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Received 23 Dec 2010
Accepted 22 Jan 2011
Available online 20 Apr 2011

Keywords:

biodiversity
biological activities
Laurencia complex
seaweeds
taxonomy
terpenoids

ISSN 0102-695X
doi: 10.1590/S0102-695X2011005000064

Overview of the taxonomy and of the major secondary metabolites and their biological activities related to human health of the *Laurencia* complex (Ceramiales, Rhodophyta) from Brazil

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Abstract: In Brazil, the *Laurencia* complex is represented by twenty taxa: *Laurencia* s.s. with twelve species, *Palisada* with four species (including *Chondrophycus furcatus* now that the proposal of its transference to *Palisada* is in process), and *Osmundea* and *Yuzurua* with two species each. The majority of the Brazilian species of the *Laurencia* complex have been phylogenetically analyzed by 54 *rbcL* sequences, including five other Rhodomelacean species as outgroups. The analysis showed that the *Laurencia* complex is monophyletic with high posterior probability value. The complex was separated into five clades, corresponding to the genera: *Chondrophycus*, *Laurencia*, *Osmundea*, *Palisada*, and *Yuzurua*. A bibliographical survey of the terpenoids produced by Brazilian species showed that only six species of *Laurencia* and five of *Palisada* (including *C. furcatus*) have been submitted to chemical analysis with 48 terpenoids (47 sesquiterpenes and one triterpene) isolated. No diterpenes were found. Of the total, 23 sesquiterpenes belong to the bisabolane class and eighteen to the chamigrene type, whose biochemical precursor is bisabolane, two are derived from lauranes and four are triquinols. Despite the considerable number of known terpenes and their ecological and pharmacological importance, few experimental biological studies have been performed. In this review, only bioactivities related to human health were considered.

Introduction

The red algae of the *Laurencia* complex comprehend 430 species (and infraspecific taxa) listed in the database at present, of which 134 have been flagged as currently accepted taxonomically. They are reported worldwide from the temperate to tropical shores of the world, occurring from the intertidal to the subtidal zone up to 65 m in depth (Guiry & Guiry, 2010). *Laurencia sensu lato* is an extremely rich source of halogenated secondary metabolites with diverse structural features (Fenical, 1975; Erickson, 1983) that can be divided into two groups according to their biogenetic origin. The first one is the nonterpenoid group, which contains the acetogenins derived from the metabolism of fatty acids. The other one is the terpenoid group, in which the sesquiterpenes are the most abundant, but also containing diterpenes and triterpenes (Fernández et al.,

2005).

The taxonomy of the *Laurencia* complex has undergone several changes based on the use of new vegetative morpho-anatomical and reproductive features, cladistic analyses of morphological characters and molecular approaches based on the plastidial *rbcL* gene (Nam et al., 1994; Garbary & Harper, 1998; Nam, 1999, 2006, 2007; Martin-Lescanne et al., 2010). These changes include the resurrection of the genus *Osmundea* Stackhouse (Nam et al., 1994), the elevation of the subgenus *Chondrophycus* Tokida & Saito (in Saito, 1967) to the generic rank (Garbary & Harper, 1998), the new delineations of the genera *Chondrophycus*, *Laurencia* and *Osmundea* (Nam, 1999), the definition of the proposal of the genus *Palisada* (Yamada) K.W. Nam based on Yamada's (1931) section *Palisadae* (Nam, 2006) and its later validation (Nam, 2007), and the establishment of the genus *Yuzurua* (K.W. Nam

Martin-Lescanne based on Nam's (1999) subgenus *Yuzurua* (Martin-Lescanne et al., 2010). Thus, five genera are currently assigned to the *Laurencia* complex: *Laurencia* J.V. Lamouroux itself, *Osmundea*, *Chondrophycus*, *Palisada* and *Yuzurua*. Several morpho-anatomical and reproductive characters used in the taxonomy of the complex have been shown to have diagnostic value at the generic level only (Saito, 1967; Nam et al., 1994; Garbary & Harper, 1998; Nam, 1999, 2006). Many species have no defined taxonomic boundaries and present extensive morphological plasticity, making their taxonomic delimitation difficult. In this context, the use of molecular markers has proven to be useful for delimiting the taxa and inferring their phylogenetic relationships and has corroborated the current classification system (Nam et al., 2000; McIvor et al., 2002; Abe et al., 2006; Fujii et al., 2006; Díaz-Larrea et al., 2007; Cassano et al., 2009; Gil-Rodríguez et al., 2009; Martin-Lescanne et al., 2010; Rocha-Jorge et al., 2010).

The genera are distinguished by a combination of both vegetative and reproductive characteristics: number of pericentral cells per vegetative axis, position of the first pericentral cell relative to the trichoblast, origin of the tetrasporangia, absence or presence of fertility of the second pericentral cell, number of sterile pericentral cells in the tetrasporangial axis, origin of the spermatangial branches, formation pattern of the spermatangial branches on trichoblasts, the number of pericentral cells in procarp-bearing segments of female trichoblasts, and probably post-fertilization features associated with the formation time of the auxiliary cell. Many of these characters overlap among the genera. Effectively, the genus *Laurencia* is distinct from the other four genera by the presence of four pericentral cells per axial segment; two pericentral cells occur in *Osmundea*, *Chondrophycus*, *Palisada* and *Yuzurua* (Nam et al., 1994; Garbary & Harper, 1998; Nam, 1999, 2006; Martin-Lescanne et al., 2010). The genus *Osmundea* is distinct from the other genera by the tetrasporangial production from random cortical cells rather than from particular pericentral cells and filament-type rather than trichoblast-type spermatangial development (Nam et al., 1994). The genus *Chondrophycus* is characterized by spermatangial branches produced from two laterals on the suprabasal cell of trichoblasts, but remaining partly sterile, and a tetrasporangial axis with the first and second pericentral cells never fertile (Nam, 1999). In the genus *Palisada*, the spermatangial branches are produced from one of two laterals on the suprabasal cells of trichoblasts and the second pericentral cell in the tetrasporangial axis is always fertile; the resulting axis has one sterile pericentral cell (Nam, 2006). The genus *Yuzurua* shares the majority of the morphological characters of *Palisada*, from which it was recently

segregated, but differs by not having palisade-like cells, by the presence of secondary pit-connections between cortical cells, and by procarp-bearing segments with five pericentral cells rather than four (Fujii et al., 1996).

The species of the *Laurencia* complex are widely distributed along the Brazilian coast from Ceará (Pinheiro-Joventino et al., 1998) to Rio Grande do Sul (Baptista, 1977), growing in different types of habitats (Fujii & Senties, 2005) and constituting an important element of Brazilian phycological flora (Oliveira Filho, 1977).

The members of this complex, in particular *Laurencia s.s.*, are prolific synthesizers of structurally elaborate halogenated secondary metabolites and have been reported to produce a numerous diversity of unique compounds, especially terpenes (Martín & Darias, 1978; Erickson, 1983; Pereira & Teixeira, 1999). Although the function of these secondary metabolites has not yet been clearly defined, it has been suggested that these metabolites play a major role in mediating ecological interactions such as algae/herbivore interactions (Hay et al., 1987; Hay & Steinberg, 1992), with these compounds acting as a defense against being eaten or as a deterrent against epibiota, *i.e.*, an antifouling activity (da Gama et al., 2002; Cassano et al., 2008; Lhullier et al., 2009), or protection against pathogens (König & Wright, 1997). Thus, ecological pressures such as competition for space, fouling of the surface, predation, and successful reproduction have led to the evolution of unique secondary metabolites with various biological activities (Ireland et al., 2000). The prominent biological activity of marine terpenes is evident in their ecological role in the marine environment and makes them interesting as potential drugs. Many of these natural products are pharmacologically active and marine algae, especially those from tropical and subtropical seas, are able to produce a wide range of compounds, many of which exhibit at least some degree of bioactivity (Fernández et al., 1998, 2005; da Gama et al., 2002; Cassano et al., 2008; Lhullier et al., 2009; Machado et al., 2011; Santos et al., 2010). In fact, the marine environment represents a treasure trove of useful products awaiting discovery for the treatment of infectious and parasitic diseases (Vairappan et al., 2004; Morales et al., 2006), cancer (Mohammed et al., 2004; Stein et al., 2011), cognitive diseases, inflammatory processes, and viral infections (Sakemi et al., 1986). Despite the many structures known and their ecological and pharmacological importance, only a few biosynthetic studies have been performed on marine terpenoid compounds (Gross & König, 2006). In this paper, the current status of the taxonomy of the *Laurencia* complex in Brazil is outlined, together with the diversity of secondary metabolites produced

and their biological activities of relevance to human health.

Materials and Methods

The present work is a compilation of the data on the *Laurencia* complex from Brazil, including the current results on the taxonomy and phylogeny of the group, secondary metabolites and their biological activities related to human health.

We performed a phylogenetic analysis using 54 *rbcL* sequences, with seventeen samples from Brazil (Table 1). Multiple alignments for sequences were constructed using the computer program BioEdit 7.0.4.1 (Hall, 1999). A total of 250 nucleotides were removed from all *rbcL* sequences at the beginning and end of the sequences because many sequences from the GenBank

were incomplete, producing a data set of 1217 base pairs. Phylogenetic relationships were inferred with MrBayes v.3.0 beta 4 (Huelsenbeck & Ronquist, 2001). The model used in the Bayesian analysis was selected based on maximum likelihood ratio tests implemented by the software Modeltest version 3.06 (Posada & Crandall, 1998) with a significance level of 0.01 by the Akaike information criterion. For the Bayesian analysis, four chains of the Markov chain Monte Carlo (one hot and three cold) were used, sampling one tree every ten generations for 1,000,000 generations starting with a random tree. The 50,000 generations were discarded as 'burn in'. The model used in the Bayesian analysis for *rbcL* sequences was the general-time-reversible model of nucleotide substitution with invariant sites and gamma distributed rates for the variable sites (GTR+I+G).

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

Samples	Collection data	GenBank accession numbers (if available)
<i>Bostrychia radicans</i> (Montagne) Montagne in Orbigny	USA, Mississippi, St. Louis Bay, 11 Feb. 1998, C.F.D. Gurgel	AF259497
<i>Polysiphonia muelleriana</i> J. Agardh	New Zealand, Deas Cove, Thompson Sound, Fiordland, 03 Oct. 2000, S. Wing and N. Goebel	AY588412
<i>Bryocladia cuspidata</i> (J. Agardh) De Toni	USA, Texas, Port Aransas, 17 May 1998, S. Fredericq and C.F.D. Gurgel	AF259498
<i>Chondria collinsiana</i> M.A. Howe	Brazil, Rio de Janeiro, Armação dos Búzios, Praia Rasa, 13 Jan. 2005, V. Cassano and J.C. De-Paula	GU330225
<i>C. dasyphylla</i> (Woodward) C. Agardh	USA, North Carolina, New Hanover Co., Wrightsville Beach	U04021
<i>Chondrophycus furcatus</i> (Cordeiro-Marino & M.T. Fujii) Senties & M.T. Fujii	Brazil, Paraíba, Praia de Tambaú, 24 Feb. 2004, M.T. Fujii	GU330226
<i>C. cf. undulatus</i>	New Caledonia, Loyalty Is., Maré, 22 Mar. 2005, C. Payri	FJ785307
<i>Chondrophycus</i> sp. 1	New Caledonia, Loyalty Is., Lifou, 26 Mar. 2005, C. Payri	FJ785309
<i>Chondrophycus</i> sp. 2	New Caledonia, Loyalty Is., Maré, 21 Mar. 2005, C. Payri	FJ785310
<i>Chondrophycus</i> sp. 3	New Caledonia, Loyalty Is., Beaufort/Beaupré, 06 Apr. 2005, C. Payri	FJ785311
<i>Laurencia aldingensis</i> Saito & Womersley	Brazil, Espírito Santo, Anchieta, Ilhote de Ubu, 30 Jun. 2007, E. Stein	-
<i>L. aldingensis</i>	Brazil, Rio de Janeiro, Armação dos Búzios, Praia Rasa, 13 Jan. 2005, V. Cassano and J.C. De-Paula	-
<i>L. cf. brongniartii</i> J. Agardh	Australia, Tarcoola Beach, S. Fredericq, 1993	EF061654
<i>L. cf. brongniartii</i>	Taiwan, Makang Harbour, S. Fredericq, 11 Jul. 1993	AF465814
<i>L. caduciramulosa</i> Masuda & Kawaguchi	Brazil, Rio de Janeiro, Angra dos Reis, Praia do Velho, 19 Apr. 2006, V. Cassano and J.C. De-Paula	-
<i>L. caduciramulosa</i>	Spain, Canary Islands, Tenerife, Punta del Hidalgo, 06 May 2008, M.C. Gil-Rodríguez, M.T. Fujii, V. Cassano and J. Díaz-Larrea	-
<i>L. caraibica</i> P.C. Silva	Mexico, Quintana Roo, Cancún, Isla Mujeres, 23 Feb. 2006, A. Senties	EF658642
<i>L. catarinensis</i> Cordeiro-Marino & M.T. Fujii	Brazil, Santa Catarina, Florianópolis, Prainha da Barra da Lagoa, 16 Jul. 2008, P.A. Horta	-
<i>L. catarinensis</i> (as <i>L. intricata</i>)	Brazil, Espírito Santo, Anchieta, Ponta dos Castelhanos, 05 Oct. 2006, M.T. Fujii and V. Cassano	-
<i>L. catarinensis</i> (as <i>L. intricata</i>)	Brazil, Rio Grande do Norte, Maracajaú, 24 Jun. 2006, M.T. Fujii and I.B. Silva	-
<i>L. dendroidea</i> J. Agardh [as <i>L. majuscula</i> (Harvey) A.H.S. Lucas]	Brazil, Rio de Janeiro, Angra dos Reis, Praia do Velho, 20 Jul. 2006, V. Cassano and J.C. De-Paula	GU330232

<i>L. dendroidea</i> (as <i>L. arbuscula</i>)	Brazil, São Paulo, Ubatuba, Praia do Felix, 31 Aug. 2000, M.T. Fujii	AF465810
<i>L. dendroidea</i> (as <i>L. majuscula</i>)	Spain, Canary Islands, Tenerife, Puerto de la Cruz, 13 Jul. 2006, M.C. Gil-Rodríguez, M.T. Fujii and A. Senties	EF686000
<i>L. flexuosa</i> Kützing	South Africa, S. KwaZulu-Natal, Palm Beach, 07 Feb. 2001, S. Fredericq	AF465815
<i>L. intricata</i> J.V. Lamouroux	Mexico, Yucatan, Campeche Bay, 14 Feb. 1999, C.F.D. Gurgel	AF465809
<i>L. intricata</i>	USA, Florida, Long Key, Channel 5, 10 Dec. 1998, B. Wysor and T. Frankovich	AY588410
<i>L. intricata</i>	Cuba, Ciego de Ávila, Cayo Coco, 25 Sep. 2005, M.T. Fujii	GU330238
<i>L. marilzae</i> Gil-Rodríguez, Senties, Díaz-Larrea, Cassano & M.T. Fujii	Spain, Canary Islands, Tenerife, Punta del Hidalgo, M.C. Gil-Rodríguez, 12 Jul. 2006	EF686002
<i>L. marilzae</i>	Brazil, São Paulo, Laje de Santos Marine State Park, Parcel do Sul, 25 Mar. 2007, R. Rocha-Jorge	GU938189
<i>L. obtusa</i> (Hudson) J.V. Lamouroux	Ireland, County Donegal, Fanad Head, 06 Jul. 1998, C.A. Maggs	AF281881
<i>L. oliveirana</i> Yoneshigue	Brazil, Rio de Janeiro, Arraial do Cabo, Ponta da Cabeça, 07 Jul. 2008, V. Cassano and J.C. De-Paula	-
<i>L. translucida</i> M.T. Fujii & Cordeiro-Marino	Brazil, Espírito Santo, Marataizes, 15 Sep. 2001, M.T. Fujii	AY588408
<i>L. venusta</i> Yamada	Mexico, Quintana Roo, Puerto Morelos, Punta Brava, J. D. Larrea and A. Senties, 18.04.2004	EF061655
<i>L. viridis</i> Gil-Rodríguez & Haroun	Spain, Canary Islands, Tenerife, Punta del Hidalgo, Roca Negra, 06 Oct. 2005, M.C. Gil-Rodríguez	EF685999
<i>Laurencia</i> sp. 1	Brazil, Rio de Janeiro, Armação dos Búzios, Praia Rasa, 13 Jan. 2005, V. Cassano and J.C. De-Paula	-
<i>Osmundea blinksii</i> (Hollenberg & Abbott) K.W. Nam	USA, California, San Mateo Co., Año Nuevo, Greyhound Rock, 17 Jul. 1996, M.H. Hommersand	AY172575
<i>O. oederi</i> (Gunnerus) G. Furnari [as <i>O. ramosissima</i> (Oeder) Athanasiadis]	Ireland, Co. Donegal, St. John's Point, 12 Oct. 1999, C.A. Maggs	AF281880
<i>O. osmunda</i> (S.G. Gmelin) K.W. Nam	Ireland, County Donegal, St. John's Point, 12 Oct. 1999, C.A. Maggs	AF281877
<i>O. pinnatifida</i>	France, Brittany, Penmarch	AF259495
<i>O. sinicola</i> (Setchell & Gardner) K.W. Nam	USA, California, Orange Co., Crescent Beach, 28 May 2002, S. Murray	AY588407
<i>O. spectabilis</i> (Postels & Ruprecht) K.W. Nam var. <i>spectabilis</i>	Mexico, Baja California, Punta Santo Thomas, 2 Jul. 1996, M.H. Hommersand	AY172574
<i>O. splendens</i> (Hollenberg) K.W. Nam	Mexico, Baja California, Bahia Colnett, Drift, 2 Jul. 1996, M.H. Hommersand and J. Hughey	AY172576
<i>O. truncata</i> (Kützing) K.W. Nam & Maggs	Ireland, Lough Hyne, Co. Cork, 11 Nov. 1999, C.A. Maggs	AF281879
<i>Palisada corallopsis</i> (Montagne) Senties, M.T. Fujii & Díaz-Larrea	Mexico, Quintana Roo, Cancún, Chaac-Mol Beach, 21 Aug. 2005, J. Díaz-Larrea and A. Senties	EF061646
<i>P. flagellifera</i> (J. Agardh) K.W. Nam	Brazil, Rio de Janeiro, Rio das Ostras, Areias Negras, 03 Aug. 2005, V. Cassano and M.B. Barros-Barreto	GU330221
<i>P. patentiramea</i> (Montagne) Cassano, Senties, Gil-Rodríguez & M.T. Fujii	Philippines	AF489862
<i>P. perforata</i> (Bory) K.W. Nam	Brazil, Rio de Janeiro, Parati, Praia Vermelha, 30 Dec. 2005, V. Cassano	EU256331
<i>P. perforata</i>	Brazil, Rio de Janeiro, Areias Negras, Rio das Ostras, 03 Aug. 2005, V. Cassano and M.B. Barros-Barreto	EU256330
<i>Palisada</i> cf. <i>robusta</i>	New Caledonia, Lifou, 23 Mar. 2005, C. Payri	FJ785321
<i>P. thuyoides</i> (Kützing) Cassano, Senties, Gil-Rodríguez & M.T. Fujii	Philippines	AF489863
<i>Yuzurua poiteaui</i> (J.V. Lamouroux) Martin-Lescanne var. <i>gemmifera</i> (Harvey) M. J. Wynne	Mexico, Quintana Roo, Puerto Morelos, Ojo de Agua, 16 Apr. 2004, J. Díaz-Larrea and A. Senties	EF061648
<i>Y. poiteaui</i> var. <i>gemmifera</i>	Cuba, La Habana, Rincon de Guanabo, 29 Jul. 2005, J. Díaz-Larrea and A. A. Mallea	EF061650
<i>Y. poiteaui</i> var. <i>poiteaui</i>	USA, Florida, Long Key, Ocean Side, 1998, S. Fredericq	EF061652
<i>Y. poiteaui</i> var. <i>poiteaui</i>	Mexico, Quintana Roo, Playa del Carmen, 15 Mar 2005, J. Díaz-Larrea and A. Senties	EF061653

Table 2. Species of the *Laurencia* complex referred from Brazil and their regional geographic distribution.

Taxa	Regional distribution along the Brazilian coast	References
<i>Laurencia aldingensis</i> Saito & Womersley	Northeastern and Southeastern	Carvalho et al., 2003; 2006; Guimarães, 2006; Cassano, 2009; Torrano Silva, 2010; Silva, 2010.
<i>L. caduciramulosa</i> Masuda & Kawaguchi	Northeastern and Southeastern	Cassano et al., 2006; Torrano Silva, 2010.
<i>L. caraibica</i> P.C. Silva	Northeastern	Oliveira Filho & Ugadim, 1974; 1976) and Oliveira Filho, 1977 as <i>L. pygmaea</i> Weber-van Bosse; Fujii & Villaça, 2003; Silva, 2010.
<i>L. catarinensis</i> Cordeiro-Marino & M.T. Fujii	Northeastern, Southeastern, and South	Baptista, 1977 as <i>L. nana</i> Howe; Cordeiro-Marino & Fujii, 1985; Fujii & Senties, 2005; Széchy et al., 2005 as <i>L. intricata</i> J.V. Lamouroux; Guimarães, 2006; Silva, 2010.
<i>L. dendroidea</i> J. Agardh	Northeastern, Southeastern, and South	Joly, 1965; Oliveira Filho, 1969; Cordeiro-Marino, 1978; Pinheiro-Joventino et al., 1998; Figueiredo et al., 2004 as <i>L. microcladia</i> Kützinger; Joly, 1965; Oliveira Filho, 1969; Pedrini, 1980; Paes e Mello & Pereira, 1990; Figueiredo-Creed & Yoneshigue-Valentin, 1997; Pinheiro-Joventino et al., 1998 as <i>L. obtusa</i> (Hudson) J.V. Lamouroux; Oliveira Filho, 1969 as <i>L. composita</i> Yamada <i>pro parte</i> ; Oliveira Filho, 1969 as <i>L. heteroclada</i> Harvey; Oliveira Filho, 1977, Fujii, 1990; Széchy & Nassar, 2005; Amado Filho et al., 2006 as <i>L. scoparia</i> J. Agardh; Fujii, 1990; Figueiredo-Creed & Yoneshigue-Valentin, 1997 as <i>L. catarinensis pro parte</i> , Nunes, 1998; Széchy & Nassar, 2005 as <i>Laurencia arbuscula</i> Sonder; Fujii, 1998; Pinheiro-Joventino et al., 1998; Pereira et al., 2002; 2005 as <i>L. filiformis</i> (C. Agardh) Montagne; Széchy & Nassar, 2005 as <i>L. majuscula</i> (Harvey) A.H.S. Lucas; Cassano, 2009; Rocha-Jorge, 2010; Torrano Silva, 2010; Silva, 2010.
<i>L. marilzae</i> Gil-Rodríguez, Senties, Díaz-Larrea, Cassano & M.T. Fujii	Southeastern	Rocha-Jorge et al., 2010.
<i>L. oliveirana</i> Yoneshigue	Southeastern and South	Joly, 1965 as <i>Laurencia</i> sp.; Baptista, 1977 as <i>Laurencia</i> sp.; Yoneshigue, 1985; Fujii, 1990; Nunes, 1998; Amado Filho et al., 2006; Cassano 2009.
<i>L. translucida</i> M.T. Fujii & Cordeiro-Marino	Northeastern and Southeastern	Oliveira Filho, 1969 as <i>L. composita</i> Yamada <i>pro parte</i> ; Fujii, 1990 as <i>Laurencia</i> sp.1; Fujii & Cordeiro-Marino, 1996; Fujii, 1998; Nunes, 1998; Pereira et al., 2002; Fujii & Senties, 2005 as <i>Chondrophycus translucidus</i> ; Silva, 2010.
<i>L. venusta</i> Yamada	Southeastern	Fujii et al., 2005.
<i>Laurencia</i> sp. 1	Southeastern	Oliveira Filho, 1969 as <i>L. clavata</i> Sonder; Cassano, 2009.
<i>Laurencia</i> sp. 2 (taxon previously identified as <i>L. intricata</i>)	Northeastern and Southeastern	Oliveira Filho, 1969 as <i>Laurencia</i> sp.; Nunes, 1998, Guimarães, 2006; Fujii & Senties, 2005 as <i>L. intricata</i> .
<i>Laurencia</i> sp. 3 (previously misidentified as <i>L. implicata</i> / <i>L. intricata</i>)	Northeastern and Southeastern	Fujii, 1990; Széchy & Paula, 1997 as <i>L. implicata</i> J. Agardh; Amado Filho et al., 2006 as <i>L. intricata</i> .
<i>*Osmundea hybrida</i> (A.P. de Candole) K.W. Nam		Oliveira Filho, 1977 as <i>Laurencia hybrida</i> .
<i>O. lata</i> (M. Howe & W.R. Taylor) Yoneshigue-Valentin, M.T. Fujii & Gurgel	Northeastern and Southeastern	Howe & Taylor, 1931; Horta, 2000 as <i>Laurencia lata</i> ; Yoneshigue-Valentin et al., 2003; Fujii & Senties, 2005; Nunes, 2005.
<i>*O. pinnatifida</i> (Hudson) Stackhouse	Southeastern	Oliveira Filho, 1977 as <i>Laurencia pinnatifida</i> .
<i>Osmundea</i> sp.	Southeastern	Rocha-Jorge, 2010.
<i>Palisada corallopsis</i> (Montagne) Senties, M.T. Fujii & Díaz-Larrea	Northeastern and Southeastern	Fujii, 1990; Nunes, 1998 as <i>Laurencia corallopsis</i> .
<i>P. flagellifera</i> (J. Agardh) K.W. Nam	Northeastern, Southeastern, and South	Joly, 1965 as <i>Laurencia scoparia</i> ; Oliveira Filho, 1969; Cordeiro-Marino, 1978; Pedrini, 1980, Pedrini et al., 1989; Széchy et al., 1989, Fujii, 1990; 1998; Paes e Mello & Pereira, 1990; Cocentino, 1994; Nunes, 1998; Pinheiro-Joventino et al., 1998; Pereira et al., 2002; Széchy & Nassar, 2005 as <i>Laurencia flgellifera</i> ; Fujii et al., 2006 as <i>Chondrophycus flagelliferus</i> ; Cassano, 2009.

<i>P. perforata</i> (Bory) K.W. Nam	Northeastern, Southeastern, and South	Joly, 1965; Oliveira Filho, 1969; Pedrini, 1980; Pedrini et al., 1989; Széchy et al., 1989; Fujii, 1990; Paes e Mello & Pereira, 1990; Cocentino, 1994; Figueiredo-Creed & Yoneshigue-Valentin, 1997 as <i>L. catarinensis pro parte</i> , Nunes, 1998; Pinheiro-Joventino et al., 1998; Brito et al., 2002; Pereira et al., 2002; Széchy & Nassar, 2005 as <i>Laurencia papillosa</i> (C. Agardh) K.W. Nam; Széchy et al., 1989, Nunes, 1998; Pereira et al., 2002 as <i>Laurencia perforata</i> ; Torrano Silva, 2010 as <i>Chondrophycus papillosus</i> ; Cassano et al., 2009.
<i>Chondrophycus furcatus</i> (Cordeiro-Marino & M.T. Fujii) M.T. Fujii & Senties (the proposal for transference to <i>Palisada</i> is in process)	Northeastern and Southeastern	Cordeiro-Marino et al., 1994; Fujii, 1998; Nunes, 1998, Pinheiro-Joventino et al., 1998; Pereira et al., 2002 as <i>Laurencia furcata</i> ; Fujii & Senties, 2005; Silva, 2010.
* <i>Yuzurua poiteaui</i> (J.V. Lamouroux) Martin-Lescanne var. <i>poiteaui</i>	Southeastern	Oliveira Filho, 1977 as <i>Laurencia poitei</i> .
<i>Y. poiteaui</i> var. <i>gemmafer</i> (Harvey) M. J. Wynne	Northeastern	Taylor, 1960 as <i>Laurencia gemmafer</i> ; Cocentino et al., 2006 as <i>Chondrophycus gemmaferus</i> .

Northeastern: from State of Ceará to Bahia, Southeastern: from State of Espírito Santo to São Paulo, and South: from State of Paraná to Rio Grande do Sul. * need to be confirmed.

Results and Discussion

In Brazil, the red algae of the *Laurencia* complex are represented by four of the five genera that integrate the complex: *Laurencia* itself, *Palisada*, *Osmundea*, and *Yuzurua*. The first is the most diverse with twelve species, followed by *Palisada* (including *Chondrophycus furcatus*) with four species and *Osmundea* and *Yuzurua* with two species each (Table 2). The habit of several representatives of the *Laurencia* complex from Brazil and some generic morphological diagnostic characters are displayed in Figures 1-25.

The topology of the Bayesian tree with corresponding Bayesian posterior probabilities values (PP) is shown in Figure 26. The phylogenetic analysis shows a monophyletic *Laurencia* complex with high PP support (100%) in relation to the members of the outgroup, corroborating the previous results verified for the group (Abe et al., 2006; Fujii et al., 2006; Martin-Lescanne et al., 2010). The *Laurencia* complex was separated into five clades, corresponding to the genera: *Laurencia*, *Osmundea*, *Palisada*, *Chondrophycus*, and *Yuzurua*. The earliest diverging clade was the genus *Palisada* with six species and high support (100% PP), which included also *Chondrophycus furcatus*, an endemic species from Brazil. This result shows clearly that *C. furcatus* must be transferred to the genus *Palisada* and, with its future nomenclatural change, there will be no more representatives of *Chondrophycus* in Brazil. The monophyletic genera *Chondrophycus* and *Osmundea* were sister groups with a posterior probability of 86%. The monophyletic clade that corresponds to the genus *Yuzurua* showed higher molecular affinity with *Laurencia* than *Palisada*, from which it was recently segregated. The genus *Laurencia* included fifteen taxa with a posterior probability of 80%. *Laurencia*

marilzae formed a monophyletic clade with high support (100% PP) and was separated from all other *Laurencia* s.s., forming a distinct lineage, suggesting that *L. marilzae* represents a new genus within the *Laurencia* complex.

The bibliographical survey on the terpenoids produced by species of the *Laurencia* complex from the Brazilian coast shows that only five species of *Laurencia* and three of *Palisada* (including *C. furcatus*) have been submitted to chemical analysis and that, so far, 48 terpenoids have been isolated: 47 sesquiterpenes and one triterpene. Diterpenes have not been found in Brazilian species (Table 3).

The compounds isolated from the native algae include 21 sesquiterpenes belonging to the bisabolane class, seventeen belonging to the chamigrane type, whose biochemical precursor is bisabolane, and four triquinols, that possess a rare structure but are derived from the same biogenetic origin as the bisabolane- and chamigrane-derived terpenoids [2E,6E-farnesylpyrophosphate (FPP)]. Besides bisabolane and chamigrane terpenoids, the introduced seaweed *Laurencia caduciramulosa* produces two laurane-type compounds not found in Brazilian native algae (Table 3).

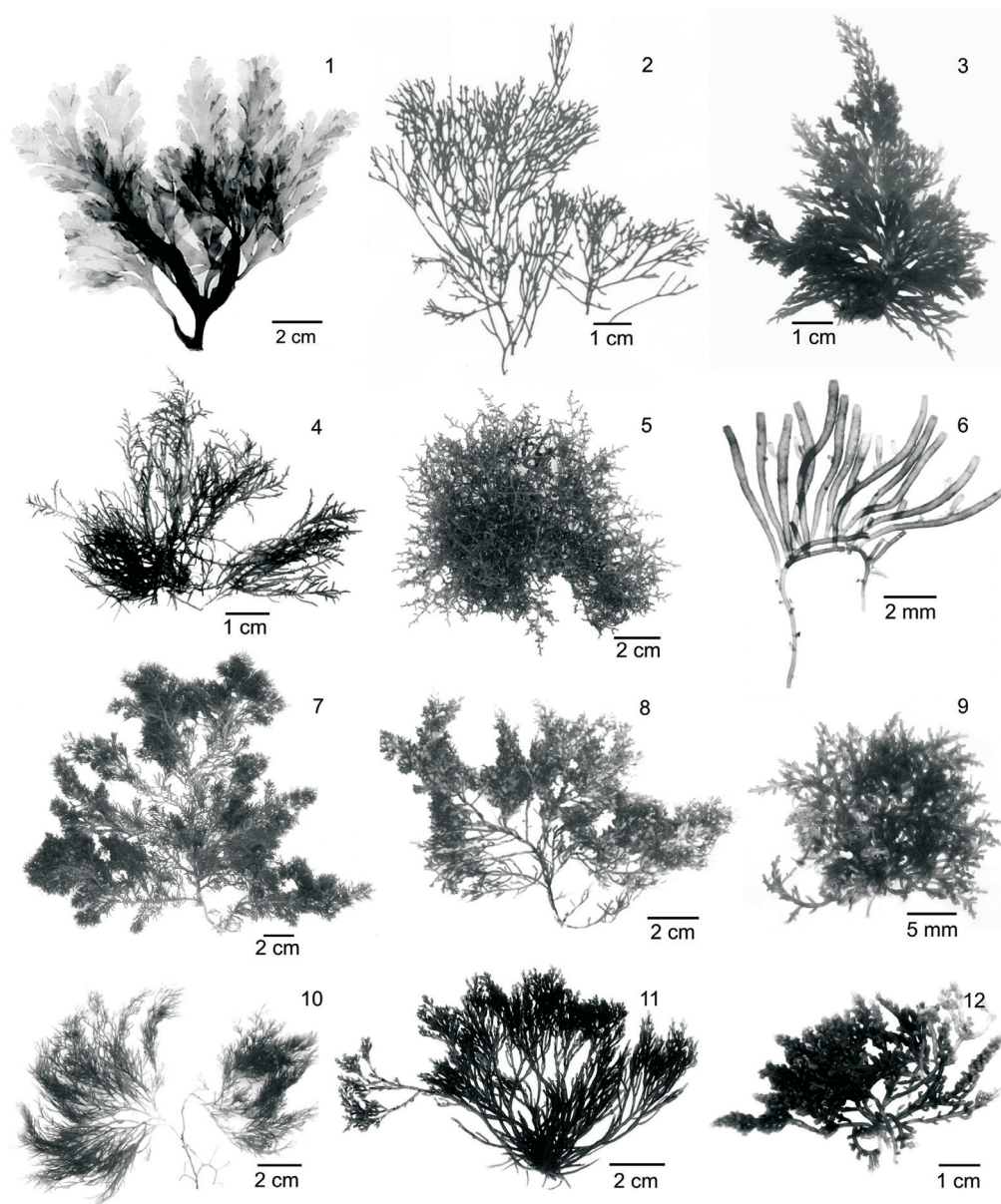
With respect to *Palisada perforata* and *P. flagellifera*, they generally do not produce sesquiterpenoids or acetogenins, classical metabolites produced by *Laurencia*. Although the presence of sesquiterpenes was not expected in this group, triquinane alcohols (compounds 47 and 26) were found in *P. perforata* by using a high sensitivity extraction method (HS-SPME) (Gressler et al., 2011). These compounds were not active against bacterial strains or the yeast *Candida albicans*, but showed some antioxidant activity. *Chondrophycus furcatus* is distinct from the other members of *Palisada*

by producing only triterpenoids (Rodríguez-Concepción, 2006) that are synthesized via the same precursor (FPP) as the sesquiterpenoids from Brazilian *Laurencia* species. However, on the basis of morphology, it does not fit perfectly into either *Laurencia* or *Palisada* due to the presence of secondary pit-connections between adjacent cortical cells, a characteristic more related to *Laurencia*, and to the production of two pericentral cells, instead of four per each axial segment, a characteristic shared by *Chondrophycus*, *Palisada*, *Yuzurua* and *Osmundea* (Fujii & Senties, 2005).

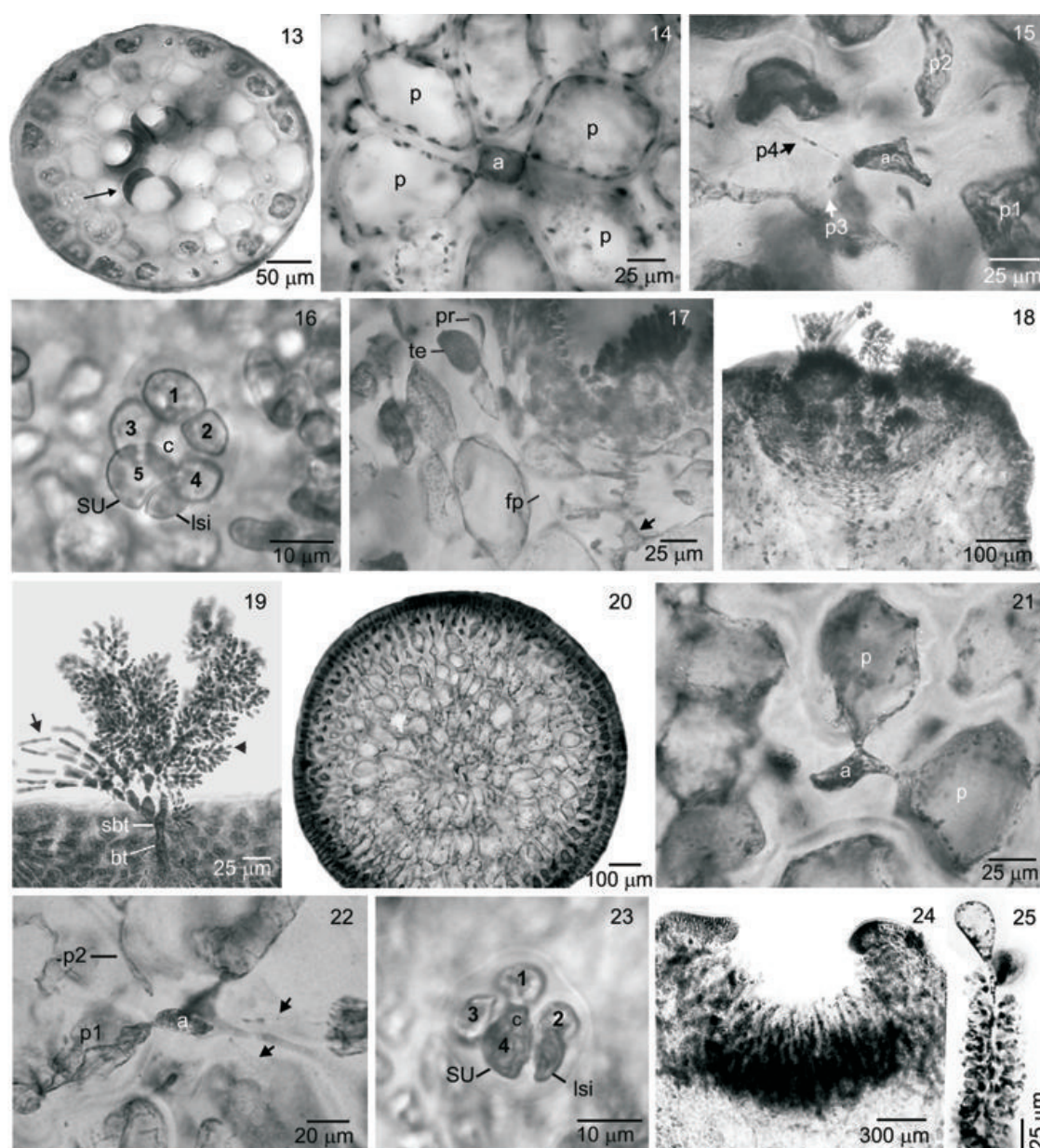
Most of the metabolites (15) that have been isolated from *Laurencia dendroidea*, *L. scoparia*, *L.*

microcladia, and *L. obtusa* [denominations that, in Brazil, refer to the same botanical species (Cassano, 2009)] are derived from chamigrane, with very similar or even identical structures, such as elatol found in *L. dendroidea* and *L. microcladia*; *L. scoparia* produces five sesquiterpenoids from bisabolane and two triquinols. Both *L. aldingensis* and *L. catarinensis* synthesize metabolites whose precursor is bisabolane, exhibiting a high degree of similarity between them, as can be seen in Figure 26.

Although species of the *Laurencia* complex are known to produce interesting active metabolites that possess important pharmacological potential, experimental biological activity assays have been performed with only



Figures 1-12. Habits of plants. 1. *Osmundea lata*. 2. *Chondrophycus furcatus*. 3. *Laurencia aldingensis*. 4. *L. caduciramulosa*. 5. *L. catarinensis*. 6. *L. oliveirana*. 7. *L. dendroidea*. 8. *L. translucida*. 9. *L. marilzae*. 10. *Laurencia* sp. 1. 11. *Palisada flagellifera*. 12. *P. perforata*.



Figures 13-25. Vegetative and reproductive characteristics of the *Laurencia* complex. 13-19. Characteristics of *Laurencia*. 20-23. Characteristics of *Palisada*. 24-25. Characteristics of *Osmundea*. 13. Transverse section of a thallus of *Laurencia*. Note the lenticular thickenings (arrow). 14. Transverse section of a thallus showing four pericentral cells (p) and an axial cell (a), typical of the genus *Laurencia*. 15. Transverse section near the apex of a branchlet of *Laurencia* showing the tetrasporangial axial segment formed by four pericentral cells: the first and the second pericentral cells remain vegetative (p1 and p2), the third and fourth become fertile (p3 and p4, arrows), axial cell (a). 16. Procarp-bearing segment with five pericentral cells, the fifth becoming the supporting cell (SU) of the carpogonial branch, central cell of procarp-bearing segment (c), lateral sterile group initial (lsi). 17. Longitudinal section through an apical portion of a tetrasporangial branchlet showing the origin of the tetrasporangia (te) from the axial cell (arrow), fertile pericentral cells (fp) and pre-sporangial cover cells (pr). 18. Longitudinal section through a male branchlet showing trichoblast-type spermatangial branches in cup-shaped tips. 19. Detail of trichoblast-type spermatangial branches; spermatangial branches on trichoblast (bt) with two laterals, sterile (arrow) and fertile (arrowhead) branches on its suprabasal cell (sbt). 20. Transverse section of a thallus of *Palisada*. 21. Transverse section of a thallus showing two pericentral cells (p) and an axial cell (a). 22. Transverse section near the apex of a branchlet of *Palisada* showing the tetrasporangial axial segment formed by two pericentral cells: the first (p1) remains vegetative, the second (p2) becomes fertile, and two additional fertile pericentral cells are formed in the opposite position (arrows). 23. Procarp-bearing segment with four pericentral cells, the fourth becoming the supporting cell (SU) of the carpogonial branch, central cell of procarp-bearing segment (c), lateral sterile group initial (lsi). 24. Longitudinal section through a male branchlet showing filament-type spermatangial branches in cup-shaped tips. 25. Detail of filament-type spermatangial branches, typical of *Osmundea*.

with six species: *Laurencia catarinensis*, *L. dendroidea*, *L. translucida*, *L. aldingensis*, *L. caduciramulosa*, and *Palisada flagellifera*. The three former are native Brazilian species and the most studied of these is *L. dendroidea*. More than twenty compounds were identified in this species and several of them showed biological activities such as anthelmintic activity against the parasitic stage of *Nippostrongylus brasiliensis* (Davyt, 2003; 2006), antileishmanial activity against the insect-stage

promastigotes of *Leishmania amazonensis* (Machado et al., 2011), human pathogenic antifungal properties (Stein et al., 2011), and significant levels of toxicity towards a model tumor cell line (human uterine sarcoma, MES-SA) (Stein et al., 2011). Thus, studies on the biological activities of the secondary metabolites isolated from the *Laurencia* complex should be encouraged with the goal of finding new sources with pharmaceutical applications.

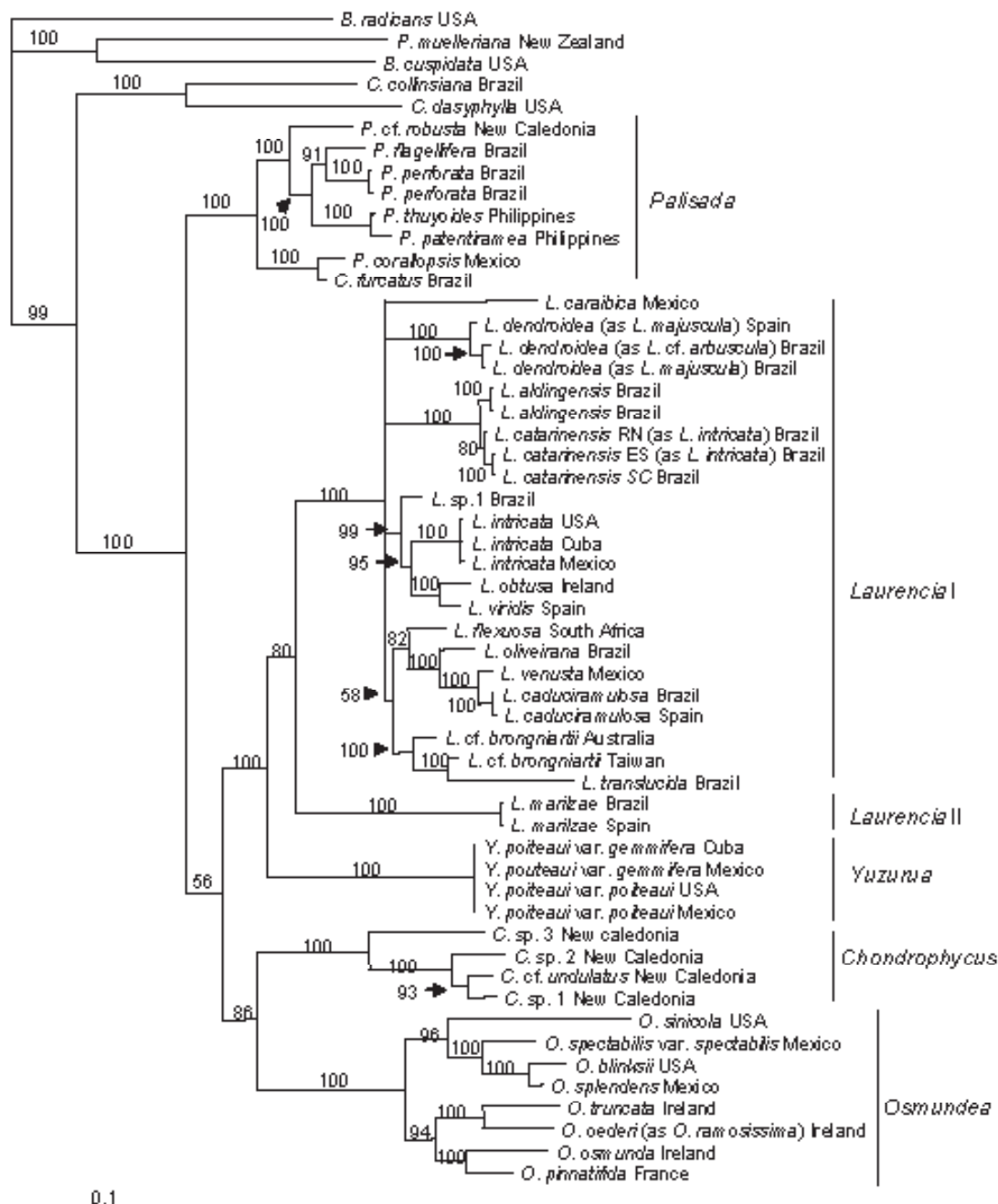
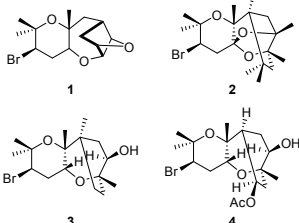
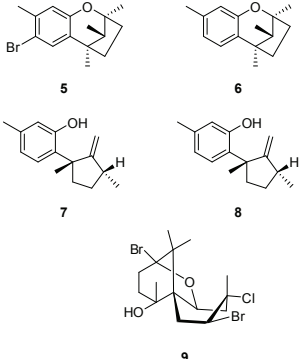
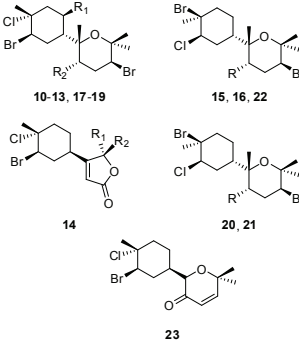
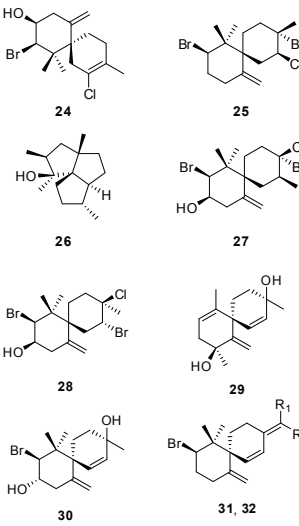
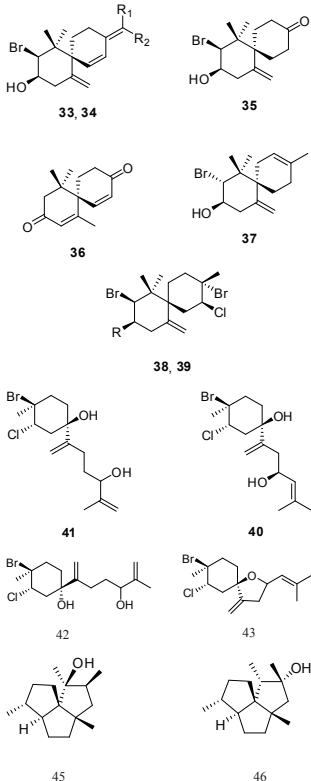
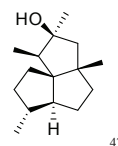


Figure 26. Bayesian phylogram inferred from analyses of *rbcL* sequences. Numbers on branches correspond to support values for Bayesian inference posterior probability.

Table 3. Structural formulas, names and origin of terpenoids isolated from Brazilian species of the *Laurencia* complex, and biological activities related to human health.

Species	Structural formula	Name	Structural class	Human health related activity tests	References
<i>Laurencia aldingensis</i>		1 Aldingenin A 2 Aldingenin B 3 Aldingenin C 4 Aldingenin D	1-4 α -Bisabolane	Polar and non-polar extracts showed no cytotoxic effects toward primary model tumor cell line (MES-SA)	Carvalho et al., 2003; 2006; Stein et al., 2011
<i>L. caduciramulosa</i> *		5 Filiformin 6 Debromofiliformin 7 Allolaurinterol 8 Debromoallolaurinterol 9 Pacifenol	5, 6 δ -Bisabolane 7, 8 Laurane 9 Chamigrane	NB	Cassano et al., 2008
<i>L. catarinensis</i>		10 R ₁ =OAc, R ₂ =OH 11 R ₁ =OH, R ₂ =OAc 12 R ₁ =OAc, R ₂ =OAc 13 R ₁ =OAc, R ₂ =H 17 R ₁ =H, R ₂ =OH 18 R ₁ =H, R ₂ =OAc 19 R ₁ =R ₂ =H 15 R ₁ =Me, R ₂ =OMe 16 R ₁ =OMe, R ₂ =Me 22 R ₁ =Me, R ₂ =OH 20 R=OH 21 R=H	10-23 Bisabolane	<i>in vitro</i> cytotoxicity using HT29, MCF7, and A431 cell lines: 17 = IC ₅₀ <10 μ M; 10,18,19 and 23 = IC ₅₀ <20 μ M for all cell lines Non-polar extracts showed high level ($\geq$ 80% of cell kill) of cytotoxic effects toward primary model tumor cell line (MES-SA)	Lhullier et al., 2010 Stein et al., 2011
<i>L. dendroidea</i>		24 Elatol 25 Obtusane 26 Triquinane 27 Obtusol 28 Cartilagineol 24 Elatol	24, 25, 27, 28 Chamigrane 24 Chamigrane 29-39 Chamigrane	Antileishmanial test 24, 25 =IC ₅₀ ranging from 3.9 to 9.7 μ g/mL ¹ 24 =IC ₅₀ of 4.0 μ M and 0.45 μ M ² for promastigote and the amastigote forms Non-polar extracts showed high level ($\geq$ 80% of cell kill) of cytotoxic effects toward primary model tumor cell line (MES-SA) <i>In vitro</i> anthelmintic essay using <i>Nippostrongylus brasiliensis</i> :	1) Santos et al., 2010 Machado et al., 2011 Stein et al., 2011 2) Lhullier et al., 2009
1) as <i>L. obtusa</i>					
2) as <i>L. microcladia</i>					

3) as <i>L. scoparia</i>	 33, 34 35 36 37 38, 39 40 41 42 43 45 46	30, 33, 34, 35, 36, 37 and 11 - moderate activity (lower than 100 μM), 31 and 33 demonstrated higher activity than 32 and 34	
		40-42 β-bisabolane 43, 44, oxa-bicyclic stereoisomers 45, 46, triquinanes	Compounds 40-42, 44, and 46 were tested <i>in vitro</i> using <i>Nippostrongylus brasiliensis</i> Compound 40 EC₅₀=0.11 mM 3) Davyt et al., 2001; 2006
<i>L. translucida</i>	Absence of terpenes and acetogenins	Non-polar extracts showed high level ($\geq 80\%$ of cell kill) of cytotoxic effects toward primary model tumor cell line (MES-SA)	Fistarol & Carvalho, 2002; Stein et al., 2011
<i>Chondrophycus furcatus</i>	Triterpenes	NB	Estevam & Carvalho, 2002 as <i>Laurencia furcata</i>
<i>Palisada perforata</i>	1. Absence of terpenes and acetogenins 2.	NB	1) Estevam & Carvalho, 2001 as <i>Chondrophycus papillosus</i>
	 47	Human pathogenic antimicrobial properties absent	2) Gressler et al., 2011
<i>P. flagellifera</i>	Absence of terpenes and acetogenins	“Crude” methanol extracts showed moderate level (50-79% of cell kill) of cytotoxic effects toward primary model tumor cell line (MES-SA)	Carvalho et al., 2000 as <i>C. flagelliferus</i> ; Stein et al., 2011

NB: none biological activity essay was performed; *introduced algae.

Acknowledgements

This study was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico

(Proc. 473322/2008-0), and the Fundação de Amparo à Pesquisa do Estado de São Paulo (Proc. 10/50193-1, Proc. 10/52244-2). Additional support was provided by the Ministerio de Ciencia e Innovación of the Spanish

Government (CGL 2010-14881). MT Fujii thanks the CNPq for a Research Productivity Fellowship (Proc. 301438/2009-9) and EM Stein thanks FAPESP for a Master's Student Fellowship (Proc. 2008/07775-0). Beneficiary of financial support from CAPES-Brazil.

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