841*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	La Paloma, Bahía Salinas, Guancaste	Costa Rica	11°02'00.1" 85°44'59.4"	28-07-09	C. Fernández-A. Planas
CFCR-846*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	La Paloma, Bahía Salinas, Guancaste	Costa Rica	11°02'00.1" 85°44'59.4"	28-07-09	C. Fernández-A. Planas
CFCR-847*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Isla Despensa, Bahía Salinas, Guancaste	Costa Rica	11°00'09.5" 85°44'51.2"	28-07-09	C. Fernández-A. Planas
CFCR-853*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	La Penca, Bahía Culebra, Guancaste	Costa Rica	10°34'29.2" 85°41'53.0"	29-07-09	C. Fernández-A. Planas
CFCR-864	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Punta Arenita, Bahía Culebra, Guancaste	Costa Rica	10°36'17.2" 85°38'54.1"	30-07-09	A. Planas, JJ Alvarado-C. Sanchez
CFCR-865*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Punta Arenita, Bahía Culebra, Guancaste	Costa Rica	10°36'17.2" 85°38'54.1"	30-07-09	A. Planas, JJ Alvarado-C. Sanchez
CFCR-871*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Punta Arenita, Bahía Culebra, Guancaste	Costa Rica	10°36'17.2" 85°38'54.1"	30-07-09	A. Planas, JJ Alvarado-C. Sanchez

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
CFCR-880*	<i>Caulerpa intermedia laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Bahía Virador, Bahía Culebra, Guancaste	Costa Rica	10°36'51.6" 85°41'25.0"	01-08-09	A. Planas, JJ Alvarado-C. Sanchez
CFCR-889*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Cabo Vela, Parque Nacional Marino Las Baulas, Guancaste	Costa Rica	10°20'52.0" 85°52'10.1"	02-08-09	C. Fernández-A. Planas
CFCR-899*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Los Conejos, Parque Nacional Marino Las Baulas, Guancaste	Costa Rica	10°22'05.2" 85°51'52.9"	02-08-09	C. Fernández-A. Planas
CFCR-912*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Tortugas, Golfo de Nicoya, Puntarenas	Costa Rica	09°45'50.3" 84°53'51.1"	03-08-09	C. Fernández-A. Planas
CFIC-916	<i>Caulerpa serrulata</i>	<i>Caulerpa serrulata</i>	Punta Ulloa, Isla del Coco	Costa Rica	05°33.054 87°02.095	14-09-09	J. Cortés
CFIC-919*	<i>Caulerpa serrulata</i>	<i>Caulerpa serrulata</i>	Punta Ulloa, Isla del Coco	Costa Rica	05°33.054 87°02.095	14-09-09	J. Cortés
CFIC-920	<i>Caulerpa serrulata</i>	<i>Caulerpa serrulata</i>	Punta Ulloa, Isla del Coco	Costa Rica	05°33.054 87°02.095	14-09-09	J. Cortés
CFIC-921	<i>Caulerpa serrulata</i>	<i>Caulerpa serrulata</i>	Punta Ulloa, Isla del Coco	Costa Rica	05°33.054 87°02.095	14-09-09	J. Cortés
CFIC-922	<i>Caulerpa serrulata</i>	<i>Caulerpa serrulata</i>	Punta Ulloa, Isla del Coco	Costa Rica	05°33.054 87°02.095	14-09-09	J. Cortés
CFIC-923	<i>Caulerpa serrulata</i>	<i>Caulerpa serrulata</i>	Punta Ulloa, Isla del Coco	Costa Rica	05°33.054 87°02.095	14-09-09	J. Cortés
CFMX-925*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Isla Espíritu Santo, La Paz, Baja California Sur	México	24°23'25.97" 110°19'7.44"	11-11-09	C. Fernández
CFMX-926*	<i>Caulerpa peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Isla Espíritu Santo, La Paz, Baja California Sur	México	24°23'25.97" 110°19'7.44"	11-11-09	C. Fernández
CFPA-1004	<i>Caulerpa macrophysa</i>	<i>Caulerpa racemosa</i> var. <i>macrophysa</i>	Coiba Noreste, Golfo de Chiriquí	Panama	07°38'01" 81°44'9.5"	22-06-10	C. Fernández
CFPA-1009	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Jicarita, Golfo de Chiriquí	Panama	07°12'49.1" 81°47'57.0"	23-06-10	C. Fernández
CFPA-1012	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Bahía Damas, Golfo de Chiriquí	Panama	07°25'19" 81°41'44.2"	23-06-10	C. Fernández

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
CFPA-1016	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Canales de Afuera, Golfo de Chiriquí	Panama	07°41'44" 81°37'59"	23-06-10	C. Fernández
CFPA-1017*	<i>Caulerpa verticillata</i>	<i>Caulerpa verticillata</i>	Playa Hermosa, Chiriquí	Panama	8°12'55.80" 82°09'23.80"	16-06-10	O. Tejada
CUVC-40308	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Playa Azufrada, Isla Gorgona	Colombia	2°57'17.70" 78°10'37.12"	Nov-2010	E. Peña-Salamanca
CUVC-40319	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Isla Palma, Bahía Malaga	Colombia	3°54'09.36" 77°21'41.48"	Nov-2010	E. Peña-Salamanca
CUVC-46409	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Estero Natal, Tumaco	Colombia	1°45'53.83" 78°43'32.02"	Nov-2010	E. Peña-Salamanca
CUVC-46410	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Isla Palma, Bahía Malaga	Colombia	3°54'09.36" 77°21'41.48"	Nov-2010	E. Peña-Salamanca
CUVC-40309	<i>Caulerpa macrophysa</i>	<i>Caulerpa racemosa</i> var. <i>mucronata</i>	Playa Azufrada, Isla Gorgona	Colombia	2°57'17.70" 78°10'37.12"	Nov-2010	E. Peña-Salamanca
001	<i>Caulerpa racemosa</i>	<i>Caulerpa racemosa</i> var. <i>mucronata</i>	Playa Escondida, Esmeraldas	Ecuador	0°48'52.83" 79°56'47.32"	12-03-10	A. Franco Campos
002	<i>Caulerpa racemosa</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Estero del Platano, Esmeraldas	Ecuador	0°46'34.90" 80°05' 0.21"	20-02-10	A. Franco Campos
003	<i>Caulerpa racemosa</i>	<i>Caulerpa racemosa</i> var. <i>mucronata</i>	Punta Galera, Esmeraldas	Ecuador	0°48'51.60" 80°02' 2.49"	19-04-11	A. Franco Campos
BW-4838*	<i>Caulerpa intermediae</i> <i>laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Isla Canales de Afuera, NE end, Golfo de Chiriquí	Panama	7°41'45.42" 81°36'52.45"	14-01-11	C. Fernández
BW-4973*	<i>Caulerpa macrophysa</i>	<i>Caulerpa racemosa</i> var. <i>mucronata</i>	Isla Coiba, near Punta Baltazar, Golfo de Chiriquí	Panama	7°37'23.40" 81°46'39.98"	15-01-11	C. Fernández-B. Wysor
MX-0077*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Mazunte, Oaxaca	Mexico	15°39.705 96°33.365	15-02-09	L.Tyberghein-H. Verbruggen
MX-0174*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Canal de Boca Chica, Acapulco, Guerrero	Mexico	16.8271 -99.9119	19-02-09	L.Tyberghein-H. Verbruggen
MX-0191*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Canal de Boca Chica, Acapulco, Guerrero	Mexico	16.8271 -99.9119	20-02-09	L.Tyberghein-H. Verbruggen

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
MX-0315*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	El Acuario, Bahía Tenacatita, Jalisco	Mexico	19.2815 -104.8724	25-02-09	L.Tyberghein-H. Verbruggen
MX-0316*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	El Acuario, Bahía Tenacatita, Jalisco	Mexico	19.2815 -104.8724	25-02-09	L.Tyberghein-H. Verbruggen
MX-0317*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	El Acuario, Bahía Tenacatita, Jalisco	Mexico	19.2815 -104.8724	25-02-09	L.Tyberghein-H. Verbruggen
MX-0346*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Nayarit: Punta de Mita: Playa Careyero	Mexico	20.78431 -105.5118	27-02-09	L.Tyberghein-H. Verbruggen
MX-0379*	<i>Caulerpa racemosa</i> var. <i>laetevirens</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Nayarit: Sayulita: Punta los Muertos	Mexico	20.8728 -105.4454	01-03-09	L.Tyberghein-H. Verbruggen
MX-0382*	<i>Caulerpa cupressoides</i>	<i>Caulerpa cupressoides</i>	Nayarit: Lo de Marcos: playa en Lo de Marcos	Mexico	20.9539 -105.3623	01-03-09	L.Tyberghein-H. Verbruggen
Others Pacific							
GC-10	<i>Caulerpa verticillata</i>	<i>Caulerpa verticillata</i>	Calerita, Baja California Sur	Mexico	24°21'16.41" 110°17'0.08"	22-11-07	R. Riosmena-J. Hernández
GC-11*	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Calerita, Baja California Sur	Mexico	24°21'16.41" 110°17'0.08"	22-11-07	R. Riosmena-J. Hernández
GC-15	<i>Caulerpa racemosa</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Calerita, Baja California Sur	Mexico	24°21'16.41" 110°17'0.08"	22-11-07	R. Riosmena-J. Hernández
GC-87	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Mulege, Baja California Sur	Mexico	26°54'6.9" 111°57'11.1"	22-04-06	J.M. Lopez-J. Hernández
GC-89*	<i>Caulerpa vanbossea</i>	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Requeson, Baja California Sur	Mexico	26°38'26.8" 111°49'45.5"	24-04-06	J.M. Lopez-J. Hernández
GC-90	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Requeson, Baja California Sur	Mexico	26°38'26.8" 111°49'45.5"	24-04-06	J.M. Lopez-J. Hernández
GC-91*	<i>Caulerpa</i> sp.	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Las Pocitas, Baja California Sur	Mexico	26°34'45.7" 111°47'07.6"	24-04-06	J.M. Lopez-J. Hernández
GC-92*	<i>Caulerpa racemosa</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Isla Venados, Sinaloa	Mexico	23°15'0" 106°28'48"	31-05-05	J.M. Lopez-J. Hernández
GC-93	<i>Caulerpa racemosa</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Cerritos, Sinaloa	Mexico	23°8'35.99" 106°29'23.99"	01-06-05	J.M. Lopez-J. Hernández

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
GC-94*	<i>Caulerpa</i> sp.	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Cerritos, Sinaloa	Mexico	23°8'35.99" 106°29'23.99"	01-06-05	J.M. Lopez-J. Hernández
GC-96*	<i>Caulerpa racemosa</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Calerita, Baja California Sur	Mexico	24°21'16.41" 110°17'0.08"	27-05-04	J.M. Lopez-J. Hernández
GC-97	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Isla Bledos, Sinaloa	Mexico	25°36'0.00" 108°58'60.0"	20-06-07	J.M. Lopez-J. Hernández
GC-121*	<i>Caulerpa</i> sp.	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Playa La Concha, Baja California Sur	Mexico	24°12'07.36" 110°18'03.10"	19-08-07	J. Hernández, H. Verbruggen
GC-123*	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Playa La Concha, Baja California Sur	Mexico	24°12'07.36" 110°18'03.10"	19-08-07	J. Hernández, H. Verbruggen
GC-124*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Playa El Pulguero	Mexico	24°20'53.43" 110°18'00.45"	19-08-07	J. Hernández, H. Verbruggen
GC-125*	<i>Caulerpa racemosa</i> var <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Calerita, Baja California Sur	Mexico	24°21'16.41" 110°17'0.08"	19-08-07	J. Hernández, H. Verbruggen
GC-126*	<i>Caulerpa racemosa</i> var <i>turbinata</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Calerita, Baja California Sur	Mexico	24°21'16.41" 110°17'0.08"	19-08-07	J. Hernández, H. Verbruggen
GC-127*	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	El Coyote, Baja California Sur	Mexico	24°18'30.1" 110°14'22.3"	21-08-07	J. Hernández, H. Verbruggen
GC-128*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	El Sausoso, Baja California Sur	Mexico	24°19'47.99" 110°13'59.87"	21-08-07	J. Hernández, H. Verbruggen
GC-130*	<i>Caulerpa</i> sp.	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	El Faro de San Rafael, Baja California Sur	Mexico	24°17'53.37" 110°20'45.36"	27-08-07	J. Hernández, H. Verbruggen
GC-131	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Agua de Yepiz, San Juan de la Costa, Baja California Sur	Mexico	24°35'00" 110°66'00"	01-09-07	C. Valdez
GC-132*	<i>Caulerpa vanbossea</i>	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Agua de Yepiz, San Juan de la Costa, Baja California Sur	Mexico	24°35'00" 110°66'00"	01-09-07	C. Valdez
GC-164*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	El Sargento, Baja California Sur	Mexico	24°4'59.88" 109°58'48"	20-10-07	J.M. Lopez-J. Hernández
GC-165	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	El Sargento, Baja California Sur	Mexico	24°4'59.88" 109°58'48"	20-10-07	J.M. Lopez-J. Hernández
GC-171*	<i>Caulerpa racemosa</i>	<i>Caulerpa cupressoides</i>	Punta Perico, Baja California Sur	Mexico	24°2'3.11" 109°48'18"	28-01-08	J.M. Lopez-J. Hernández

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
GC-187*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Cabo San Lucas, Baja California Sur	Mexico	22°53'14.99" 109°54'0"	29-01-08	J.M. Lopez-J. Hernández
GC-263*	<i>Caulerpa vanbossea</i>	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Mangrove, Isla San Jose, Baja California Sur	Mexico	24° 53' 12" 110° 34' 12.5"	12-02-08	J.M. Lopez-J. Hernández
GC-265*	<i>Caulerpa vanbossea</i>	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Mangrove, Isla San Jose, Baja California Sur	Mexico	26° 53' 12" 112° 34' 12.5"	12-02-08	J.M. Lopez-J. Hernández
GC-273*	<i>Caulerpa vanbossea</i>	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Isla San Jose, behind El Pardo, Baja California Sur	Mexico	24° 51' 10.7" 110° 34' 52.1"	12-02-08	J.M. Lopez-J. Hernández
GC-274	<i>Caulerpa paspaloides</i>	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Isla San Jose, behind El Pardo, Baja California Sur	Mexico	25° 51' 10.7" 111° 34' 52.1"	12-02-08	J.M. Lopez-J. Hernández
GC-277	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Isla San Jose, behind El Pardo, Baja California Sur	Mexico	26° 51' 10.7" 112° 34' 52.1"	12-02-08	J.M. Lopez-J. Hernández
GC-501	<i>Caulerpa verticillata</i>	<i>Caulerpa verticillata</i>	Playa La Concha, Baja California Sur	Mexico	24°12'07.36" 110°18'03.10"	30-04-08	J.M. Lopez-J. Hernández
GC-502*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Mangrove, Balandra, Baja California Sur	Mexico	24°19'04.4" 110°19'10.9"	30-04-08	J.M. Lopez-J. Hernández
GC-614*	<i>Caulerpa</i> sp.	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	San Pedro Nolasco, Sonora	Mexico	27° 58' 2.0" 111° 22' 22.4"	26-05-08	J.M. Lopez-J. Hernández
GC-615*	<i>Caulerpa</i> sp.	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	San Pedro Nolasco, Sonora	Mexico	27° 58' 2.0" 111° 22' 22.4"	26-05-08	J.M. Lopez-J. Hernández
GC-616*	<i>Caulerpa</i> sp.	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	San Pedro Nolasco, Sonora	Mexico	27° 58' 2.0" 111° 22' 22.4"	26-05-08	J.M. Lopez-J. Hernández
GC-687*	<i>Caulerpa vanbossea</i>	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Miramar, Sonora	Mexico	27°54'21.36" 110°57'57.72"	27-05-08	J.M. Lopez-J. Hernández
GC-688*	<i>Caulerpa vanbossea</i>	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Miramar, Sonora	Mexico	27°54'21.36" 110°57'57.72"	27-05-08	J.M. Lopez-J. Hernández
GC-689*	<i>Caulerpa vanbossea</i>	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Miramar, Sonora	Mexico	27°54'21.36" 110°57'57.72"	27-05-08	J.M. Lopez-J. Hernández
GC-717*	<i>Caulerpa</i> sp.	<i>Caulerpa chemnitzia</i>	Playa Norte, Mazatlán	Mexico	23°14'13.68" 110°20'45.36"	09-01-08	R. Riosmena
GC-725*	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Palmilla, San Jose del Cabo, Baja California Sur	Mexico	22°59'23.99" 109°42'0"	11-01-09	R. Riosmena

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
GC-1088*	<i>Caulerpa vanbossea</i>	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Isla San Pedro Martir, Barra baya, Baja California Sur	Mexico	28°38'62.3" 112°31'24.5"	12-05-09	J.M. Lopez-J. Hernández
GC-1089*	<i>Caulerpa vanbossea</i>	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Isla San Pedro Martir, Barra baya, Baja California Sur	Mexico	28°38'62.3" 112°31'24.5"	12-05-09	J.M. Lopez-J. Hernández
GC-1168*	<i>Caulerpa nummularia</i>	<i>Caulerpa chemnitzia</i> ecad <i>vanbossea</i>	Playa El Tecolote, Baja California Sur	Mexico	24°20'23.99" 110°19'11.99"	18-07-09	J.M. Lopez-J. Hernández
HV-1922	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Kashiwajima, Kochi Prefecture, Shikoku	Japan	32.773 -132.625	26-07-09	H. Verbruggen
HV-1923*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Kashiwajima, Kochi Prefecture, Shikoku	Japan	32.773 -132.625	26-07-09	H. Verbruggen
HV-1928*	<i>Caulerpa intermediae laetevirens-peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>intermedia</i>	Kashiwajima, Kochi Prefecture, Shikoku	Japan	32.773 -132.625	26-07-2009	H. Verbruggen
HV-2022*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Shirahama, Wakajama Prefecture, Honshu	Japan	33.578 -135.417	29-07-2009	H. Verbruggen
HV-2030*	<i>Caulerpa racemosa</i> var. <i>peltata</i>	<i>Caulerpa chemnitzia</i> ecad <i>peltata</i>	Shirahama, Wakajama Prefecture, Honshu	Japan	33.578 -135.417	29-07-2009	H. Verbruggen
JAP120*	<i>Caulerpa racemosa</i>	<i>Caulerpa chemnitzia</i> ecad <i>laetevirens</i>	Kyushu, Kagoshima, Nangunn-Motomachi	Japan	31.2632 -130.22	28-07-09	K. Pauly
Others Atlantic							
HV985*	<i>Caulerpa prolifera</i>	<i>Caulerpa prolifera</i>	Florida Keys, Florida	USA	24.893 -80.622	24-08-04	H. Verbruggen
HV986*	<i>Caulerpa ashmeadii</i>	<i>Caulerpa ashmeadii</i>	Florida Keys, Florida	USA	24.893 -80.622	24-08-04	H. Verbruggen
HV987*	<i>Caulerpa racemosa</i>	<i>Caulerpa chemnitzia</i>	Florida Keys, Florida	USA	24.893 -80.622	24-08-04	H. Verbruggen
HV988*	<i>Caulerpa cupressoides</i>	<i>Caulerpa cupressoides</i>	Florida Keys, Florida	USA	24.893 -80.622	24-08-04	H. Verbruggen
BW06031*	<i>Caulerpa cupressoides</i>	<i>Caulerpa cupressoides</i>	Mimbi Timbi, Bocas del Toro	Panama	9.440 -82.280	14-08-09	N. Schubert
BW06111*	<i>Caulerpa cupressoides</i>	<i>Caulerpa cupressoides</i>	Bocas del Toro	Panama		17-08-09	L. Quan-Young
BW06034*	<i>Caulerpa racemosa</i>	<i>Caulerpa chemnitzia</i>	Bocas del Toro	Panama		15-08-09	E. Lacey

Sample Code	Species name based on morphological identification	Species name based on molecular identification	Collecting site	Country	Coordinates (°N-°W)	Collecting date (D-M-Y)	Collector
BW06035*	<i>Caulerpa verticillata</i>	<i>Caulerpa verticillata</i>	STRI Station, Bocas del Toro	Panama	9.352 -82.256	15-08-09	O. Tejada
BW06100*	<i>Caulerpa verticillata</i>	<i>Caulerpa verticillata</i>	Bocas del Toro	Panama		15-08-09	C. Fernández
BW06036*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Bocas del Toro	Panama		15-08-09	C. Fernández
BW06096*	<i>Caulerpa sertularioides</i>	<i>Caulerpa sertularioides</i>	Flat Rock Beach, Bocas del Toro	Panama	9.380 82.238	19-08-09	C. Fernández
BW06099*	<i>Caulerpa racemosa</i>	<i>Caulerpa chemnitzia</i>	Flat Rock Beach, Bocas del Toro	Panama	9.380 82.238	19-08-09	C. Fernández

Tabla S2. Lista de secuencias del género *Caulerpa* de GenBank utilizadas en el análisis de UPGMA.

Table S2. List of GenBank *Caulerpa* sequences used in the UPGMA analysis.

Sequences from GenBank	
C_ambigua_XX_AJ417963_Haw	C_prolifera_GB.FL188_DQ652382_FL
C_ashmeadii_GB.FL064_DQ652363_FL	C_prolifera_GB.FL201_DQ652383_FL
C_ashmeadii_GB.FL065_DQ652364_FL	C_prolifera_GB.FL202_DQ652384_FL
C_ashmeadii_GB.FL066_DQ652365_FL	C_prolifera_GB.FL205_DQ652385_FL
C_ashmeadii_GB.FL130_DQ652367_FL	C_prolifera_GB.FL206_DQ652386_FL
C_ashmeadii_GB.FL171_DQ652368_FL	C_prolifera_GB.FL223_DQ652387_Bah
C_ashmeadii_GB.FL213_DQ652369_FL	C_prolifera_GB.FL242_DQ652389_Bah
C_ashmeadii_GB.FL215_DQ652370_FL	C_prolifera_GB.FL243_DQ652388_FL
C_ashmeadii_GB.FL216_DQ652371_FL	C_prolifera_GB_AJ417942_Indo
C_ashmeadii_GB_AJ417941_FL	C_prolifera_GB_AJ417943_FL
C_bartoniae_G118_FJ810426_RSA	C_racemosa.lae.pel.tur_GB.FL010_DQ652469_FL
C_cactoides_GB_AJ417969_Aus	C_racemosa.lae.pel.tur_GB.FL055_DQ652474_FL
C_cupressoides.lycop_GB_AJ512414_Phil	C_racemosa.lae.pel.tur_GB.FL057_DQ652475_FL
C_cupressoides.lycop_GB_AJ512466_Phil	C_racemosa.lae.pel.tur_GB.FL209_DQ652483_FL
C_cupressoides_GB.FL018_DQ652330_FL	C_racemosa.lae.pel.tur_GB.FL210_DQ652484_FL
C_cupressoides_GB.FL046_DQ652332_Virg	C_racemosa.lae.pel.tur_GB.FL238_DQ652485_Bah
C_cupressoides_GB.FL060_DQ652333_Bah	C_racemosa.lae.pel.tur_GB.FL245_DQ652487_FL
C_cupressoides_GB.FL132_DQ652334_FL	C_racemosa.lae.pel.tur_GB_AJ417948_Pan
C_cupressoides_GB.FL167_DQ652335_FL	C_racemosa.lae.pel.tur_GB_AJ417949_Pan
C_cupressoides_GB.FL176_DQ652336_FL	C_racemosa.lae.pel.tur_GB_AJ417950_Pan
C_cupressoides_GB.FL196_DQ652337_FL	C_racemosa.mucri_GB.FL045_DQ652425_Virg
C_cupressoides_GB.FL203_DQ652338_FL	C_racemosa.mucri_GB.FL108_DQ652426_FL
C_cupressoides_GB.FL222_DQ652340_FL	C_racemosa.mucri_GB.FL159_DQ652429_FL
C_cupressoides_GB.FL229_DQ652343_Bah	C_racemosa.mucri_GB.FL160_DQ652430_FL
C_cupressoides_GB.FL237_DQ652344_Bah	C_racemosa.mucri_GB.FL161_DQ652431_FL
C_cupressoides_GB_AJ417928_Jap	C_racemosa.mucri_GB_AJ417947_Pan
C_cupressoides_GB_AJ417929_StBarth	C_racemosa.mucri_GB_AJ417956_FL
C_cupressoides_GB_AJ417930_AtPan	C_racemosa.mucri_GB_AJ512417_Phil
C_filiformis_GB_AJ417964_Aus	C_racemosa.mucri_GB_AJ512418_Phil
C_flexilis_GB_AJ417970_Aus	C_racemosa.rac.cor.lam_GB_AJ417954_Jap
C_flexilis_GB_AJ512426_Aus	C_racemosa.rac.cor.lam_GB_AJ417957_Egypt
C_integerrima_G086_FJ810425_Isr	C_racemosa.rac.cor.lam_GB_AJ512413_Phil
C_integerrima_G088_FJ810424_Isr	C_racemosa.rac.cor.lam_GB_AJ512423_Phil
C_lanuginosa_GB.FL166_DQ652496_FL	C_racemosa.rac.cor.lam_GB_AJ512424_Phil
C_lanuginosa_GB.FL207_DQ652497_FL	C_racemosa.rac.cor.lam_GB_AJ512425_Phil
C_lanuginosa_GB.FL208_DQ652498_FL	C_racemosa.rac.cor.lam_GB_AJ512467_Phil
C_lanuginosa_GB_AJ417959_FL	C_scalpelliformis_GB_AJ417971_Aus

C_mexicana_GB.FL003_DQ652433_FL	C_scalpelliformis_GB_AJ417972_Leba
C_mexicana_GB.FL005_DQ652434_FL	C_sedoides.geminata_GB_AJ417960_Aus
C_mexicana_GB.FL008_DQ652435_FL	C_sedoides.geminata_GB_AJ417968_Aus
C_mexicana_GB.FL016_DQ652436_FL	C_selago_GB_AJ417973_Egypt
C_mexicana_GB.FL017_DQ652437_FL	C_serrulata_GB_AJ417931_Egypt
C_mexicana_GB.FL020_DQ652438_FL	C_serrulata_GB_AJ417932_Phil
C_mexicana_GB.FL048_DQ652440_FL	C_serrulata_GB_AJ417933_Pan
C_mexicana_GB.FL050_DQ652442_FL	C_serrulata_GB_AJ512411_Phil
C_mexicana_GB.FL068_DQ652443_FL	C_serrulata_GB_AJ512412_Phil
C_mexicana_GB.FL069_DQ652444_FL	C_sertular.brevipes_GB_AJ512420
C_mexicana_GB.FL075_DQ652445_FL	C_sertular.brevipes_GB_AJ512422
C_mexicana_GB.FL077_DQ652446_FL	C_sertular.longipes_GB_AJ512419
C_mexicana_GB.FL177_DQ652452_FL	C_sertular.longipes_GB_AJ512421
C_mexicana_GB.FL191_DQ652453_FL	C_sertular_GB.FL002_DQ652394_FL
C_mexicana_GB.FL192_DQ652454_FL	C_sertular_GB.FL007_DQ652396_FL
C_mexicana_GB.FL195_DQ652455_FL	C_sertular_GB.FL051_DQ652404_FL
C_mexicana_GB.FL198_DQ652456_FL	C_sertular_GB.FL178_DQ652411_FL
C_mexicana_GB.FL199_DQ652457_FL	C_sertular_GB_AJ417944_Mart
C_mexicana_GB.FL214_DQ652458_FL	C_sertular_GB_AJ417945_Pan
C_mexicana_GB.FL221_DQ652459_FL	C_sertular_GB_AJ417946_Pan
C_mexicana_GB.FL232_DQ652460_Bah	C_sertular_HV989_FJ432654_FL
C_mexicana_GB.FL233_DQ652461_Bah	C_sp.1_GB_AJ417962_FL
C_mexicana_GB_AJ417951_Cuba	C_subserrata_GB_AJ417934_Phil
C_mexicana_GB_AJ417952_FL	C_subserrata_GB_AJ417935_Jap
C_mexicana_GB_AJ417953_Egypt	C_taxifolia_GB.CA057_DQ652358
C_microphysa_GB.FL146_DQ652520_Hond	C_taxifolia_GB.FL131_DQ652361_FL
C_microphysa_GB_AJ417961_TX	C_taxifolia_GB_AJ417936_Aus
C_paspaloides_GB.FL013_DQ652499_FL	C_taxifolia_GB_AJ417937_Egy
C_paspaloides_GB.FL072_DQ652500_FL	C_taxifolia_GB_AJ417938_PueRi
C_paspaloides_GB.FL078_DQ652501_FL	C_taxifolia_GB_AJ417939_KZN
C_paspaloides_GB.FL172_DQ652505_FL	C_taxifolia_GB_AJ417940_Aus.distichophylla
C_paspaloides_GB.FL173_DQ652506_FL	C_taxifolia_GB_DQ652356
C_paspaloides_GB.FL190_DQ652507_FL	C_verticillata_GB.FL006_DQ652525_FL
C_paspaloides_GB.FL220_DQ652508_FL	C_verticillata_GB.FL009_DQ652526_FL
C_paspaloides_GB.FL240_DQ652509_Bah	C_verticillata_GB.FL015_DQ652527_FL
C_paspaloides_GB_AJ417965_FL	C_verticillata_GB.FL021_DQ652528_FL
C_prolifera_GB.FL053_DQ652374_FL	C_verticillata_GB.FL175_DQ652530_FL
C_prolifera_GB.FL054_DQ652375_FL	C_verticillata_GB_AJ417967_FL
C_prolifera_GB.FL157_DQ652379_FL	C_webbiana_GB_AJ417958_Egyp
C_prolifera_GB.FL174_DQ652380_FL	C_webbiana_GB_AJ417966_KZN
C_prolifera_GB.FL184_DQ652381_FL	

Tabla S3. Listado de especímenes colectados del género *Padina* del Pacífico Tropical Oriental.
 Table S3. List of *Padina* specimens collected from the Eastern Tropical Pacific.

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFES-015	<i>Padina durvillei</i>	1-2 m	Pirigallo Sur, Golfo de Fonseca, La Unión	El Salvador	13°10'00.2"N 87°41'08.7"W	22-01-09	C. Fernández, A. Planas
CFES-021	<i>Padina durvillei</i>	2-3 m	Pirigallo Oeste, Golfo de Fonseca, La Unión	El Salvador	13°10'27.6"N 87°41'14.3"W	22-01-09	C. Fernández, A. Planas
CFES-025	<i>Padina durvillei</i>	2-3 m	Pirigallo Este, Golfo de Fonseca, La Unión	El Salvador	13°10'27.6"N 87°41'14.3"W	22-01-09	C. Fernández, A. Planas
CFES-029	<i>Padina durvillei</i>	1-2 m	Pirigallo Este, Golfo de Fonseca, La Unión	El Salvador	13°10'27.6"N 87°41'14.3"W	22-01-09	C. Fernández, A. Planas
CFES-036	<i>Padina durvillei</i>	1-3 m	Suroeste Isla Meanguera, Golfo de Fonseca, La Unión	El Salvador	13°10'8.8"N 87°43'22.2"W	22-01-09	C. Fernández, A. Planas
CFES-048	<i>Padina durvillei</i>	1-2 m	Suroeste Isla Meanguera, Golfo de Fonseca, La Unión	El Salvador	13°10'8.8"N 87°43'22.2"W	22-01-09	C. Fernández, A. Planas
CFES-057	<i>Padina caulescens</i>	Intertidal	El Pital, La Libertad	El Salvador	13°30'44.0"N 89°36'15.6"W	27-01-09	C. Fernández, A. Planas
CFES-073	<i>Padina caulescens</i>	Intertidal	La Vega, La Libertad	El Salvador	13°29'56.4" N 89°28'55.7" W	28-01-09	C. Fernández, A. Planas
CFES-075	<i>Padina caulescens</i>	Intertidal	La Vega, La Libertad	El Salvador	13°29'56.4" N 89°28'55.7" W	28-01-09	C. Fernández, A. Planas
CFES-086	<i>Padina caulescens</i>	Intertidal	Playa El Faro, Los Cobanos	El Salvador	13°31'19.3"N 89°48'26.7"W	30-01-09	C. Fernández, A. Planas
CFES-109	<i>Padina caulescens</i>	2-3 m	Frente al Hotel De Cameron, Poza salinas, Los Cóbano	El Salvador	13°31'47.0"N 89°49'09.6"W	31-01-09	C. Fernández, A. Planas
CFES-147	<i>Padina caulescens</i>	Intertidal	Playa El Privado, Los Cóbano	El Salvador	13°31'38.0"N 89°48'40.8"W	01-02-09	C. Fernández, A. Planas
CFES-149	<i>Padina caulescens</i>	Intertidal	Playa El Privado, Los Cóbano	El Salvador	13°31'38.0"N 89°48'40.8"W	01-02-09	C. Fernández, A. Planas
CFES-150	<i>Padina caulescens</i>	Intertidal	Playa El Privado, Los Cóbano	El Salvador	13°31'38.0"N 89°48'40.8"W	01-02-09	C. Fernández, A. Planas

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFES-157	<i>Padina durvillei</i>	2-3 m	Playa Maculiz, La Unión	El Salvador	13°09'4.2"N 87°55'19.6"W	07-02-09	C. Fernández, J.J. Alvarado
CFMX-184	<i>Padina mexicana</i>	1-3 m	Playa El Panteon, Puerto Angel, Oaxaca	Mexico	15°39.842N 96°29.725W	13-02-09	C. Fernández
CFMX-187	<i>Padina caulescens</i>	1-3 m	Playa El Panteon, Puerto Angel, Oaxaca	Mexico	15°39.842N 96°29.725W	13-02-09	C. Fernández
CFMX-190	<i>Padina durvillei</i>	1-3 m	Playa El Panteon, Puerto Angel, Oaxaca	Mexico	15°39.842N 96°29.725W	13-02-09	C. Fernández
CFMX-203	<i>Padina concrescens</i>	2-3m	Togolunda, Bahía de Huatulco, Oaxaca	Mexico	15°39.900N 96°29.775W	14-02-09	C. Fernández
CFMX-205	<i>Padina concrescens</i>	2-3m	Togolunda, Bahía de Huatulco, Oaxaca	Mexico	15°39.900N 96°29.775W	14-02-09	C. Fernández
CFMX-208	<i>Padina caulescens</i>	Intertidal	Togolunda, Bahía de Huatulco, Oaxaca	Mexico	15°39.900N 96°29.775W	14-02-09	C. Fernández
CFMX-220	<i>Padina durvillei</i>	2-3 m	Mazunte, Oaxaca	Mexico	15°39.705N 96°33.365W	15-02-09	C. Fernández
CFMX-233	<i>Padina durvillei</i>	2-4 m	Puerto Angelito, Oaxaca	Mexico	15°51.432N 97°04.464W	16-02-09	C. Fernández
CFMX-247	<i>Padina concrescens</i>	3-4 m	Puerto Escondido, Oaxaca	Mexico	15°51.453N 97°03.940W	17-02-09	C. Fernández
CFMX-256	<i>Padina durvillei</i>	3 m	NW de la Isla Roqueta 1, Acapulco, Guerrero	Mexico	16°49.504N 99°54.668W	19-02-09	C. Fernández
CFMX-289	<i>Padina mexicana</i>	Intertidal	Playa del Palmar, Ixtapa	Mexico	17°39.139N 101°36.019W	21-02-09	C. Fernández
CFMX-306	<i>Padina concrescens</i>	7-13 m	Caleta de Chon, Zihuatanejo	Mexico	17°36.938N 101°33.314W	22-02-09	C. Fernández
CFMX-324	<i>Padina mexicana</i>	Intertidal	Playa La Audiencia, Manzanillo	Mexico	19°06.300N 104°21.122W	23-02-09	C. Fernández
CFMX-325	<i>Padina caulescens</i>	Intertidal	Playa La Audiencia, Manzanillo	Mexico	19°06.300N 104°21.122W	23-02-09	C. Fernández
CFMX-328	<i>Padina caulescens</i>	Intertidal	Playa La Audiencia, Manzanillo	Mexico	19°06.300N 104°21.122W	23-02-09	H. Verbruggen

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFMX-334	<i>Padina conrescens</i>	6-9 m	Roca Elefante, Manzanillo	Mexico	19°05.391N 104°23.651W	24-02-09	C. Fernández
CFMX-363	<i>Padina durvillei</i>	Intertidal	Playa Mismaloya, Puerto Vallarta, Jalisco	Mexico	20°31.927N 105°17.598W	26-02-09	C. Fernández
CFMX-364	<i>Padina mexicana</i>	Intertidal	Playa Mismaloya, Puerto Vallarta, Jalisco	Mexico	20°31.927N 105°17.598W	26-02-09	C. Fernández
CFMX-384	<i>Padina durvillei</i>	6-8 m	Majahuitas, Puerto Vallarta, Jalisco	Mexico	20°30.410N 105°23.571W	28-02-09	C. Fernández
CFMX-394	<i>Padina conrescens</i>	5-9 m	Caletas, Puerto Vallarta, Jalisco	Mexico	20°30.299N 105°22.480W	28-02-09	C. Fernández
CFMX-403	<i>Padina conrescens</i>	9 m	Bajo del Cristo, cerca de los arcos, Puerto Vallarta, Jalisco	Mexico	20°32.797N 105°17.269W	28-02-09	C. Fernández
CFPA-416	<i>Padina durvillei</i>	5-6 m	Islotes antes de Saboga, Archipiélago de las Perlas	Panama	8°38.787N 79°03.314W	04-06-09	C. Fernandez
CFPA-420	<i>Padina durvillei</i>	6 m	Isla Saboga, Archipiélago de las Perlas	Panama	8°37.732N 79°03.309W	04-06-09	C. Fernandez
CFPA-426	<i>Padina durvillei</i>	6.5 m	Isla Pacheca, Archipiélago de las Perlas	Panama	8°39.729N 79°03.199W	04-06-09	C. Fernandez
CFPA-436	<i>Padina durvillei</i>	2-3 m	Otoque Sur, Archipiélago de las Perlas	Panama	8°34.059N 79°35.454W	10-06-09	C. Fernandez
CFPA-457	<i>Padina durvillei</i>	2-3 m	Isla Taboga, Archipiélago de las Perlas	Panama	8°47.363N 79°32.739W	17-06-09	C. Fernandez
CFPA-477	<i>Padina durvillei</i>	1-2 m	Isla Mogo-Mogo, Archipiélago de las Perlas	Panama	8°34.692N 79°01 698W	24-06-09	C. Fernández
CFPA-486	<i>Padina durvillei</i>	1-2 m	Isla Contadora, Archipiélago de las Perlas	Panama	8°37.681N 79°01.628W	24-06-09	C. Fernández
CFPA-496	<i>Padina durvillei</i>	2-3 m	Islote Trapiche, Isla Pedro González, Archipiélago de las Perlas	Panama	8°25.554N 79°06.549W	25-06-09	C. Fernández
CFPA-499	<i>Padina durvillei</i>	1-3 m	Isla Bayoneta, Archipiélago de las Perlas	Panama	8°29'15.29N 79°04'03.53"W	25-06-09	C. Fernández

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFNI-505	<i>Padina caulescens</i>	Intertidal	Playa El Tránsito, León	Nicaragua	12° 02' 54.2"N 86° 42' 17.0"W	30-06-09	C. Fernández, A. Alvarez, JJ Alvarado, J. Aguirre
CFNI-521	<i>Padina caulescens</i>	Intertidal	Playa El Tránsito, León	Nicaragua	12° 02' 54.2"N 86° 42' 17.0"W	30-06-09	C. Fernández, A. Alvarez, JJ Alvarado, J. Aguirre
CFNI-534	<i>Padina conrescens</i>	17.5 m	La Flor, San Juan del sur, Rivas	Nicaragua	11°08'09.0"N 85°48'04.2"W	02-07-09	C. Fernández
CFNI-546	<i>Padina durvillei</i>	13 m	La Cagada, San Juan del Sur, Rivas	Nicaragua	11°07'23.7"N 85°47'43.1"W	02-07-09	C. Fernández
CFNI-549	<i>Padina conrescens</i>	13 m	La Cagada, San Juan del Sur, Rivas	Nicaragua	11°07'23.7"N 85°47'43.1"W	02-07-09	C. Fernández
CFNI-563	<i>Padina conrescens</i>	13 m	La Cagada, San Juan del Sur, Rivas	Nicaragua	11°07'23.7"N 85°47'43.1"W	02-07-09	J. Aguirre
CFNI-564	<i>Padina conrescens</i>	11 m	La Peña Rota, Rivas	Nicaragua	11°14'00.3"N 85°52'01.5"W	02-07-09	C. Fernández
CFNI-578	<i>Padina conrescens</i>	11 m	La Peña Rota, Rivas	Nicaragua	11°14'00.3"N 85°52'01.5"W	02-07-09	C. Fernández
CFNI-595	<i>Padina conrescens</i>	11 m	Gigante, Rivas	Nicaragua	11°23'07.9"N 86°02'12.4"W	03-07-09	C. Fernandez
CFNI-607	<i>Padina caulescens</i>	11 m	Gigante, Rivas	Nicaragua	11°23'07.9"N 86°02'12.4"W	03-07-09	J. Aguirre
CFNI-628	<i>Padina conrescens</i>	5.5 m	Guacalito, Rivas	Nicaragua	11°21'17.3"N 86°00'06.9"W	03-07-09	C. Fernandez, J. Aguirre
CFNI-656	<i>Padina conrescens</i>	7.6 m	Punta El Clavo, Rivas	Nicaragua	11°19'12.6"N 85°56'43.0"W	04-07-09	J. Aguirre
CFNI-697	<i>Padina caulescens</i>	Intertidal	Pochomil, Managua	Nicaragua	11°45'28.1"N 86°29'32.5"W	05-07-09	C. Fernandez, A. Alvarez, JJ Alvarado, J. Aguirre

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFNI-706	<i>Padina mexicana</i>	Intertidal	Masachapa, Managua	Nicaragua	11°47'01.3"N 86°31'03.3"W	06-07-09	C. Fernandez
CFNI-712	<i>Padina conrescens</i>	Intertidal	Masachapa, Managua	Nicaragua	11°47'01.3"N 86°31'03.3"W	06-07-09	C. Fernandez
CFNI-721	<i>Padina durvillei</i>	Intertidal	Masachapa, Managua	Nicaragua	11°47'01.3"N 86°31'03.3"W	06-07-09	C. Fernandez
CFNI-748	<i>Padina durvillei</i>	Intertidal	Playa Hermosa, León Roca Tres Hermanas, Parque Nacional Marino Ballena,	Nicaragua	12°06'21.7"N 86°44'09.2W	09-07-09	C. Fernandez
CFCR-768	<i>Padina caulescens</i>	3-4 m	Puntarenas Roca Tres Hermanas, Parque Nacional Marino Ballena,	Costa Rica	09°06'14.84"N 83°42'28.30"W	16-07-09	C. Fernández
CFCR-776	<i>Padina caulescens</i>	3-4 m	Puntarenas Roca Tres Hermanas, Parque Nacional Marino Ballena,	Costa Rica	09°06'14.84"N 83°42'28.30"W	17-07-09	C. Fernández
CFCR-777	<i>Padina conrescens</i>	3-4 m	Puntarenas Bajo Tres Hermanas, Parque Nacional Marino Ballena,	Costa Rica	09°06'14.84"N 83°42'28.30"W	16-07-09	C. Fernández
CFCR-782	<i>Padina conrescens</i>	4-5 m	Puntarenas Bajo Tres Hermanas, Parque Nacional Marino Ballena,	Costa Rica	09°06'25.65"N 83°42'39.33"W	16-07-09	C. Fernández
CFCR-783	<i>Padina caulescens</i>	4-5 m	Puntarenas	Costa Rica	09°06'25.65"N 83°42'39.33"W	16-07-09	C. Fernández
CFCR-783	<i>Padina conrescens</i>			Costa Rica			
CFCR-787	<i>Padina caulescens</i>	4-5 m	Bajo Tres Hermanas, Parque Nacional Marino Ballena, Puntarenas	Costa Rica	09°06'25.65"N 83°42'39.33"W	16-07-09	C. Fernández
CFCR-799	<i>Padina mexicana</i>	Intertidal	Punta Dominicalito, Puntarenas Cueva del tiburón, Reserva Biológica Isla del Caño,	Costa Rica	09°13'15.7"N 83°50'19.0"W	16-07-09	C. Fernández
CFCR-820	<i>Padina mexicana</i>	8 m	Puntarenas	Costa Rica	08°42'45.7N 83°53'23.2"W	20-07-09	C. Fernández
CFCR-833a	<i>Padina conrescens</i>	2-3 m	San Josecito, Puntarenas	Costa Rica	8°40'15.4"N 83°43'6.5"W	21-07-09	C. Fernández

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFCR-851	<i>Padina conrescens</i>	7 m	Isla Despensa, Bahía Salinas, Guanacaste	Costa Rica	11°00'09.5"N 85°44'51.2"W	28-07-09	C. Fernández, Andrea Planas
CFCR-868	<i>Padina durvillei</i>	4 m	Punta Arenita, Bahía Culebra, Guanacaste	Costa Rica	10°36'17.2"N 85°38'54.1"W	30-07-09	A. Planas, J.J. Alvarado, Celeste Sanchez
CFCR-882	<i>Padina conrescens</i>	5-6 m	Bahía Virador, Bahía Culebra, Guanacaste	Costa Rica	10°36'51.6"N 85°41'25.0"W	01-08-09	A. Planas, J.J. Alvarado, Celeste Sanchez
CFCR-895	<i>Padina durvillei</i>	9-10 m	Los Conejos, Parque Nacional Marino Las Baulas, Guancaste	Costa Rica	10°22'05.2"N 85°51'52.9"W	02-08-09	C. Fernández, A. Planas
CFCR-903	<i>Padina conrescens</i>	13 m	Isla Negritos, Golfo de Nicoya, Puntarenas	Costa Rica	09°48'59.2"N 84°51'48.7"W	03-08-09	C. Fernández, A. Planas
CFCR-905	<i>Padina conrescens</i>	13 m	Isla Negritos, Golfo de Nicoya, Puntarenas	Costa Rica	09°48'59.2"N 84°51'48.7"W	03-08-09	C. Fernández, A. Planas
CFCR-915	<i>Padina sp</i>	12 m	Tolinga, Lado Sur de Islas Tortugas, Golfo de Nicoya, Puntarenas	Costa Rica	09°45'50.3"N 84°53'51.1"W	03-08-09	C. Fernández, A. Planas
CFCR-910	<i>Padina conrescens</i> , <i>Vaughaniella stage</i>	12 m	Tolinga, Lado Sur de Islas Tortugas, Golfo de Nicoya, Puntarenas	Costa Rica	09°45'50.3"N 84°53'51.1"W	03-08-09	C. Fernández
CFCR-1003	<i>Padina mexicana</i>	3-4 m	Isla Uva, Golfo Chiriquí	Panama	07°48'57"N 81°45'33"W	22-06-10	C. Fernandez
CFPA-1006		3-4 m	Coiba Noreste, Golfo de Chiriquí	Panama	07°38'01"N 81°44'9.5"W	22-06-10	C. Fernandez
CFPA-1010		5.5 m	Jicarita, Golfo de Chiriquí	Panama	07°12'49.1"N 81°47'57.0"W	23-06-10	C. Fernandez
BW-4675	<i>Padina mexicana</i>	2 m	Servimarina I canales de tierra	Panama	7.74438N 81.57861W	Ene-11	C. Fernandez
BW-4926	<i>Padina conrescens</i>		Punta Cirilo	Panama	7.58898N 81.83492W	Ene-11	C. Fernandez

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
BW-4641	<i>Padina conrescens</i>		Isla Burica	Panama	8.01865N 82.88390W	Ene-11	C. Fernandez
BW-4598	<i>Padina caulescens</i>		Punta Burica	Panama	8.03042N 82.87574W	Ene-11	C. Fernandez, N. León
BW-4602	<i>Padina mexicana</i>		Punta Burica	Panama	8.03042N 82.87574W	Ene-11	C. Fernandez, N. León
CFMX-1021	<i>Padina durvillei</i>	1 m	San Juan de la Costa, Baja California Sur	Mexico	24°15'38.17"N 110°36'48.15"W	28-08-11	C. Fernández
CFMX-1022	<i>Padina mexicana</i>	1 m	San Juan de la Costa, Baja California Sur	Mexico	24°15'38.17"N 110°36'48.15"W	28-08-11	C. Fernández
AM-005	<i>Padina mexicana</i>	Intertidal	Calerita, Golfo de California, Baja California Sur Puertecitos, San Luis	Mexico	24°21' N 110°16' W	22-11-07	J. Hernández Kantún
AM-307	<i>Padina arborescens</i>	Intertidal	Gonzaga, Golfo de California, Baja California Sur Puertecitos, San Luis	Mexico	29°48'53"N 114°23'16"W	24-02-08	J. Hernández Kantún
AM-308	<i>Padina arborescens</i>	Intertidal	Gonzaga, Golfo de California, Baja California Sur Puertecitos, San Luis	Mexico	29°48'53"N 114°23'16"W	24-02-08	J. Hernández Kantún
AM-309	<i>Padina arborescens</i>	Intertidal	Gonzaga, Golfo de California, Baja California Sur	Mexico	29°48'53"N 114°23'16"W	24-02-08	J. Hernández Kantún
AM-391	<i>Padina</i>	Intertidal	Playa El Huerfanito, Golfo de California, Baja California Sur	Mexico	29°50'22"N 114°18'0"W	25-02-08	G. Andrade
AM-392	<i>Padina</i>	Intertidal	Playa El Huerfanito, Golfo de California, Baja California Sur	Mexico	29°50'22"N 114°18'0"W	25-02-08	G. Andrade
AM-393	<i>Padina</i>	Intertidal	Playa El Huerfanito, Golfo de California, Baja California Sur	Mexico	29°50'22"N 114°18'0"W	25-02-08	G. Andrade
AM-442	<i>Padina</i>	Intertidal	Isla Miramar, Golfo de California, Sonora	Mexico	27°55'114"N 110°56'50"W	25-02-08	I. Pacheco
AM-443	<i>Padina</i>	Intertidal	Isla Miramar, Golfo de California, Sonora	Mexico	27°55'114"N 110°56'50"W	25-02-08	I. Pacheco
AM-444	<i>Padina</i>	Intertidal	Isla Miramar, Golfo de California, Sonora	Mexico	27°55'114"N 110°56'50"W	25-02-08	I. Pacheco

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
AM-541	<i>Padina arborescens</i>	Intertidal	Isla San Pedro Martir, Golfo de California, Baja California Sur	Mexico	28°24'56"N 112°16'22"W	29-10-08	COBI
AM-716	<i>Padina durvillei</i>	Intertidal	Los Cerritos, Sinaloa	Mexico		09-01-08	R. Riosmena-Rodríguez
AM-971	<i>Padina sp 3</i>	7 m	La Guanera, Isla Natividad, Baja California Sur	Mexico	27°53'06.13"N 115°10'27.22"W	28-03-09	A. Suarez
AM-1030	<i>Padina arborescens</i>	Intertidal	Las Cuevas, Isla Natividad, Baja California Sur	Mexico	27°50'57.85"N 115°10'27.22"W	31-03-09	R. Riosmena-Rodríguez

Tabla S4. Listado de especímenes colectados del género *Dictyota* del Pacífico Tropical Oriental.
 Table S4. List of *Dictyota* specimens collected from the Eastern Tropical Pacific.

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFES-016	<i>Dictyota stolonifera</i>	1-2 m	Pirigallo Sur, Golfo de Fonseca, La Unión	El Salvador	13°10'00.2"N 87°41'08.7"W	22-01-09	C. Fernández A. Planas
CFES-023	<i>Dictyota centroamericana</i>	2-3 m	Pirigallo Oeste, Golfo de Fonseca, La Unión	El Salvador	13°10'27.6"N 87°41'14.3"W	22-01-09	C. Fernández A. Planas
CFES-034	<i>Dictyota humifusa</i>	1-2 m	Isla Meanguera, Playa Mahaul, Golfo de Fonseca, La Unión	El Salvador	13°10'02.9"N 87°42'55.1"W	22-01-09	C. Fernández A. Planas
CFES-039	<i>Dictyota humifusa</i>	1-3 m	Suroeste Isla Meanguera	El Salvador	13°10'8.8"N 87°43'22.2"W	22-01-09	C. Fernández A. Planas
CFES-042	<i>Dictyota humifusa</i>	1-3 m	Suroeste Isla Meanguera	El Salvador	13°10'8.8"N 87°43'22.2"W	22-01-09	C. Fernández A. Planas
CFES-059	<i>Dictyota centroamericana</i>	Intertidal	El Pital, La Libertad	El Salvador	13°30'44.0"N 89°36'15.6"W	27-01-09	C. Fernández A. Planas
CFES-153	<i>Dictyota humifusa</i>	7-8 m	La Pared, Los Cobanos	El Salvador	13°30'10.9"N 89°48'40.3"W	02-02-09	C. Fernández A. Planas
CFES-155	<i>Dictyota centroamericana</i>		La Loredona, Los Cobanos	El Salvador	13°30'56"N 89°50'26.9"W	03-02-09	C. Fernández A. Planas
CFES-175	<i>Dictyota stolonifera</i>	2-3 m	Playa Maculiz	El Salvador	13°09'4.2"N 87°55'19.6"W	07-02-09	C. Fernández J.J. Alvarado
CFES-177	<i>Dictyota stolonifera</i>	2-3 m	Playa Maculiz	El Salvador	13°09'4.2"N 87°55'19.6"W	07-02-09	C. Fernández J.J. Alvarado
CFES-180	<i>Dictyota stolonifera</i>	2-3 m	Playa Maculiz	El Salvador	13°09'4.2"N 87°55'19.6"W	07-02-09	C. Fernández J.J. Alvarado
CFMX-182	<i>Dictyota ceylanica</i>	1-3 m	Playa El Panteon, Puerto Angel, Oaxaca	México	15°39.842N 96°29.725W	13-02-09	C. Fernández
CFMX-186	<i>Dictyota humifusa</i>	1-3 m	Playa El Panteon, Puerto Angel, Oaxaca	México	15°39.842N 96°29.725W	13-02-09	C. Fernández
CFMX-189	<i>Dictyota ceylanica</i>	1-3 m	Playa El Panteon, Puerto Angel, Oaxaca	México	15°39.842N 96°29.725W	13-02-09	C. Fernández

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFMX-196	<i>Dictyota ceylanica</i>	1-3 m	Playa El Panteon, Puerto Angel, Oaxaca	México	15°39.842N 96°29.725W	13-02-09	C. Fernández
CFMX-199	<i>Dictyota humifusa</i>	2-3m	Togolunda, Bahía de Huatulco, Oaxaca	México	15°39.900N 96°29.775W	14-02-09	C. Fernández
CFMX-200	<i>Dictyota humifusa</i>	2-3m	Togolunda, Bahía de Huatulco, Oaxaca	México	15°39.900N 96°29.775W	14-02-09	C. Fernández
CFMX-201	<i>Dictyota humifusa</i>	2-3m	Togolunda, Bahía de Huatulco, Oaxaca	México	15°39.900N 96°29.775W	14-02-09	C. Fernández
CFMX-206	<i>Dictyota crenulata</i>	Intertidal	Togolunda, Bahía de Huatulco, Oaxaca	México	15°39.900N 96°29.775W	14-02-09	C. Fernández
CFMX-207	<i>Dictyota stolonifera</i>	Intertidal	Togolunda, Bahía de Huatulco, Oaxaca	México	15°39.900N 96°29.775W	14-02-09	C. Fernández
CFMX-213	<i>Dictyota humifusa</i>	2-3m	Mazunte, Oaxaca	México	15°39.705N 96°33.365W	15-02-09	C. Fernández
CFMX-219	<i>Dictyota ceylanica</i>	4 m	Mazunte, Oaxaca	México	15°39.705N 96°33.365W	15-02-09	C. Fernández
CFMX-221	<i>Dictyota stolonifera</i>	Intertidal	Mazunte, Oaxaca	México	15°39.705N 96°33.365W	15-02-09	C. Fernández
CFMX-227	<i>Dictyota crenulata</i>	2-3 m	Mazunte, Oaxaca	México	15°39.705N 96°33.365W	15-02-09	H. Verbruggen
CFMX-234	<i>Dictyota ceylanica</i>	2-4 m	Puerto Angelito, Oaxaca	México	15°51.432N 97°04.464W	16-02-09	C. Fernández
CFMX-235	<i>Dictyota ceylanica</i>	2-4 m	Puerto Angelito, Oaxaca	México	15°51.432N 97°04.464W	16-02-09	C. Fernández
CFMX-237	<i>Dictyota humifusa</i>	2-4 m	Puerto Angelito, Oaxaca	México	15°51.432N 97°04.464W	16-02-09	C. Fernández
CFMX-243	<i>Dictyota humifusa</i>	5-7 m	Puerto Escondido 1, Oaxaca	México	15°51.453N 97°03.940W	17-02-09	C. Fernández
CFMX-244	<i>Dictyota ceylanica</i>	5-7 m	Puerto Escondido 1, Oaxaca	México	15°51.453N 97°03.940W	17-02-09	C. Fernández
CFMX-248	<i>Dictyota ceylanica</i>	3-4 m	Puerto Escondido 1, Oaxaca	México	15°51.453N 97°03.940W	17-02-09	C. Fernández

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFMX-266	<i>Dictyota ceylanica</i>	10 m	NW de la Isla Roqueta, Acapulco, Guerrero	México	16° 49.430 99° 54.731	20-02-09	C. Fernández
CFMX-268	<i>Dictyota ceylanica</i>	10 m	NW de la Isla Roqueta, Acapulco, Guerrero	México	16° 49.430 99° 54.731	20-02-09	C. Fernández
CFMX-269	<i>Dictyota ceylanica</i>	10 m	NW de la Isla Roqueta, Acapulco, Guerrero	México	16° 49.430 99° 54.731	20-02-09	C. Fernández
CFMX-270	<i>Dictyota stolonifera</i>	10 m	NW de la Isla Roqueta, Acapulco, Guerrero	México	16° 49.430 99° 54.731	20-02-09	C. Fernández
CFMX-271	<i>Dictyota humifusa</i>	9 m	Otro lado del canal (continente), Acapulco, Guerrero	México	16°49.630N 99°54.715W	20-02-09	C. Fernández
CFMX-275	<i>Dictyota humifusa</i>	10 m	Isla de la Virgen, Acapulco, Guerrero	México	16°49'26.85"N99°54'01.32"W	20-02-09	C. Fernández
CFMX-277	<i>Dictyota stolonifera</i>	10 m	Isla de la Virgen, Acapulco, Guerrero	México	16°49'26.85"N99°54'01.32"W	20-02-09	C. Fernández
CFMX-294	<i>Dictyota ceylanica</i>	5-7 m	Manzanillo, Zihuatanejo, Guerrero	México	17°37.260N 101°31.300W	22-02-09	C. Fernández
CFMX-295	<i>Dictyota stolonifera</i>	5-7 m	Manzanillo, Zihuatanejo, Guerrero	México	17°37.260N 101°31.300W	22-02-09	C. Fernández
CFMX-299	<i>Dictyota ceylanica</i>	5-7 m	Manzanillo, Zihuatanejo, Guerrero	México	17°37.260N 101°31.300W	22-02-09	C. Fernández
CFMX-310	<i>Dictyota ceylanica</i>	8.8 m	Playa Las Gatas, Zihuatanejo, Guerrero	México	17°37.351N 101°33.333W	22-02-09	C. Fernández
CFMX-318	<i>Dictyota adpressa</i>	Intertidal	Playa La Audiencia, Manzanillo, Colima	México	19°06.300N 104°21.122W	23-02-09	C. Fernández
CFMX-321	<i>Dictyota crenulata</i>	Intertidal	Playa La Audiencia, Manzanillo, Colima	México	19°06.300N 104°21.122W	23-02-09	C. Fernández
CFMX-323	<i>Dictyota crenulata</i>	Intertidal	Playa La Audiencia, Manzanillo, Colima	México	19°06.300N 104°21.122W	23-02-09	C. Fernández
CFMX-329	<i>Dictyota stolonifera</i>	6-9 m	Roca Elefante, Manzanillo, Colima	México	19°05.391N 104°23.651W	24-02-09	C. Fernández
CFMX-331	<i>Dictyota ceylanica</i>	6-9 m	Roca Elefante, Manzanillo, Colima	México	19°05.391N 104°23.651W	24-02-09	C. Fernández

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFMX-332	<i>Dictyota stolonifera</i>	6-9 m	Roca Elefante, Manzanillo, Colima	México	19°05.391N 104°23.651W	24-02-09	C. Fernández
CFMX-336	<i>Dictyota humifusa</i>	6-9 m	Roca Elefante, Manzanillo, Colima	México	19°05.391N 104°23.651W	24-02-09	C. Fernández
CFMX-341	<i>Dictyota ceylanica</i>	8 m	Roca Elefante, Manzanillo, Colima	México	19°05.913N 104°23.415W	24-02-09	C. Fernández
CFMX-342	<i>Dictyota ceylanica</i>	8 m	Roca Elefante, Manzanillo, Colima	México	19°05.913N 104°23.415W	24-02-09	C. Fernández
CFMX-343	<i>Dictyota stolonifera</i>	8 m	Roca Elefante, Manzanillo, Colima	México	19°05.913N 104°23.415W	24-02-09	C. Fernández
CFMX-370	<i>Dictyota ceylanica</i>	1.5 m	Playa Careyero, Pta Mita, Puerto Vallarta, Jalisco	México	20°47.059N 105°30.710W	27-02-09	C. Fernández
CFMX-372	<i>Dictyota ceylanica</i>	1.5 m	Playa Careyero, Pta Mita, Puerto Vallarta, Jalisco	México	20°47.059N 105°30.710W	27-02-09	C. Fernández
CFMX-373	<i>Dictyota mexicana</i>	1.5 m	Playa Careyero, Pta Mita, Puerto Vallarta, Jalisco	México	20°47.059N 105°30.710W	27-02-09	C. Fernández
CFMX-374	<i>Dictyota ceylanica</i>	1.5 m	Playa Careyero, Pta Mita, Puerto Vallarta, Jalisco	México	20°47.059N 105°30.710W	27-02-09	C. Fernández
CFMX-382	<i>Dictyota stolonifera</i>	6-8 m	Majahuitas, Puerto Vallarta, Jalisco	México	20°30.410N 105°23.571W	28-02-09	C. Fernández
CFMX-383	<i>Dictyota stolonifera</i>	6-8 m	Majahuitas, Puerto Vallarta, Jalisco	México	20°30.410N 105°23.571W	28-02-09	C. Fernández
CFMX-389	<i>Dictyota azureus</i>	5-9 m	Caletas, Puerto Vallarta, Jalisco	México	20°30.299N 105°22.480W	28-02-09	C. Fernández
CFMX-393	<i>Dictyota crenulata</i>	5-9 m	Caletas, Puerto Vallarta, Jalisco	México	20°30.299N 105°22.480W	28-02-09	C. Fernández
CFMX-401	<i>Dictyota stolonifera</i>	10 m	Colomitos, Puerto Vallarta, Jalisco	México	20°30.755N 105°19.532W	28-02-09	C. Fernández
CFPA-413	<i>Dictyota centroamericana</i>	5-6 m	Islotes antes de Saboga	Panamá	8°38.787N 79°03.314W	04-06-09	C. Fernandez
CFPA-414	<i>Dictyota humifusa</i>	5-6 m	Islotes antes de Saboga	Panamá	8°38.787N 79°03.314W	04-06-09	C. Fernandez

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFPA-415	<i>Dictyota centroamericana</i>	5-6 m	Islotes antes de Saboga	Panamá	8°38.787N 79°03.314W	04-06-09	C. Fernandez
CFPA-419	<i>Dictyota humifusa</i>	6 m	Isla Saboga	Panamá	8°37.732N 79°03.309W	04-06-09	C. Fernandez
CFPA-432	<i>Dictyota humifusa</i>	6.5 m	Isla Pacheca	Panamá	8°39.729N 79°03.199W	04-06-09	C. Fernandez
CFPA-437	<i>Dictyota centroamericana</i>	2-3 m	Otoque Sur	Panamá	8°34.059N 79°35.454W	10-06-09	C. Fernandez
CFPA-445	<i>Dictyota humifusa</i>	2-3 m	Isla Urabá	Panamá	8°46.933N 79°32.178W	10-06-09	C. Fernandez
CFPA-452	<i>Dictyota centroamericana</i>	6-9m	Isla Taboguilla	Panamá	8°48.162N 79°34.082W	17-06-09	C. Fernandez
CFPA-458	<i>Dictyota humifusa</i>	2-3m	Isla Taboga	Panamá	8°47.363N 79°32.739W	17-06-09	C. Fernandez
CFPA-463	<i>Dictyota humifusa</i>	2-3m	Isla Taboga	Panamá	8°47.363N 79°32.739W	17-06-09	C. Fernandez
CFPA-465	<i>Dictyota humifusa</i>	2-3m	Isla Taboga	Panamá	8°47.363N 79°32.739W	17-06-09	C. Fernandez
CFPA-479	<i>Dictyota centroamericana</i>	1-2 m	Isla Mogo-Mogo	Panamá	8°34.692N 79°01.698W	24-06-09	C. Fernández
CFPA-483	<i>Dictyota humifusa</i>	1-2m	Isla Contadora	Panamá	8°37.681N 79°01.628W	24-06-09	C. Fernández
CFPA-492	<i>Dictyota centroamericana</i>	2-3m	Islote Trapiche, Isla Pedro González	Panamá	8°25.554N 79°06.549W	25-06-09	C. Fernández
CFNI-538	<i>Dictyota humifusa</i>	17.5 m	La Flor, San Juan del sur	Nicaragua	11°08'09.0"N 85°48'04.2"W	02-07-09	C.Fernández
CFNI-540	<i>Dictyota stolonifera</i>	17.5 m	La Flor, San Juan del sur	Nicaragua	11°08'09.0"N 85°48'04.2"W	02-07-09	C.Fernández
CFNI-548	<i>Dictyota stolonifera</i>	13 m	La Cagada, San Juan del Sur	Nicaragua	11°07'23.7"N 85°47'43.1"W	02-07-09	C. Fernández
CFNI-550	<i>Dictyota humifusa</i>	13 m	La Cagada, San Juan del Sur	Nicaragua	11°07'23.7"N 85°47'43.1"W	02-07-09	C. Fernández

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFNI-554	<i>Dictyota stolonifera</i>	13 m	La Cagada, San Juan del Sur	Nicaragua	11°07'23.7"N 85°47'43.1"W	02-07-09	C. Fernández
CFNI-555	<i>Dictyota stolonifera</i>	13 m	La Cagada, San Juan del Sur	Nicaragua	11°07'23.7"N 85°47'43.1"W	02-07-09	J. Aguirre
CFNI-557	<i>Dictyota stolonifera</i>	13 m	La Cagada, San Juan del Sur	Nicaragua	11°07'23.7"N 85°47'43.1"W	02-07-09	J. Aguirre
CFNI-559	<i>Dictyota humifusa</i>	13 m	La Cagada, San Juan del Sur	Nicaragua	11°07'23.7"N 85°47'43.1"W	02-07-09	J. Aguirre
CFNI-565	<i>Dictyota stolonifera</i>	11 m	La Peña Rota, Rivas	Nicaragua	11°14'00.3"N 85°52'01.5"W	02-07-09	C. Fernández
CFNI-566	<i>Dictyota stolonifera</i>	11 m	La Peña Rota, Rivas	Nicaragua	11°14'00.3"N 85°52'01.5"W	02-07-09	C. Fernández
CFNI-568	<i>Dictyota stolonifera</i>	11 m	La Peña Rota, Rivas	Nicaragua	11°14'00.3"N 85°52'01.5"W	02-07-09	C. Fernández
CFNI-570	<i>Dictyota stolonifera</i>	11 m	La Peña Rota, Rivas	Nicaragua	11°14'00.3"N 85°52'01.5"W	02-07-09	C. Fernández
CFNI-575	<i>Dictyota centroamericana</i>	11 m	La Peña Rota, Rivas	Nicaragua	11°14'00.3"N 85°52'01.5"W	02-07-09	C. Fernández
CFNI-580	<i>Dictyota stolonifera</i>	11 m	La Peña Rota, Rivas	Nicaragua	11°14'00.3"N 85°52'01.5"W	02-07-09	C. Fernández
CFNI-597	<i>Dictyota humifusa</i>	11 m	Gigante	Nicaragua	11°23'07.9"N 86°02'12.4"W	03-07-09	C. Fernandez
CFNI-602	<i>Dictyota stolonifera</i>	11 m	Gigante	Nicaragua	11°23'07.9"N 86°02'12.4"W	03-07-09	C. Fernandez
CFNI-608	<i>Dictyota humifusa</i>	11 m	Gigante	Nicaragua	11°23'07.9"N 86°02'12.4"W	03-07-09	J. Aguirre
CFNI-616	<i>Dictyota stolonifera</i>	7 m	La Anciana	Nicaragua	11°21'10.6"N 86°00'08.0"W	03-07-09	C. Fernandez
CFNI-617	<i>Dictyota stolonifera</i>	7 m	La Anciana	Nicaragua	11°21'10.6"N 86°00'08.0"W	03-07-09	C. Fernandez
CFNI-619	<i>Dictyota stolonifera</i>	7 m	La Anciana	Nicaragua	11°21'10.6"N 86°00'08.0"W	03-07-09	C. Fernandez

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFNI-626	<i>Dictyota stolonifera</i>	7 m	La Anciana	Nicaragua	11°21'10.6"N 86°00'08.0"W	03-07-09	J. Aguirre
CFNI-633	<i>Dictyota centroamericana</i>	5.5 m	Guacalito	Nicaragua	11°21'17.3"N 86°00'06.9"W	03-07-09	C. Fernandez J. Aguirre
CFNI-635	<i>Dictyota stolonifera</i>	5.5 m	Guacalito	Nicaragua	11°21'17.3"N 86°00'06.9"W	03-07-09	C. Fernandez J. Aguirre
CFNI-639	<i>Dictyota stolonifera</i>	5.5 m	Guacalito	Nicaragua	11°21'17.3"N 86°00'06.9"W	03-07-09	C. Fernandez J. Aguirre
CFNI-641	<i>Dictyota stolonifera</i>	5.5 m	Guacalito	Nicaragua	11°21'17.3"N 86°00'06.9"W	03-07-09	C. Fernandez J. Aguirre
CFNI-654	<i>Dictyota stolonifera</i>	7.6 m	Punta El Clavo	Nicaragua	11°19'12.6"N 85°56'43.0"W	04-07-09	C. Fernandez
CFNI-671	<i>Dictyota stolonifera</i>	6.6 m	Costa Blanca	Nicaragua	11°18'57.20"N 85°56'23.90"W	04-07-09	C. Fernandez
CFNI-747	<i>Dictyota centroamericana</i>	Intertidal	Playa Hermosa, León	Nicaragua	12°06'21.7"N 86°44'09.2W	09-07-09	C. Fernandez
CFCR-770	<i>Dictyota stolonifera</i>	3-4 m	Roca Tres Hermanas, PNMB	Costa Rica	09°06'14.84"N 83°42'28.30"W	16-07-09	C Fernández
CFCR-771	<i>Dictyota centroamericana</i>	3-4 m	Roca Tres Hermanas, PNMB	Costa Rica	09°06'14.84"N 83°42'28.30"W	16-07-09	C Fernández
CFCR-773	<i>Dictyota stolonifera</i>	3-4 m	Roca Tres Hermanas, PNMB	Costa Rica	09°06'14.84"N 83°42'28.30"W	16-07-09	C Fernández
CFCR-779	<i>Dictyota humifusa</i>	3-4 m	Roca Tres Hermanas, PNMB	Costa Rica	09°06'14.84"N 83°42'28.30"W	16-07-09	C Fernández
CFCR-781	<i>Dictyota humifusa</i>	4-5 m	Bajo Tres Hermanas, PNMB	Costa Rica	09°06'25.65"N 83°42'39.33"W	16-07-09	C Fernández
CFCR-804	<i>Dictyota stolonifera</i>	10 m	Catarata 1, Isla del Caño	Costa Rica	08°42'52.7"N 83°52'03.0"W	18-07-09	C Fernández J.J. Alvarado
CFCR-808	<i>Dictyota humifusa</i>	10 m	Catarata 2, Isla del Caño	Costa Rica	08°42'24.0"N 83°51'58.9"W	18-07-09	C Fernández J.J. Alvarado
CFCR-810	<i>Dictyota stolonifera</i>	10 m	Catarata 2, Isla del Caño	Costa Rica	08°42'24.0"N 83°51'58.9"W	18-07-09	C Fernández J.J. Alvarado

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFCR-811	<i>Dictyota stolonifera</i>	10 m	Catarata 2, Isla del Caño	Costa Rica	08°42'24.0"N 83°51'58.9"W	18-07-09	C Fernández J.J. Alvarado
CFCR-812	<i>Dictyota stolonifera</i>	10 m	Catarata 2, Isla del Caño	Costa Rica	08°42'24.0"N 83°51'58.9"W	18-07-09	C Fernández J.J. Alvarado
CFCR-821	<i>Dictyota centroamericana</i>	8 m	La Cueva del Tiburón, Isla del Caño	Costa Rica	08°42'45.7N 83°53'23.2"W	20-07-09	C Fernández J.J. Alvarado
CFCR-822	<i>Dictyota stolonifera</i>	8 m	La Cueva del Tiburón, Isla del Caño	Costa Rica	08°42'45.7N 83°53'23.2"W	20-07-09	C Fernández J.J. Alvarado
CFCR-823	<i>Dictyota humifusa</i>	8 m	La Cueva del Tiburón, Isla del Caño	Costa Rica	08°42'45.7N 83°53'23.2"W	20-07-09	C Fernández J.J. Alvarado
CFCR-824	<i>Dictyota stolonifera</i>	8 m	La Cueva del Tiburón, Isla del Caño	Costa Rica	08°42'45.7N 83°53'23.2"W	20-07-09	C Fernández J.J. Alvarado
CFCR-827	<i>Dictyota stolonifera</i>	2-3m	Isla Bolaños, Bahía Salinas	Costa Rica	11°02'53.6"N 85°42'43.1"W	28-07-09	C Fernández A. Planas
CFCR-828	<i>Dictyota humifusa</i>	2-3m	Isla Bolaños, Bahía Salinas	Costa Rica	11°02'53.6"N 85°42'43.1"W	28-07-09	C Fernández A. Planas
CFCR-829	<i>Dictyota stolonifera</i>	2-3m	Isla Bolaños, Bahía Salinas	Costa Rica	11°02'53.6"N 85°42'43.1"W	28-07-09	C Fernández A. Planas
CFCR-832	<i>Dictyota centroamericana</i>	2-3m	Isla Bolaños, Bahía Salinas	Costa Rica	11°02'53.6"N 85°42'43.1"W	28-07-09	C Fernández A. Planas
CFCR-835	<i>Dictyota stolonifera</i>	2-3m	Isla Bolaños, Bahía Salinas	Costa Rica	11°02'53.6"N 85°42'43.1"W	28-07-09	C Fernández A. Planas
CFCR-836	<i>Dictyota stolonifera</i>	2-3m	Isla Bolaños, Bahía Salinas	Costa Rica	11°02'53.6"N 85°42'43.1"W	28-07-09	C Fernández A. Planas
CFCR-842	<i>Dictyota stolonifera</i>	7 m	La Paloma, Bahía Salinas	Costa Rica	11°02'00.1"N 85°44'59.4"W	28-07-09	C Fernández A. Planas
CFCR-844	<i>Dictyota centroamericana</i>	7 m	La Paloma, Bahía Salinas	Costa Rica	11°02'00.1"N 85°44'59.4"W	28-07-09	C Fernández A. Planas
CFCR-850	<i>Dictyota humifusa</i>	7 m	Isla Despensa, Bahía Salinas	Costa Rica	11°00'09.5"N 85°44'51.2"W	28-07-09	C Fernández A. Planas
CFCR-855	<i>Dictyota centroamericana</i>	4 m	La Penca, Bahía Culebra	Costa Rica	10°34'29.2"N 85°41'53.0"W	29-07-09	C Fernández A. Planas

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFCR-858	<i>Dictyota humifusa</i>	4 m	La Penca, Bahía Culebra	Costa Rica	10°34'29.2"N 85°41'53.0"W	29-07-09	C Fernández A. Planas
CFCR-861	<i>Dictyota humifusa</i>	6 m	Cacique, Bahía Culebra	Costa Rica	10°34'25.3"N 85°41'56.6"W	29-07-09	C Fernández A. Planas
CFCR-862	<i>Dictyota humifusa</i>	4 m	Punta Arenita, Bahía Culebra	Costa Rica	10°36'17.2"N 85°38'54.1"W	30-07-09	A. Planas J.J. Alvarado C. Sanchez
CFCR-878	<i>Dictyota humifusa</i>	5-6m	Bahía Virador, Bahía Culebra	Costa Rica	10°36'51.6"N 85°41'25.0"W	01-08-09	A. Planas J.J. Alvarado C. Sanchez
CFCR-886	<i>Dictyota humifusa</i>	8-9 m	Cabo Vela, PNM Baulas	Costa Rica	10°20'52.0"N 85°52'10.1"W	02-08-09	C Fernández A. Planas
CFCR-892	<i>Dictyota stolonifera</i>	8-9 m	Cabo Vela, PNM Baulas	Costa Rica	10°20'52.0"N 85°52'10.1"W	02-08-09	C Fernández A. Planas
CFCR-893	<i>Dictyota humifusa</i>	8-9 m	Cabo Vela, PNM Baulas	Costa Rica	10°20'52.0"N 85°52'10.1"W	02-08-09	C Fernández A. Planas
CFCR-894	<i>Dictyota humifusa</i>	8-9 m	Cabo Vela, PNM Baulas	Costa Rica	10°20'52.0"N 85°52'10.1"W	02-08-09	C Fernández A. Planas
CFCR-896	<i>Dictyota stolonifera</i>	9-10 m	Los Conejos, PNM Baulas	Costa Rica	10°22'05.2"N 85°51'52.9"W	02-08-09	C Fernández A. Planas
CFCR-897	<i>Dictyota humifusa</i>	9-10 m	Los Conejos, PNM Baulas	Costa Rica	10°22'05.2"N 85°51'52.9"W	02-08-09	C Fernández A. Planas
CFCR-900	<i>Dictyota stolonifera</i>	13 m	Isla Negritos, Golfo de Nicoya	Costa Rica	09°48'59.2"N 84°51'48.7"W	03-08-09	C Fernández A. Planas
CFCR-902	<i>Dictyota centroamericana</i>	13 m	Isla Negritos, Golfo de Nicoya	Costa Rica	09°48'59.2"N 84°51'48.7"W	03-08-09	C Fernández A. Planas
CFCR-906	<i>Dictyota humifusa</i>	12 m	Tolinga, Lado Sur de Islas Tortugas, Golfo de Nicoya	Costa Rica	09°45'50.3"N 84°53'51.1"W	03-08-09	C Fernández A. Planas
CFCR-913	<i>Dictyota stolonifera</i>	12 m	Tolinga, Lado Sur de Islas Tortugas, Golfo de Nicoya	Costa Rica	09°45'50.3"N 84°53'51.1"W	03-08-09	C Fernández A. Planas
CFPA-1008	<i>Dictyota stolonifera</i>	3 - 4 m	Coiba Noreste	Panama	07°38'01"N 81°44'9.5"W	22-06-10	C Fernandez

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFPA-1010	<i>Dictyota humifusa</i>	5.5	Jicarita	Panama	07°12'49.1"N 81°47'57.0"W	23-06-10	C Fernandez
CFPA-1014	<i>Dictyota stolonifera</i>	2 m	Canales de afuera	Panama	07°41'44"N 81°37'59"W	23-06-10	C Fernandez

Tabla S5. Listado de especímenes colectados del género *Amphiroa* del Pacífico Tropical Oriental.
 Table S5. List of *Amphiroa* specimens collected from the Eastern Tropical Pacific.

Sample Code	Species name	Depth	Collecting Site	Country	Coordenates	Collecting Date	Collector
CFES-004	<i>Amphiroa</i> complex C	2 m	Isla Zacatillo, Golfo de Fonseca, La Unión	El Salvador	13°17'29.6" N 87°46'05.5"W	22/01/2009	C. Fernández A. Planas
CFES-046	<i>Amphiroa</i> complex C	1-2 m	Isla Meanguera, Playa Mahual, Golfo de Fonseca, La Unión	El Salvador	13°10'02.9"N 87°42'55.1"W	22/01/2009	C. Fernández A. Planas
CFES-058	<i>Amphiroa</i> complex C	Intertidal	El Pital, La Libertad	El Salvador	13°30'44.0"N 89°36'15.6"W	27/01/2009	C. Fernández A. Planas
CFES-070	<i>Amphiroa</i> complex B	Intertidal	La Vega, La Libertad	El Salvador	13°29'56.4" N 89°28'55.7" W	28/01/2009	C. Fernández A. Planas
CFES-139	<i>Amphiroa</i> complex C	Intertidal	Playa El Privado, Los Cóbano	El Salvador	13°31'38.0"N 89°48'40.8"W	01/02/2009	C. Fernández A. Planas
CFES-143	<i>Amphiroa</i> complex C	Intertidal	Playa El Privado, Los Cóbano	El Salvador	13°31'38.0"N 89°48'40.8"W	01/02/2009	C. Fernández A. Planas
CFES-152	<i>Amphiroa</i> complex B	Intertidal	Playa El Privado, Los Cóbano	El Salvador	13°31'38.0"N 89°48'40.8"W	01/02/2009	C. Fernández A. Planas
CFMX-181	<i>Amphiroa</i> complex D	1-3 m	Playa El Panteon, Puerto Angel, Oaxaca	México	15°39.842N 96°29.725W	13/02/2009	C. Fernández
CFMX-210	<i>Amphiroa</i> complex E	2-3 m	Togolunda, Bahía de Huatulco, Oaxaca	México	15°39.900N 96°29.775W	14/02/2009	H. Verbruggen
CFMX-211	<i>Amphiroa</i> complex C	2-3 m	Togolunda, Bahía de Huatulco, Oaxaca	México	15°39.900N 96°29.775W	14/02/2009	H. Verbruggen
CFMX-214	<i>Amphiroa</i> complex D	2-3 m	Mazunte, Oaxaca	México	15°39.705N 96°33.365W	15/02/2009	C. Fernández
CFMX-225	<i>Amphiroa</i> complex B	Intertidal	Mazunte, Oaxaca	México	15°39.705N 96°33.365W	15/02/2009	C. Fernández
CFMX-246	<i>Amphiroa</i> complex C	5-7 m	Puerto Escondido 1, Oaxaca	México	15°51.453N 97°03.940W	17/02/2009	C. Fernández
CFMX-253	<i>Amphiroa</i> complex E	15 m	Puerto Escondido 2, Oaxaca	México	15°51.898N 97°06.603W	17/02/2009	C. Fernández
CFMX-255	<i>Amphiroa</i> complex D	15 m	Puerto Escondido 2, Oaxaca	México	15°51.898N 97°06.603W	17/02/2009	C. Fernández

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFMX-285	Amphiroa complex E	Intertidal	Playa del Palmar, Ixtapa	México	17°39.139N 101°36.019W	21/02/2009	C. Fernández
CFMX-356	Amphiroa complex E	3 m	Playa Tenacatita, Jalisco	México	19°16.894N 104°52.348W	25/02/2009	L.Tyberghein
CFMX-358	Amphiroa complex E	3 m	Playa Tenacatita, Jalisco	México	19°16.894N 104°52.348W	25/02/2009	L.Tyberghein
CFMX-379	Amphiroa complex E	6-8 m	Majahuitas, Puerto Vallarta, Jalisco	México	20°30.410N 105°23.571W	28/02/2009	C. Fernández
CFMX-380	Amphiroa complex D	6-8 m	Majahuitas, Puerto Vallarta, Jalisco	México	20°30.410N 105°23.571W	28/02/2009	C. Fernández
CFMX-397	Amphiroa complex E	10 m	Colomitos, Puerto Vallarta, Jalisco	México	20°30.755N 105°19.532W	28/02/2009	C. Fernández
CFPA-412	Amphiroa complex C	5-6 m	Islotes antes de Saboga, Perlas Arquipelgo	Panamá	8°38.787N 79°03.314W	04/06/2009	C. Fernandez
CFPA-421	Amphiroa complex B	6 m	Isla Saboga, Perlas Arquipelgo	Panamá	8°37.732N 79°03.309W	04/06/2009	C. Fernandez
CFPA-422	Amphiroa complex B	6 m	Isla Saboga, Perlas Arquipelgo	Panamá	8°37.732N 79°03.309W	04/06/2009	C. Fernandez
CFPA-439	Amphiroa complex E	2-3 m	Otoque Sur, Perlas Arquipelgo	Panamá	8°34.059N 79°35.454W	10/06/2009	C. Fernandez
CFPA-446	Amphiroa complex B	2-3 m	Isla Urabá, Perlas Arquipelgo	Panamá	8°46.933N 79°32.178W	10/06/2009	C. Fernandez
CFPA-447	Amphiroa complex A	2-3 m	Isla Urabá, Perlas Arquipelgo	Panamá	8°46.933N 79°32.178W	11/06/2009	C. Fernandez
CFPA-480	Amphiroa complex C	1-2 m	Isla Mogo-Mogo, Perlas Arquipelgo	Panamá	8°34.692N 79°01.698W	24/06/2009	C. Fernández
CFPA-489	Amphiroa complex C	2-3 m	Islote Trapiche, Isla Pedro González, Perlas Arquipelgo	Panamá	8°25.554N 79°06.549W	25/06/2009	C. Fernández
CFPA-494	Amphiroa complex C	2-3 m	Islote Trapiche, Isla Pedro González, Perlas Arquipelgo	Panamá	8°25.554N 79°06.549W	25/06/2009	C. Fernández
CFNI-504	Amphiroa complex E	Intertidal	Playa El Tránsito, León	Nicaragua	12° 02' 54.2"N 86° 42' 17.0"W	30/06/2009	C. Fernández A. Alvarez, JJ Alvarado, J. Aguirre

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFNI-519	Amphiroa complex E	Intertidal	Playa El Tránsito, León	Nicaragua	12° 02' 54.2"N 86° 42' 17.0"W	30/06/2009	C. Fernández A. Alvarez, JJ Alvarado, J. Aguirre
CFNI-532	Amphiroa complex B	Intertidal	Playa El Tránsito, León	Nicaragua	12° 02' 54.2"N 86° 42' 17.0"W	30/06/2009	C. Fernández A. Alvarez, JJ Alvarado, J. Aguirre
CFNI-535	Amphiroa complex E	17.5 m	La Flor, San Juan del sur	Nicaragua	11°08'09.0"N 85°48'04.2"W	02/07/2009	C.Fernández
CFNI-545	Amphiroa complex D	13 m	La Cagada, San Juan del Sur	Nicaragua	11°07'23.7"N 85°47'43.1"W	02/07/2009	C. Fernández
CFNI-577	Amphiroa complex E	11 m	La Peña Rota, Rivas	Nicaragua	11°14'00.3"N 85°52'01.5"W	02/07/2009	C. Fernández
CFNI-579	Amphiroa complex D	11 m	La Peña Rota, Rivas	Nicaragua	11°14'00.3"N 85°52'01.5"W	02/07/2009	C. Fernández
CFNI-605	Amphiroa complex D	11 m	Gigante	Nicaragua	11°23'07.9"N 86°02'12.4"W	03/07/2009	C. Fernandez
CFNI-614	Amphiroa complex C	7 m	La Anciana	Nicaragua	11°21'10.6"N 86°00'08.0"W	03/07/2009	C. Fernandez
CFNI-618	Amphiroa complex D	7 m	La Anciana	Nicaragua	11°21'10.6"N 86°00'08.0"W	03/07/2009	C. Fernandez
CFNI-667	Amphiroa complex E	6.6 m	Costa Blanca	Nicaragua	11°18'57.20"N 85°56'23.90"W	04/07/2009	C. Fernandez
CFNI-669	Amphiroa complex D	6.6 m	Costa Blanca	Nicaragua	11°18'57.20"N 85°56'23.90"W	04/07/2009	C. Fernandez
CFNI-686	Amphiroa complex D	5.6 m	Marsella, Rivas	Nicaragua	11°16'59.20"N 85°54'22.50"W	04/07/2009	C. Fernandez
CFNI-716	Amphiroa complex B	Intertidal	Masachapa, Managua	Nicaragua	11°47'01.3"N 86°31'03.3"W	06/07/2009	C. Fernandez

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFCR-793	Amphiroa complex E	15-16 m	Isla Ballena, costado sur, PNMB	Costa Rica	9°06'1606"N 83°43'36.95"W	16/07/2009	C. Fernandez
CFCR-815	Amphiroa complex D	4 m	El Jardín, Isla del Caño	Costa Rica	08°42'55.7"N 83°52'28.3"W	19/07/2009	C. Fernandez
CFCR-818	Amphiroa complex E	4 m	El Jardín, Isla del Caño	Costa Rica	08°42'55.7"N 83°52'28.3"W	19/07/2009	C. Fernandez
CFCR-825	Amphiroa complex E	8 m	La Cueva del Tiburón, Isla del Caño	Costa Rica	08°42'45.7N 83°53'23.2"W	20/07/2009	C. Fernandez
CFCR-831a	Amphiroa complex D	2-3 m	San Josecito	Costa Rica	8°40'15.4"N 83°43'6.5"W	21/07/2009	C. Fernandez
CFCR-837	Amphiroa complex C	7 m	La Paloma, Bahía Salinas	Costa Rica	11°02'00.1"N 85°44'59.4"W	28/07/2009	C. Fernández A. Planas
CFCR-854	Amphiroa complex D	4 m	La Penca, Bahía Culebra	Costa Rica	10°34'29.2"N 85°41'53.0"W	29/07/2009	C. Fernández A. Planas
CFCR-857	Amphiroa complex D	4 m	La Penca, Bahía Culebra	Costa Rica	10°34'29.2"N 85°41'53.0"W	29/07/2009	C. Fernández A. Planas
CFCR-859	Amphiroa complex D	4 m	La Penca, Bahía Culebra	Costa Rica	10°34'29.2"N 85°41'53.0"W	29/07/2009	C. Fernández A. Planas
CFCR-860	Amphiroa complex C	4 m	La Penca, Bahía Culebra	Costa Rica	10°34'29.2"N 85°41'53.0"W	29/07/2009	C. Fernández A. Planas
CFCR-866	Amphiroa complex C	4 m	Punta Arenita, Bahía Culebra	Costa Rica	10°36'17.2"N 85°38'54.1"W	30/07/2009	A. Planas, J.J. Alvarado C. Sanchez
CFCR-867	Amphiroa complex D	4 m	Punta Arenita, Bahía Culebra	Costa Rica	10°36'17.2"N 85°38'54.1"W	30/07/2009	A. Planas, J.J. Alvarado C. Sanchez
CFCR-884	Amphiroa complex C	5-6 m	Bahía Virador, Bahía Culebra	Costa Rica	10°36'51.6"N 85°41'25.0"W	01/08/2009	A. Planas, J.J. Alvarado C. Sanchez
CFCR-891	Amphiroa complex D	8-9 m	Cabo Vela, PNM Baulas	Costa Rica	10°20'52.0"N 85°52'10.1"W	02/08/2009	C. Fernández A. Planas
CFCR-901	Amphiroa complex E	13 m	Isla Negritos, Golfo de Nicoya	Costa Rica	09°48'59.2"N 84°51'48.7"W	03/08/2009	C. Fernández A. Planas

Sample Code	Species name	Depth	Collecting Site	Country	Coordinates	Collecting Date	Collector
CFCR-908	Amphiroa complex E	12 m	Tolinga, Lado Sur de Islas Tortugas, Golfo de Nicoya	Costa Rica	09°45'50.3"N 84°53'51.1"W	03/08/2009	C. Fernández A. Planas
CFIC-1018	Amphiroa complex C	10-15 m	Punta Ulloa, Isla del Coco	Costa Rica	05°33.054N 87°02.095W		J. Cortés