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Review

An overview of odoriferous marine seaweeds of the *Dictyopteris* genus: insights into their chemical diversity, biological potential and ecological roles

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ABSTRACT

Since the middle of the twentieth century the marine algae have attracted attention as a source of new drugs. *Dictyopteris* is an important group of marine seaweeds and is widely distributed in tropical, subtropical and temperate regions. This genus is known by its characteristic "ocean smell". Some species show a distinct phytochemistry, with specific secondary metabolites, including C_{11}-hydrocarbons, sulfur compounds and quinone derivatives, not usually found in marine seaweeds and described for the first time in the literature. Furthermore, several terpenes, steroids and halogenated compounds have been described. This chemical diversity gives it interesting biological properties, including cytotoxic, antimicrobial, antioxidant, anti-inflammatory and anti-herbivory activities. These findings highlight the importance to continue investigations on this genus and the need to compile the data available so far, since the species are quite heterogeneous, notably in relation to the chemical constitution. This paper reviews the literature on the *Dictyopteris* genus, focusing on its secondary metabolites and biological activities, in order to build the base for further studies.

Introduction

More than 70% of the earth's surface is covered by ocean, an enormous ecosystem that is a source of novel opportunities in the field of biotechnology. Marine secondary metabolites have demonstrated outstanding structural and functional diversity related to their different metabolic pathways (Shanura Fernando et al., 2016). Some current applications for high-value marine-derived products are in drug discovery, antifoulants, biofilm inhibitors, bioremediation, human and animal tissue repair, nutraceuticals, and personal care products (Allen and Jaspars, 2009).

While the fragrances of terrestrial plants have attracted the attention of man since antiquity, these odors being associated with monoterpenes, phenols, and simple aliphatic esters, the fragrance of marine plants is much less familiar, and relatively few marine plants possess odor (Moore, 1977). A typical "sea-breeze" fragrance has interesting nuances for perfumery, eliciting a sense of peace, well-being and lightness. The trend in marine fragrances is relatively recent compared to other scents used in traditional perfumery (Oigman et al., 2015), such as amber and musk, which are perhaps the oldest fragrances, and have been used since ancient times, in religious traditions, cultures, cuisine, and beautification. The chemistry of marine fragrance is mainly associated with four groups of organic compounds of natural or synthetic origin: cyclic and alicyclic C_{11}-hydrocarbons (which act as pheromones); polyunsaturated aldehydes from the degradation of fatty acids; synthetic benzodioxepanes (such as Calone 1951®, an unusual structure that was patented by Pfizer in 1969); and halogenated phenols, which is believed to be the main component in the flavor of several seafoods (Oigman et al., 2015).

Marine macroalgae (seaweeds) are multicellular photosynthetic organisms, belonging to the lower plants category. These organisms are thallophytes, which means that they are constituted by leaf-like thallus instead of roots, stems, and leaves. According to the specific combination of photosynthetic pigments, they can be classified into three groups: green (Chlorophyta, mainly chlorophyll *a* and *b*), brown (Phaeophyceae, mainly chlorophyll *a* and *c*, β-carotene and xanthophylls) and red algae (Rhodophyta, mainly chlorophyll *a*, phycoerythrin and phycocyanin) (Reviers, 2006).

The brown algae of the genus *Dictyopteris* are among the few odoriferous types of seaweed (Pettus Jr. and Moore, 1971). These species contain C_{11}-hydrocarbons, which are structurally similar to sexual attractants and act as odoriferous compounds. In this con-

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text, due to its spicy taste and agreeable odor, *D. plagiogramma* (known as "limu lipoa") has been used by Hawaiians instead of pepper and sage, as a condiment with raw fish and other foods (Pettus Jr., 1971; Moore, 1977). Some patents have also been registered for formulations containing its odoriferous compounds (Chapuis, 1992; Gaudin and Morel, 1992; Kajiwara et al., 2003).

The genus *Dictyopteris* J.V. Lamouroux (from Greek *Dictyon* = network, and *Pteris* = fern) was first proposed by Lamouroux in 1809 (Nizamuddin and Saifullah, 1966) and belongs to the Dictyotales order (Silberfeld et al., 2014). It includes species with flattened, generally dichotomously branched thalli with a distinct central midrib. Thalli are attached by a matted rhizoidal holdfast, up to 60 cm long, subdichotomously to laterally branched, branches 0.5–25 mm broad. Growth is via a row of meristematic cells that lie in a shallow depression on the branch apex. The genus comprises 35 species and considerable morphological and anatomical variation may occur between the small and the larger robust species (Phillips and Huisman, 1998; Guiry and Guiry, 2018).

The species are widely distributed in oceans of tropical, subtropical and temperate regions (Nizamuddin and Saifullah, 1966; Guiry and Guiry, 2016). Fig. 1 shows the geographic distribution of eighteen *Dictyopteris* species, which have already been studied for their chemical and biological properties. Fig. 2 shows two *Dictyopteris* species (*D. plagiogramma* and *D. jolyana*).

The review is organized into three main sections. The first section covers its chemical diversity (focusing on C_{11}-hydrocarbons, sulfur compounds, terpenes, meroditerpenes, halogenated compounds and sterols), followed by the first reports and context of its discovery. The subsequent section covers further chemical and biological reports by species.

Methods

A literature search was conducted covering the period from January 1951 to December 2017, using the keywords "Dictyopteris" and all the names of the individual species, including synonyms. Searches were conducted on the electronic databases Web of Science, Scopus, Springer, Science Direct, Pub Med and Google Scholar. Reference lists of the identified papers were also searched, and additional research traced online. Inclusion criteria were papers reporting the isolation or identification of compounds and biological activities related to the *Dictyopteris* genus.

Chemical diversity

A number of investigations have demonstrated a wide chemical diversity for the species of the *Dictyopteris* genus that showed interesting biological activities, which are presented in Box 1. Isolated metabolites from the genus include C_{11}-hydrocarbons and their derivatives, terpenes, meroditerpenes, sulfur compounds, steroids, halogenated compounds, simple volatile compounds, sulfated polysaccharides, and fatty acids. It is known that envi-

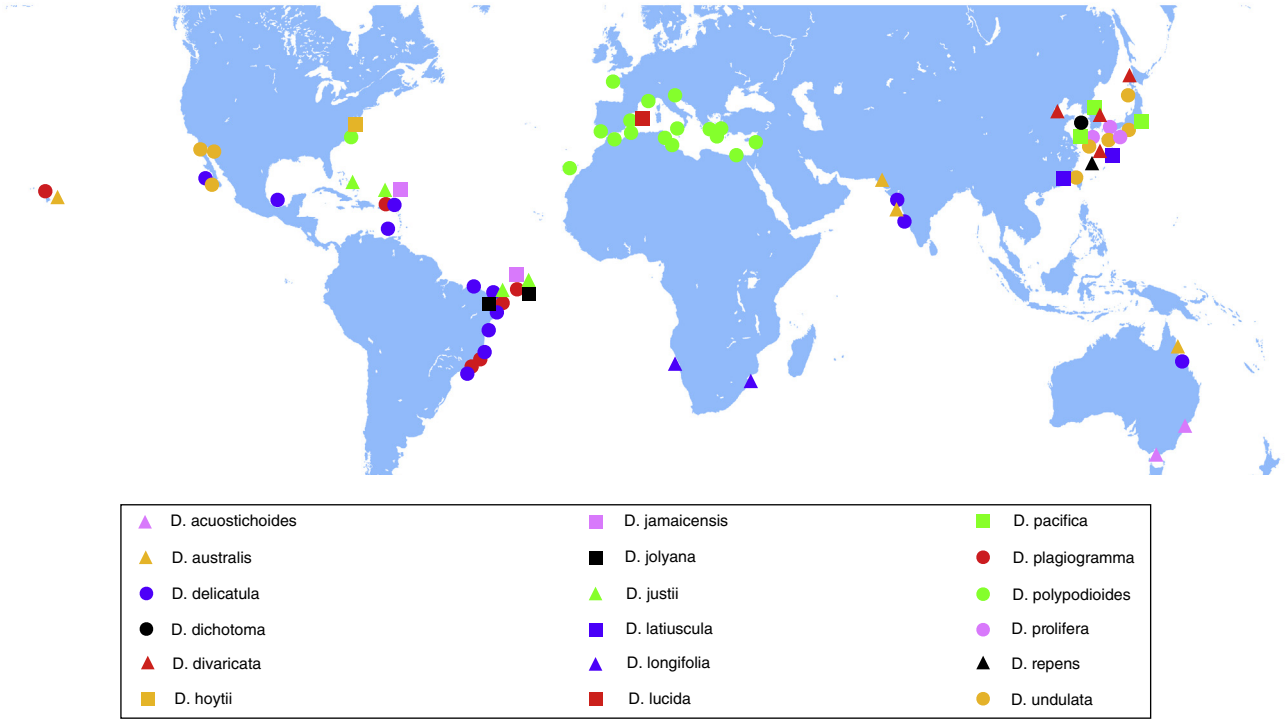


Fig. 1. Geographic distribution of *Dictyopteris* species which have already been studied for their chemical and biological properties.

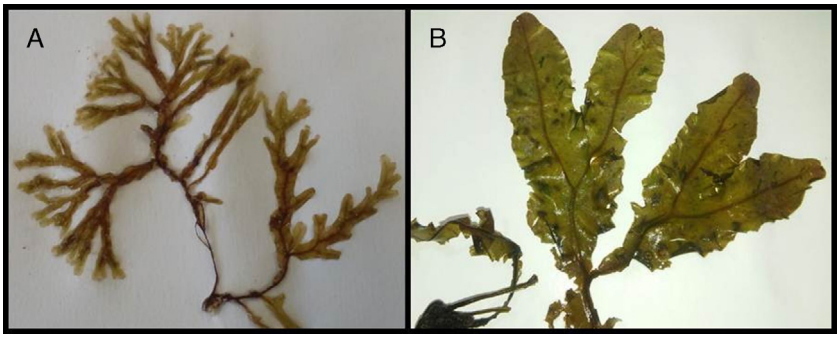


Fig. 2. Dictyopteris species. (A) *D. plagiogramma*; (B) *D. jolyana*.

Table 1
Distribution of isolated or identified compounds of *Dictyopteris* genus by species.

	Dac	Dau	Dde	Ddi	Dju	Dla	Dpl	Dpo	Dpr	Dun
C_{11}	15	12	2	2	0	14	12	16	16	8
Suphur	0	5	0	0	0	0	9	10	1	0
Terpenes	0	0	5	53	0	2	2	21	1	4
Meroditerpenes	0	0	1	4	0	0	0	2	0	13
Halogenated	0	0	0	2	0	0	0	2	0	0
Steroids	0	0	8	2	1	0	8	3	0	12
Other volatile	0	0	0	1	2	15	4	29	1	1
Total	15	17	16	64	3	31	35	83	19	38

Dac, *D. acuostichoides*; Das, *D. australis*; Dde, *D. delicatula*; Ddi, *D. divaricata*; Dju, *D. justii*; Dla, *D. latiuscula*; Dpl, *D. plagiogramma*; Dpo, *D. polypolioides*; Dpr, *D. prolifera*; Dun, *D. undulata*.

ronmental factors, such as the level and quality of light, nutrient levels and composition, CO_2 availability, temperature, salinity, pH, contaminants and biotic impacts due to the distribution of grazers and endo- and epibionts, as well as seasonal vegetative and reproductive development, may influence the synthesis and activity of primary and secondary metabolites (Stengel et al., 2011).

Besides the influence of environmental aspects, differences in chemical composition are also determined by genetic profile. A phylogenetic analysis by Bittner et al. (2008) showed that the genus *Dictyopteris* is polyphyletic: the seven species included in the study were separated into two clusters, the first consisting of *D. undulata* and *D. divaricata*, and the second consisting of *D. delicatula*, *D. prolifera*, *D. latiuscula*, *D. polypodioides* and *D. australis*. This is in agreement with the fact that *D. undulata* and *D. divaricata* produce higher amounts of terpenes than the other species, which produce C_{11}-compounds as major metabolites.

Some of the metabolites isolated from *Dictyopteris* have already proven to be correlated with chemical defense and communication between species (acting as sex pheromones). Box 2 shows a summary of the ecological reports for this genus, including the study of feeding preferences, antifouling and allelopathy.

In view of the high diversity of compounds of the genus *Dictyopteris*, this review focuses only on its secondary metabolites. Furthermore, simple volatile hydrocarbons, aldehydes and alcohols were identified as minor compounds in essential oils (EO) of some species, mainly *D. latiuscula* and *D. polypodioides* (Supporting information).

An overview of the main metabolite groups report is shown below, followed by a detailed summary focusing on the main species of *Dictyopteris*. All these compounds are listed also in Supporting information.

C_{11}-hydrocarbons and derivatives

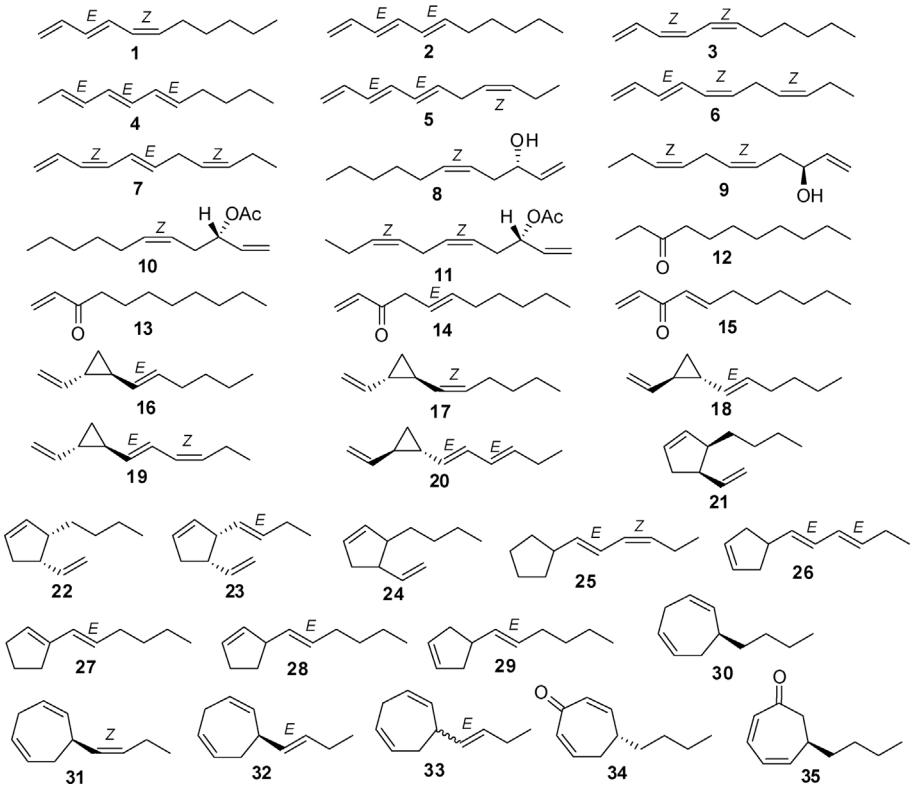
The "ocean smell" of the EO from *Dictyopteris* is mainly due to the non-isoprenoid C_{11}-hydrocarbons (**1**–**35**). The *Dictyopteris* species produce bouquets of C_{11}-metabolites, some of which act as pheromones that stimulate gamete release or attract sperm to eggs following release (Boland, 1995). Several C_{11}-hydrocarbons and their derivatives have been isolated from diverse groups of brown algae (*e.g.* the *Zonaria*, *Desmarestia*, *Dictyota*, *Ectocarpus*, *Laminaria* and *Fucus* genera), and have also been detected in diatom cultures, blooms of freshwater microalgae, and higher plants (Boland, 1995). Although they occur in this wide range of organisms, they appear to be most abundant in brown algae of the genus *Dictyopteris* (Moore, 1977), and have been shown to be present in almost all the species studied (Table 1).

These biologically active compounds comprise several different linear or alicyclic unsaturated hydrocarbons and their stereoisomers. Their structural similarities suggest a common biosynthetic origin derived from the aliphatic terminus of C_{20} polyunsaturated fatty acids by oxidative cleavage (Pohnert and Boland, 2002; Rui and Boland, 2010), while in terrestrial plants, these compounds are generated by unsaturated C_{12} precursors (Stratmann et al., 1992). According to their molecular structures, C_{11}-compounds can be classified into four groups: acyclic olefins (**1**–**15**), cyclopropanes (**16**–**20**), cyclopentenes (**21**–**29**) and cycloheptadienes (**30**–**35**). Among these compounds, the dialkenylcyclopropane dictyopterenes A (**16**) and B (**19**) (known also as hormosirene) are usually present in high amounts (Moore et al., 1974; Yamamoto et al., 2001; Hattab et al., 2002; Hattab et al., 2007a), while in the female gametes of the marine brown alga *Analipus japonicus* and in the flowering plant *Senecio isatideus* dictyopterene D (**31**) (also known as ectocarpene) is the most abundant (Boland and Mertes, 1985; Müller et al., 1990). Dictyopterene C′ (also known as dictyotene) (**30**) was found as a minor compound in EO of vegetative parts of *Dictyopteris* (Pettus Jr. and Moore, 1971), and also in freshly released eggs of marine brown alga *Dictyota dichotoma*, as the substance that attracts spermatozoids (Müller et al., 1981). Interestingly some studies have reported the identification of dictyopterenes in natural biofilm established in plastic pipes used at the drinking water supply, which were associated with algae and cyanobacteria present in the raw water source (Skjevrak et al., 2004). These *Dictyopteris* pheromones are included in some patents for the preparation of cosmetics or pharmaceutical compositions, including fragrances, and in the composition of antiperspirants and deodorants (Chapuis, 1992; Gaudin and Morel, 1992; Kajiwara et al., 2003; Gedouin et al., 2007; Cetti et al., 2016).

Some acyclic olefins, such as undecatriene (**1**–**4**) and undecatetraenes (**5**–**7**), were also found in the brown alga *Giffordia mitchellae*, which presents giffordene as the main metabolite (Boland et al., 1987), and also are commonly found as odoriferous compounds in some fruits, such as mango (Munafo et al., 2014, 2016), pineapple (Steingass et al., 2014), mandarin (Naef and Velluz, 2001), yuzu and jabara (a Japanese citrus fruit) (Omori et al., 2011; Miyazato and Hashimoto, 2012), and apricot (Takeoka et al., 1990).

Box 1
Biological assays related to therapeutic potential of some *Dictyopteris* compounds.

Species	Compounds	Activity	Reference
D. divaricata	**66**, **73**, **76–79**, **81**, **83**, **84**, **108–117**, **135**, **138**, **143**, **154**	Cytotoxicity against several human cancer cell lines (KB, PC-3M, Ketr 3, A549, Bel7402, BGC-823, HCT-8, and MCF-7): inactive	Song et al., 2004; Song et al., 2005a; Song et al., 2006
D. polypodioides	**44**, **45**, **47–50**, **53**	Antibacterial against resistant strains of *S. aureus* and *E. coli* (inactive)	Dimou et al., 2016
		Anti-inflammatory (LPS stimulation assay): **45** and **53** were active (IC_{50} = 3.8 and 14.2 μM, respectively) and showed growth inhibition above 45 and 85 μM, respectively	Dimou et al., 2016
D. sp	**53**	Phospholipase A2 inhibition (inactive)	Mayer et al., 1993
D. undulata	**125**, **126**	Antifungal (*Phytophthora cinnamomi*, *Rhizoctonia solani*, *Sclerotinia sclerotiorum*, and *Sclerotium rolfsii*): moderate	Fenical et al., 1973
	125	Anti-angiogenic properties	Castro et al., 2004
	126	Phospholipase A2 inhibition: 52%	Mayer et al., 1993
	126	Inhibition of inflammatory bowel disease in a mouse model of ulcerative colitis	Yamada et al., 2014
	126	Neuroprotection by activating the Nrf2/ARE pathway	Shimizu et al., 2015
	130	Phospholipase A2 inhibition: 76%	Mayer et al., 1993
	137	Antifungal (12.5–25 μg/ml) against *Saccharomyces cerevisiae*, *Sclerotinia libertiana*, *Aspergillus niger*, and *A. oryzae*	Ochi et al., 1979a,b
	Mixture of **163** and **164**, and **168**	Inhibition of PTP1B (IC_{50} = 1.88 and 3.47 mM)	Feng et al. (2018)
	Mixture of **163** and **164**, and **165**, **166**, **167**, **168**, **169**	Cytotoxicity against human cancer cell lines HL-60 (IC_{50} from 1.02 to 2.70 mM) and A-549 (IC_{50} from 1.35 to 2.85 mM)	Feng et al. (2018)



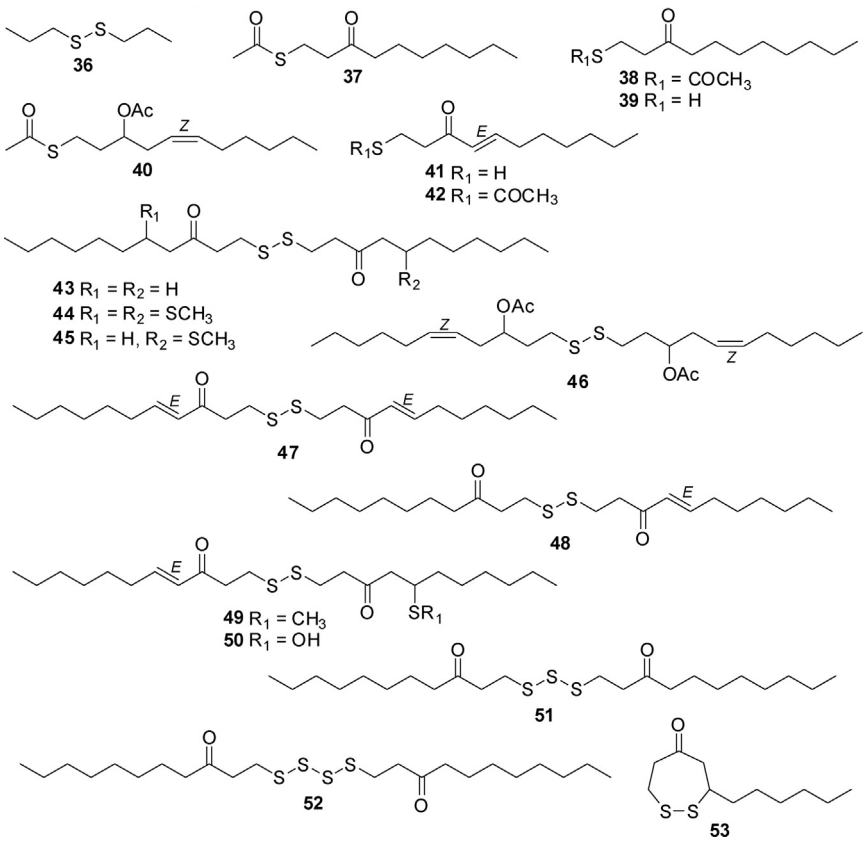
Sulfur compounds

There are relatively few polysulfides in nature, but many of those that exist possess biological activity. Due to the relatively high sulfate concentration in seawater, and the particularly high sulfide concentration in anoxic environments, it was expected that many sulfides would occur in the marine environment (Faulkner, 1977). Nevertheless, few taxa were reported to present sulfides as secondary metabolites. Some examples include the cyclic polysulfides reported for red alga *Chondria californica*, which are responsible for its antibiotic activity (Wratten and Faulkner, 1976) and several polysulfides from hyperthermophilic archaea in marine hydrothermal vents, such as the *Thermococcus* species (Ritzau et al., 1993; Prieur et al., 1995).

As part of this single group, some *Dictyopteris* species produce significant amounts of sulfur-containing compounds (**36–53**),

Box 2
Biological assays related to ecological aspects for *Dictyopteris* species.

Species	Algal material	Active compounds	Activity	Reference
D. acrostichoides	CH_2Cl_2 surface extract and whole-cell extracts	–	Antifouling test: whole-cell extract inhibits settlement and germling development of *Ulva australis* gametes, while the CH_2Cl_2 extract had no significant effect. Both whole-cell and CH_2Cl_2 extracts had no effects in inhibition of settlement of *Polysiphonia* spores	Nylund et al., 2007
D. delicatula	Whole alga	**16**, **19**	Herbivory test: *D. delicatula* was intermediate in the preference of the fishes, while amphipods preferentially consumed *D. delicatula*. Compounds 16 and 19 significantly deterred fish grazing but had no effect on grazing by amphipods	Hay et al., 1988
	CH_2Cl_2 extract	–	Antifouling test: no fouling inhibition using the common fouling organism mussel *Perna perna*	Medeiros et al., 2007
	Aqueous extract	–	Antiparasitic activity: Weak effect on the life cycle of the monogenean ectoparasite, *Neobenedenia* sp., infecting farmed barramundi (*Lates calcarifes*)	Hutson et al., 2012
D. divaricata	MeOH extract	–	Herbivory test: deterred feeding by the sea urchin *Strongylocentrotus nudus* and the abalone *Haliotis discus hannai*	Shiraishi et al., 1991
D. hoytii	Whole alga	–	Herbivory test: no activation of chemical defenses following damage by herbivores	Cetrulo and Hay, 2000
	Whole alga	–	Herbivory test: feeding preference of amphipod *A. longimana* in comparison of *D. polypodioides* (which contains C_{11}-sulfur compounds)	Schnitzler et al., 2001
D. jamaicensis	Whole alga	–	Herbivory test: no feeding preference by fishes	Marques et al., 2006
D. jolyana	Whole alga		Herbivory test: the alga was less consumed by fishes in comparison to other alga species	Longo et al., 2015
D. justii	$CHCl_2$/MeOH and MeOH extract	**156**	Herbivory test: The crude extracts were inactive, but the mixture of epimers 156 has inhibitory effect against the crab *Pachygrapsus transversus*	Teixeira et al., 2006
D. plagiogramma	Whole alga	–	Herbivory test: least susceptibility to consumption by herbivorous fishes	Mendes et al., 2015
	Whole alga	–	Herbivory test: the alga was less consumed by fishes in comparison to other alga species	Longo et al., 2015
D. polypodioides	Whole alga	**53**	Herbivory test: deterring feeding by the amphipod *A. longimana*, without effect on feeding by the sea urchin *Arbacia punctulata*	Schnitzler et al., 1998
	Whole alga	–	Herbivory test: not preferred by the amphipod *A. longimana* in the herbivory test when compared to *D. hoytii* and *D. polypodioides* that had lost the ability to produce C_{11} sulfur compounds	Schnitzler et al., 2001
	Whole alga	–	Herbivory test: reducing feeding but not palatability in response to direct amphipod-attacks	Yun et al., 2007
	Whole alga	–	Herbivory test: predominated in the diet of Lessepsian migrant *Siganus luridus*	Stergiou, 1988
	Diethyl ether extract	–	Antifouling activity and variable antimicrobial activity against some representative species of the major groups. of fouling organisms	Hellio et al., 2001
D. undulata	Methanol extract	**125**–**127**, **129**, **130**, **135**, **142**	Piscicidal activity: the extract and isolated compounds were toxic to fish	Dave et al., 1984
	Neutral and acidic fractions methanol extract	**125**, **126**, **129**–**131**, **135**	Herbivory test: potent inhibitory activity against young abaone *Haliotis discus hanai*	Kurata et al., 1996
	Methanol extract	**125**, **126**, **132**, **134**–**137**	Algicidal activity: moderate to high cell lysis activity against the red tide microalgal species	Ishibashi et al., 2013
	Ethanol extract	–	Antifouling test: no activity against *Ciona intestinalis*, *Bugula neritina*, *Spirorbis* sp., but enhanced the settling of *Ciona intestinalis*	Bakus and Kawaguchi, 1984
	Methanol extract	**125**, **126**	Antifungal activity: moderate activity against *Phytophthora cinnamomi*, *Rhizoctonia solani*, *Sclerotinia sclerotiorum* and *Sclerotium rolfsii*	Fenical et al., 1973



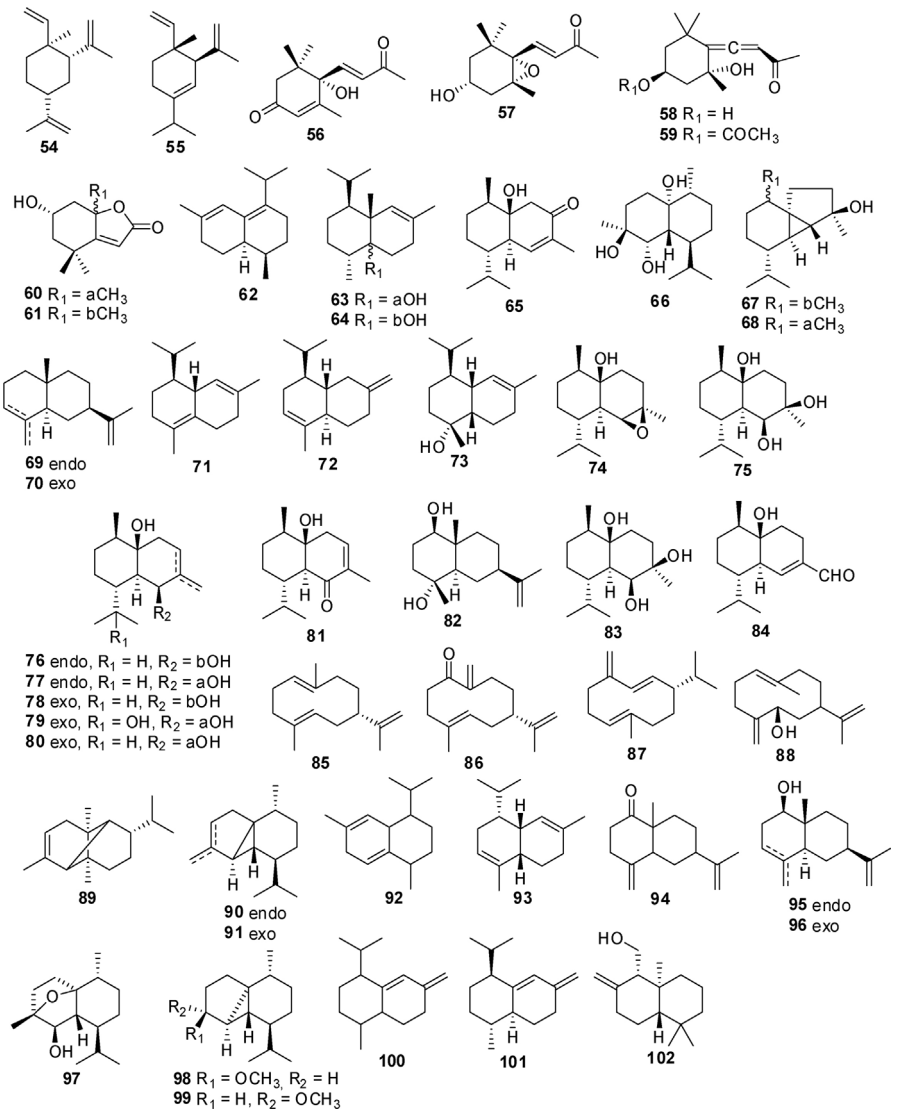
many of them found in *D. polypodioides*. Most of them appear to be biosynthetically related to C_{11} pheromones, and may originate from oxidative degradation of highly unsaturated eicosanoids via oxygenated intermediates. These compounds are produced in the thalli and act as chemical defenses against herbivory, which is a key factor for controlling the biomass and community structure of macroalgae (Hay et al., 1988). Dithiepanone (**53**), isolated from the methanol/chloroform extract of *D. polypodioides* collected at Villefranche-sur-mer, France, strongly deterred feeding by the amphipod *Ampithoe longimana*, but had no effect on feeding by the sea urchin *Arbacia punctulata* (Schnitzler et al., 1998). The fresh seaweed was not preferred by the amphipod *A. longimana* in the herbivory test when compared to *D. hoytii* (which lacks C_{11}-sulfur compounds) and cultivated *D. polypodioides* that had lost the ability to produce sulfur compounds (Schnitzler et al., 2001). Also as a form of chemical defense, the annelid worm *Lumbriconereis heteropoda* produces the cyclic disulfide nereistoxin, which possesses insecticidal activity (Okaichi and Hashimoto, 1962). With the exception of compound **53**, which was also identified in EO of brown alga *Hormophysa cuneiformes* (Hattab et al., 2007b), these C_{11} sulfur metabolites seem to be restricted to the *Dictyopteris* genus.

Terpenes

Interestingly, in contrast to other species, *D. undulata* and *D. divaricata* seem to produce terpenes in higher amounts, compared with C_{11}-compounds. However, it should be kept in mind that the extraction methods differed among different authors, and with different species. The sesquiterpenes found in the *Dictyopteris* genus belong to two main classes, depending on whether they are of mixed biosynthetic origin (*i.e.* class II – meroditerpenes) or not (*i.e.* class I). Terpenes of *D. undulata* are mainly meroditerpenes and are discussed in the next topic. Without considering the meroditerpenes, so far, 71 terpenes have been reported for the *Dictyopteris* genus (**54**–**124**), most of them produced by *D. divaricata*. A total of eight monoterpenes (from *D. divaricata*, *D. latiscula* and *D. plagiogramma*) (**54**–**61**), 59 sesquiterpenes (mainly from *D. divaricata*, along with *D. undulata*, *D. membranacea*, *D. latiuscula*, *D. delicatula* and *D. prolifera*) (**62**–**120**) and four diterpenes (from *D. delicatula* and *D. polypodioides*) (**121**–**124**) have been reported. These sesquiterpenes derive from a 1,10 cyclization of t,t-farnesol, leading to a germacrane-type intermediate which furnishes (by a known sequence of transcyclization steps, or via a Cope rearrangement) the cadinane, copaane, cubebane, selinane, and elemane skeletons (Fleury et al., 1989).

Meroditerpenes

Meroditerpenes consist of a terpenic part with a linear or cyclic structure and an aromatic part, often consisting of quinone or derivatives. Eighteen such compounds have been found in *Dictyopteris* (**125**–**142**), mainly produced by *D. undulata* from the coupling of a farnesene-type precursor to a *p*-hydroquinone or *p*-hydroxybenzoic acid moiety, with or without further cyclization, to yield substituted drimane or farnesene sesquiterpenes (Fleury et al., 1989). These compounds are mainly found in marine organisms, predominantly sponges and brown algae, and have received considerable attention for their abundant structural variants and numerous biological activities. For example, it was demonstrated that avarol and avarone, isolated from the Mediterranean sponge *Dysidea*, inhibits HIV replication *in vitro* (Sarin et al., 1987). In addition, bolinaquinone, dysidenones, and dysidine, also from *Dysidea* spp, exhibited potent anti-inflammatory effect (Giannini et al., 2001; Lucas et al., 2003). Some examples reported for brown algae from Oceania include pycnanthuquinone C, isolated from *Cystophora harveyi* (Laird et al., 2007) and a bis-prenylated quinone from *Perithalia capillaris* (Kita et al., 2007a,b).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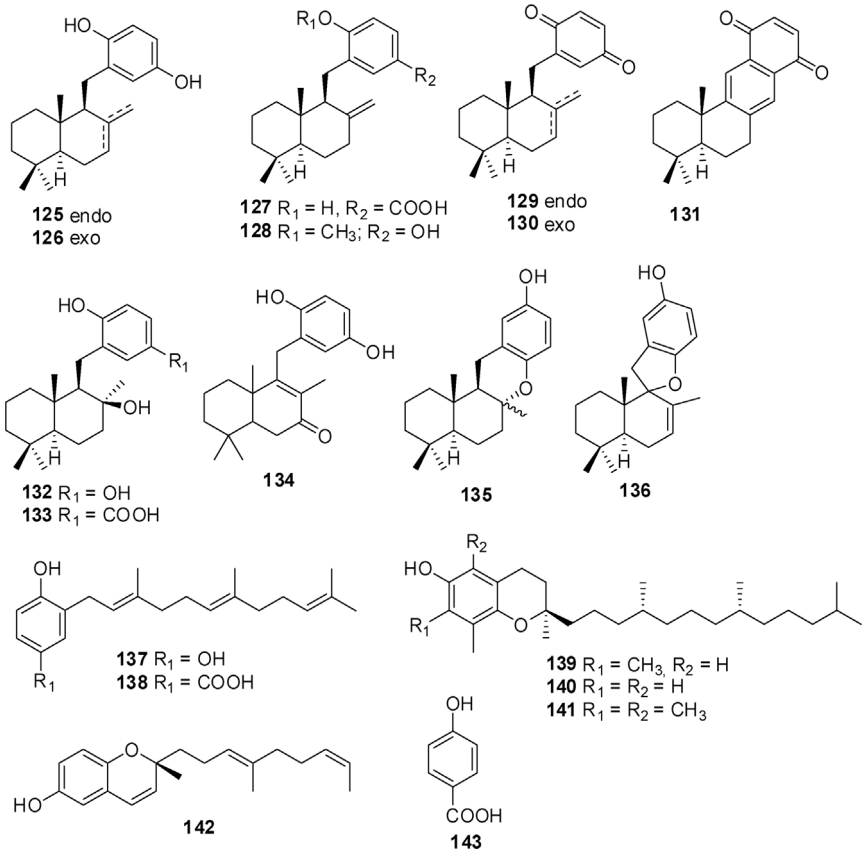


Zonarol (**126**) and isozonarol (**125**) were the first farnesyl hydroquinones with a drimane skeleton to be isolated from a marine organism (Fenical et al., 1973). The co-occurrence of **126** and **127** may be an indication that 4-hydroxybenzoic acid (**143**), which was further isolated from *D. divaricata* (Song et al., 2006), is the ring precursor as in ubiquinone biogenesis (Cimino et al., 1975). Compound **126** was also obtained from the rhizome of *Phytolacca* species (Jia and Qin, 2003).

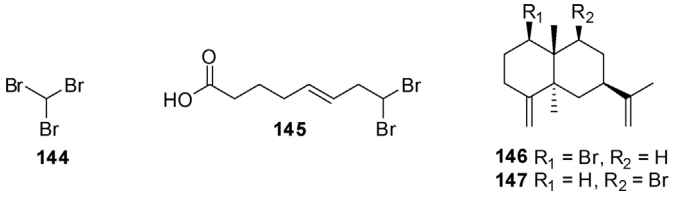
Along with the biological activities showed in Box 2, there is a patent that provides **126**, **125** and yahazunol (**132**) as active ingredients in pharmaceuticals, food or beverages aiming inhibition of lipase activity or fat absorption (Koyama et al., 2015). Chromazonarol (**135**) is included in a patent for an inhibitor of diatom adhesion containing lipid-soluble fractions from marine algae (Okino et al., 2007).

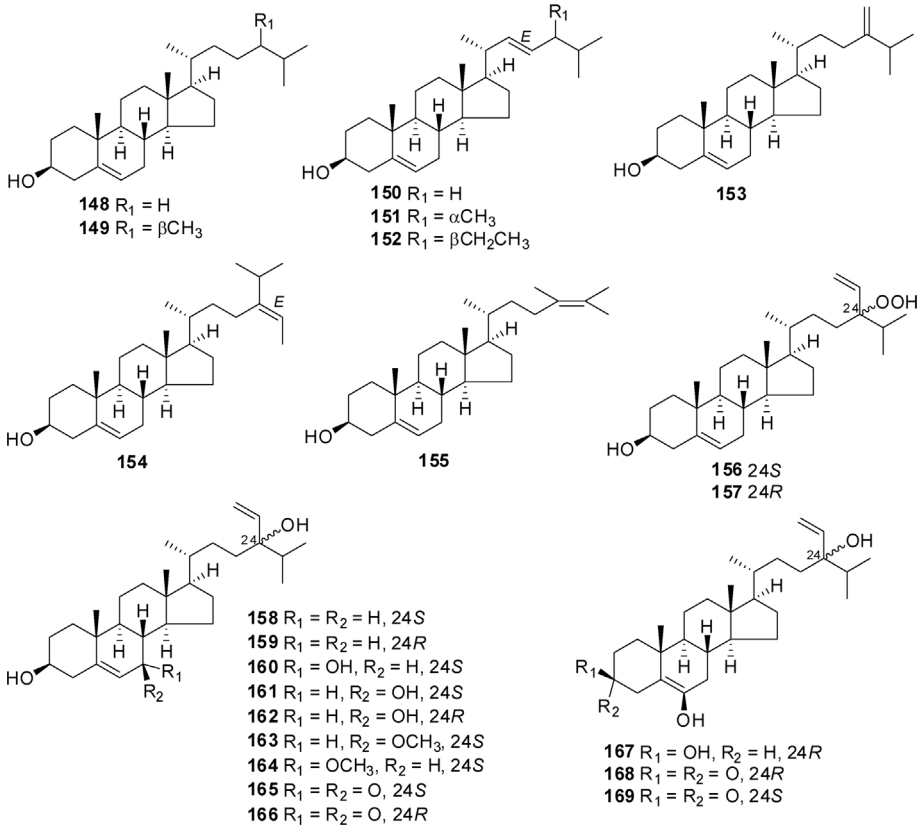
Prenylated aromatic compounds with a smaller side chain and without further substituents on the aromatic ring, such as the linear sesquiterpenoids 2-geranylhydroquinone (**137)** and 3-farnesyl-*p*-hydroxybenzioc acid (**138**), and dictyochromenol (**142**), are relatively rare among metabolites of brown algae, being more common in other marine organisms (Rosa and Tommonaro, 2012) and some terrestrial plants. Thus, compound **138** was previously isolated from the trichomes of *Turricula* and *Phacelia* genus as an allergen (Reynolds et al., 1985; Reynolds and Rodriguez, 1986), and also from *Piper* species (Ampofo et al., 1987; Maxwell and Rampersad, 1988), along with a series of prenylated phenolics. Metabolite **142** was found in *Piper tricuspe* and showed antimalarial and antioxidant activities, as well as cytotoxicity (Vega et al., 2008). Compounds **137** and **126** are claimed to inhibit NO production (Yazawa et al., 2010); and compound **138** was patented for the treatment of cognitive, neurodegenerative or neuronal diseases or disorders (Lopez Ogalla et al., 2009).

As meroditerpenes, α- (**141**), δ- (**140**) and γ- (**139**) tocopherols were reported for the *Dictyopteris* genus, and have also been isolated and characterized from various brown algae including *Sargassum* and *Cystoseira*. These molecules have shown a variety of functions in terrestrial vascular plants, but their ecological functions in algae are unclear; they may function in similar form to vascular plants, given the high exposure of many macroalgae to UV radiation (Paige Stout et al., 2010).

Halogenated compounds

Although halogenated compounds are unusual in brown algae, which can be partially explained due to the low activity of bromoperoxidase (Moore et al., 1996; La Barre et al., 2010), some brominated compounds have been reported for *Dictyopteris* (**144**–**147**). The first halogenated compounds were bromoform (**144**) and 8,8-dibromooct-5-enoic acid (**145**), identified in the EO of *D. polypodioides* collected on the coast of England (Hattab et al., 2002). More recently, new sesquiterpenes with a brominated selinane skeleton, as the isomers 1- (**146**) and 9-bromoselin-4(14),11-diene (**147**), have been isolated from *D. divaricata* collected on the coast of China; according to the authors, they may act as chemical defense against marine herbivores (Ji et al., 2009). These two isomers were further reported for the red alga *Laurencia composita* (Li et al., 2012).





Sterols

Sterols, which are constituents of cell membranes, have been reported for *Dictyopteris* species (**148**–**169**). Although fucosterol (**154**) is considered the typical sterol of brown algae, cholesterol (**148**) may be found as the dominant steroid in some *Dictyopteris* species (Fleury et al., 1994b). The major function of sterols in any organism is to maintain the structure and fluidity of the cell membrane; however, their ecological roles remain unclear. The isolation of a mixture of unusual hydroperoxide sterols 24*S* (**156**) and 24*R* (**157**) of 24-hydroperoxy-24-vinylcholesterol from *D. justii* may suggest an ecological function as a defense against herbivory, since these compounds inhibited herbivory by the crab *P. transversus* (Teixeira et al., 2006).

First reports and context of the discovery – the attractive "beach smell"

The first chemical investigations have been conducted on the odoriferous constituents of this genus. From the steam distillate of dried *D. divaricata*, which grows on the cost of Japan, Takaoka and Ando (1951) obtained an oil with a "beach odor" that has been shown, by Irie et al. (1964), to be a mixture of sesquiterpenes of the cadinene type: α-copaene (**89**), γ-cadinene (**72**), cadalene (**118**), β-elemene (**54**), δ-cadinol (**73**) and a non-identified sesquiterpene alcohol. Two years later, the selinane type sesquiterpenes dictyopterone (**94**) and α-dictyopterol (**95**) were isolated (Kurosawa et al., 1966). From another species collected in Japan (*D. dichotoma*), a viscous yellowish brown oil with a peculiar beach smell was obtained, and the presence of sesquiterpenes (structures not determined), along with palmitic acid, hexadecenoic acid, and *n*-parafines, was identified (Ando, 1953).

In contrast to the *Dictyopteris* species that grow along the coasts of Japan, the Hawaiian *D. plagiogramma* and *D. australis* develop non-isoprenoid C_{11}-compounds instead of sesquiterpenes. These species grew together on the sublittoral reef flats surrounding the Hawaiian Island, and large amounts of the seaweed are deposited on the shores during the summer months by heavy surf. The odor of *Dictyopteris* can frequently be detected in the air around the beaches (Pettus Jr., 1971; Moore, 1977). Therefore, the group of Professor Moore extensively studied the EO of the mixture of these algae, seeking to isolate and characterize the odoriferous constituents. The EO of the fresh wet algae (unseparated species, ratio of about 4:1) was analyzed by preparative gas chromatography, leading to the isolation of the C_{11}-hydrocarbon **16** (Moore and Pettus Jr., 1968). Subsequent work led to the isolation of undecapolyenes **19** (Pettus Jr. and Moore, 1970), **30** and **31** (Pettus Jr. and Moore, 1971). Several acyclic undecapolyenes were found with dictyopterenes in the EO in moderate to trace amounts, including compound **1**, *trans*, *trans*-undeca-1,3,5-triene (**2**), *cis*,*trans*-undeca-1,3,5-triene (**3**), *trans*,*trans*-2,4,6-undecatriene (**4**), *trans*,*trans*,*cis*-undeca-1,3,5,8-tetraene (**5**), and *trans*,*cis*,*cis*-undeca-1,3,5,8-tetraene (**6**) (Moore et al., 1974).

Study of the extract (chloroform-methanol) of the mixture of *D. plagiogramma* and *D. australis* led to the isolation of the new sulfur compounds **37**, bis-(3-oxoundecyl) trisulphide (**51**), bis-(3-oxoundecyl) tetrasulphide (**52**) (Moore, 1971), *S*-(−)-3-acetoxyundec-5-enyl thioacetate (**40**) and (−)-bis-(3-acetoxyundec-5-enyl) disulfide (**46**) (Moore et al., 1972). From the extract of *D. plagiogramma* other C_{11}-sulfur compounds were obtained, as *S*-(3-oxoundecyl) thioacetate (**38**), *S*-(trans)-(3-oxoundec-4-enyl) thioacetate (**42**), bis-(3-oxoundecyl) disulfide (**43**), along with **53** (Roller and Moore, 1971). It was supposed that these compounds may be precursors of hydrocarbons found in the EO of both species (Roller and Moore, 1971; Moore et al., 1972). Moreover, other minor C_{11}-metabolites, namely dihydrotropones (**34** and **35**), structurally related to **30**, were isolated from *D. plagiogramma* and *D. australis* extracts (Moore and Yost, 1973).

Box 3
Biological assays reported for less studied *Dictyopteris* species.

Species	Activity	Algal material	Reference
D. dichotoma	Tyrosine inhibition	EtOH extract	Kwak et al., 2016
D. jamaicensis	Antibacterial, antifungal	$CHCl_3$/MeOH extract (2:1)	Ballantine et al., 1987
D. jolyana	Antibacterial, antifungal, antiprotozoal (all inactive)	CH_2Cl_2/MeOH extract (2:1)	Bianco et al., 2013b
D. longifolia	Antibacterial	EtOH extract	Vlachos et al., 1997, 1999
	Antioxidant	EtOH, MeOH, Aqueous extracts	Matsukawa et al., 1997; Lee et al., 2011; Lee and Kim, 2015
	Cytotoxic, anti-inflammatory	EtOH extract	Lee et al., 2008

Also in the 1970s, some works were performed on *D. undulata* from North America. The sesquiterpene zonarene (**62**) was isolated from the hexane extract of *D. undulata* collected in Puerto Peñasco, Mexico, as the first example of a conjugated diene member of cadinene hydrocarbons (Fenical et al., 1972). Fenical et al. (1973) also reported the isolation of the isomeric C_{21}-hydroquinones **125** and **126** from methanol extracts of *D. undulata* collected in San Diego and in the Gulf of California. Furthermore, two new sesquiterpene chromanols, **135** and **136**, were obtained as minor constituents of chloroform extract (Fenical and McConnell, 1975); a further sesquiterpene, zonaroic acid (**127**), in which the bicyclic isoprenoid moiety is attached to 4-hydroxybenzoic acid (**143**), was also reported for the chloroform extract (Cimino et al., 1975).

Further chemical and biological reports by species

Dictyopteris polypodioides is described first, because it is the holotype of the genus *Dictyopteris*. After that, the species are described in alphabetical order. Species with no reported chemical studies, for which there are only biological reports, are described in Box 3.

Dictyopteris polypodioides (synonym: *D. membranacea*)

Dictyopteris polypodioides (A.P. De Candolle) J.V. Lamouroux (basionym: *Ulva polypodioides* A.P. De Candolle) is the type species (holotype) of the genus *Dictyopteris*. *D. membranacea* is regarded as a taxonomic synonym of *D. polypodioides*, which is the currently accepted name (Guiry and Guiry, 2016). This species has been reported in South America (Brazil), Atlantic Islands, North America, Caribbean Islands, Africa, Asia and Europe (Guiry and Guiry, 2016). Despite this wide distribution, chemical and biological studies are concentrated mainly in the Mediterranean Sea (Fig. 1). There are 83 compounds described for this species, highlighting C_{11}-hydrocarbons (France, England and Algeria), sulfur compounds (France, Greece and USA) and terpenes (Egypt and Algeria) (Table 1).

The first work was performed by Boland and Müller (1987), who analyzed the volatile components of *D. polypodioides* collected in two habitats of the French Mediterranean coast, near Nice: Beaulieu harbour, and the Station Zoologique pier at Villefranche-sur-mer. Those authors observed remarkable qualitative and quantitative differences in the EO composition, which they attributed to genetic factors of the populations and/or to different conditions of the habitats. Moreover, two new cyclic C_{11}-hydrocarbons **29** and **33** were isolated for the first time, besides known compounds (**2**, **7**, **10**, **12**, **24**, **30**).

A different pattern was reported by Hattab et al. (2002), who studied the EO of *D. polypodioides* in two works. From a sample collected in Atlantic coast of Brittany (England), they reported the presence of the C_{11}-hydrocarbons and derivatives **10**, **13**, **14**, **16**, **24**, **27**, **30**, along with the halogenated metabolites **144** and **145** and other volatile minor compounds (Supporting information). In another study, with samples collected in Algeria, the same group observed an important variation in chemical composition using three distinct methods for the extraction of volatile metabolites. C_{11}-hydrocarbons (**4**, **10**, **12**, **13**, **15**, **16**, **24**, **28**, **30**) were mainly extracted by hydrodistillation. Focused microwave-assisted hydrodistillation led to the sesquiterpenes **62**, 1,10-di-epi-cubebol (**68**), δ-cadinene (**71**), germacrene D (**87**), **89**, α-cubebene (**90**), β-cubebene (**91**), **92**, α-amorphene (**93**), **100**, epi-bicyclosesquiphellandrene (**101**), albicanol (**102**), aromadendrene (**103**), axenol (**104**), vulgarol B (**105**), β-bourbonene (**106**), sativene (**107**), and α-calacorene (**119**), while sulfur compounds (**39**, **41**, and **53**) were obtained by the supercritical fluid extraction method. As reported in the previous study, some volatile minor compounds were identified (Supporting information) (Hattab et al., 2007a).

Ozdemir et al. (2006) worked with a sample of *D. polypodioides* collected on the Izmir coast, Turkey, and identified C_{11}-hydrocarbons as the main constituents of the EO using the distillation method. Compound **30** was the major compound (43.21%), along with simple volatile compounds (Supporting information). Furthermore, the EO and the methanol, hexane and chloroform extracts showed antibacterial and antifungal activities (Ozdemir et al., 2006).

Several sulfur compounds were recently isolated from the chloroform/methanol extract of *D. polypodioides* collected at Gerolimenas Bay, Greece, including six new (**44**, **45**, **47**–**50**) and two previously reported disulfides (**43** and **53**), along with **34**, **139** and **140**. Metabolite **45** inhibited NO production using a lipopolysaccharide (LPS) stimulation assay, and none of the compounds displayed antibacterial activity (Dimou et al., 2016).

Moreover, from petroleum ether, dichloromethane and chloroform extracts of *D. polypodioides* collected on the Mediterranean coast of Egypt, diterpenes 18,19-epoxyxenic-4-one-6,9,13-triene (**122**), dictyolactone (**123**) and 4-acetoxycrenulide (**124**) were isolated, along with steroids **148** and **154** (Aboutabl et al., 2010). Chalinasterol (**153**) was also found in *D. polypodioides* (Amico et al., 1976; Guven and Kizil, 1983; Kanias et al., 1992). Furthermore, some extracts showed a wide range of antimicrobial activity against fungi and Gram positive and negative bacteria, along with free radical scavenging and anti-inflammatory activities, with significant inhibition of rat paw edema induced by carrageenan (Aboutabl et al., 2010).

This species is also rich in fatty acids and lipids (Pohl et al., 1968; Eichenberger et al., 1993; Hofmann and Eichenberger, 1997, 1998; Karaki et al., 2013), and in sulfated polysaccharides, which present antioxidant, anticoagulant, antitumoral, antimicrobial,

antiviral, gastroprotective and hypolipidemic activities (Pelivan and Lutkic, 1994; Sokolova et al., 2011; Karaki et al., 2013; Abou Zeid et al., 2014; Matloub et al., 2015; Ammar et al., 2018).

Mannino et al. (2014) reported the highest phenolic content during winter and autumn in ethanol extract of *D. polypodioides* collected on the coast of Sicily. The seasonal variation was also reported in the same study for another species of algae, *Cystoseira amentacea*. However, a distinct seasonal pattern of phenolic compounds was observed for this species, with maximum levels in summer. Other publication of the same group (Mannino et al., 2017) suggests also the influence of a combination of factors, such as growth form, depth, and exposition to solar radiation in the total phenolic content. Lower content of phenolic compounds was observed for 70% aqueous methanol extract of a sample from the Canary Islands, but the authors did not mention when the sample was collected (Chkhikvishvili and Ramazanov, 2000). Recently, Akremi et al. (2017) analyzed the total phenolic, flavonoid and tannin contents and antibacterial, antifungal and antitubercular activities of the crude extract obtained with dichloromethane/methanol 1:1 (v/v), and fractions of *D. polypodioides* collected in Tunisia. The acetone fraction presented higher phenolic and tannin contents, while the ethanolic fraction had higher flavonoid content. The two fractions presented promising activities. The dichloromethane/methanol fraction presented lower phenolic, tannin and flavonoid contents and did not exhibit antimicrobial and antifungal activities. It was also observed that the solvents influenced the content of compounds and also the biological activity. Antioxidant activity was reported for the dichloromethane extract of *D. polypodioides* from Crete, Greece (Nahas et al., 2007), and chloroform and ethyl acetate extracts of *D. polypodioides* from Tunisia by DPPH and hydroxyl radical-scavenging activity, and reducing power. Furthermore, chloroform and ethyl acetate extracts, along with aqueous extract, exhibited high anti-inflammatory potential in the carrageenan-induced rat paw edema assay, comparable to acetylsalicylate lysine, and antibacterial and antifungal activities (Aoun et al., 2010).

Different organic extracts of *D. polypodioides* from the Canary Islands, Morroco, Libya and Turkey showed antibacterial and antifungal activities against some human pathogenic microorganisms (González del Val et al., 2001; Tüney et al., 2006, 2007; Salvador et al., 2007; Chiheb et al., 2009; Alghazeer et al., 2013a,b; Khallil et al., 2015). Cytotoxicity against human epidermoid oral carcinoma (KB cells) and kidney cells of monkey (CV-1) was reported for the aqueous, ethanol 30% and chloroform extracts of *D. polypodioides* from the Gulf of Trieste (North Adriatic Sea) (Kosovel et al., 1988, 1991) and methanol/toluene extract of *D. polypodioides* from the Western Mediterranean (Ballesteros et al., 1992). Furthermore, *D. polypodioides* from the northwest coast of Spain showed selective agglutinating activity for *C. guillermondii* var. soya and may be a valuable reagent for the identification of yeast strains (Fabregas et al., 1989).

Dictyopteris acrostichoides

Dictyopteris acrostichoides (J.Agardh) Bornet (basionym: *Haliseris acrostichoides* J.Agardh) is found in some places of Africa, Asia and Oceania (Guiry and Guiry, 2016). Despite being found in different locations, chemical and biological reports only exist for samples collected in Australia (Fig. 1). Several C_{11}-hydrocarbons were identified by GC–MS, such as some dictyopterenes (**16**, **19**, **30** and **31**), and the olefins **1**, **2**, **6**, cyclopropane **20**, cyclopentenes **21**–**26**, **29**, and cycloheptadiene **32** (Wirth et al., 1992).

Dictyopteris australis

Dictyopteris australis (Sonder) Askenasy (basionym: *Haliseris australis* Sonder) is widely distributed in the Pacific region (including the Pacific Islands, Australia, New Zealand, and temperate coast of South America), the Indian Ocean Islands, and Southwest Asia (Gosch et al., 2015; Guiry and Guiry, 2016). Besides the lack of studies on the species, the chemistry of *D. australis* has only been studied together with *D. polypodioides*, as already described. That study reports mainly C_{11}-hydrocarbons and derivatives, such as sulfur compounds from samples collected in Hawaii. Material from this species collected on the coast of Pakistan (Karachi coast) and Australia (North Queensland) has been reported as a rich source of fatty acids (Aslam et al., 1994; Saikh et al., 2009; Shahnaz and Shameel, 2009; Valeem and Shameel, 2012; Gosch et al., 2015). The sample collected in Pakistan showed antibacterial, antifungal, cytotoxic and phytotoxic activities (Aslam et al., 1994; Shahnaz and Shameel, 2009). Methanol extract of *D. australis* from India showed high cytotoxicity with a dose-dependent activity using the brine shrimp lethality assay, and also antioxidant activity, with higher ferrous ion chelating activity than the other tested brown seaweeds (Vinayak et al., 2011).

Dictyopteris delicatula

Dictyopteris delicatula J.V. Lamouroux is widely distributed in the world, including North, Central and South America, Africa, Asia, Australia and New Zealand, and also the Atlantic, the Caribbean and the Indian Ocean Islands (Guiry and Guiry, 2016). According to Taylor et al. (1960, apud Hay et al., 1988) this alga commonly grows epiphytically on other algae in shallow waters in the Caribbean, but also occurs at depths of up to 30 m. As shown in Fig. 1, there are chemical and biological studies on *D. delicatula* from Brazil, Australia, India, Mexico, Porto Rico, the Caribbean and Venezuela. Samples from Brazil and India were studied mainly for their steroid composition, along with polysaccharides, lipids and fatty acids; terpenes were reported for *D. delicatula* from Australia, while C_{11}-compounds were isolated from samples from the Caribbean.

The C_{11}-compounds **16** and **19** were isolated from the extract of a Caribbean alga, which significantly deterred fish grazing but had no effect on grazing by amphipods (Hay et al., 1988). Later, the diterpene **121** (dolabellane type), which possesses two epoxide groups, was isolated from *D. delicatula* collected in Queensland, Australia (Wright and Coll, 1990), and also the new sesquiterpenes 4β,5α-dihydroxycubenol (**66**) and cubenol-3-one (**65**), the previously reported cubenol (**63**), and a non-racemic mixture of **73** (König and Wright, 1995).

The sterol composition of *D. delicatula* collected on the coast of Rio de Janeiro, Brazil, was determined by GC-MS, and eight steroids were identified, including cholesterol (**148**) as the major compound, besides campesterol (**149**), 22,23-didehydrocholesterol (**150**), brassicasterol (**151**), stigmasterol (**152**), chalinasterol (**153**), **154**, and 24-methyldesmosterol (**155**) (Fleury et al., 1994b). Furthermore, *D. delicatula* collected in India and Brazil seems to be a source of lipids and fatty acids, also showing the presence of polyphenolics, β-carotene and α-tocopherol (**141**) (Fleury et al., 1994a; Sousa et al., 2008; Fleury et al., 2011; Kumari et al., 2013, 2014). A polysaccharide-rich extract of *D. delicatula* collected in Natal, Brazil, exhibited some biological activities, including anticoagulant, antiproliferative and antioxidant activities (Costa et al., 2010). The polysaccharide constituents of brown seaweed containing substantial percentages of L-fucose and sulfate ester groups are called fucoidans, and their potential as anticoagulant agents is by far the most widely studied activity (Li et al., 2008). Fucoidans isolated in a further work from *D. delicatula* also exhibited anticoagulant, antiproliferative and antioxidant activities (Magalhaes et al., 2011).

The following studies did not include isolation of bioactive compounds, reporting only biological activities from extracts. Aqueous extract of *D. delicatula* collected in Porto Rico had weak antibacterial activity against *S. aureus* and *Mycobacterium smegmatis* (Burkholder et al., 1960). Likewise, ethanol extract of *D. delicatula* collected in Venezuela and Mexico showed activity against *S. aureus* and *S. pyogenes* (Perez et al., 1990).

The dichloromethane/methanol (2:1) extract of *D. delicatula* collected in Pernambuco (Brazil) showed antioxidant activity in different *in vitro* antioxidant assays (DPPH and ABTS scavenging, metal chelating and ferric reducing antioxidant power). These results may correlate to phenolic contents (Vasconcelos et al., 2017). The methanol extract of *D. delicatula* from Anjuna Beach, Goa, India, showed cytotoxic activity in the brine shrimp lethality test and potential antioxidant activity in several assays, with high phenolic content (Vinayak et al., 2011). The dichloromethane/methanol (1:1) extract of *D. delicatula* collected in Rasa Beach, Rio de Janeiro, Brazil, showed antiviral activity against acyclovir resistant *Herpes simplex* virus types 1 and 2, without cytotoxicity against Vero cells (Soares et al., 2012). On the other hand, dichloromethane/methanol extract (2:1) of *D. delicatula* from Calhetas Beach, Pernambuco, Brazil, presented weak larvicidal activity against *Aedes aegypti* (Bianco et al., 2013a).

Dictyopteris divaricata

Dictyopteris divaricata (Okamura) Okamura (basionym: *Haliseris divaricata* Okamura) is reported in several locations of Africa, South America, Asia, Europe and Oceania, and also the Atlantic Islands (Guiry and Guiry, 2016). However, despite the wide occurrence, there are only chemical and biological reports of samples collected in Japan, China and Korea (Fig. 1), and the latter is restricted to biological works. In general, terpenes are the most important class of compounds, comprising 53 isolated and/or identified compounds in the extracts and EO.

As already reported, *D. divaricata* was the first *Dictyopteris* species to be studied in relation to its chemical composition. The EO of *D. divaricata* from the cost of Japan presented a mixture of sesquiterpenes of the cadinene (**54**, **72**, **73**, **89**, **118**) (Takaoka and Ando, 1951; Irie et al., 1964) and selinane types (**94**, **95**) (Kurosawa et al., 1966). Some of them were further isolated from the species colleted in other places of Japan and China (Kajiwara et al., 1980; Song et al., 2004; Song et al., 2005a; Song et al., 2006; Ji et al., 2009; Qiao et al., 2009), along with several other sesquiterpenes, such as epicubenol (**64**), epicubebol (**67**) (Suzuki et al., 1981), germacrene A (**85**) (Segawa et al., 1990; Song et al., 2004), β-dictyopterol (**96**) (Kurosawa et al., 1966; Ji et al., 2009), and compounds **63** (Suzuki et al., 1981; Kajiwara et al., 1989; Mayer et al., 1993; Qiao et al., 2009), **71** (Kajiwara et al., 1980; Suzuki et al., 1981), **86** (Segawa et al., 1990; Song et al., 2004), **87** (Kajiwara et al., 1989), **88** (Suzuki et al., 1990), **90** (Suzuki et al., 1981), **91** (Kajiwara et al., 1980; Suzuki et al., 1981), **98** and **99** (Suzuki et al., 1981), along with the unusual prenylated aromatic type compound **138** (Segawa et al., 1990; Song et al., 2004).

Song et al. (2004, 2005, 2006) between the years 2004 and 2006, published three studies that showed a wide variety of terpenes that have been isolated from ethanolic extract of *D. divaricata*, collected on the coast of Qingdao, China, in May 2002. The first work reported seven cadinane sesquiterpenes **76**–**79**, **81**, **83** and **84**, a new sesquiterpene-substituted phenol named dictyvaric acid (**133**), and some known compounds, including the monoterpenes dehydrovomifoliol (**56**), loliolide (**60**) and isololiolide (**61**), sesquiterpenes **57** and **66**, the meroditerpene **135** and the steroid **154** (Song et al., 2004). In sequence, it was reported the isolation of three bisnorsesquiterpenes (**108**–**110**) and one norsesquiterpene (**117**) (Song et al., 2005b) and also the compounds **111**–**115**, which bear two novel carbon skeletons, as well as oplapane sesquiterpene (**116**) (Song et al., 2006). The authors suggested that the novel skeletons may be derived from the co-occurring cadinanes by different ring contraction rearrangements, and may also be biogenetic intermediates of the co-occurring bisnorsesquiterpenes (Song et al., 2006). The monoterpenes **58** and **59** were reported for samples collected on the coast of Qingdao, China (Xu et al., 2012).

From material collected in China in July 2008, Qiao et al. (2009) reported the isolation of 4β,5β-epoxycadinan-1β-ol (**74**), cadinan-1,4,5-triol (**75**), and **65** and **76** from chloroform/methanol (1:1) extract. In the same year, Ji et al. (2009) showed the isolation of α-selinene (**69**), β-selinene (**70**), cyperusol C (**82**), 1,4-epoxymuurolan5β-ol (**97**) and two brominated selinane sesquiterpenes (**146** and **147**) from chloroform/methanol (1:1) extract of material collected on the coast of Yantai, China in July 2008. Recently, Ji et al. (2016) reported the sesquiterpenes cadinan-4(15)-ene-1β,5α-diol (**80**) and trans-3-norisocalamenen-4-ol (**120**) from material collected in the same place.

Other compounds identified in the essential oil of *D. divaricata* collected in Japan include the two C_{11}-hydrocarbons **30** and **31** (Kajiwara et al., 1997), while the steroid **157** was identified from the benzenic extract (Ikekawa et al., 1968).

Studies of biological activities performed with *D. divaricata* showed cytotoxicity against human cancer cell lines for ethanol and ethyl acetate extracts from a sample collected in Jeju Island, South Korea (Kim et al., 2009), and less polar extracts from a sample collected on the coast of China (Xu et al., 2001, 2004). In addition, dichloromethane/methanol and ethanol extracts of *D. divaricata* from the coast of the Yellow Sea, China, inhibited the enzyme α-glucosidase, important target for the treatment of diabetes, hyperlipoproteinemia and obesity (Xiancui et al., 2005; Jeong et al., 2012). Ethanol extract of *D. divaricata* from the Korean coast showed anti-inflammatory activity (Lee et al., 2008; Yang et al., 2014).

Antioxidant activity, usually related to the presence of phenolic compounds, was reported for organic extracts of *D. divaricata* from Korea and China. The extracts exhibited radical scavenging activity, reducing power, cellular NO inhibition, β-carotene bleaching activity and effects on lipid accumulation by attenuation of oxidative damage (Zhang et al., 2007; Kim et al., 2008; Lee et al., 2011; Lee and Kim, 2015).

Dictyopteris justii

Dictyopteris justii J.V. Lamouroux was found on the American continent, in some Atlantic and Caribbean Islands and also in the Western Atlantic (Guiry and Guiry, 2016). There are a few chemical and biological studies for samples from Brazil, Porto Rico and Bahamas. From a sample collected in Fernando de Noronha Archipelago, Brazil, a mixture of epimers 24*R* and 24*S* (**156**) was isolated, comprising the major component of the sterol fraction, and showed defensive properties against the crab *Pachygrapsus transversus* (Teixeira et al., 2006). From material from the same site, several fatty acids were identified by the CG-MS technique, along with simple volatile compounds (Supporting information) (Ferreira et al., 2012). Sulfated polysaccharides were determined from the proteolytic digestion of *D. justii* collected in Maxaranguape, Brazil, and showed antioxidant activity, along with inhibition of calcium oxalate crystal formations (Melo et al., 2013). Chloroform/methanol (2:1) extract of *D. justii* from the Caribbean showed antimicrobial activity against *B. subtilis* (Ballantine et al., 1987), *S. aureus*, *E. coli*, *M. smegmatis*, and *Candida albicans* (Burkholder et al., 1960).

Dictyopteris latiuscula

Dictyopteris latiuscula (Okamura) Okamura (basionym: *Haliseris latiuscula* Okamura) is reported only for Asia (China, Japan, Korea) (Guiry and Guiry, 2016) and only four studies about this species were found in the literature. As Hattab et al. (2007a) found for *D. polypodioides*, using simultaneous distillation extraction, Yamamoto et al. (2001) also identified C_{11}-hydrocarbons as major constituents from the EO of a sample collected on the west coast of Hikoshima Island, Japan. Compound **16** was identified as the major constituent (40.1%), along with other C_{11}-hydrocarbons (**2**, **6**, **8**–**11**, **18**, **19**, **21**, **29**, **30**, **31**, **33**), the sesquiterpene δ-elemene (**55**) and some minor volatile aldehydes and alcohols (Supporting information), and the sesquiterpene **62**.

The lipid profile of methanol extract of *D. latiuscula* from Japan was also determined (Eichenberger et al., 1993) and showed high lipase inhibition activity (90%) (Bitou et al., 1999). The methanol/toluene extract (3:1) of *D. latiuscula* from Fujian, China, showed antibacterial activity (Zheng et al., 2001).

Dictyopteris plagiogramma

Dictyopteris plagiogramma (Montagne) Vickers (basionym: *Haliseris plagiogramma* Montagne) occurs in North, Central and South America, Asia, Africa, Australia and New Zealand, the Atlantic and Pacific Islands, the Caribbean Islands and the Indian Ocean Islands (Guiry and Guiry, 2016). Nevertheless, there are only studies on samples collected in Hawaii, Brazil and Porto Rico (Fig. 1). In general, *D. plagiogramma* from Hawaii proved to be rich in C_{11}-hydrocarbons and sulfur compounds, while Brazilian *D. plagiogramma* was most studied for its terpene, steroid (Fleury et al., 1994b; Ferreira et al., 2012), lipid, fatty acids (Fleury et al., 1994a) and polysaccharide composition (Percival et al., 1981; Briggs et al., 1982), along with other volatile constituents (Ferreira et al., 2012).

The material collected in Fernando de Noronha Archipelago, Brazil, showed the presence of the monoterpenes **60** and **61**, along with simple volatile compounds (Supporting information) (Ferreira et al., 2012). As was also reported for *D. delicatula*, the steroids **148**–**155** were identified in *D. plagiogramma* collected in Rio de Janeiro, Brazil, and cholesterol showed to be the major component (Fleury et al., 1994b). The methanol extract of *D. plagiogramma* collected in Makai Pier, Oahu (Hawaii), showed weak antioxidant activity compared to other brown algae (Kelman et al., 2012). *D. plagiogramma* collected in Porto Rico demonstrated both promoting and inhibiting properties in relation to various marine bacteria (Burkholder et al., 1960).

Dictyopteris prolifera

Dictyopteris prolifera (Okamura) Okamura (basionym: *Haliseris prolifera* Okamura) is found mainly in Japan, China and some Atlantic Islands (Guiry and Guiry, 2016). Nevertheless, phytochemical investigations were performed only with samples collected in Japan, while biological reports are related to samples collected in Korea. *D. prolifera* proved to be rich in C_{11}-compounds and terpenes.

From EO of the species collected in Japan, the dictyopterenes **16**, **19**, **30** and **31** were identified (Yamada et al., 1979; Kajiwara et al., 1980; Kajiwara et al., 1989; Fujimura et al., 1994; Kajiwara et al., 1997; Yamamoto et al., 2001), along with other C_{11}-compounds as **2**, **6**, **17**, **21**, **22**, **24**, **33** and **29** (Kajiwara et al., 1989; Fujimura et al., 1994; Kajiwara et al., 1997). Possible precursors for dictyopterenes were also identified, such as dictyoprolenol (**8**), neodictyoprolenol (**9**) (Yamamoto et al., 2001), neodictyoprolene (**11**) (Yamada et al., 1980; Yamamoto et al., 2001), and metabolite **10** (Tan et al., 1979; Yamada et al., 1979; Kajiwara et al., 1989; Fujimura et al., 1994; Yamamoto et al., 2001). With the exception of **10**, these compounds were first isolated from *D. undulata* (see in the next item). Yamada et al. (1986) also reported a synthesis and biosynthesis study involving compounds **10** and **11**. Other reported compounds include sesquiterpene **63** (Kajiwara et al., 1989; Fujimura et al., 1994) and dipropyl disulfide (**36**) (Fujimura et al., 1994).

Several ethanol and methanol extracts of *D. prolifera* from Jeju Islands, Korea, were submitted to biological assays and showed antioxidant (Lee et al., 2011; Lee and Kim, 2015) and anti-inflammatory activities (Yang et al., 2014), along with inhibitory activity of α-glucosidase (Jeong et al., 2012). The methanol extract from a sample collected in Japan showed pancreatic lipase activity inhibition (Bitou et al., 1999).

Dictyopteris undulata

Dictyopteris undulata Holmes (formerly *D. zonarioides*), known as "Shiwayahazu" in Japan (Ochi et al., 1979b), occurs also in Taiwan, China, Korea, Philippines, California and Mexico (Guiry and Guiry, 2016). As verified for *D. prolifera*, there are chemical studies of *D. undulata* from Mexico, the USA and Japan, while samples collected in Korea and Taiwan were mainly investigated for their biological potential. The species presents mainly meroditerpenes (Asia and North America) and C_{11}-compounds (mostly found in Japan).

Besides works described in the topic 'First reports and context of the discovery', investigation of the methanol extract of *D. undulata* collected in the Bay of Tosa, Japan, led to the isolation of a new sesquiterpene-substituted hydroquinone (**132**) with strong antifungal activity, along with **125**, **126** and **127** (Ochi et al., 1979b). The prenylated hydroquinone **137**, isolated from the methanol extract as a possible precursor of these sesquiterpene-substituted phenols, also showed antifungal activity (Ochi et al., 1979a).

Dave et al. (1984) found that methanol extract of *D. undulata* from Izu-Shimoda beach, Japan, possesses remarkable toxicity to fish; the bioactive compounds were isolated, including a new chromenol (**142**), along with **125**–**127**, isozonarone **(129)**, zonarone (**130**), **135** and **136**. A new derivative, cyclozonarone (**131**), along with **125**, **126**, **129**, **130** and **135**, were also isolated from the methanol extract of *D. undulata* collected at Tobi, Akita prefecture, Japan, and showed potent feeding-deterrent activity toward young abalones (Kurata et al., 1996).

The dichloromethane extract of *D. undulata* collected in Catalina Island (California, USA), showed antimycobacterial activity, and the bioassay-guided fractionation led to the isolation of the new sesquiterpene hydroquinone (**128**), together with **125**, **126** and **132** (Joshi Bipin et al., 2012). The bioassay-guided fractionation (algicidal activity) of a methanol extract of *D. undulata* collected in Japan led to the isolation of zonarenone (**134**), another novel sesquiterpene hydroquinone, together with the known compounds **125**–**127**, **132**, **134**, **136** and **137** (Ishibashi et al., 2013).

The characteristic "ocean smell" of *D. undulata* from Japan was studied by Kajiwara et al. (1980), and proved to be related to a mixture of dictyopterenes **16**, **19**, **30** and **31** and the sesquiterpenes **89**, **91**, **71**, along with other non-identified C_{11}-compounds. The presence of dictyopterenes was also demonstrated in subsequent works, together with **8**–**11** (Kajiwara et al., 1982; Kajiwara et al., 1991; Kajiwara et al., 1997; Yamamoto et al., 2001).

Recently, ten new stigmastane-type steroids bearing unusual Δ^{28}-24-hydroxy side chains (**160**–**169**), together with two previously reported analogs of saringosterol (**158**–**159**), were isolated from *D. undulata* collected from the Zhanjiang coastline in the South China Sea, and exhibited promising PTP1B inhibitory activity and cytotoxicity activity (Box 1) (Feng et al., 2018).

Potent antibacterial activity against several methicillin-resistant *S. aureus* (MRSA) strains was demonstrated for the

methanol extract of *D. undulata* from Japan (Horikawa et al., 1999). Another study showed antibacterial potential against foodborne pathogens, such as *Salmonella choleraesuis*, *Bacillus cereus*, *S. aureus* and *Listeria monocytogenes* (Jang and Lee, 2015).

Different extracts of *D. undulata* collected off the coasts of Taiwan (Lin et al., 2012) and Korea (Lee et al., 2011; Lee and Kim, 2015) showed antioxidant potential. Moreover, treatment with *D. undulata* significantly inhibited adipocyte differentiation and reactive species of oxygen (ROS) production during differentiation of 3T3-L1 preadipocytes, which may protect against oxidative stress linked to obesity (Lee et al., 2011).

The ethanol extract of *D. undulata* from the Jeju Islands, Korea, inhibited the production of pro-inflammatory factors in the murine macrophage cell line RAW 264.7 activated with LPS (Kang et al., 2012). Other studies showed cytotoxic and apoptotic effects on colon cancer and human melanoma cells lines, an effect that may be due to the induction of endoplasmic reticulum stress and reactive oxygen species (Kang et al., 2014; Kim et al., 2014, 2015).

Conclusion

After more than sixty years of research on the *Dictyopteris* species, hundreds of metabolites have been isolated, including many unique molecules, such as uncommon sulfur compounds and meroditerpenes, which were reported for the first time. The biological activities reported to some *Dictyopteris* species suggest them to have a high medicinal potential. *D. polypodioides*, *D. delicatula*, *D. divaricata*, *D. prolifera*, and *D. undulata*, in particular, presented interesting results related to their antimicrobial and cytotoxic activities, constituting important targets for in depth investigations. Additionally, the related metabolites also proved to present promising biotechnological applications (pharmaceuticals, cosmetics, food and shipping industries). Therefore, more studies should be carried out, including toxicological investigations, since these species hold great potential for pharmacological and clinical studies, and may afford new drugs in the future.

Authors' contributions

All authors contributed in collecting and analyzing data besides drafting parts of the paper. GAZ and ACP (PhD students) contributed also drawing the structures. MF organized the data and contributed to critical reading of the manuscript. All the authors have read the final manuscript and approved the submission.

Conflicts of interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.bjp.2018.01.005.

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