



Concise review of the genus *Dictyota* J.V. Lamouroux

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Abstract

The genus *Dictyota* (Dictyotales, Phaeophyceae) comprises parenchymatous algae occurring predominantly in tropical to warm-temperate waters and has gathered attention due to its diverse secondary metabolites with antibiofouling and pharmaceutical potential, its oil content, and its potential as animal feed. This has resulted in an increase in economic potential during the last decade. In this review, we summarise the recent knowledge on the genus and concentrate on the applications and the economic potential of *Dictyota*. In addition, the review summarises the taxonomy, anatomy, cytology, genetic data, life history, chemical composition, nutritional value and ecological and economic importance of *Dictyota* species. Currently, around 100 species are recognised together with the morphologically similar and closely related genera *Dilophus*, *Canistrocarpus* and *Rugulopteryx* (tribus Dictyoteae). The thallus is characterised by one or more lens-shaped apical cells that divide into cortical and medullary cell layers. Species typically grow in rocky intertidal pools and subtidal areas. *Dictyota* is consumed locally in the Caribbean, Malayan-Indonesian and Hawaiian regions. Extracts of *Dictyota* which contain active compounds, such as diterpenes and phlorotannins, have been attributed antimicrobial, health and wellness promoting effects which render them promising candidates for the design of functional foods, phytomedicinal products, and cosmetics. The high fraction of lipids and fatty acids has propelled emerging applications in the biofuel industry and as a feedstock species.

Keywords *Dictyota* · Taxonomy · Biofuel · Pharmaceutical uses · Antioxidants · Chemical composition · Diterpenes

Identity

Pachydictyon J. Agardh, 1894; *Bicrista* Kuntze 1898 ;
Glossophorella M. Nizamuddin & A.C.Campbell, 1995.

Nomenclature and taxonomy

Valid scientific name

Jean Vincent Félix Lamouroux (1809) described the genus *Dictyota* but only much later, *Dictyota dichotoma* (Hudson) Lamouroux was selected as the lectotype of the genus. The name *Dictyota* is derived from the Greek word ‘Διχτυον’ meaning ‘net’ or ‘network’, which refers to the aspect of medulla and cortical cells when observed under a microscope.

Nomenclatural synonyms

Heterotypic synonyms: *Dichophyllum* Kützing 1843;
Dilophus J. Agardh, 1882; *Glossophora* J. Agardh, 1882;

Vernacular names

Although vernacular names do exist, e.g. Divided Net Weed, Brown Fan Weed, Brown Forkweed (Bunker et al. 2010), these are not commonly used. Most authors refer to ‘*Dictyota*’, using the latin name of the taxon.

Taxonomy

Dictyota is one of the 19 genera of the order Dictyotales. Together with the Sphacelariales, Syringodermatales and Onslowiales, the Dictyotales are member of the SSDO-clade, which diverged early from the rest of the Phaeophyceae (Bittner et al. 2008, Phillips et al. 2008). The Dictyotaceae, the only family in the Dictyotales, is subdivided in two tribes, Dictyoteae and Zonarieae. The Dictyoteae are characterised by the presence of a single lens-shaped apical cell and thereby stand out from the Zonarieae which have a row or cluster of apical cells. The definition of the Dictyoteae and its genera has evolved considerably over time.

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In the nineteenth century, the concept of *Dictyota* was gradually narrowed down from a broadly defined genus that initially included all known representatives of the Dictyotales, Cutleriales and the odd red alga, to a very narrowly defined genus differentiated by related genera on the number of medulla and cortex layers. J. Agardh (1882, 1894) was largely responsible for a very narrow concept of *Dictyota*. He segregated *Dilophus*, *Glossophora* and *Pachydictyon* from *Dictyota* restricting the latter to include species with a single-layered medulla and cortex, while *Dilophus* and *Pachydictyon* are characterised by a multilayered medulla or cortex, respectively. Last, *Glossophora* was chiefly characterised by the presence of multiple surface proliferations. Late in the twentieth century *Glossophorella* was described (Nizamuddin and Campbell, 1995) to accommodate a species from the Arabian Sea similarly characterised by surface proliferations but a variable number of cortex and medulla layers. The distinction among these genera has been the subject of considerable debate, as some species are particularly hard to assign to one or another genus (Setchell and Gardner 1925, Taylor 1945, Dawson 1950). Following observations that the number of cell layers can be manipulated in culture in several *Dictyota* or *Dilophus* species, Hörnig et al. (1992a, b) merged *Dilophus* in *Dictyota*, abandoning the narrow genus concept proposed by J. Agardh. Using DNA sequence data, De Clerck et al. (2006) demonstrated that also *Glossophora*, *Glossophorella* and *Pachydictyon* are embedded in *Dictyota*, resulting in synonymisation of these genera with *Dictyota*. The phylogenetic analyses also led to the exclusion of certain species from *Dictyota* and the description of *Canistrocarpus* and *Rugulopteryx*. The latter are distinguished by a combination of characters related to male reproductive structures (e.g. paraphyses, sterile cells surrounding the antheridia) and meiospores (e.g. the number of stalk cells supporting the sporangium). The phylogenetic analyses by De Clerck et al. (2006) were inconclusive regarding the status of *Dilophus*, since the generitype (*Dil. gunnianus*) was missing from the dataset. More recently, however, Küpper et al. (2019) presented a phylogeny of *Dictyota* and related genera that included *Dilophus gunnianus* as well as *Dilophus fastigiatus*. Both species were resolved as a clade separate from *Dictyota* proper. These results argue in favor of a genus *Dilophus*, distinct from *Dictyota* which most likely includes the Australian species characterised by a multilayered medulla and sporangia borne on 2 stalk cells.

Morphology/anatomy

External morphology

Dictyota is a parenchymatous alga, with flat, ribbon-like axes, which grow from well-defined apical meristems that differentiate into an outer cortical layer and an inner

medullary layer. Thalli branch via dichotomous primary branching by longitudinal cell divisions of the apical meristem cells (Gaillard et al., 1986) (Fig. 1a) or by adventitious branching after re-differentiation of cortical cells (Gaillard and L'Hardy-Halos, 1990) or other cortical differentiations such as male paraphyses and dedifferentiated reproductive cells (Hwang et al., 2005). Dichotomous branching may range from isotomous (equal branches) to anisotomous (unequal branches) (Fig. 1b, c), a process that is controlled by light, nutrients and apparently also the base of the thallus (Gaillard and L'Hardy-Halos, 1977, 1979, 1980, 1984). Branches may curve back forming 'recurved' branches (*Canistrocarpus cervicornis* Kützing f. *pseudohamata* (Cribb) De Clerck & Coppejans). Unequal branches may differentiate as falcate branchlets (*Dictyota hamifera* Setchell), which likely serve as additional attachment structures in exposed habitats (De Clerck, 2003) (Fig. 1d). Cervicorn branching results from anisotomous dichotomous branching combined with spirally twisted axes (*Castinocarpus cervicornis* Kützing) (Fig. 1d). The shape of the apical meristems can be truncate, rounded or acute (Fig. 1d). Branching patterns and apical morphologies may show in some species a large degree of morphological plasticity, most notably in *Dictyota dichotoma* (Hudson) Lamouroux (Schnetter and Hörnig 1987; Tronholm et al., 2010). Adventitious branching is typically induced by grazing or loss of the apical meristem activity where they take over the function of the main axis (Tanaka et al. 2016), but may also be a common phenomenon in some species. Cortical cells from the margins may dedifferentiate into meristematic cells and grow small teeth (*Dictyota ciliolata* Sonder ex Kützing) or cortex from the center of the thalli may develop adventitious branches or 'ligulae' (for example *Dictyota kunthii* (C. Agardh) Greville). Apart from the occurrence of above mentioned outgrowths and fertile structures (discussed below), thalli develop tufts of hair 20–50 µm in diameter. Hair formation is under control of ecological factors such as blue light (Müller and Clauss, 1976).

Attachment of the thallus is accomplished by means of multicellular, uniseriate, branching, hyaline rhizoids that may be differentiated terminally into fixing disks that firmly adhere the algae to the substratum (Gaillard et al., 1986). Depending on the species they may have a single point of attachment or have several points of attachment, resulting in a large variety of growth forms ranging from fully erect to creeping thalli firmly attached to the substrate (De Clerck, 2003). A few species attach to the substrate via terete stoloniferous holdfasts (e.g. *D. spiralis*, *D. stolonifera*). Living thalli range from straw colour to dark brown or sometimes greenish, depending on the species (Fig. 2). In situ, many species show a yellowish to deep blue-green iridescence, which is lost upon removal from the water (for example *D. friabilis*, Fig. 2b).

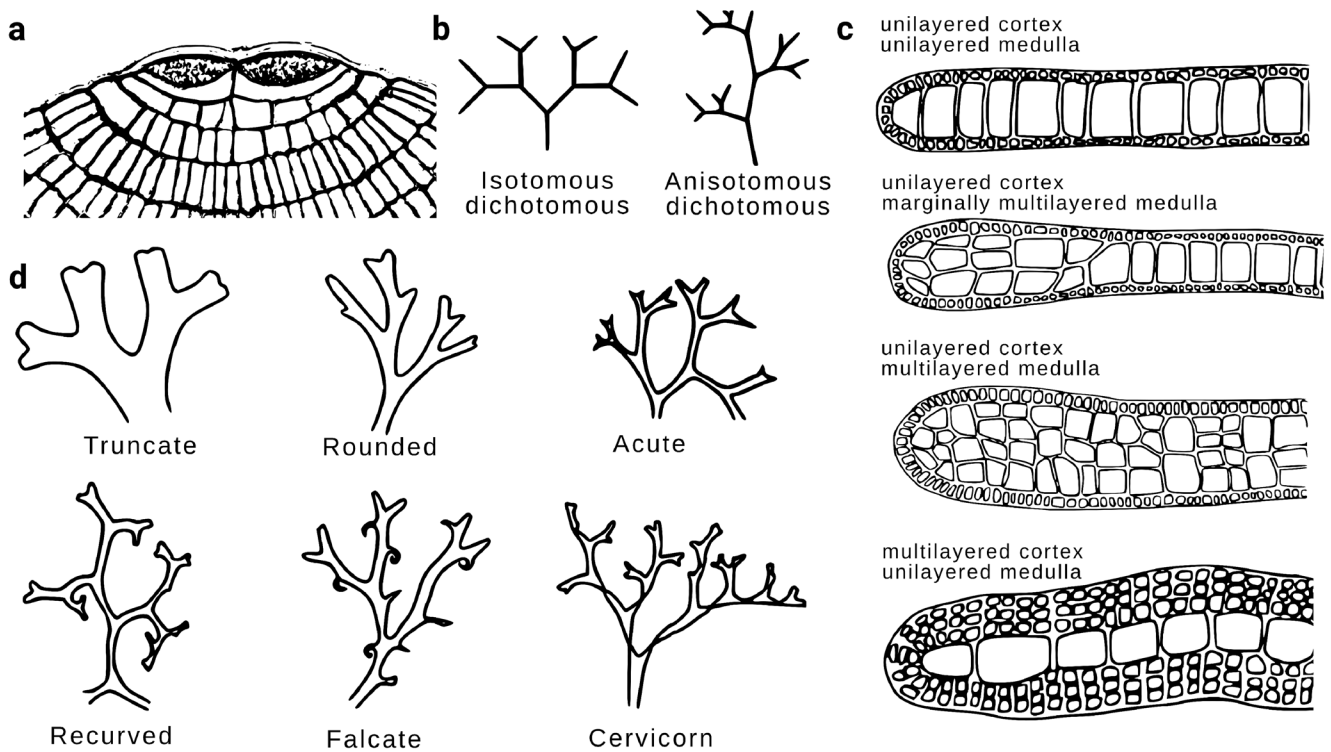


Fig. 1 Morphology and anatomy of *Dictyota*. **a** Apical meristem with a transverse lens-shaped apical cell which has recently divided longitudinally resulting in two lens-shaped apical cells and consequently a dichotomous branching. **b** Isotomous vs anisotomous dichotomous branching. **c**

Cross section of thalli of different species showing variations in cortex and medullary layer. **d** Shape of apical segments (upper) and specialised branching patterns. **b**, **c** and **d** are modified from De Clerck (2003)

Anatomy and cytology

Plants are parenchymatous with apical meristems dividing into a three-dimensional multicellular structure (Gaillard and L’Hardy-Halos, 1984; Katsaros and Galatis, 1985). The apical meristem contains a lens-shaped apical cell dividing transversely with a discoid subapical cell as result (Fig. 1a). This subapical cell will divide twice parallel to the thallus surface, resulting in a primary medullary cell and two surrounding primary cortical cells. While the cortical cell layers undergo

further cell divisions perpendicular to the surface that keep track of cell expansion of the segments, the medullary cell layer divides less frequently and almost exclusively longitudinally. The large medullary cells are hyaline and highly vacuolated with a central nucleus often surrounded by a cluster of lipid vesicles or physodes and sparse chloroplasts. The small cortical cells contain many physodes and chloroplasts without pyrenoids. In both cases, the nuclei are positioned centrally. The size differences of cortical and medullary cells have proven to be a useful taxonomic character (Weber-Peukert, 1985).

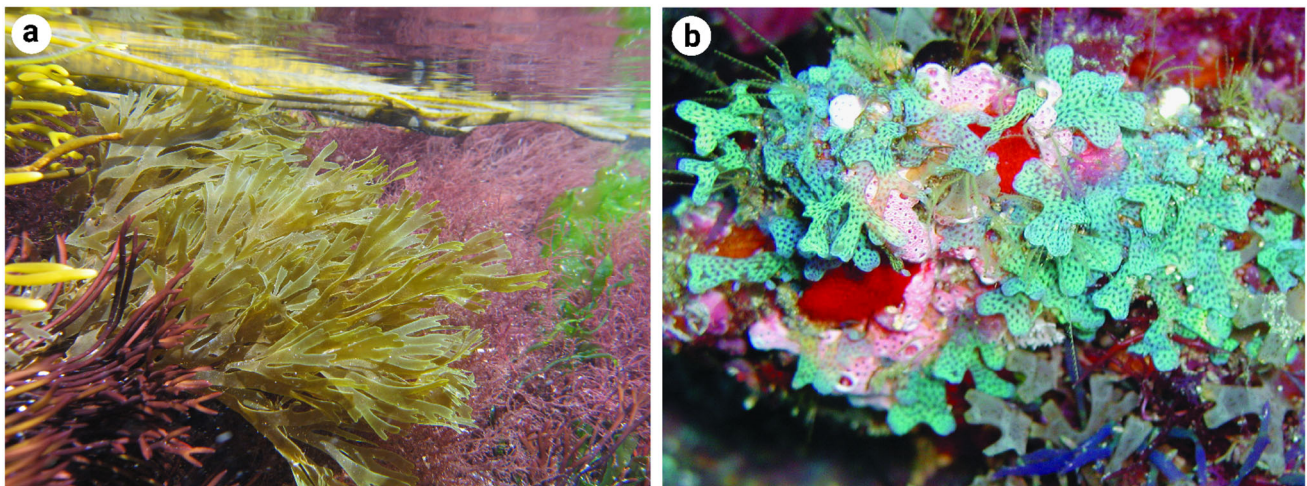


Fig. 2 Illustrations of two *Dictyota* species. **a** *Dictyota dichotoma*. Photo: Heroen Verbruggen (Roscoff, Bretagne, France). **b** *Dictyota friabilis*. Photo: Olivier De Clerck (South Africa)

In some species, the medulla may be multilayered in the entire thallus or only at the base or margins (Fig. 1c). A multilayered cortex is also present in some species. Cell walls are characterised by large pitfields containing many plasmodesmata ensuring symplastic continuity (Terauchi et al., 2012).

Genetic data

Chromosomes and nuclear content

In *Dictyota*, haploid chromosome numbers generally range from 9 to 32 (Lewis, 1996; Hörnig et al., 1992a). Both Cole (1967) and Lewis (1996) indicated the basic chromosome number of the Dictyotales to be 8 or 12, while Hörnig et al. (1992a) suggested a basic chromosome number of 4. In several cases multiple chromosome numbers have been reported for the same species. For example, both haploid chromosome numbers of $n = 16$ (Mottier, 1900; Williams, 1904a, b; Giraud, 1956) and $n = 32$ (Yabu, 1958; Kumagae and Inoh, 1960) have been described for *Dictyota dichotoma*, tempting authors to conclude the occurrence of polyploidy (Lewis, 1996). However, these observations can most likely be attributed to misidentifications, given the current knowledge on the distribution of *D. dichotoma* (Tronholm et al., 2008; Tronholm et al., 2010).

Next to chromosome numbers, several studies have determined the DNA content of algal nuclei by means of DAPI microspectrophotometry. Kapraun (2005) indicated a haploid genome size of 1.1 pg for *Dictyota dichotoma*, while Ribera Siguan et al. (2011) reported nuclear DNA contents ranging from 0.7–0.9 pg for 5 *Dictyota* species, with a nuclear content of 0.9 pg in the narrow growth form of *Dictyota dichotoma* (*var. intricata*). By comparing these values to nuclear DNA contents obtained for other taxa within the Dictyotales, the authors concluded that *Dictyota* species displayed a more narrow range of haploid nuclear genome sizes. This narrower range may represent a synapomorphy, although the authors acknowledge that more species should be examined to make more conclusive statements.

Molecular data

Given the high morphological plasticity of *Dictyota*, molecular techniques are indispensable for species identification. For example, Tronholm et al. (2010) adopted a multigene approach, using up to 6 markers derived from chloroplast, mitochondrial, and nuclear DNA, to resolve the taxonomic positions of members of the genus *Dictyota* in Europe. The most common molecular markers used include *psbA*, *rbcL* and *cox1*.

At the moment no complete *Dictyota* genome is available, although a whole genome sequence of *D. dichotoma* is expected as an outcome of ongoing research initiatives.

Transcriptomic data (Bogaert et al. 2017a) and a complete mitochondrial genome (length 31,617 bp) are available for *D. dichotoma* (Oudot-Le Secq et al., 2006).

Distribution, ecology and metabolism

Distribution

At the genus level, *Dictyota* is characterised by a near cosmopolitan distribution, only lacking representatives in polar seas. *Dictyota* is essentially a tropical to warm-temperate genus, with only a handful of species adapted to colder waters (e.g. *D. decumbens* from Macquarie Island; Ricker 1987 and *D. falklandica* from the Falkland Islands and Tierra del Fuego; Küpper et al. 2019) (Fig. 3). *D. dichotoma* grows up to southern Norway, where it is a summer species and its biomass disappears in winter. Distribution ranges are inadequately characterised for many species still, but from detailed studies in Europe and the Atlantic Ocean, a pattern emerges of species with predominantly regional distributions confined to realms or provinces (sensu Spalding et al. 2007), but some species definitely have large ranges spanning more than one ocean basin (Tronholm et al. 2010, 2012, 2012). At least one species, *D. cyanoloma* has been shown to be introduced, probably from southern Australia to the Mediterranean Sea (Steen et al. 2017).

Ecology

Growing in upper subtidal areas and intertidal rock pools, *Dictyota* species occupy a broad range of ecological niches worldwide (Tronholm et al., 2010). While the genus is distributed widely, abundance data are mainly available for the northern Atlantic region, with particular focus on coral reef communities in the northwest Atlantic and island communities in the northeast Atlantic archipelagos (Table 1). These abundances have repeatedly been shown to vary seasonally and are influenced by a combination of both abiotic and biotic factors (Lirman, 2001; Thacker et al., 2001; Diaz-Pulido and Garzón-Ferreira, 2002; Tronholm et al., 2008; Gauna et al., 2013). *Dictyota* species may reach considerable abundances at their seasonal peak (Table 1) and have been reported to bloom in the Florida Keys (Beach and Walters 2000) and as an invasive in the Strait of Gibraltar (*Rugulopteryx okamurae*, formerly known as *D. okamurae*) where it dominates subtidal vegetations (> 90% coverage) at 10–20-m depth since 2016, causing large supralittoral wrack deposits (García-Gómez et al. 2020).

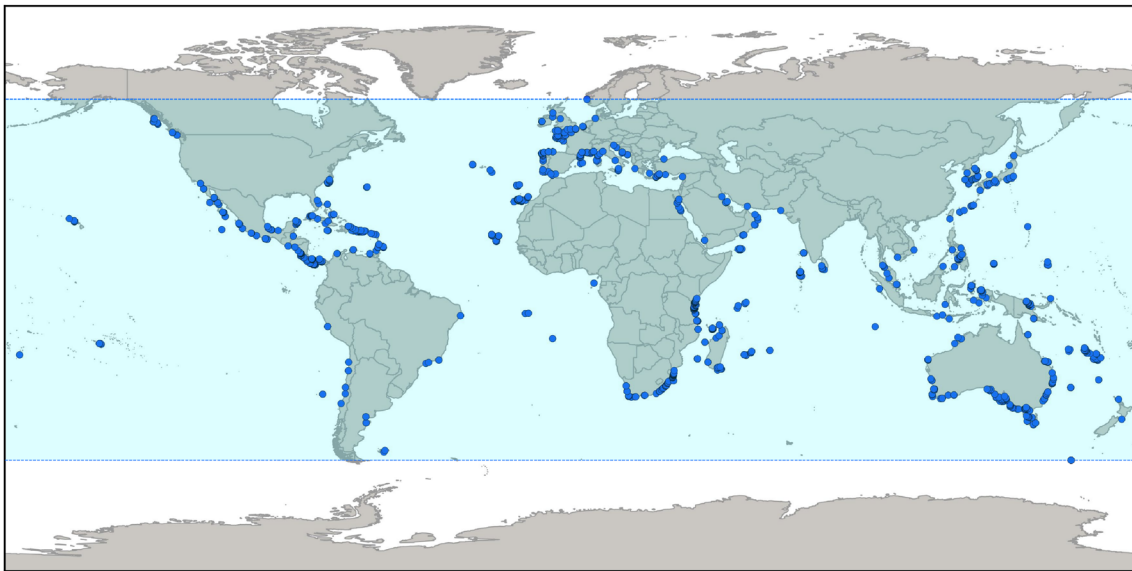


Fig. 3 Distribution map of the genus *Dictyota*. The light blue area denotes the range delimited by the most northerly and southerly reported occurrence (blue dotted lines).

Seasonality

Seasonality in abundance and reproduction has been observed for several *Dictyota* species in temperate regions. In the case of *D. dichotoma*, these seasonal patterns seem to be largely regulated by temperature and therefore vary along the latitudinal range of the species. Specifically, southern populations of this warm temperate species tend to be present throughout most of the year but virtually disappear during the warmest months, surviving this period as microscopic stages (Tronholm et al., 2008; Steen et al., 2019). In contrast, northern populations show high abundance and fertility during summer but are absent in winter, when sea surface temperatures are lowest (Steen et al., 2019). Next to temperature, both daylength and solar radiation have also been shown to play an important role in the seasonality of *Dictyota* species (Ferrari et al., 2012; Gauna et al., 2013). Several studies examined the seasonal dynamics of algal assemblages, including *Dictyota*, indicating the existence of seasonal trends in occurrence, abundance, size, and fertility within the genus *Dictyota* (Diaz-Pulido and Garzón-Ferreira, 2002; Quan-Young et al., 2004; Peña and Bárbara, 2010). Besides phenological characters, the chemical compositions of the biomass is also influenced as seasonal variation in protein and fatty acid content has been reported (see the “Protein and amino acids” and “Biodiesel” sections).

Abiotic interactions

Important environmental factors affecting *Dictyota* species include light, temperature, nutrient availability, pH and water motion (Cronin and Hay 1996; Renken et al., 2010; Dailer et al., 2012; Ho and Carpenter, 2017). Among these, the

effects of nutrient availability and light conditions have received considerable attention and will therefore be discussed here in more detail.

Light Several studies examined the effects of the quality and quantity of irradiance on members of the genus *Dictyota*. Regarding light quality, Kühlenkamp et al. (2001) demonstrated a strong reduction in growth rate when germlings of *D. dichotoma* were exposed to UV radiation (UVR). In accordance with these findings, *Dictyota ciliolata* showed reduced growth and survival, as well as a decrease in the production of secondary metabolites after prolonged exposure to surface levels of UVR (Cronin and Hay 1996). However, Flores-Moya et al. (1999) found that the recovery of photosynthesis after high solar radiation was impaired in the absence of UV-B in *D. dichotoma*, suggesting that this type of radiation may have beneficial effects on photoprotective processes.

Next to these studies, which focus mainly on the effects of UV radiation, extensive efforts have been made in elucidating the response of *Dictyota* species to different irradiance levels. In general, species of the genus *Dictyota* tolerate a wide range of light intensities, being able to maintain high photosynthetic rates even at low irradiances (Dawes and Kovach, 1992; Peckol and Ramus, 1992). This allows them to obtain high abundances in certain deep-water habitats, such as the deep-water seaweed assemblages of Bermuda, where they constitute one of the most dominant groups (Searles and Schneider, 1987). A wide bathymetric distribution has also been observed for temperate species, such as *D. dichotoma*, which may be linked to changes in photosynthetic pigment concentration with depth (Perez-Bermudez et al., 1981). In addition to low-light tolerance, *Dictyota* species possess several mechanisms aimed at protecting the photosynthetic apparatus from

Table 1 Abundance of *Dictyota* species at different locations. Values indicate maximum values, unless stated otherwise. Species names should be treated carefully given the large degree of morphological plasticity displayed by *Dictyota* species. Abbreviations: FW, fresh weight; DW, dry weight

Species	Location	Depth	Abundance	Reference
<i>Dictyota bartayresiana</i>	Cape Verde	5–25 m	0.22% cover ^a	Sangil et al. (2018)
	Chengue Bay, Colombia	9–12 m	30.0% cover	Diaz-Pulido and Garzón-Ferreira (2002)
<i>Dictyota crenulata</i>	Canary Islands	5–25 m	0.01% cover ^a	Sangil et al. (2018)
<i>Dictyota cymatophila</i>	Punta del Hidalgo, Tenerife ^d	Eulittoral zone	32 individuals m ⁻²	Tronholm et al. (2010)
<i>Dictyota dichotoma</i>	Azores	5–25 m	16.95% cover ^a	Sangil et al. (2018)
	Canary Islands	5–25 m	0.39% cover ^a	Sangil et al. (2018)
	Cape Verde	5–25 m	17.09% cover ^a	Sangil et al. (2018)
	Punta del Hidalgo, Tenerife ^d	Sublittoral zone	6.2 individuals m ⁻²	Tronholm et al. (2008)
<i>Dictyota fasciola</i>	Canary Islands	5–25 m	0.006% cover ^a	Sangil et al. (2018)
<i>Dictyota hamifera</i>	Chengue Bay, Colombia	9–12 m	0.4% cover	Diaz-Pulido and Garzón-Ferreira (2002)
<i>Dictyota implexa</i>	Cape Verde	5–25 m	0.33% cover ^a	Sangil et al. (2018)
<i>Dictyota jamaicensis</i>	Cape Verde	5–25 m	0.05% cover ^a	Sangil et al. (2018)
<i>Dictyota linearis</i>	Canary Islands	5–25 m	0.005% cover ^a	Sangil et al. (2018)
<i>Dictyota menstrualis</i>	Cape Verde	5–25 m	0.01% cover ^a	Sangil et al. (2018)
<i>Dictyota paffii</i>	Canary Islands	5–25 m	0.23% cover ^a	Sangil et al. (2018)
	Cape Verde	5–25 m	0.04% cover ^a	Sangil et al. (2018)
	Chengue Bay, Colombia	9–12 m	7.2% cover	Diaz-Pulido and Garzón-Ferreira (2002)
	Chengue Bay, Colombia	9–12 m	3.2% cover	Diaz-Pulido and Garzón-Ferreira (2002)
<i>Dictyota pinnatifida</i>	Canary Islands	5–25 m	0.006% cover ^a	Sangil et al. (2018)
	Chengue Bay, Colombia	9–12 m	0.1% cover	Diaz-Pulido and Garzón-Ferreira (2002)
	Glovers Reef, Belize (exposed)	8 m	32.3% cover	Renken et al. (2010)
	Glovers Reef, Belize (sheltered)	8 m	5.4% cover	Renken et al. (2010)
	<i>Dictyota spp.</i>	Bajo pepito, Mexico	NA	6.1% cover ^a
<i>Dictyota pulchella</i>	Conch Reef, Florida Keys ^b	7 m	29.6 g FW m ⁻² a	Beach et al. (2003)
	Conch Reef, Florida Keys ^b	21 m	30.1 g FW m ⁻² a	Beach et al. (2003)
	Bache Shoals, Florida Keys ^c	3–5 m	12.2 g DW m ⁻²	Lirman and Biber (2000)
	Elkhorn Reef, Florida Keys ^c	3–5 m	8.2 g DW m ⁻²	Lirman and Biber (2000)
	Pacific Reef, Florida Keys ^c	3–5 m	20.4 g DW m ⁻²	Lirman and Biber (2000)
	Triumph Reef, Florida Keys ^c	3–5 m	19.7 g DW m ⁻²	Lirman and Biber (2000)

^a Values indicate mean values^b Species reported as '*Dictyota menstrualis*' and '*Dictyota pulchella*'^c Species reported as '*Dictyota bartayresiana*', '*Dictyota pulchella*' and '*Dictyota cervicornis*' (now *Canistrocarpus cervicornis*)^d Species have been identified based on DNA sequence data

damage induced by excessive irradiance levels, allowing them to withstand strong light exposure. Mostly studied in the species *D. dichotoma*, examples of these mechanisms include dynamic photoinhibition (Nultsch et al., 1987), the reversible conversion of violaxanthin to antheraxanthin and eventually zeaxanthin in the xanthophyll cycle (Uhrmacher et al., 1995), and chromatophore displacement (Hanelt and Nultsch, 1991).

Nutrients The effects of nutrients on *Dictyota* species have mainly been studied in tropical ecosystems, where they were

predominantly evaluated in the context of community studies. In general, species of *Dictyota* are considered opportunistic macroalgae, owing to their ability to rapidly take up nutrients upon supply (i.e. surge uptake) (Aisha et al., 1995; Raikar and Wafar, 2006; Clausing and Fong, 2016, den Haan et al., 2016). Extra nutrients, in turn, may provide several fitness-enhancing effects, such as increases in growth rate, photosynthetic capacity and saturation irradiance (Dailer et al., 2012). Moreover, the capability for rapid uptake after episodic nutrient inputs can be largely maintained in the dark, which may

represent an ecological advantage in nutrient-poor waters (Raikar and Wafar, 2006). However, the effects of nutrient enrichment have been shown to interact with other variables including herbivory (Sotka and Hay, 2009), environmental context (Clausing and Fong, 2016), and dissolved inorganic carbon (DIC) concentration (Martins et al., 2016), emphasising the need to consider multiple factors in order to draw realistic inferences.

Biotic interactions

Owing to their significant abundance in various intertidal and shallow subtidal habitats (Table 1), *Dictyota* species constitute a food source for a wide range of marine organisms, including sea turtles, sea urchins, amphipods and certain fish species (Azzurro et al., 2007; Carrión-Cortez et al. 2010; McCarty and Sotka, 2013; Moreno-Sánchez et al. 2014; Cabanillas-Terán et al. 2016). In the specific case of the amphipod *Ampithoe longimana*, several studies indicated local adaptation of feeding preferences, with populations that are naturally coexisting with *Dictyota* showing higher feeding preference for and greater fitness when feeding on *Dictyota*, compared to populations that are not (Sotka and Hay, 2002; Sotka et al., 2003; McCarty and Sotka, 2013). These differences in fitness are shown to be heritable and persist even after rearing multiple generations in the laboratory (Sotka and Hay, 2002; Sotka et al., 2003). Overall, these findings indicate that *Dictyota* may play an important role in the genetic differentiation of its associated marine herbivores.

Next to its role as a food source, *Dictyota* provides substrate and shelter to numerous marine organisms. A study conducted in the Abrolhos Bank, Brazil, identified 9 higher taxa of marine invertebrates associated with the genus *Dictyota*, with further analyses of the most abundant taxa resulting in 64 families and 120 species (Cunha et al., 2013). The most abundant families belonged to the polychaetes, isopods, gastropods, and amphipods. For certain amphipod species, including *A. longimana*, *Dictyota*'s value as a protective refuge also plays a role in its prevalence as a food source, indicating these interactions to be driven by a combination of the need for qualitative food and effective shelter (Duffy and Hay 1991; Lasley-Rasher et al., 2011). Next to its association with macrofaunal communities, *Dictyota* species have been shown to harbour a wide diversity of dinoflagellate species as well as diatoms (Irola-Sansores et al., 2018; Park et al., 2018; Boisnoir et al., 2019). Finally, they can also play a role as shelter for larger species. For example, decorator crabs selectively use *Dictyota menstrualis* as camouflage on their backs in order to reduce their susceptibility to predation, while juvenile parrotfishes have been shown to use *Dictyota* patches as an effective recruitment microhabitat when there is a lack of coral cover (Stachowicz and Hay, 1999; Paddock and Sponaugle, 2008).

While beneficial interactions between *Dictyota* species and their associated biota are plentiful, this genus is also known to exert negative effects on various marine organisms. One of the most studied examples of such effects includes the competitive interactions between *Dictyota* and corals. Over the past decades, numerous reefs in the Atlantic and Pacific have undergone a marked phase-shift from coral-dominated communities to communities dominated by macroalgae (Done, 1992; Hughes, 1994; Edmunds, 2002). Especially in the Caribbean region, Florida and Fiji, the genus *Dictyota* constitutes an important component of the reef flora (Shulman and Robertson, 1996; Lapointe et al. 1997; Lirman and Biber, 2000; Ferrari et al., 2012; Bonaldo and Hay, 2014). *Dictyota* species have repeatedly been shown to reduce survival and recruitment of coral larvae, and to cause bleaching, reduced photosynthetic efficiency, and death when in direct contact with adult coral tissue (Kuffner et al., 2006; Rasher and Hay, 2010; Paul et al., 2011; Shearer et al., 2012; Olsen et al., 2015). These effects can, at least partly, be linked to the production of allelopathic secondary metabolites that are deployed at the seaweed surface (Longo and Hay, 2017). In addition, algae of the genus *Dictyota* have been linked to changes in coral-associated bacterial communities, expanding their impact to the holobiont level (Barott et al., 2012; Morrow et al. 2011).

Life history

Life cycle

The life cycle of *Dictyota* was one of the first cases where the alternation of generations was demonstrated to be accompanied by a change in ploidy (Svedelius, 1927; Haig, 1984). This discovery supported the theory of Strasburger (1894) which linked alternation of generations with ploidy change. *Dictyota* is characterised by an isomorphic life cycle (Fig. 4a), in which the gametophyte phase and the sporophyte phase are morphologically similar (Williams, 1897, 1904a, 1904b; Hoyt, 1910). This morphological similarity is also reflected in nutritional quality and chemical defense against predators in both sporophytes and gametophytes (Cronin and Hay 2009). Gametophytes produce motile gametes that, upon fertilisation, produce a diploid sporophyte that will bear sporangia undergoing a reduction division with each sporangium producing a tetrad of 4 haploid spores (Williams, 1904a; Hoyt, 1910) (Fig. 4b). Spores grow into both male and female gametophytes in about equal amounts (Hoyt, 1910).

The life cycle is relatively simple. Unlike *Fucus*—which shows both dioecious and monoecious species—all studied species of *Dictyota* are dioecious (Phillips et al., 1990; Phillips, 1992; De Clerck, 2003). While for example the life

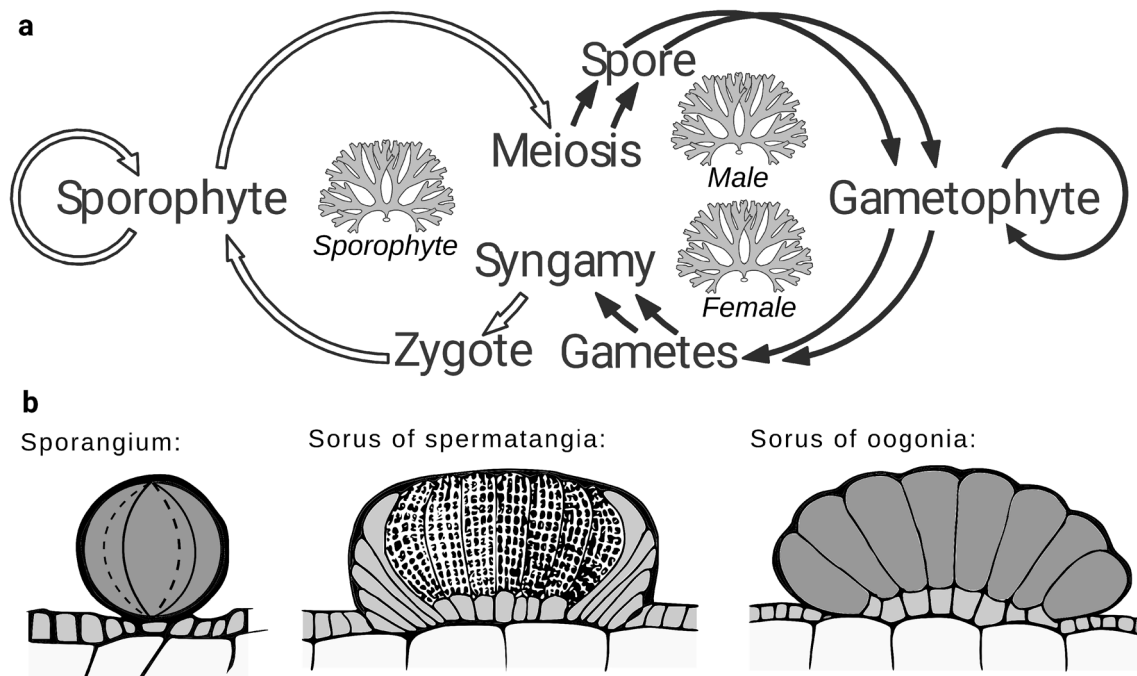


Fig. 4 Life cycle and reproduction in *Dictyota*. **a** Life cycle of *Dictyota*. Bold black arrows denote haploid stages, white arrows denote diploid stage. Both sporophytes and gametophytes may reproduce asexually (see text for details). Modified from Bogaert et al. (2013). **b** Schematic

drawing of cross section of sexual reproductive organs of sporophyte (left), male gametophyte (middle) and female gametophyte (right). Modified from De Clerck (2003)

cycle of *Ectocarpus*—a model system for life cycle research in brown algae—shows a very complex life cycle and possible deviations from the classic alternations of ploidy (Müller, 1972; Bothwell et al., 2010), no deviations from this alternation of haploid gametophytes to diploid sporophytes have been described for *Dictyota*. Unfertilised eggs invariably die after 2–3 (aberrant) cell divisions (Williams, 1904b).

Reproduction

Reproduction in *Dictyota* has been relatively well-studied compared to other seaweed genera. Male gametophytes develop antheridia that are organised in ellipse or puzzle-shaped white sori (Williams, 1904b; Phillips et al., 1990; Phillips, 1992; Phillips and Clayton, 1993). The antheridia are surrounded by sterile elongated cells, ‘paraphyses’, which persist after release of the gametes. Paraphyses are unicellular, contrary to *Canistrocarpus* where paraphyses are multicellular. Gametogenesis is constant for all species and occurs by the swelling of a group of cortical cells which undergo a mitotic cell division parallel to the surface to form an antheridial stalk cell and an antheridial initial. The antheridial initial divides frequently to produce 16–26 tiers consisting each of 16 loculi, containing a single spermatozoid each. Atypical for heterokont algae, *Dictyota* spermatozooids bear only the anterior flagellum, the posterior flagellum has been completely reduced.

Female gametophytes develop oogonia that are similarly organised in ellipsoid sori, except for a single species (*D. robusta*) where the oogonia are not organised in groups. Like the male sori, they develop after outward expansion of the cortex, followed by a cell division parallel to the surface, producing a stalk cell and an oogonium (Williams, 1904b; Foster et al., 1972). Central oogonia are generally larger than the peripheral ones. Each oogonium only produces a single egg cell.

Spores are formed by diploid sporophytes in unilocular sporangia. A cortical cell expands outwardly after which a mitotic division form the tetraspore mother cell and a stalk cell (Williams, 1904a; Phillips, 1992). The tetraspore mother cell finally undergoes a meiotic cell division shortly prior to release resulting in four cruciately arranged meiospores. In most species, sporangia can be easily discerned from oogonia by their scattered arrangement throughout the thallus, but some species possess sporangia that are organised in sori as well, potentially confounding discrimination of female gametophytes and sporophytes (Foster et al., 1972). Gametangia and sporangia may differentiate all over the thallus with a minimal distance of a couple of centimeters from actively growing meristems.

Gametes are released with both a diurnal and lunar periodicity (Williams, 1905). Gametes are typically released about 20–30 min in the early morning after first light (Kumke, 1973; Phillips et al., 1990). The male gametes show chemotaxis and are attracted by the release of the oxylipin n-butyl-cyclohepta-

2,5-diene (dictyotene) (Muller et al., 1981; Phillips et al., 1990). In the presence of male gametes, oogonia become fertilised after which they elongate in about 90 s (Bogaert et al., 2017a). The elongation results into a ‘rugby’ ball-shaped cell with two poles of which one eventually will develop into the rhizoid tip and the other into the apical cell (Bogaert et al., 2017a). The shape change is accompanied by the immediate production of an adhesive layer in which a dense halo of male superfluous gametes may be embedded (Bogaert et al., 2017b). After attachment to the substrate, the cell will undergo an asymmetric cell division with a thallus and a rhizoid cell as a result (Bogaert et al., 2017a). Similar to *Fucus* zygotes, *Dictyota* uses the light direction to determine which one of the poles will develop into the rhizoid side, a process which involves the phytohormone auxin (Bogaert et al., 2019).

Besides a diurnal periodicity, gametophytes of *Dictyota* are the best studied brown algae with a clear lunar periodicity (Tessmar-Raible et al., 2011). *D. dichotoma* releases its gametes with two peaks a month (bilunar) (Williams, 1905; Hoyt, 1907, 1927; Müller, 1962). Under controlled conditions, the periodicity can be induced and controlled by illuminating the algae during one night every 28 days, mimicking the full moon (Müller, 1962). The release periodicity of most other reported species is lunar instead of bilunar: *D. menstrualis*, *D. diemensis* and *D. gunniana* gametes are released only once a month (Hoyt, 1927; Phillips et al., 1990; Phillips, 1992), while species like *D. fastigiata* Sonder or *D. binghamiae* apparently do not show a lunar periodicity (Foster et al., 1972; Phillips, 1992).

Apart from sexual reproduction, *Dictyota* is able to propagate asexually (Fig. 4a). This mode of reproduction may contribute to the large biomasses often observed in warmer regions (Herren et al., 2006). Many adventitious branches or ligulae in species such as *D. kunthii* are likely adaptations for vegetative propagation. In *Dictyota*, the loss of the apical meristem, typically induces a fast proliferation of new adventitious branching (Tanaka et al., 2016). Adventitious branches have a tendency to break off easily, which may explain how *Dictyota* can withstand high predation pressures. Similarly, in a Korean *Dictyota* species, some populations tend to propagate by the formation of *in situ* germlings. These germlings form by the apomictic development of the spore mother cell into a multicellular propagule (Hwang et al., 2005).

Chemical composition

The water content of *Dictyota* species fluctuates around 86.4–99.0% (McDermid and Stuercke, 2003; Taylor et al., 2003; McDermid et al., 2007; Tabarsa et al., 2012) (Table 2). It is not known whether the chemical content is species-specific

because considerable variation has been observed between samples from the same species taken at different localities and during different seasons (Taylor et al., 2003; Gosch et al., 2015).

Inorganic elements

Like most seaweeds, *Dictyota* is rich in minerals and has an ash content of around 17.2–30.1% of dry weight (DW) (Table 2). Species may therefore be useful as mineral supplements. *Dictyota* species appear significantly enriched in iron compared to other screened species from the same locality with concentrations higher than 29,774 $\mu\text{g g}^{-1}$ DW (Tabarsa et al., 2012; Billah et al., 2017), but values 2 to 3 orders of magnitude lower have also been reported (McDermid and Stuercke, 2003; Deyab et al., 2017). Varying amounts of heavy metals have been observed in *Dictyota* (Table 2). Especially copper and chromium might be relevant (Chakraborty et al., 2014). While *Dictyota* was reported to be enriched in iodine (EL-Naggar, 2009), relatively moderate quantities are reported in other studies (Grimm, 1952; Solimabi and Das 1977).

Carbohydrates

The reported total carbohydrate fraction varies between 10.8 and 54.2% of DW (Table 2). Total soluble carbohydrates (fucans, laminarans and monosaccharides) are reported to range from 5.9 to 26.7% in the field (McDermid and Stuercke, 2003; Martins et al., 2018). These can be artificially increased to ~50% of DW by addition of nitrogen and CO₂ in a bioreactor setup in *D. menstrualis* (Martins et al., 2016). The crude fraction of fibers ranges between 10.2 and 14.1% of DW (Tabarsa et al., 2012; Mwalugha et al., 2015). The cellulose microfibrils in the cell wall of brown algae are embedded in a matrix of polysaccharides comprising alginates and fucans (Abdel-Fattah et al., 1978), which are estimated to comprise respectively 7.4–22.9% and 22.2% of DW (García-Ríos et al., 2012; Deyab et al., 2017). Storage polysaccharides are laminarans and mannitol (0.4–7.8% of DW) (Table 2). The fucoidan fractions have been particularly well-studied due to their antiviral, ROS scavenging and anti-coagulant properties (García-Ríos et al., 2012; Rabanal et al., 2014). Despite the lower content in fucans and alginates compared to, for example, Fucales, polysaccharides of Dictyotales are of particular interest due to the presence of some O-acetyl groups (García-Ríos et al., 2012). More than 60 subfractions of sulfated heteropolysaccharides can be obtained, all differing in their relative proportions of residues of D-arabinose, D-fucose, D-galactose, D-glucose, D-mannose, D-rhamnose, D-uronic acid and xylose (Hussein et al., 1979; Rabanal et al., 2014).

Table 2 Chemical composition in different species of *Dictyota*. Abbreviations: DW, dry weight; EAAs, essential amino acids; MUFAs, monounsaturated fatty acids; nonEAAs, non-essential amino acids; PUFAs, polyunsaturated fatty acids; SFAs, saturated fatty acids; TFAs, total fatty acids

	Unit	Min	Max	Species	References
Water	% of fresh weight	86.4	90.0	<i>D. dichotoma</i> , <i>Dictyota</i> sp., <i>D. acutiloba</i> , <i>D. sandvicensis</i>	(Munda and Gubensek, 1986; McDermid and Stuercke, 2003; Tabarsa et al., 2012)
Ash	% of DW	17.2	30.1	<i>Dictyota</i> sp., <i>D. bartayresiana</i> , <i>D. acutiloba</i> , <i>D. sandvicensis</i>	(Burkholder et al., 1971; Montgomery and Gerking, 1980; Munda and Gubensek, 1986; McDermid and Stuercke, 2003; Pillans et al., 2004; Tabarsa et al., 2012; Machado et al., 2014)
Carbohydrates	% of DW	10.8	54.2	<i>Dictyota</i> sp., <i>D. ceylanica</i>	(Montgomery and Gerking, 1980; Chakraborty et al., 2008; Deyab et al., 2017)
Soluble carbohydrates	% of DW	5.9	26.7	<i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>D. menstrualis</i>	(McDermid and Stuercke, 2003; Martins et al., 2018)
Crude fiber	% of DW	10.2	14.1	<i>Dictyota</i> sp., <i>D. bartayresiana</i> , <i>C. cervicornis</i>	(Burkholder et al., 1971; Tabarsa et al., 2012; Mwalugha et al., 2015)
Fucoidan	% of DW	22.2	22.2	<i>D. caribaea</i>	(García-Ríos et al., 2012)
Alginates	% of DW	7.4	22.9	<i>D. caribaea</i> , <i>Dictyota</i> sp.	(García-Ríos et al., 2012; Deyab et al., 2017)
Mannitol	% of DW	0.4	7.8	<i>D. caribaea</i> , <i>D. dichotoma</i>	(Munda and Gubensek, 1986; García-Ríos et al., 2012)
Energy	cal/g	2424	3500	<i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Montgomery and Gerking, 1980; McDermid and Stuercke, 2003; Pillans et al., 2004)
Total N	% of DW	1.0	4.4	<i>Dictyota</i> sp., <i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>D. dichotoma</i> , <i>D. bartayresiana</i>	(Nasr et al., 1968; Munda and Gubensek, 1986; McDermid and Stuercke, 2003; Pillans et al., 2004; Machado et al., 2014; Deyab et al., 2017)
Total protein %	% of DW	1.7	27.6	<i>Dictyota</i> sp., <i>D. bartayresiana</i> , <i>D. ceylanica</i> , <i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>D. dichotoma</i> , <i>D. menstrualis</i> , <i>D. ceylanica</i>	(Nasr et al., 1968; Burkholder et al., 1971; Montgomery and Gerking, 1980; Munda and Gubensek, 1986; McDermid and Stuercke, 2003; Chakraborty et al., 2008; Tabarsa et al., 2012; Mwalugha et al., 2015; Deyab et al., 2017; Martins et al., 2018)
Total/crude lipid %	% of DW	0.5	20.2	<i>D. bartayresiana</i> , <i>Dictyota</i> sp., <i>D. ceylanica</i> , <i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>D. menstrualis</i>	(Montgomery and Gerking, 1980; McDermid and Stuercke, 2003; Chakraborty and Santra, 2008; Gosch et al., 2012; Tabarsa et al., 2012; Mwalugha et al., 2015; Deyab et al., 2017; Martins et al., 2018)
TFAs	mg g ⁻¹ DW	14.0	54.2	<i>Dictyota</i> sp., <i>D. bartayresiana</i> , <i>D. menstrualis</i>	(Gosch et al., 2012; Gosch et al., 2015; Martins et al., 2018)
Phenolics	% of DW	0.01	1.34	<i>D. dichotoma</i> , <i>Dictyota</i> sp., <i>D. divaricata</i> , <i>D. bartayresiana</i>	(Targett et al., 1992; Targett et al., 1995; Chkhikvishvili and Ramazanov, 2000)
Elements					
C	µg g ⁻¹ DW	297,000	332,800	<i>D. bartayresiana</i> , <i>D. dichotoma</i>	(Pillans et al., 2004; Machado et al., 2014)
N	µg g ⁻¹ DW	9800	28,700	<i>D. bartayresiana</i> , <i>D. dichotoma</i> , <i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>Dictyota</i> sp.	(McDermid and Stuercke, 2003; Pillans et al., 2004; Machado et al., 2014; Deyab et al., 2017)
Na	µg g ⁻¹ DW	5300	23,598	<i>Dictyota</i> sp., <i>D. bartayresiana</i>	(Tabarsa et al., 2012; Machado et al., 2014; Deyab et al., 2017)
P	µg g ⁻¹ DW	1300	1953	<i>Dictyota</i> sp., <i>D. bartayresiana</i>	(McDermid and Stuercke, 2003; Deyab et al., 2017)
K	µg g ⁻¹ DW	27,000	72,600	<i>D. bartayresiana</i> , <i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>Dictyota</i> sp.	(McDermid and Stuercke, 2003; Tabarsa et al., 2012; Machado et al., 2014; Deyab et al., 2017)
Mg	µg g ⁻¹ DW	51	13,600	<i>D. bartayresiana</i> , <i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>Dictyota</i> sp.	(McDermid and Stuercke, 2003; Deyab et al., 2017)
Ca	µg g ⁻¹ DW	10,300	35,200	<i>D. bartayresiana</i> , <i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>Dictyota</i> sp.	(McDermid and Stuercke, 2003; Tabarsa et al., 2012; Machado et al., 2014; Deyab et al., 2017)

Table 2 (continued)

	Unit	Min	Max	Species	References
S	μg g ⁻¹ DW	12,000	22,100	<i>D. bartayresiana</i> , <i>D. acutiloba</i> , <i>D. sandvicensis</i>	(McDermid and Stuercke, 2003; Machado et al., 2014)
B	μg g ⁻¹ DW	95	172	<i>D. bartayresiana</i> , <i>D. acutiloba</i> , <i>D. sandvicensis</i>	(McDermid and Stuercke, 2003; Machado et al., 2014)
Zn	μg g ⁻¹ DW	5	407	<i>D. dichotoma</i> , <i>D. bartayresiana</i> , <i>Dictyota</i> sp., <i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>D. ceylanica</i>	(McDermid and Stuercke, 2003; Chakraborty and Santra, 2008; Laib and Leghouchi, 2012; Billah et al., 2017)
Mn	μg g ⁻¹ DW	6	2480	<i>D. dichotoma</i> , <i>D. bartayresiana</i> , <i>Dictyota</i> sp., <i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>D. ceylanica</i>	(McDermid and Stuercke, 2003; Chakraborty and Santra, 2008; Tabarsa et al., 2012; Billah et al., 2017; Deyab et al., 2017)
Fe	μg g ⁻¹ DW	19	29,774	<i>D. dichotoma</i> , <i>D. bartayresiana</i> , <i>Dictyota</i> sp., <i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>D. ceylanica</i>	(McDermid and Stuercke, 2003; Chakraborty and Santra, 2008; Tabarsa et al., 2012; Billah et al., 2017; Deyab et al., 2017)
Cu	μg g ⁻¹ DW	3	153	<i>Dictyota</i> sp., <i>D. bartayresiana</i> , <i>D. acutiloba</i> , <i>D. sandvicensis</i> , <i>D. ceylanica</i>	(McDermid and Stuercke, 2003; Chakraborty and Santra, 2008; Laib and Leghouchi, 2012; Tabarsa et al., 2012; Billah et al., 2017; Deyab et al., 2017)
Ni	μg g ⁻¹ DW	0.6	23.6	<i>D. bartayresiana</i> , <i>Dictyota</i> sp., <i>D. ceylanica</i>	(Chakraborty and Santra, 2008; Tabarsa et al., 2012; Deyab et al., 2017)
Co	μg g ⁻¹ DW	4.5	8.1	<i>Dictyota</i> sp.	(Tabarsa et al., 2012; Deyab et al., 2017)
Pb	μg g ⁻¹ DW	0.9	1.5	<i>D. bartayresiana</i> , <i>D. dichotoma</i> , <i>D. ceylanica</i>	(Chakraborty and Santra, 2008; Laib and Leghouchi, 2012)
I	μg g ⁻¹ DW	544	2030	<i>D. divaricata</i> , <i>D. bartayresiana</i>	(Solimabi and Das 1977; EL-Naggar, 2009)
Sr	μg g ⁻¹ DW	1.2	1.2	<i>D. bartayresiana</i>	(Machado et al., 2014)
Cr	μg g ⁻¹ DW	0.8	6.2	<i>D. bartayresiana</i> , <i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Chakraborty and Santra, 2008; Laib and Leghouchi, 2012; Deyab et al., 2017)
Cd	μg g ⁻¹ DW	0.1	2.2	<i>D. bartayresiana</i> , <i>D. dichotoma</i>	(Chakraborty and Santra, 2008; Laib and Leghouchi, 2012)
Amino acids					
Nonessential amino acids					
Asp	mg g ⁻¹ DW	10.3	13.4	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Glu	mg g ⁻¹ DW	15.0	22.7	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Ser	mg g ⁻¹ DW	4.6	6.4	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Gly	mg g ⁻¹ DW	6.0	7.6	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Arg	mg g ⁻¹ DW	5.6	7.0	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Ala	mg g ⁻¹ DW	3.2	8.9	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Pro	mg g ⁻¹ DW	3.0	5.8	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Tyr	mg g ⁻¹ DW	4.0	4.0	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Cys	mg g ⁻¹ DW	0.4	0.4	<i>D. dichotoma</i>	(Munda and Gubensek, 1986)
Essential amino acids					
His	mg g ⁻¹ DW	1.9	5.9	<i>Dictyota dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Thr	mg g ⁻¹ DW	4.9	6.3	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Val	mg g ⁻¹ DW	5.8	6.9	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Met	mg g ⁻¹ DW	0.7	3.4	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Ile	mg g ⁻¹ DW	4.3	5.7	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Leu	mg g ⁻¹ DW	8.5	10.3	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Phe	mg g ⁻¹ DW	4.9	6.2	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)
Lys	mg g ⁻¹ DW	5.9	6.2	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Munda and Gubensek, 1986; Tabarsa et al., 2012)

Table 2 (continued)

	Unit	Min	Max	Species	References
Fatty acids (composition)					
SFAs	% of total fatty acids methyl esters	26.0	56.9	<i>Dictyota</i> sp., <i>D. ceylanica</i> , <i>D. pinnatifida</i> , <i>D. bartayresiana</i> , <i>D. dichotoma</i> , <i>C. cervicornis</i> , <i>D. ciliolata</i> , <i>D. haukiana</i>	(Chakraborty and Santra, 2008; Tabarsa et al., 2012; Kumari et al., 2013)
MUFAs	% of total fatty acids methyl esters	11.3	22.2	<i>Dictyota</i> sp., <i>Dictyota ceylanica</i> , <i>D. pinnatifida</i> , <i>D. bartayresiana</i> , <i>D. dichotoma</i> , <i>C. cervicornis</i> , <i>D. ciliolata</i> , <i>D. haukiana</i>	(Chakraborty and Santra, 2008; Tabarsa et al., 2012; Kumari et al., 2013)
PUFAs	% of total fatty acids methyl esters	18.3	58.0	<i>Dictyota</i> sp., <i>D. ceylanica</i> , <i>D. pinnatifida</i> , <i>D. bartayresiana</i> , <i>D. dichotoma</i> , <i>C. cervicornis</i> , <i>D. ciliolata</i> , <i>D. haukiana</i>	(Chakraborty and Santra, 2008; Tabarsa et al., 2012; Kumari et al., 2013)
PUFAs ω 6	% of total fatty acids methyl esters	7.5	7.5	<i>Dictyota</i> sp.	(Tabarsa et al., 2012)
PUFAs ω 3	% of total fatty acids methyl esters	10.7	10.7	<i>Dictyota</i> sp.	(Tabarsa et al., 2012)
Fatty acids (dry weight basis)					
SFAs	mg g ⁻¹ DW	5.3	35.2	<i>D. bartayresiana</i> , <i>Dictyota</i> sp., <i>D. menstrualis</i>	(Gosch et al., 2012; Gosch et al., 2015; Martins et al., 2018)
MUFAs	mg g ⁻¹ DW	4.5	30.8	<i>D. bartayresiana</i> , <i>Dictyota</i> sp., <i>D. menstrualis</i>	(Gosch et al., 2012; Gosch et al., 2015; Martins et al., 2018)
PUFAs	mg g ⁻¹ DW	4.3	39.1	<i>D. bartayresiana</i> , <i>Dictyota</i> sp., <i>D. menstrualis</i>	(Gosch et al., 2012; Gosch et al., 2015; Martins et al., 2018)
PUFAs ω 6	mg g ⁻¹ DW	1.9	16.7	<i>D. bartayresiana</i> , <i>Dictyota</i> sp., <i>D. menstrualis</i>	(Gosch et al., 2012; Gosch et al., 2015; Martins et al., 2018)
PUFAs ω 3	mg g ⁻¹ DW	1.0	22.9	<i>D. bartayresiana</i> , <i>Dictyota</i> sp., <i>D. menstrualis</i>	(Gosch et al., 2012; Gosch et al., 2015; Martins et al., 2018)
ω 6/ ω 3		0.3	3.9	<i>Dictyota</i> sp., <i>D. ceylanica</i> , <i>D. pinnatifida</i> , <i>D. bartayresiana</i> , <i>D. dichotoma</i> , <i>C. cervicornis</i> , <i>D. ciliolata</i> , <i>D. haukiana</i> , <i>D. menstrualis</i>	(Chakraborty and Santra, 2008; Gosch et al., 2012; Tabarsa et al., 2012; Kumari et al., 2013; Gosch et al., 2015; Martins et al., 2018)
Vitamins					
Vit E	μ g g ⁻¹ FW	24.5	42.8	<i>Dictyota</i> sp.	(Jayasree et al. 1985; de Sousa et al. 2008)
β -Carotene	μ g g ⁻¹ FW	4.7	4.7	<i>Dictyota</i> sp.	(de Sousa et al. 2008)
Vit A	μ g g ⁻¹ FW	0.8	0.8	<i>Dictyota</i> sp.	(de Sousa et al. 2008)
Pigments					
Chlorophyll <i>a</i>	mg g ⁻¹ DW	1.9	6.1	<i>Dictyota</i> sp., <i>D. dichotoma</i> , <i>D. ceylanica</i> , <i>D. menstrualis</i>	(Perez-Bermudez et al., 1981; Chakraborty and Santra, 2008; Deyab et al., 2017; Martins et al., 2018)
Chlorophyll <i>c</i>	mg g ⁻¹ DW	0.6	2.0	<i>Dictyota</i> sp., <i>D. dichotoma</i> , <i>D. ceylanica</i>	(Perez-Bermudez et al., 1981; Chakraborty and Santra, 2008; Deyab et al., 2017)
Carotenoids	mg g ⁻¹ DW	0.03	0.03	<i>D. ceylanica</i>	(Chakraborty and Santra, 2008)
Fucoxanthin	mg g ⁻¹ DW	0.1	2.3	<i>D. dichotoma</i> , <i>Dictyota</i> sp.	(Perez-Bermudez et al., 1981; Deyab et al., 2017)

Protein and amino acids

As a fast-growing alga, especially in warm temperate to tropical environments, *Dictyota* may be of interest as a food, feed or protein source. Protein levels are highly variable, with estimates varying between 1.7 and 27.6% of DW depending on the local conditions, seasonality and nitrogen availability. It should be noted that many of the protein estimates are obtained using a traditional nitrogen-to-protein factor of 6.25, which is unsuitable for seaweeds and has been estimated as 4.55 ± 0.38 for *D. menstrualis* and 18 other tropical seaweeds by Lourenço et al. (2002) while Angell et al. (2016) have suggested a mean value of 5. In a bioreactor setup, the protein content can be increased by addition of nitrogen irrespective of CO₂ addition (Martins et al., 2016).

Lipid and fatty acids

Estimates of total lipid content varies from 0.5 to 20.2% of DW (McDermid and Stuercke, 2003; Deyab et al., 2017). In multispecies comparisons, *Dictyota* is often among the brown algae displaying the highest fatty acids fractions (Burkholder et al., 1971; Montgomery and Gerking, 1980; McDermid and Stuercke, 2003; Gosch et al., 2012; Machado et al., 2014; Martins et al., 2018) and rendering a relatively high caloric content ranging from 2424 to 3500 cal g⁻¹ (Montgomery and Gerking, 1980; McDermid and Stuercke, 2003; Pillans et al., 2004). Consequently, species of *Dictyota* are seen as a suitable feedstock species because the total fatty acid content is reported to exceed that of any other seaweed (Gosch et al., 2015). Furthermore, *Dictyota* contains large amounts of ω 3 fatty acids with a low ω 6/ ω 3 ratio ranging from 0.3 to 3.9 on a DW basis (Table 2). *Dictyota* is therefore appealing for its use in bio-oil industry and as a healthy food source (Tabarsa et al., 2012; Martins et al., 2016, 2018). Lipid content (Gosch et al., 2012; Radulovich et al., 2015; Deyab et al., 2017) and total fatty acids content (Gosch et al., 2012) can be highly variable in *Dictyota* and can be modulated depending on nitrogen and CO₂ contents (Martins et al., 2016). Fatty acids spectra have been characterised for different *Dictyota* species (Heiba et al., 1997; Chakraborty and Santra, 2008; Gosch et al., 2012, 2015; Tabarsa et al., 2012; Martins et al., 2016, 2018) and may show a high content in PUFAs in especially *D. bartayresiana* (Gosch et al., 2012, 2015; Machado et al., 2014) and *Dictyota* sp. (Gosch et al., 2012) (Table 2).

Besides fatty acids, *Dictyota* possesses phenolics and phlorotannins that are included in small vesicles (physodes), which play a role in cell wall crosslinking (Deniaud-Bouët et al., 2017) and potentially antiherbivore defense (Targett et al., 1995). The phenolic content is of pharmaceutical

interest. *Dictyota* species, however, contain relatively low contents of phenolics (0.01–1.34% of DW) compared to other brown algae (Targett et al., 1992, 1995; Targett and Arnold, 1998; Chkhikvishvili and Ramazanov, 2000). Bioflavonoids such as rutin, quercetin and kaempferol have been detected in relatively high percentages (Al-Saif et al. 2014).

Like all brown algae, *Dictyota* is characterised by the presence of oxylipins, C₁₁-carbohydrates that are derived from fatty acids (Pohnert and Boland, 2002). Both adult thalli (Schnitzler et al., 2001; Wiesemeier et al., 2008) and female gametes (Phillips et al., 1990) release a blend of oxylipins. The blend of female gametes contains the pheromone, dictyotene, that attracts sperm cells (Maier and Muller, 1986). Oxylipins also function as grazing deterrent, protecting the zygotes and adult thalli (Hay et al., 1998).

Pigments

Four kinds of pigments are present in the fucoxanthin-chlorophyll *a/c* protein assemblies (FCPA) that perform the energy transfer that supports photosynthesis in *D. dichotoma* chloroplasts: Chl *a*, Chl *c*, fucoxanthin and violaxanthin in a molar ratio of 13:3:10:1 (Mimuro et al., 1990). However, water-depth effects modulate the ratios, with the ratio of chl *c*/chl *a* decreasing in light exposed samples (Perez-Bermudez et al., 1981). The carotenoid composition of adult thalli is 69% fucoxanthin, 19% violaxanthin and 12% β -carotene (Kato et al., 1989). Violaxanthin can be interconverted to antheraxanthin or zeaxanthin in response to photoinhibition (Uhrmacher et al., 1995). *Dictyota* undergoes a fast recovery after photoinhibition, which suggests photoinhibition is an adaptation to strong light exposure (Nultsch et al., 1987).

Vitamins

Dictyota contains large quantities (24.5–42.8 μ g g⁻¹ fresh weight) of vitamin E, also known as α -tocopherol (Jayasree et al. 1985; de Sousa et al. 2008). The algae also contain vitamin A (4.7 μ g g⁻¹ fresh weight) and β -carotene (0.8 μ g g⁻¹ fresh weight) (de Sousa et al. 2008), but overall little is known about the vitamin content in *Dictyota*.

Secondary metabolites

Dictyota is a rich source of secondary metabolites which are under increasing interest due to their bioactivity. Several phenols (Zouaoui and Ghalem, 2017), sterols (Bouzidi et al., 2008), fatty acids (Gosch et al., 2015) and polysaccharides (Rabanal et al., 2014) display significant bioactivity. The main class of secondary metabolites of interest, however, are diterpenes. Diterpenes are often specific to certain species of *Dictyota* (Teixeira and Kelecom, 1988). The rich complement of secondary metabolites is thought to enable the survival in

environments with large pressure from herbivores and pathogens and the diversity between species or even populations has been suggested to result from different evolutionary pressures in different localities (de Paula et al., 2011). *Dictyota* regulates the release of diterpenes after wounding which influences susceptibility to grazers (Wiesemeier et al., 2008). Up until now, more than 230 diterpenes have been isolated from *Dictyota* species (recently reviewed by Chen et al. 2018).

The diterpenes have been grouped in three categories depending on the first formal cyclisation of the precursor.

- Group I diterpenes are derived by the first cyclisation between C1 and C10 of the geranyl-geraniol precursor (Teixeira and Kelecom, 1988). They contain mainly the prenylated-guaiane diterpenes. But also some prenylated-germacrane diterpenes (Sun and Fenical, 1979; König et al., 1991), and an prenylated-*epi*-elemene diterpene (Wright et al., 1993) and two prenylated-cadiene diterpenes (Kolesnikova et al., 2006) have been isolated.
- Group II is the largest group and consists of the diterpenes that have resulted from a cyclisation of the geranyl-geraniol precursor between C1 and C11 (Teixeira and Kelecom, 1988). Based on their diterpene skeletons, they are subdivided into the dolebellane, dolestone and secodolestone diterpenes (Chen et al., 2018). One dictyoxetane diterpene was isolated (Sullivan et al., 1986).
- Group III diterpenes are derived from a cyclisation between C2 and C10 or by ring contraction of the prenylated-germacrane. They are subdivided in the xenicane, crenulidane, dichotomane and crenulane diterpenes (Chen et al., 2018).

Utilisation

At present no published reports of cultivation of *Dictyota* are available and harvesting of the genus has not been industrialised as is the case for species like *Porphyra*, *Undaria* or *Saccharina*. Thalli are generally collected from natural populations (Kaliaperumal and Chennubhotla 2017). In Hawaii *D. acutiloba* is often grown in what are known as “algal gardens” (Pereira 2016).

Food for human consumption

Documented use of *Dictyota* appears restricted to the Caribbean, Malayan-Indonesian and Hawaiian regions where some species are either eaten raw, cooked in coconut milk, pickled or ground as flour (Pereira 2016, Brandham et al. 2002). Alginates extracted from *Dictyota* are also being used in various food products (Ravi et al. 2019).

Health and wellness applications

There is considerable interest in the pharmaceutical application of secondary metabolites of *Dictyota* (and other Dictyotales). There is a large body of literature describing the effects of diverse extracts containing secondary metabolites of *Dictyota* against many diseases. Because of the increasing need for bioactive molecules due to side effects or antibiotic resistance, many of the above mentioned isolated phenolics, fucans, laminarans and especially diterpenes are being tested for a diverse range of bioactivities, ranging from antioxidant to anticancer activity. While it is clear that different diterpenes may have different bioactivity, the choice of study species by the different labs is largely driven by the local availability.

Neuroprotective effect

Alzheimer’s disease is a chronic neurological disorder that has taken epidemic proportions in developed countries. Increasing the acetylcholine concentrations by inhibition of the enzyme butyrylcholinesterase (BuChE) is considered as an effective treatment against the disease (Mehta et al., 2012). Methanolic extracts of *Dictyota* have been shown to inhibit this enzyme and therefore are expected to have a neuroprotective effect (Stirk et al., 2007; Suganthi et al., 2010). In addition, two dolastane diterpenes present in at least several species have an inhibitory effect on Na⁺K⁺-ATPase, which is involved in the physiology of Alzheimer’s disease and a diverse range of other pathologies (Garcia et al., 2009).

Anticoagulant and antihemolytic activity

Dysfunction in coagulation and platelet aggregation may lead to diverse cardiovascular pathologies. Therefore, there is an interest in phytochemicals with an antihemostatic effect for drug design. The most available and used is heparin. Heterofucans of *Dictyota* (and *C. cervicornis*) are of interest because of their strong anticoagulant activity (Garcia et al., 2009; Costa et al., 2010). Interestingly the purified heterofucans have a higher anticoagulant activity than heparin (Albuquerque et al., 2004). Besides heterofucans, some diterpenes have also been attributed an anticoagulative effect (Moura et al. 2011; 2014). Secodolastane diterpenes from *C. cervicornis* where attributed an inhibitory effect against the clotting and proteolytic effects of crude snake venom of *Lachesis muta*, a South-American pit viper (Domingos et al., 2011). The same diterpenes did also inhibit the hemolytic effect of phospholipase A2 (a component in the venom) but could not inhibit the hemolytic effect of the crude venom (Domingos et al., 2011). Similarly, the coagulation activity and hemolytic effects of the venom of *Lonomia obliqua*, a toxic caterpillar, can be inhibited by extracts from *Dictyota*

species (Domingos et al. 2009). The activities can be specific to particular diterpenes because both *C. cervicornis* and *D. pfaffii* extracts do inhibit the coagulation activity but only extracts from *D. pfaffii* inhibit also the hemolytic activity (Domingos et al. 2009). In vivo studies have shown that CH₂Cl₂/MeOH extracts from *D. pulchella* induce vasorelaxation in rats (Queiroz et al., 2011).

Anti-inflammatory activity

CH₂Cl₂ fractions of methanolic extracts or specific isolated diterpenes from *Dictyota* have been shown to be efficient inhibitors of nitric oxide and PGE₂ generation in macrophages, suggesting these contain interesting compounds for anti-inflammatory drug discovery (Lee et al., 2008; Yoon et al., 2009; Cheng et al., 2014; Zhao et al., 2015). Anti-inflammatory effects are not confined to diterpenes, because also heterofucans may provide candidates as anti-inflammatory or antinociceptive molecules (Albuquerque et al., 2013).

Antimelanogenesis

Excess production of melanin in the skin may cause hyperpigmentation phenomena such as freckles and aging spots. A diterpene of *D. coriacea* was shown to exhibit antimelanogenesis effects without showing cell toxicity (Ko et al., 2013).

Anticancer activity

Extracts from *Dictyota* have been demonstrated to show a particularly strong cytotoxic effect on cancer cell lines and to have a relatively high antiproliferative effect compared to many other algae (Zubia et al., 2009; Guedes et al., 2013; Miranda-Delgado et al., 2018; Kosanić et al., 2019), where they can induce apoptosis of the cancer cells (Gomes et al., 2015). Different molecules in the extracts have been attributed this anticancer activity. In hexane extracts, fucosterol and two diterpenes have been identified with cytotoxic activities (Caamal-Fuentes et al., 2014). Both sulfated laminarans and fucans of *Dictyota* are being explored for their anticancer activity and show synergistic effects with X-radiation (Abdel-Fattah et al., 1978; Usoltseva et al., 2018; Yousefi et al., 2018; Malyarenko et al., 2019). Additionally, the polyphenol fraction was attributed an antiproliferative effect on pancreatic cancer cells (Aravindan et al., 2013). The relatively weak selectivity of the cytotoxic effect may be seen as a disadvantage (Harada and Kamei, 1997), but may be due to the diverse nature of the effect. Potential application of fucan-coated silver nanoparticles are being studied in cancer therapy (Fernandes-Negreiros et al., 2017). Next to coating of nanoparticles with its fucans, *Dictyota* may also be used for the

environmentally friendly synthesis of anti-ruthenium nanoparticles and delivery to tumors is being explored (Yacoub et al., 2017).

Antiviral activity

Dolabelladienetriol, a dolabellane diterpene isolated from *D. pfaffii*, was shown to have activity against herpes simplex virus Type-1 (HSV-1), where it inhibits the replication by inhibiting reverse transcriptase in a non-competitive manner (Barbosa et al., 2004; Abrantes et al. 2010; Cirne-Santos et al. 2008). The potential drug showed low cytotoxicity in preclinical tests (Cirne-Santos et al., 2008; Abrantes et al. 2010; Miceli et al. 2012) and has shown to be non-toxic in experimental animals (Garrido et al., 2011; Garrido et al. 2017). Experiments on mice showed crude extracts from *C. cervicornis* are potential treatments of HSV-1 cutaneous lesions (Barros et al. 2017). The effect has been attributed to two dolastane diterpenes which represent promising anti-HSV-1 molecules (Vallim et al. 2010). The effect against HSV-1 is specific to some diterpenes, because for example isopachydictyolal from *D. dichotoma* and 4- α -acetyldictyodial from *D. linearis* did not show such a strong effect (Siamopoulou et al. 2004). CH₂Cl₂/MeOH extracts and isolated diterpenes from different species of *Dictyota* were shown to exhibit anti-HIV-1 and anti-ZIKV (Zika virus) effect, where they inhibit replication of the virus in cell cultures (Pereira et al. 2004; Abrantes et al. 2010; Barros et al. 2017; Cirne-Santos et al. 2019). The effect in *D. pfaffii* has been attributed to dolabelladienol A and dolabelladienol B, which showed to be even more effective against HIV-1 than dolabelladienetriol and non-cytotoxic against the tested cell lines (Pardo-Vargas et al. 2014). In *D. menstrualis* the anti-HIV-1 effect was attributed to two dichotomane diterpenes (Pereira et al. 2005), while in *D. friabilis* the effect has been attributed to dolabelladienetriol (Stephens et al. 2017). In *D. plectens* 2 xenicane diterpenes were found to exhibit a similar effect, while another xenicane from *D. plectens* was effective against H5N1 (Zhao et al., 2015). Also, antiviral activities (against HSV-1 and CVB3) of the galactofucan rich subfractions of fucoidans have been demonstrated (Rabanal et al. 2014).

Antifungal activity

Methanolic extracts of *Dictyota* are also of interest for their antifungal activity against *Candida albicans* (ATCC 10231, ATCC 14053), *Aspergillus niger* MTCC109 (Stirk et al., 2007; Solomon and Santhi 2008; Manzo et al., 2009; Zouaoui and Ghalem, 2017; Kosanić et al., 2019), and other fungi (Reichelt & Borowitzka 1984). One xenicane has been shown to have a mild antifungal activity against *Candida albicans* ATCC14053 (Manzo et al., 2009), however,

diterpenes with an antifungal activity appear to be much more common in other Dictyotales species like *Dictyopteris* (de Paula et al. 2011).

Antibacterial activity

Although extracts of *Dictyota* spp. have shown *in vitro* antibiotic activity (Reichelt & Borowitzka 1984) they have not led to new antibiotics. Beta-lactam antibiotics comprise almost half of the total fraction of the global antibiotic usage. Their effectivity is under threat due to prolonged usage and the evolution of beta-lactamases that hydrolyse the antibiotics and render bacterial strains resistant. *Dictyota* methanolic extracts were shown to effectively inhibit beta-lactamases and therefore may be a source of new beta-lactamase inhibitors (Houchi et al., 2019). Several compounds from *Dictyota* have been attributed an antibacterial activity (see Chen et al., (2018) for a review).

Antileishmanial and antitrypanosomal activity

Different diterpenes, including dolabelladienetriol, from *Dictyota* showed interesting activity against *Leishmania amazonensis* and *Trypanosoma cruzi* responsible for respectively leishmaniasis and trypanosomiasis (Chagas disease) (León-Deniz et al., 2009; Soares et al., 2012; Alançia et al., 2014; Lira et al., 2016; Chiboub et al., 2019), an activity that is not shared by extracts from other marine algae and vertebrates (Bianco et al., 2013).

Antioxidant activity

Although similar antioxidant activities are not confined to *Dictyota* and related species, several multispecies comparisons have demonstrated that especially *Dictyota* (and Dictyotales) extracts have high antioxidant activity compared to other tested seaweeds (Martins et al., 2013; Tariq et al., 2015). Polysaccharide content is at least a part of the explanation of this high activity (Camara et al., 2011; Tariq et al., 2015). Also, the phenolic content of *Dictyota* is of interest for their antioxidant activities (Zouaoui and Ghalem, 2017; Miranda-delgado et al., 2018); however, the high antioxidant effect does not always correlate with the total phenolic content in the extract (Tariq et al., 2011; Martins et al., 2013; Van et al., 2013; Tariq et al., 2015; Chale-Dzul et al., 2017). Due to its high antioxidant potential and anti-inflammatory effects the extracts of *D. coriacea* are among the most chemopreventive ones among 30 seaweeds with an estimated chemoprevention index (the ratio between the cytotoxicity and the quinone reductase activity) of 4.36 using Hepa1c17 cells (Lee et al., 2008).

Biodiesel

While other macroalgae have low prospect for biodiesel production because of their low lipid content, the high lipid fraction in *D. bartayresiana* and *Dictyota* sp. (10.8–11.9% of DW) (Gosch et al., 2012) of up to 16.1% and 20.2% of DW in *D. acutiloba* and *D. sandvicensis*, respectively, suggests they may be comparable to or exceeding that of several microalgal species such as *Tetraselmis*, *Rhodomonas* and *Scenedesmus* and strains of *Skeletonema* and *Isochrysis* (Gosch et al., 2012; Kumari et al., 2013). However, also lower estimates (0.5–4.2% of DW) have been reported (Chakraborty and Santra, 2008; Deyab et al., 2017; Mwalugha et al., 2015; Tabarsa et al., 2012). Consequently, bioreactor-based cultures have been explored which modulate the lipid and fatty acids content of *Dictyota* (Martins et al., 2016) and seasonal and spatial variation of lipid and TFA contents has been monitored (Gosch et al., 2012, 2015). A protocol for nano-catalyzed biodiesel production from the lipids of *D. dichotoma* has been described (Khan et al., 2017).

Biofouling

Several studies have explored the effect of *Dictyota* extracts against biofouling (Barbosa et al., 2007; Ktari et al. 2010; Murugan and Begum, 2010; Othmani et al., 2013; Bakar et al., 2019). Larvae of invertebrates show mortality and abnormal development in response to application of diterpenes (Schmitt et al., 1998). Diterpenes of *Canistrocarpus* and *Dictyota* were shown to inhibit byssal threads of mussels (Bianco et al., 2009; Siless et al., 2018). Furthermore, coral mortality was induced in the presence of *Dictyota* species (Kuffner et al., 2006). Several other studies demonstrated the antibacterial activity of a range of diterpenes (reviewed by Chen et al., 2018) and sterols (Bakar et al., 2019), which can consequently inhibit bacterial biofilm formation (Viano et al., 2009; Othmani et al., 2013).

Animal feed

Traditionally dried and ground *Dictyota* is utilised as supplements to cattle, poultry and fish feed (Kaliaperumal and Chennubhotla, 2017). Recently, it was established that the addition of supplements of *D. bartayresiana* may reduce *in vitro* methane production of ruminants with 92.2%, and therefore offers a promising alternative for mitigating enteric CH₄ emissions (Machado et al., 2014).

Conclusions

Dictyota is characterised by a thin parenchymatous thallus structure with a meristem region developing in a thallus with

cortical and medullary cell layer(s) depending on the species. Its synchronously released and dividing zygotes are under increasing academic interest. *Dictyota* species often show a large degree of morphological plasticity. The life cycle is an isomorphic alternation of a haploid and diploid phase. As a near cosmopolitan genus, *Dictyota* only lacks from the polar seas. *Dictyota* and its taxonomically and morphologically closely associated dictyotalean sister genera can seasonally emerge as dominant species in the sublittoral and eulittoral rock pools and may form algal blooms under certain conditions. Traditionally, its commercial value has been closely connected to local uses and traditions such as food, feed or cosmetics. In more recent times, propelled by the increased interest in its secondary metabolites such as phenols, sterols, fatty acids, polysaccharides and especially diterpenes, the genus has received increased attention. Especially the demonstrated antibiofouling and pharmaceutical potential (Alzheimer's disease, anticoagulant, anti-inflammatory, anticancer, antioxidant, antibiotic and antiviral activity) of their extracts and isolated compounds stand out. Recently, some new potential applications as biofuel source and cattle feed supplement, respectively due to its reported high lipid content and its antimethanogenic effect, have emerged warranting further exploration.

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