

## Species diversity and biogeographical patterns of *Laurencia* sensu stricto (Rhodophyta) in the Atlantic Ocean

## Diversidad de especies y patrones biogeográficos de *Laurencia* sensu stricto (Rhodophyta) en el océano Atlántico

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### ABSTRACT

**Background.** Recent morphological and phylogenetic studies of *Laurencia* in the Atlantic Ocean have modified our current knowledge of the group. Approximately 23% of the worldwide generic diversity has been recorded in this region.

**Goals.** Update the checklist of the *Laurencia* species in the Atlantic and describe the distribution patterns within the genus.

**Methods.** We obtained records of *Laurencia* species in the Atlantic from a review of the literature and distributional data were used to define areas of endemism through a PAE (Parsimony of Areas of Endemism) analysis.

**Results.** We propose an updated checklist of the 30 currently recognized species of *Laurencia* in the Atlantic Ocean; this checklist also includes taxonomic synonyms, nomenclatural remarks, and a detailed distribution for each species. The distributional range for the genus in the Atlantic extends from Bermuda and Northern Europe in the North Atlantic to Brazil and South Africa in the South Atlantic. We were able to define four areas of endemism: Brazil with four endemic species, the Gulf of Guinea with four endemic species, the northeastern Atlantic with three endemic species, and South Africa with four endemic species; also documented was one secondary area (Macaronesian Islands) with the endemic species *L. viridis*. Moreover, 17 of the 30 species of the Atlantic are also distributed in the Indo-Pacific, of which five are amphi-Atlantic species.

**Conclusions.** The patterns found are related to geological events that occurred in the past, a fact that allows us to formulate a vicariance hypothesis about these species biogeographic history. Therefore, future work that will document new species and the clarification of taxonomic problems will allow researchers to continue enriching this hypothesis.

**Key words:** Area of endemism, biogeography, PAE analysis, red algae.

### RESUMEN

**Antecedentes.** Los recientes estudios morfológicos y filogenéticos de *Laurencia* para el océano Atlántico han modificado el conocimiento actual sobre la diversidad del grupo, registrándose para esta región, aproximadamente el 23% de la diversidad del género a nivel mundial.

**Objetivos.** Actualizar el listado de especies de *Laurencia* presentes en el Océano Atlántico y definir sus patrones de distribución.

**Métodos.** Se obtuvieron los registros de las especies del género a partir de una revisión bibliográfica, utilizando los datos de distribución para la definición de patrones biogeográficos mediante un análisis de PAE.

**Resultados.** Se propone un listado actualizado que contiene 30 especies de *Laurencia* reconocidas taxonómicamente para el Océano Atlántico; además se incluyen sinónimos, notas nomenclaturales y la distribución a detalle de cada una de las especies. El intervalo de distribución del género se extiende desde Bermudas y el norte de Europa para el Atlántico Norte, hasta Brasil y Sudáfrica en el Atlántico Sur. Se definieron cuatro áreas de endemismo: Brasil con cuatro especies endémicas, Golfo de Guinea con cuatro especies restringidas, Noreste del Atlántico con tres especies endémicas y Sudáfrica con cuatro especies endémicas; además de un área secundaria (Islas de la Macaronesia) con *L. viridis* como especie endémica. Por otro lado, 17 de las 30 especies registradas para el Atlántico se distribuyen también en el Indo-Pacífico, de las cuales cinco son especies anfi-Atlánticas.

**Conclusiones.** Los patrones encontrados han sido relacionados con eventos geológicos que han ocurrido en el pasado, permitiendo ofrecer una hipótesis de vicarianza sobre su historia biogeográfica. Por lo tanto, trabajos futuros sobre el reconocimiento de nuevas especies y el esclarecimiento de problemas taxonómicos permitirán continuar enriqueciendo dicha hipótesis.

**Palabras clave:** Áreas de endemismo, biogeografía, Análisis de PAE, algas rojas.

## INTRODUCTION

There is a need for an updated checklist of *Laurencia* (Rhodophyta, Ceramiales) in the Atlantic Ocean that accounts for recent morphological and phylogenetic studies that have modified our current knowledge of the group. For instance, the “*Laurencia* complex” has replaced the former concept of *Laurencia sensu lato*. The genus *Laurencia sensu stricto* (s.s.) (Garbary & Harper, 1998; Nam, 2006; Gil-Rodríguez et al., 2012), and the following seven genera belonging to the complex (mentioned above): *Osmundea* Stackhouse, *Chondrophycus* (Tokida et Saito) Garbary et J. T. Harper, *Palisada* K. W. Nam, *Yuzurua* (K.W. Nam) Martin-Lescanne, *Laurenciella* Cassano, Gil-Rodríguez, Senties, Díaz-Larrea, M. C. Oliveira et M. T. Fujii, *Coronaphycus* Metti and *Ohelopapa* F. Rousseau, Martin-Lescanne, Payri et L. Le Gall. These genera differ in the number of pericentral cells cut off by the vegetative axial segments, the origin of spermatangial branches, and the origin of tetrasporangia from determined cells (Saito, 1967; Nam et al., 1994; Garbary & Harper, 1998; Nam, 1999, 2006, 2007). Molecular phylogenetic data also support distinction among them (Martin-Lescanne et al., 2010; Cassano et al., 2012a; Metti et al., 2015; Rousseau et al., 2017).

*Laurencia* comprises 130 taxonomically recognized species worldwide (Guiry & Guiry, 2017). In particular, 18 species of the genus have been recorded for the Western Atlantic (from North Carolina to Brazil) and 21 for the Eastern Atlantic (Europe and Africa). These represent 23% of the species richness worldwide. Phylogenetic studies of some *Laurencia* species in the Atlantic have shown the artificiality of the wide ranges of distribution of some species, such as *L. microcladica* and *L. obtusa* (Cassano et al., 2012a) that have been eliminated from the Brazilian flora.

The area of endemism is defined as the sympatric congruence between two or more endemic species, based on the fact that these species share a common spatial history (Platnick, 1991; Morrone, 2007). Other areas that can be documented are the secondary areas, which have only one endemic species or the so-called relic species that are important because these areas may be later isolations where species radiation has not yet occurred (Ippi & Flores, 2001; Vargas et al., 2008). The PAE (Parsimony Areas of Endemism) analysis is a method that allows us to identify areas of endemism from area cladograms. In a manner similar to phylogenetic systematics, at least two synapomorphic characters (restricted species) will define areas of endemism (Morrone, 2013).

One important outcome of this taxonomic updating is to provide a better understanding of the biogeographical patterns. With the present updated checklist, we will discuss endemism and the widespread geographic distribution of *Laurencia* species in the Atlantic.

## MATERIALS AND METHODS

Records for *Laurencia* for the Atlantic Ocean were obtained from primary sources (these sources are indicated for each species in Results section). We complemented information with the online database Algae Base (Guiry & Guiry, 2017). Parsimony Analysis of Endemicity (PAE; Rosen, 1988) was used in a biogeographical analysis. For this analysis, an  $r \times c$  binary matrix (presence and absence) was constructed, where  $r$  (rows) displays the 17 Atlantic ecoregions proposed by Spalding et al. (2007) (Fig. 1) and  $c$  (columns) contains 24 of the 30 species recorded for the Atlantic Ocean. Because they could be found practically all over

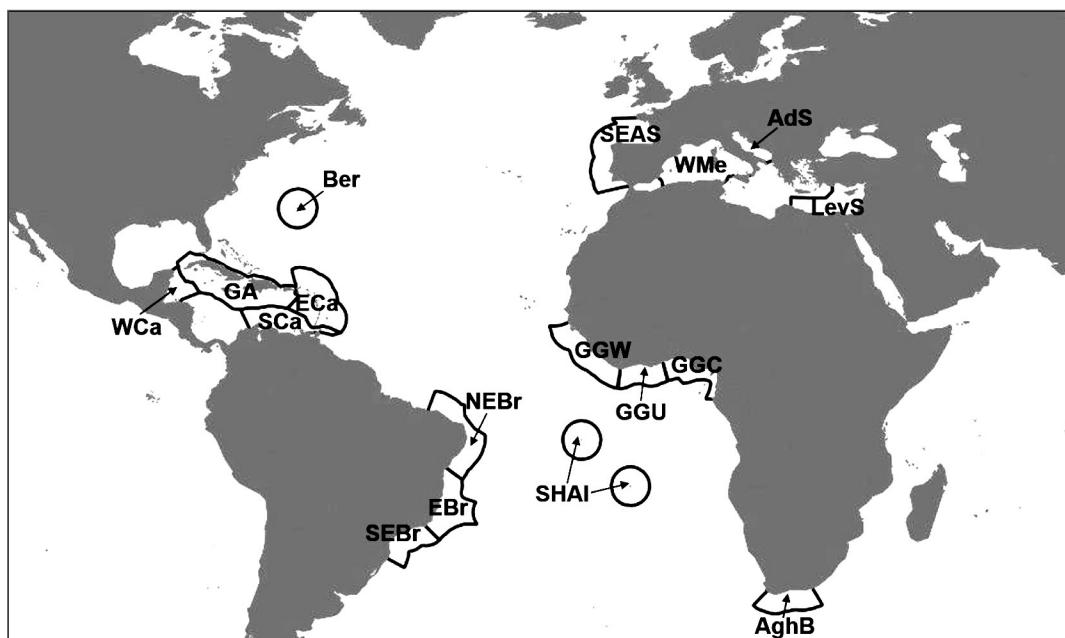


Figure 1. Marine ecoregions used in the PAE analysis, modified from Spalding et al., (2007): Adriatic Sea (AdS), Aghulas Bank (AghB), Bermuda (Ber), Eastern Brazil (EBr), Eastern Caribbean (Eca), Greater Antilles (GA), Gulf of Guinea Central (GGC), Gulf of Guinea Upwelling (GGU), Gulf of Guinea Western (GGW), Levantine Sea (LevS), Northeastern Brazil (NEBr), Southern Caribbean (Sca), South European Atlantic Shelf (SEAS), Southeastern Brazil (SEBr), St. Helena and Ascension Islands (SHAI), Western Caribbean (WCa), and Western Mediterranean (WMe).

the Atlantic, we did not include *L. bronniartii* J. Agardh, *L. caduciramulosa* Masuda et S. Kawaguchi, *L. dendroidea* J. Agardh, *L. intricata* J. V. Lamouroux, *L. microcladia* Kützing, and *L. obtusa* (Hudson) J.V. Lamouroux. In addition, the Macaronesian Islands were excluded from the analysis because they are considered to be a transition zone with species from other areas of Atlantic (see Haroun & Prud'homme van Reine, 1993; Tuya & Haroun, 2009), and may affect our distributional patterns (Medina, 2007). Parsimony analysis was done through a heuristic search using TBR+TBR routines with the NONA program, using the WinClada software (Nixon, 1999). A strict consensus tree was built from the most parsimonious trees.

Six "species inquirenda" (*L. alsidioides* Zanardini ex Fraudentfeld, *L. alsidioides* P.L. Croan et H.M. Croan, *L. botryocephala* Kützing, *L. canariensis* Montagne ex Kützing, *L. moriformis* Kützing and *L. trifaria* Kützing) did not provide information about their geographical distribution and were recorded only once by their respective authors. Null or limited herbarium material prevented us from being totally certain about these taxa. Categories of areas (patterns) were defined: Those containing an endemic species (Secondary Area); those with congruence in geographical distribution of two or more endemic species (Area of Endemism), that is, clades defined by two or more synapomorphies; and widespread species (amphi-Atlantic Areas). In addition, we defined areas containing two or more endemic species without total congruence in the geographic distribution of these, known as areas of Partial Congruence.

## RESULTS

### Checklist of *Laurencia* species

#### *Laurencia aldingensis* Saito et Womersley

Type locality: Aldinga Reef, South Australia.

Distribution: Tropical Southwestern Atlantic: BRAZIL: Espírito Santo (Carvalho et al., 2006; Fujii et al., 2011) and Rio de Janeiro (Fujii et al., 2011).

#### *Laurencia brachyclados* Pilger

Type locality: Annobon Island, Equatorial Guinea, West Africa.

Distribution: Gulf of Guinea: EQUATORIAL GUINEA: Annobon Island (John et al., 2004).

St. Helena and Ascension Islands: ASCENSION ISLAND (John et al., 2004).

#### *Laurencia bronniartii* J. Agardh

Type locality: Martinique, West Indies.

Remarks: Dizerbo & Herpe (2007) and Stokes et al. (2004) considered this an introduced species in southeast France and Ireland, respectively.

Distribution: Gulf of Guinea: GHANA (John et al., 2004).

Lusitanian: CANARY ISLANDS: El Hierro and Lanzarote (uncertain record) (Gil-Rodríguez et al., 2012). FRANCE: Brest (Dizerbo & Herpe, 2007).

Tropical Northwestern Atlantic: COSTA RICA: Punta Cocalas (Fernández & Alvarado, 2004). CUBA: Havana (Suárez, 2005). MARTINIQUE (Womersley, 2003). MEXICO: Quintana Roo (Sentíes & Fujii, 2002).

Northern European Seas: IRELAND (Stokes et al., 2004).

#### *Laurencia caduciramulosa* Masuda et Kawaguchi

Type locality: Hon Tre Island, Tien Hai Islands, Hatien, Kien-Giang Province, Vietnam.

Distribution: Lusitanian: CANARY ISLANDS: Tenerife (Gil-Rodríguez et al., 2012).

Mediterranean Sea: FRANCE: Mediterranean coast (Klein & Verlaque, 2005). GREECE: Zakynthos Island (Tsikira & Haritonidis, 2005). ITALY: Linosa Island (Furnari et al., 2001; Serio et al., 2006).

St. Helena and Ascension Islands: ASCENSION ISLAND (Tsiamis et al., 2014a).

Tropical Northwestern Atlantic: CUBA: Havana (Sentíes et al., 2010) and Rincón del Guanabo (Suárez et al., 2015). USA: Florida (Collado-Vides et al., 2014).

Tropical Southwestern Atlantic: BRAZIL: Bahia (Torrano-Silva & Oliveira, 2013) and Rio de Janeiro (Cassano et al., 2006).

#### *Laurencia caraibica* P.C. Silva

Type Locality: Abraham Bay, Mariguana (Mayaguana), Bahamas.

Distribution: Tropical Northwestern Atlantic: BAHAMAS: Abraham Bay (Schneider et al., 2010). BELIZE: Carry Bow Cay (Norris & Bucher, 1982) and Pelican Cays (Littler & Littler, 1997). CUBA: Bucunayagua, Guanahacabibes and Havana (Suarez, 2005). JAMAICA (Taylor, 1960). LESSER ANTILLES (Taylor, 1969). MÉXICO: Campeche, Quintana Roo, Tamaulipas, and Veracruz (Ortega et al., 2001; Sentíes & Fujii, 2002). VENEZUELA (Ganesan, 1990).

Tropical Southwestern Atlantic: BRAZIL: Rio Grande do Norte (Villaça et al., 2010) and Bahia (Creed et al., 2010).

Warm Temperate Northwest Atlantic: BERMUDA: Bermuda Island, Gibbet Island, and Somerset Island (Schneider et al., 2010).

#### *Laurencia catarinensis* Cordeiro-Marino et M.T. Fujii

Type locality: Mole Beach, Santa Catarina Island, Brazil.

Distribution: Lusitanian: CANARY ISLANDS: El Hierro, Fuerteventura, Gran Canaria, La Gomera, La Palma, Lanzarote and Tenerife (Machín-Sánchez et al., 2012).

Warm Temperate Southwestern Atlantic: BRAZIL: Santa Catarina (Fujii & Sentíes, 2005; Machín-Sánchez et al., 2012) and São Paulo (Fujii et al., 2006).

Tropical Southwestern Atlantic: BRAZIL: Rio Grande do Norte (Fujii & Sentíes, 2005; Machín-Sánchez et al., 2012), Espírito Santo (Machín-Sánchez et al., 2012) and Rio de Janeiro (Fujii & Sentíes, 2005).

### ***Laurencia chondrioides* Børgesen**

Type locality: Saint John Island, U. S. Virgin Islands.

Remarks: Only one record outside the Atlantic (Philippines) by Silva et al., (1987). In the Mediterranean Sea (France and Israel) it is regarded as an invasive species (Klein & Verlaque 2011; Hoffman et al., 2014).

Distribution: Lusitanian: CANARY ISLANDS: Lanzarote (Gil-Rodríguez et al., 2012).

Mediterranean Sea: FRANCE: Hyères and Porquerolles Island (Klein & Verlaque, 2011). GREECE: Zakynthos Island (Tsirika & Haritonidis, 2005). ISRAEL: Achziv Beach, Achziv Reserve, Haifa-Bat Galim Beach, Rosh Hanika and Shavei Zion (Hoffman et al., 2014). ITALY: Aeolian Islands, Lachea Island (Gómez-Garreta et al., 2001), Linosa Island (Serio et al., 2006), Tremiti Islands (Gómez-Garreta et al., 2001) and Tuscany (Rindi et al., 2002). SPAIN: Balearic Islands and Columbretes Island (Gómez-Garreta et al., 2001).

Tropical Northwestern Atlantic: CUBA: Canarreos Archipelago and Alonzo Cay (Suárez, 2005). MEXICO: Quintana Roo (Ortega et al., 2001). VIRGIN ISLANDS: St John (Klein & Verlaque, 2011).

### ***Laurencia coronopus* J. Agardh**

Type locality: "in mare Nigro ad littus Tauriae" (Black Sea).

Remarks: Gómez-Garreta et al., (2001) suggested that a revision using recent taxonomic criteria should be made to corroborate if this species actually belongs to *Laurencia* or whether it belongs to *Chondrophycus* or *Osmundea*.

Distribution: Black Sea: BULGARIA: Athopol (Gómez-Garreta et al., 2001; Kamenarska et al., 2006; Kamenarska et al., 2009). ROMANIA LITTORAL: (Caraus, 2012; Gómez-Garreta et al., 2001).

Mediterranean Sea: FRANCE: Herault (Gómez-Garreta et al., 2001).

### ***Laurencia corymbosa* J. Agardh**

Type locality: Cape of Good Hope, South Africa.

Distribution: South Africa: CAPE OF GOOD HOPE (Silva et al., 1996).

### ***Laurencia decumbens* Kützing**

Type locality: New Caledonia.

Distribution: Tropical Northwestern Atlantic: BERMUDA: Bermuda Island (Schneider & Lane, 2005). VENEZUELA (Ganesan, 1990).

Tropical Southwestern Atlantic: BRAZIL: Atol das Rocas (Villaça et al., 2010).

### ***Laurencia dendroidea* J. Agardh**

Type locality: Brazil.

Remarks: According to Cassano et al. (2012b), using molecular and morphological characters, the taxa that have been identified as *L. filiformis*, *L. majuscula*, and *L. obtusa* in Brazil

correspond to *L. dendroidea*. Similarly, *L. majuscula* in the Canary Islands corresponds to *L. dendroidea*.

Distribution: Gulf of Guinea: CAMEROON, GABON, and GHANA (John et al., 2004).

Lusitanian: CANARY ISLANDS: Fuerteventura, Gran Canaria, La Palma, Lanzarote, and Tenerife (Gil-Rodríguez et al., 2012). MADEIRA ARCHIPELAGO: Madeira (John et al., 2004). Mediterranean Sea: FRANCE [uncertain record (Gómez-Garreta et al., 2001)]. GREECE: Zakynthos Island (Tsikira & Haritonidis, 2005). ITALY: Lecce and Linosa Island (Gómez-Garreta et al., 2001; Serio et al., 2006).

Tropical Northwestern Atlantic: BARBADOS (Taylor, 1960; Wynne et al., 2014). BERMUDA (Taylor, 1960). COSTA RICA (Taylor, 1960). JAMAICA (Taylor, 1960). LESSER ANTILLES (Taylor, 1960). NETHERLANDS ANTILLES, TRINIDAD AND TOBAGO, and VENEZUELA (Taylor, 1960).

Tropical Southwestern Atlantic: BRAZIL: Bahia (Oliveira et al., 2013). Espírito Santo (Oliveira et al., 2013; Fujii et al., 2006) and Rio de Janeiro (Cassano et al., 2012b; Oliveira et al., 2013).

West African Transition Zone: CAPE VERDE ISLANDS and SALVAGE ISLANDS (John et al., 2004). GAMBIA (John et al., 2004). SENEGAL: North of Senegal (John et al., 2004).

Warm Temperate Northwest Atlantic: USA: North Carolina (Taylor, 1960).

Warm Temperate Southwestern Atlantic: BRAZIL: Santa Catarina (Creed et al., 2010) and São Paulo (Cassano et al., 2012b).

### ***Laurencia epiphylla* F. Boisset et J. C. Lino**

Type locality: Alicante: La Granadella, Jávea, the Mediterranean coast of Spain.

Distribution: Mediterranean Sea: SPAIN: Alicante (Gómez-Garreta et al., 2001).

### ***Laurencia flexuosa* Kützing**

Type locality: "Ad Caput Bonae Spei", South Africa.

Distribution: South Africa: CAPE TOWN (Stegenga et al., 1997).

West African Transition: MAURITANIA [uncertain record (John et al., 2004)].

### ***Laurencia foldatsii* N. Rodríguez de Rios**

Type locality: Taguao, Distrito Federal, Venezuela

Distribution: Tropical Northwestern Atlantic: VENEZUELA (Ganesan, 1990).

### ***Laurencia galtoffii* M. Howe**

Type locality: Pearl and Hermes Reef, Hawaiian Archipelago.

Distribution: Gulf of Guinea: GABON, GHANA, and LIBERIA (John et al., 2004).

West African Transition: CAPE VERDE ISLANDS (John et al., 2004).

### ***Laurencia griseaviolacea* M.J. Wynne**

Type locality: Clovelly, Cape Peninsula, South Africa.

Distribution: South Africa: CAPE TOWN (Stegenga *et al.*, 1997, as *Laurencia peninsularis* H. Stegenga, J. J. Bolton *et al.* R. J. Anderson not *L. peninsularis* Taylor).

### ***Laurencia intricata* J.V. Lamouroux**

Type locality: Antilles.

Remarks: According to Machín-Sánchez *et al.* (2012), records of *L. intricata* from the Canary Islands correspond to *L. catarinensis*. Therefore, we believe that a taxonomic study of this species from the rest of Macaronesian Archipelago and Western Africa is needed to verify the identity of *L. intricata* from these areas.

Distribution: GULF OF GUINEA: SAO TOMÉ AND PRÍNCIPE, and SIERRA LEONE (John *et al.*, 2004).

Mediterranean Sea: GREECE: Messolonghi (Christia *et al.*, 2011) and Zakynthos Island (Tsikira & Haritonidis, 2005). ITALY: Linosa Island (Furnari *et al.*, 2001; Gómez-Garreta *et al.*, 2001). LIBYA: Cyrenaica (Gómez-Garreta *et al.*, 2001).

Tropical Northwestern Atlantic: BAHAMAS (Taylor, 1960). BELIZE: Carrie Bow Cays (Norris & Bucher, 1992) and Pelican Cays (Littler & Littler, 1997). BERMUDA: (Taylor, 1960). CAYMAN ISLAND AND COSTA RICA (Taylor, 1960). CUBA: Canarreos Archipelago, Sabana-Camagüey Archipelago, Nuevitas Bay, Bocas de Alonzo, Coco, Gulf of Batabanó, Guanahabites, Guardalavaca, Havana, Matanzas, and Villa Clara (Suárez, 2005; Gil-Rodríguez *et al.*, 2010). HISPANIOLA ISLAND AND JAMAICA (Taylor, 1960). MARTINIQUE (Rodríguez-Prieto *et al.*, 1999). MEXICO: Campeche (Fujii *et al.*, 2006) and Quintana Roo (Sentíes & Fujii, 2002; Cassano *et al.*, 2010; Gil-Rodríguez *et al.*, 2010). PANAMA (Taylor, 1960). TRINIDAD AND TOBAGO (Duncan & Lee-Lum, 2006). USA: Florida (Collado-Vides *et al.*, 2011; Fujii *et al.*, 2006). VENEZUELA: Miranda State (Wynne, 2017). VIRGIN ISLANDS: St. Croix (Taylor, 1960).

West African Transition: CAPE VERDE ISLANDS [uncertain record (John *et al.*, 2004)] and SENEGAL (John *et al.*, 2004).

Warm Temperate Northwest Atlantic: USA: Texas (Wynne, 2008).

### ***Laurencia lauruahuertana* Mateo-Cid, Mendoza-González, Sentíes et Díaz-Larrea**

Type locality: Punta Herrero, Quintana Roo. México

Distribution: Caribbean Sea and Gulf of Mexico. MEXICO: Quintana Roo (Mateo-Cid *et al.*, 2014).

### ***Laurencia microcladina* Kützing**

Type locality: West Indies

Remarks: Records of *L. microcladina* from Brazil contain misapplied name, which correspond to *L. dendroidea* Cassano *et al.* (2012a).

Distribution: Lusitania: AZORES ISLANDS: Santa María Island and Pico (Tittley *et al.*, 2009). CANARY ISLANDS: El Hierro, Fuerteventura, Gran Canaria, La Palma, Lanzarote, and Tenerife (Gil-

Rodríguez *et al.*, 2012). MADEIRA ARCHIPELAGO: Porto Santo (Neto *et al.*, 2001). SALVAGES ISLANDS (John *et al.*, 2004).

Mediterranean Sea: ALGERIA: Alger (Gómez-Garreta *et al.*, 2001; Gil-Rodríguez *et al.*, 2012). CYPRUS: Akamas, Gazimağusa, Girne, Karpasia, Liopetri, and Salamis (Taskin *et al.*, 2013; Tsiamiset *et al.*, 2014b). EGYPT: El Daba (Gómez-Garreta *et al.*, 2001). FRANCE: Corsica (Gómez-Garreta *et al.*, 2001) and Hérault (Verlaque, 2001). GREECE: Zakynthos Island (Tsikira & Haritonidis, 2005). ITALY: Linosa Island (Serio *et al.*, 2006), Sicilia (Gómez-Garreta *et al.*, 2001), Tuscan Archipelago (Ridi *et al.*, 2002), Italian Adriatic Sea (Gómez-Garreta *et al.*, 2001), Gulf of Taranto (Gómez-Garreta *et al.*, 2001), Cherad islands, and Sardinia (Gómez-Garreta *et al.*, 2001). MALTA: Gozo Island and Malta Island (Comarci *et al.*, 1997). MOROCCO: Alhucemas, Cabo de Agua, Karia Arkemann, Muelle Colorado, Punta Negri, Punta de Rostrogordo, and Punta de Sabinilla (Gómez-Garreta *et al.*, 2001). SPAIN: Almería (Soto & Conde, 1989), Balearic Islands (Gómez-Garreta *et al.*, 2001), Catalunya (Gómez-Garreta *et al.*, 2001), and Murcia (Gil-Rodríguez *et al.*, 2012). TURKEY: Akdeniz, Izmir Bay, Gulf of Gökova, Karadeiz and Mersin (Taskin *et al.*, 2008).

Tropical Northwestern Atlantic: BAHAMAS (Taylor, 1960). BELIZE: Carrie Bow Cays (Norris & Bucher, 1982) and Pelican Cays (Littler & Littler, 1997). BERMUDA (Taylor, 1960). CAICOS ISLANDS, CAYMAN ISLANDS, COSTA RICA, JAMAICA, LESSER ANTILLES, NETHERLANDS ANTILLES, and PANAMA (Taylor, 1960). CUBA: Gulf of Batabanó (Suárez, 2005). PUERTO RICO: Arecibo and Santiago Cay (Gil-Rodríguez *et al.*, 2012). TRINIDAD AND TOBAGO (Duncan & Lum-Lee, 2006). USA: Florida (Taylor, 1960). VENEZUELA: Aves Island (Taylor, 1960) and Cumana (Gil-Rodríguez *et al.*, 2012). VIRGIN ISLANDS (Taylor, 1960).

West African Transition: CAPE VERDE ISLANDS: Ilheu Branco and San Nicolau (John *et al.*, 2004; Gil-Rodríguez *et al.*, 2012). MAURITANIA (John *et al.*, 2004). SENEGAL: North of Senegal (John *et al.*, 2004).

### ***Laurencia minuscula* Schnetter**

Type locality: Puerto López (Alta Guajira), Guajira Department, Colombia.

Distribution: Tropical Northwestern Atlantic: COLOMBIA: Guajira (Schnetter, 1976). CUBA: Havana (Sentíes *et al.*, 2010).

### ***Laurencia minuta* Vandermeulen, Garbary et Guiry**

Type locality: Eilat, Israel.

Distribution: Lusitanian: CANARY ISLANDS: Tenerife ("taxa inquira" Haroun *et al.*, 2002; John *et al.*, 2004). SPAIN: Galicia (Bárbara *et al.*, 2005).

Mediterranean Sea: CYPRUS: Girne (Taskin *et al.*, 2013). SPAIN: Alicante (Gómez-Garreta *et al.*, 2001). GREECE: Zakynthos Island (Tsikira & Haritonidis, 2005). ITALY: Apulia, Gulf Taranto, Northeastern Italy, and Sicily (Gómez-Garreta *et al.*, 2001), Linosa Island (Serio *et al.*, 2006), and Tuscany (Rindi *et al.*, 2002). MALTA: Malta Island (Gómez-Garreta *et al.*, 2001).

***Laurencia natalensis* Kylin**

Type locality: Isipingo Beach, near Durban, South Africa

Distribution: South Africa: Pearly Beach to Agulhas (Stegenga et al., 1997)

***Laurencia nidifica* J. Agardh**

Type locality: Hawaiian Islands

Distribution: Gulf of Guinea: IVORY COAST, GHANA, AND LIBERIA (John et al., 2004).

Lusitania: MADEIRA ARCHIPELAGO: Deserta Grande [uncertain record (Neto et al., 2001)].

St. Helena and Ascension Islands: ST. HELENA (John et al., 2004).

West African Transition: CAPE VERDE ISLANDS (John et al., 2004).

***Laurencia obtusa* (Hudson) J. V. Lamouroux**

Type locality: England.

Remarks: Cassano et al. (2012b) confirmed through molecular and morphological characters that records of *L. obtusa* from Brazil correspond to *L. dendroidea*.

Distribution: Black Sea: BULGARIA: Ahtopol area (Dimitrova-Konaklieva, 1981). ROMANIA: Romanian Littoral (Caraus, 2012). TURKEY: Antalya, Dikili Gelibolu, Gokceada Island, Izmir Bay, Kirkclareli, Korfezi, Mersin, and Zonguldak (Gómez-Garreta et al., 2001; Taskin et al., 2008).

Gulf of Guinea: CAMEROON. EQUATORIAL GUINEA: ANNOBON ISLAND. GHANA. SAO TOME AND PRINCIPE. SIERRA LEONE (John et al., 2004).

Lusitania: AZORES ISLANDS: Faial, Pico, Sao Miguel, Terceira, and Santa Maria (Neto, 1994; Tittley & Neto, 1994). CANARY ISLANDS: El Hierro, Fuerteaventura, Gomera, Gran Canaria, La Palma, Lanzarote Island, and Tenerife (John et al., 2004; Gil-Rodríguez et al., 2012). FRANCE: Britanny (Feldmann, 1954), Guernsey (Senties & Fujii, 2002), Herault (Ben Maizet et al., 1988), and Normandia (Dixon, 1961; Dizerbo & Herpe, 2007). MADEIRA ARCHIPELAGO: Deserta Grande, Ilhéu de Fora, Madeira, Porto Santo, Selvagem Grande, and Selvagem Pequena (John et al., 2004). SALVAGE ISLANDS (John et al., 2004). MAURITANIA (John et al., 2004). PORTUGAL: Beira Litoral, Douro Litoral, and Minho (Araujo et al., 2009). SPAIN: Asturias (Cires-Rodríguez & Cuesta-Moliner, 2010), Basquecoast (Gorostiaga et al., 2004), Cantabria (Martínez-Gil et al., 2007), Galicia (Bárbara et al., 2005; Peña & Bárbara, 2008), and Vigo (Hamel, 1928).

Mediterranean Sea: ALGERIA: Alger, Annaba, Bab El Oued, Bologhine, El Marsa, Rais Hamidou, Sidi Fredj, Southwest of Cap Bordj El Bahri, and Tipaza (Gómez-Garreta et al., 2001). CROATIA: Istria Coast (Munda, 1979). CYPRUS: Dip Karpaz, Famagusta, Gazi Mağusa, Girne, Karpasia, Kumyali, Koruçaim, Kyrenia, Liopepetri, Salamis, and Yeşilirmak (Taskin et al., 2013; Tsiamis et al., 2014b). EGYPT: Alexandria (Gómez-Garreta et al., 2001). FRANCE: Corsica (Gómez-Garreta et al., 2001; Sales & Ballesteros, 2010), Hyères (Augier et al., 1971), Pyrenees Orientales (Gómez-Garreta et al., 2001), and Var (Coppejans, 1972). GREECE: Ionian Islands (Tzikira & Haritonidis, 2005),

Kleisova (Gómez-Garreta et al., 2001; Christia et al., 2011), Rhodos Island (Diapoulis et al., 1986), and Sporades du Nord (Diannelidis, 1953). ISRAEL: Habonim (Gómez-Garreta et al., 2001). ITALY: Adriatic Sea (Furnari et al., 1999; Gómez-Garreta et al., 2001), Gulf of Taranto (Cecere et al., 1996), Napoli (Cinelli, 1971; Feoli & Bressan, 1972), Salerno (Edwards et al., 1975), Sicilia (Serio et al., 2006; Gómez-Garreta et al., 2001), Tuscany (Rindi et al., 2002), and Sardinia (Furnari et al., 2003). LIBYA: Bengazi-Sabri, Cyrenaica, Derna, and Tripoli (Gómez-Garreta et al., 2001). MALTA: Gozo Island (Cormaci et al., 1997). MOROCCO: Cabo de Agua, Cabo Quilates, Cal Iris, Cala Bonita, Cala Charranes, Cala Viñas, Cazaza, Chafarinas Islands, Karia Arkemanne, Mar Chica, Playa del Quemado, Punta Negri, Punta de Rostrogordo, and Sammar (Gómez-Garreta et al., 2001). SPAIN: Andalusia (Conde et al., 1996; Conde & Flores-Maya, 2000), Balearic Islands (Gómez-Garreta et al., 2001), Catalunya (Ballesteros, 1981; Rodríguez-Prieto & Polo-Albertí, 1988, 1998), Murcia (Pérez-Ruzafa & Honrubia, 1984; Pérez-Ruzafa, 1990), and Valencia (Barceló & Seoane, 1982). TUNISIA: Bahiret, Bechateur, Bizerte, Cap Blanc, Cap Farina, Cap Serrat, Cathage, Djerba, El Bibane, Gabès, Gammartin, Ghar El Khebir, Gulf of Gabès, Iles Cani, Kelibia, Kerkennah, Korba, Korbous, La Goulette, La Marsa, Mer de Bou Grara, Monastir, Le Galiton, Raf Raf, Raouad, Ras el Fartass, Salambô, Sidi Bou Said, Sfax, Sidi Raïs, Tabarka, Zarzis, and Zembra (Gómez-Garreta et al., 2001).

Northern European Seas: ENGLAND: Sussex and Devon (Lipkin & Silva, 2002). IRELAND: Antrim (Morton, 1994), Clare (De Valéra et al., 1979), Derry (Morton, 1994), Donegal (Morton, 2003), Down (Morton, 1994), Cork, Dublin, Galway, Kerry, Leitrim, Mayo, and Wexford (Guiry, 1978). SWEDEN (Athanasiadis, 1996).

Tropical Northwestern Atlantic: BAHAMAS: Berry Island (Senties & Fujii, 2002). BARBADOS (Wynne et al., 2014). BELIZE: Carrie Bow Cay (Norris & Bucher, 1982) and Pelican Cays (Littler & Littler, 1997). BERMUDA: St. Georges Island (Senties & Fujii, 2002; Taylor, 1960). CAICOS ISLAND, CAYMAN ISLANDS, and COLOMBIA (Taylor, 1960). CUBA: Havana City (Senties & Fujii, 2002), Camagüey, Juventud Island, and Matanzas, and Villa Clara (Suárez, 2005). DOMINICAN REPUBLIC: Santo Domingo (Senties & Fujii, 2002). GUADELOUPE: Pointe de la Verdure (Fujii et al., 2006). JAMAICA (Taylor, 1960). MARTINIQUE: Pointe des Salines and Ste. Anne (Rodríguez-Prieto & Michanek, 1999). MEXICO: Campeche, Quintana Roo, and Tamaulipas (Ortega et al., 2001; Senties & Fujii, 2002), Veracruz and Yucatán (Ortega et al., 2001). NETHERLANDS ANTILLES: Bonaire and Curaçao (Senties & Fujii, 2002). PANAMA: Galeta Point (Senties & Fujii, 2002). PUERTO RICO: Guanica and Jaobos (Senties & Fujii, 2002). TRINIDAD AND TOBAGO: Tobago (Taylor, 1960; Senties & Fujii, 2002). USA: Florida (Littler et al., 2008). VENEZUELA: Aves Island, Cabagua, Margarita Island, and Pelona Island (Taylor, 1960; Senties & Fujii, 2002; Fujii et al., 2006). VIRGIN ISLANDS (Taylor, 1960).

Warm Temperature Northwestern Atlantic: USA: Texas (Wynne, 2008).

West African Transition: CAPE VERDE ARCHIPELAGO (John et al., 2004). GAMBIA (John et al., 2004). SENEGAL: North Senegal (John et al., 2004).

***Laurencia olivirana* Yoneshigue**

Type locality: Ponta da Cabeça, Cabo Frio, Rio de Janeiro State, Brazil.

Distribution: Tropical Southwestern Atlantic: BRAZIL: Rio de Janeiro (Fujii *et al.*, 2012) and Bahia (Fujii & Senties, 2005).

Warm Temperate Southwestern Atlantic: BRAZIL: Rio Grande do Sul and São Paulo (Fujii & Senties, 2005).

***Laurencia pyramidalis* Bory ex Kützing**

Type locality: Granville, Normandy, France.

Distribution: Lusitania: AZORES: Pico, Santa Maria, and São Miguel (Machín-Sánchez *et al.*, 2014). CANARY ISLANDS: Fuerteventura, La Gomera, Lanzarote, and Tenerife (Machín-Sánchez *et al.*, 2014). FRANCE: Finistère (Bouxin & Dizerbo, 1971) and Normandy (Machín-Sánchez *et al.*, 2014). MADEIRA ARCHIPELAGO: Ponta de São Jorge-Casi, Porto Moniz-Piscinas, and Seixal-Praia da Laje (Machín-Sánchez *et al.*, 2014). PORTUGAL: Minho (Araújo *et al.*, 2009). SPAIN: Asturias (Cires-Rodríguez & Cuesta-Moliner, 2010; Díaz *et al.*, 2008), BasqueCoast (Gorrostiaga *et al.*, 2004), Cantabria (Martínez-Gil *et al.*, 2007), Galicia (Bárbara *et al.*, 2005) and Sisargas Island (Veiga *et al.*, 1998).

Mediterranean Sea: CYPRUS: Dip Karpathos and Gazi Mağusa (Taskin *et al.*, 2013). ITALY: Adriatic Sea (Furnari *et al.*, 1999) and Sardinia Island (Serio *et al.*, 2004). SPAIN: Andalusia (Conde *et al.*, 1996), Catalunya (Ballesteros, 1981), and Murcia (Pérez-Ruzafa & Honrubia, 1984).

Nothern European Seas: GREAT BRITAIN and IRELAND (Hardy & Guiry, 2003).

***Laurencia tenera* C. K. Tseng**

Type locality: Shek-O, Hong Kong.

Distribution: Gulf of Guinea: IVORY COAST, GHANA, LIBERIA, SIERRA LEONE, and Togo (John *et al.*, 2004).

West African Transition: CAPE VERDE ISLANDS, GAMBIA, MAURITANIA, and SENEGAL (John *et al.*, 2004).

St Helena and Ascension Islands: ST. HELENA (John *et al.*, 2004).

***Laurencia translucida* M. T. Fujii et Cordeiro-Marino**

Type locality: Padre beach, Aracruz, Espírito Santo State, Brazil.

Distribution: Warm Temperate Southwesern Atlantic: BRAZIL: São Paulo (Creed *et al.*, 2010).

Tropical Southwestern Atlantic: BRAZIL: Bahia, Ceará, and Pernambuco Espírito Santo (Fujii *et al.*, 2006), Rio de Janeiro (Creed *et al.*, 2010).

***Laurencia venusta* Yamada**

Type locality: Koshiki-jima, Kagoshima Prefecture and Goto-retto, Nagasaki Prefecture, Japan.

Distribution: Tropical Northwestern Atlantic: MÉXICO: Quintana Roo (Senties & Fujii, 2002).

Tropical Southwestern Atlantic: BRAZIL: Espírito Santo (Fujii & Senties, 2005).

***Laurencia viridis* Gil-Rodríguez et Haroun**

Type locality: Canary Islands: Tenerife: Punta Hidalgo-Baja Negra.

Distribution: West African Transition: CAPE VERDE ISLANDS (John *et al.*, 2004).

Macaronesian Archipelago. AZORES: Santa María (Machín-Sánchez *et al.*, 2014). CANARY ISLANDS: El Hierro, Fuerteventura, Gran Canaria, La Gomera, La Palma, Lanzarote, and Tenerife (John *et al.*, 2004; Gil-Rodríguez *et al.*, 2012; Machín-Sánchez *et al.*, 2014). MADEIRA ARCHIPELAGO: Ilhéu de Fora, Ponta de São Jorge, Porto Santo, and Salvagem Pequena (John *et al.*, 2004; Machín-Sánchez *et al.*, 2014).

***Species inquirenda******Laurencia alsidiiformis* Zanardini ex Fraudentfeld**

Type locality: Spalato, Dalmatian coast.

***Laurencia alsidioides* P. L. Crouan et H.M. Crouan**

Type locality: I. Guadeloupe, Caribbean Sea.

***Laurencia botryocephala* Kützing**

Type locality: "Ad Caput Bonae Spei" Cape of Good Hope.

***Laurencia canariensis* Montagne ex Kützing**

Remarks: Gil Rodríguez *et al.* (2012) suggested that it should be considered an uncertain species. According to John *et al.* (1994), *L. canariensis* and *L. caespitosa* are synonyms of *Osmundea hybrida* (De Candolle) K. W. Nam.

Type locality: Canary Islands.

***Laurencia moriformis* Kützing**

Type locality: Cape of Good Hope.

***Laurencia trifaria* Kützing**

Type locality: Cape of Good Hope.

**PAE Analysis.** The area cladogram obtained had the following parameters: Length = 28, Consistency Index=0.85 and Retention Index=0.88. The strict consensus tree of the 3 equally parsimonious trees is presented (Fig. 2). Cladogram topology suggests four areas of endemism: South Africa (AghB) with four restricted species, Brazil (EB, NEB, and SEB) with four restricted species, Northeastern Atlantic (WMe, SEAS, LevS, and AdS) with three restricted species, and Gulf of Guinea (SHAI, GGU, CV, GGW, and GGC) with four restricted species (Fig. 3). Some of these species, however, are also distributed in the Indo-Pacific (see Table 1). In addition, we have defined three categories of areas: partial congruence (areas with partial congruence between the areas of distribution) composed by GA, ECa, WCa, and SCa (Fig. 2), secondary areas (area with an endemic species, Ippi & Flores, 2001) and widespread species (Table 1).

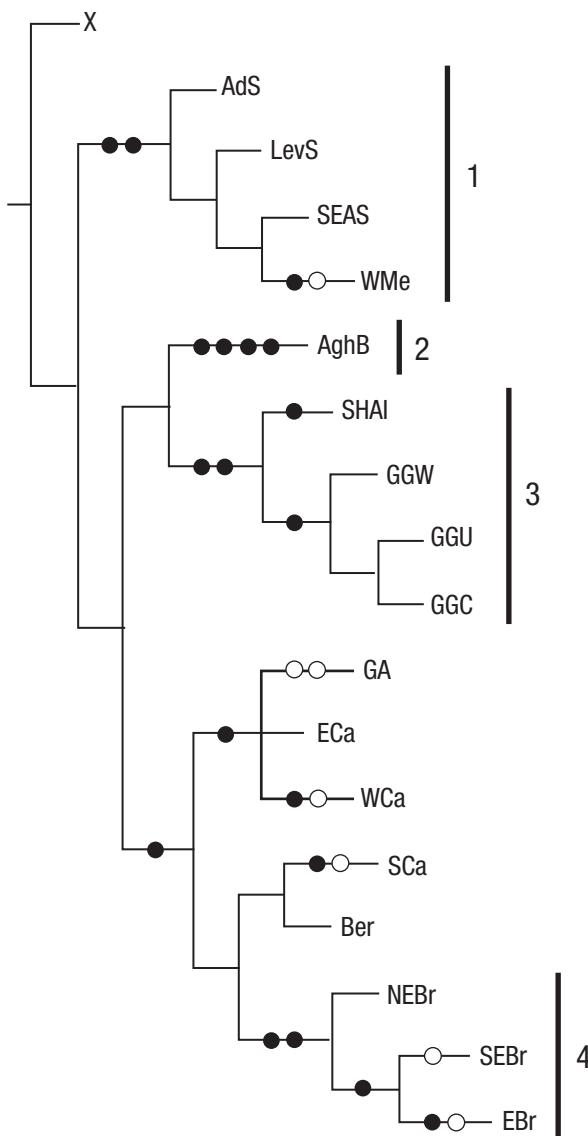


Figure 2. Areas of endemism defined in the PAE analysis. 1) Northwestern Atlantic, 2) South Africa, 3) Gulf of Guinea, and 4) Brazil. The black dots represent restricted species or synapomorphies and the white dots represent homoplasies.

## DISCUSSION

The nomenclature from genus to species, valid names, and taxonomic synonyms of *Laurencia* are a fundamental part of the checklist here proposed and a topic of continuing discussion among taxonomists. Checklists allow for the documentation of species distributions, the biodiversity within certain areas, and offer the possibility of using this information to carry out a biogeographical analysis; thus, considering the taxonomic remarks, uncertain records, reports of invasion, and introduction of species allows us to obtain biogeographical natural patterns or approximate reality. Taxonomic validity of the records and the recognition of the distribution limits of the species area are essential requirements in biogeographic works (Morrone, 2013). In turn, areas of

endemism and secondary areas can be defined, and widespread species identified.

**On endemism.** Areas of endemism (non-endemic species) are defined as the sympatric distribution congruence of two or more taxa belonging to a given category (e.g., order, family, genus or species) (Morrone, 2013). However, when we take *Laurencia*, the Caribbean Sea is defined by partial congruence in the distribution of two or more species (group GA, ECa, WCa, and SCA; see Fig. 2). Endemic species inhabit this region, such as *L. laurahuertana* in the western Caribbean, *L. foldatsii* in the southern Caribbean, *L. chondrioides*, and *L. minuscula* in the Caribbean Sea in general, but their distributional congruence is not total, and the PAE analysis does not define this area for two or more synapomorphies. Furthermore, the Caribbean Sea is the Atlantic biotic area with the highest species richness of *Laurencia* (13 spp.). This biogeographic pattern is also shared by the distributional diversity of several unrelated taxa, such as coastal fishes, mangroves, coral reefs, and seagrasses in the Atlantic Ocean (Tittensor et al., 2010).

According to Tapia-Silva et al. (2015), a mathematical analysis of the geographic distribution of the macroalgal species richness can reveal high diversity spots that, in the case of macroalgae, coincide well with the major distribution of the great marine environments in the area (mangroves, coral reefs and seagrasses): the Mexican Caribbean barrier reef, the Veracruz reef system, and the Alacran reef system at Puerto Progreso, Yucatan (Vilchis et al., in press). Studies have shown higher macroalgal diversity in the Indo-Pacific area than in the Atlantic (Kerswell, 2006), and when comparing worldwide *Laurencia* data (Tapia et al., 2015) this pattern is confirmed. Areas of endemism in the south Atlantic were also found in Brazil, Gulf of Guinea, and South Africa, which are also reported to contain endemic species (Brown & Lomolino, 1998); furthermore, it was found that the Gondwana breakup is the geological process that explains this endemism.

Other areas such as the Northwestern Atlantic, Europe, and the Caribbean Sea share *Laurencia* species with other regions (i.e., the Indo-Pacific), and the influence of vicariance events such as the closing of Isthmus of Panama and the final closure of the Tethys seaway in the Eastern Atlantic (Cowman & Bellwood, 2013) has not been studied.

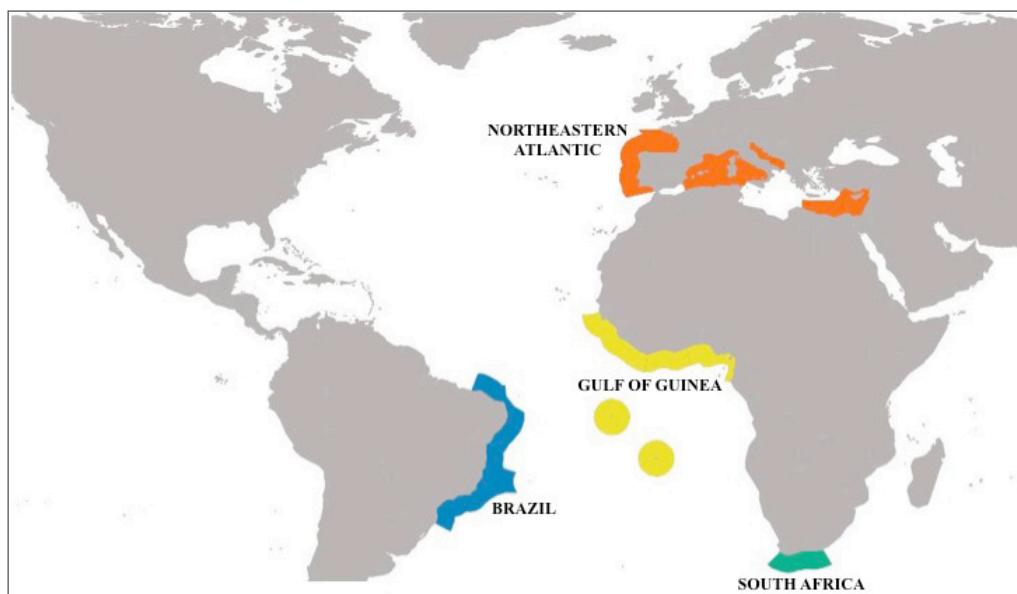
**Secondary areas.** These areas are defined by the presence of one endemic species. When this happens, for example, in the Macaronesian Archipelago with *L. viridis*, the area is inhabited mostly by species that are also distributed in other places (9 spp.), and the number of endemic species is smaller compared to the defined areas of endemism. In the Macaronesian Archipelago, the phycofloristic composition reveals elements in common with the littoral of continental Europe and the North of Africa (Haroun and Prud'Homme van Reine, 1993; Tuya & Haroun, 2009). This is because the geological origin of the Macaronesian islands dates to the early Miocene (20 my) (Brown & Lomolino, 1998), allowing the colonization of species from other areas. Thus, this region is a special biotic area that could be researched using an island-biogeography approach.

**Widespread species.** The genus *Laurencia* in the Atlantic Ocean extends from the coast of Ireland to South Africa, including the Mediterranean Sea and Black Sea; in the western Atlantic, the genus extends from North Carolina, USA, to southern Brazil. Seventeen of these species are also distributed in the Indo-Pacific, of which five are widely distributed in the Atlantic Ocean.

Table 1. Categories of areas defined for *Laurencia* in the Atlantic Ocean.

Categories	Defined Area	Species
Areas of Endemism	Atlantic Northeastern Ocean	<i>L. coronopus</i> , <i>L. minuta</i> *, <i>L. pyramidalis</i> †.
	Brazil	<i>L. aldingensis</i> *, <i>L. catarinensis</i> †, <i>L. oliveirana</i> , <i>L. translucida</i> .
	Gulf of Guinea	<i>L. brachyclados</i> *, <i>L. galtsoffii</i> *, <i>L. nidifica</i> *, <i>L. tenera</i> *
	South Africa	<i>L. corymbosa</i> *, <i>L. flexuosa</i> , <i>L. griseavilacea</i> , <i>L. natalensis</i> *
Partial Congruence	Caribbean Sea	<i>L. chondrioides</i> , <i>L. epiphylla</i> , <i>L. foldatsii</i> , <i>L. laurahuertana</i> , <i>L. minuscula</i> *
Secondary Areas	Macaronesian Islands	<i>L. viridis</i>
	American Atlantic	<i>L. caraibica</i> *, <i>L. decumbens</i> *, <i>L. venusta</i> *
Amphi-Atlantic	Northern Atlantic	<i>L. microcladia</i> * †
Widespread in the Atlantic Ocean		<i>L. bronniartii</i> *, <i>L. caduciramulosa</i> * †, <i>L. dendroidea</i> * †, <i>L. intricata</i> *, <i>L. obtusa</i> * †

\*Species also distributed in the Indo-Pacific. †Species also distributed in the Macaronesian Archipelago.

Figure 3. Map of the areas of endemism of *Laurencia* in the Atlantic Ocean.

Recent phylogenetic studies have been useful in detecting misidentifications in the Atlantic, especially in records from Macaronesia, Brazil, and the Mexican Caribbean, although only nine widespread species of *Laurencia* in the Atlantic have a molecular characterization in these places. The use of the molecular-phylogenetic approach on these species in the Atlantic Ocean should allow us to identify new lineages over a wide distribution range, as has happened with other groups of red algae (Skage *et al.*, 2005; Nuñez-Resendiz *et al.*, 2015), and achieve a much better understanding of the historical biogeography of *Laurencia* in the Atlantic Ocean.

According to Miranda and Marques (2011), the two principal obstacles in the biogeographical works are (1) the reliability of species identifications and the consequent uncertainty of the presence of species in a given area, and (2) the difficulty in producing reliable cladograms from phylogenies.

In conclusion, it has been possible to establish a biogeographic pattern in *Laurencia* from the definition of areas of endemism and partial and secondary areas. This pattern has been linked to geological events that occurred in the past. Therefore, the recognition of new species from systematics studies and the clarification of taxonomic problems will allow researchers to continue developing a biogeographic hypothesis for the genus in the Atlantic Ocean.

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