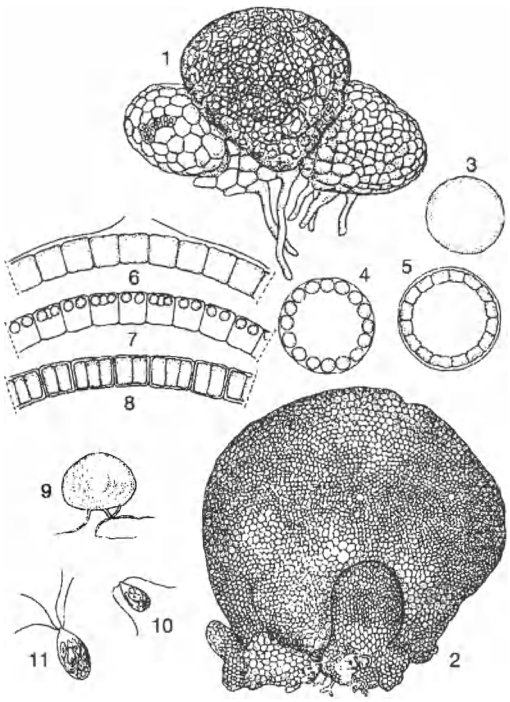


Dictyosphaeria cavernosa (Forssk.) Børgesen – 1, habit of a young specimen; 2, habit of a mature specimen; 3, cross-section of an undivided unicellular primary vesicle (diagrammatic); 4,5, formation of secondary vesicles inside the primary vesicle (cross-sections, diagrammatic); 6, the original wall of the primary vesicle has burst; 7, spherical protoplasmatic bodies are formed; 8, tertiairy vesicles have been formed (6,7,8 diagrammatic cross-sections to show formation of tertiairy vesicles); 9, habit of unicellular germling; 10, gamete with 2 flagella and an eyespot; 11, zoospore with 4 flagella and an eyespot.

divisions take place within the unicellular germlings, which are by then 3–5 mm in diameter. First many spherical protoplasmic bodies are formed, which then develop into a layer of polygonal daughter cells that together form the monostromatic mature thalli. These are attached by rhizoidal cells formed by elongation of basal cells.

Ecology *D. cavernosa* is commonly found on rocks and reefs in the intertidal zone, where it is however often poorly developed. A little lower down on the shore it reaches full size, and it has also been recorded at depths of up to 55 m. The composition and texture of the rocky substrate greatly influence communities of this alga. It often grows on white, porous shell remains, which reflect light and have a high waterholding capacity. The alga can penetrate this substrate and then grow in semiprotected niches.

Propagation and planting Phycoculture of *D. cavernosa* is not known.

Harvesting *D. cavernosa* is harvested only by hand-collecting.

Handling after harvest *D. cavernosa* is mainly used fresh.

Prospects The use of *D. cavernosa* as human food is likely to remain limited. Its antimicrobial capacity might be developed in the future.

Literature |1| Enomoto, S., Hori, T. & Okuda, K., 1982. Culture studies of Dictyosphaeria (Chlorophyceae, Siphonocladales) II. Morphological analysis of segregative cell division in Dictyosphaeria cavernosa. Japanese Journal of Phycology (Sôrui) 30: 103–112. |2| Enomoto, S. & Okuda, K., 1981. Culture studies of Dictyosphaeria (Chlorophyceae, Siphonocladales) I. Life history and morphogenesis of Dictyosphaeria cavernosa. Japanese Journal of Phycology (Sôrui) 29: 225–236.

P.Y. van Aalderen-Zen

Dictyota J.V. Lamour.

J. Bot. (Desvaux) 2: 38 (1809).
DICTYOTACEAE
$2n = 18, 24, 32, 48$

Major species and synonyms

- *Dictyota bartayresiana* J.V. Lamour., J. Bot. (Desvaux) 2: 43 (1809), synonyms: *Dictyota bartayresii* J.V. Lamour. (1809), nom. illeg., *D. patens* J. Agardh (1882), *D. neglecta* Hörnig & Schnetter (1992), non *Dictyota bartayresiana* auct. non J.V. Lamour. sensu Vickers (1908).
- *Dictyota cervicornis* Kütz., Tab. phycol. 9: 8, pl. 17, fig. 1 (1859), synonyms: *Dictyota indica* Sond. ex Kütz. (1859), *D. pardalis* Kütz. (1859).
- *Dictyota ceylanica* Kütz., Tab. phycol. 9: 11, pl. 25, fig. 1 (1859).
- *Dictyota ciliolata* Sond. ex Kütz., Tab. phycol. 9: 12, pl. 27, fig. 1 (1859), synonyms: *Dictyota ciliata* J. Agardh (1841), *D. beccariana* Zanardini (1872).
- *Dictyota crispata* J.V. Lamour., J. Bot. (Desvaux) 2: 44 (1809), synonyms: *Dictyota bartayresiana* auct. non J.V. Lamour. sensu Vickers (1908), *D. apiculata* auct. non J. Agardh sensu Weber Bosse (1913), *D. dentata* auct. non J.V. Lamour. sensu Vannajan & Trono (1978), *D.*

mertensii auct. non (Mart.) Kütz. sensu Trono (1997).

- *Dictyota dichotoma* (Huds.) J.V. Lamour. var. *dichotoma*, J. Bot. (Desvaux) 2: 38 (1809), synonyms: *Dictyota acuta* Kütz. (1845), *D. volubilis* Kütz. (1849).
- *Dictyota dichotoma* (Huds.) J.V. Lamour. var. *intricata* (C. Agardh) Grev., Alg. brit.: 58 (1830), synonyms: *Dictyota divaricata* J.V. Lamour. (1809), *D. dichotoma* (Huds.) J.V. Lamour. var. *implexa* (Desf.) Gray (1821), *D. cirrhosa* Suhr (1839).
- *Dictyota friabilis* Setch., Univ. Calif. Publ. Bot. 12: 91–92 (1926), synonym: *Dictyota ceylanica* Kütz. var. *rotundata* Weber Bosse (1913).

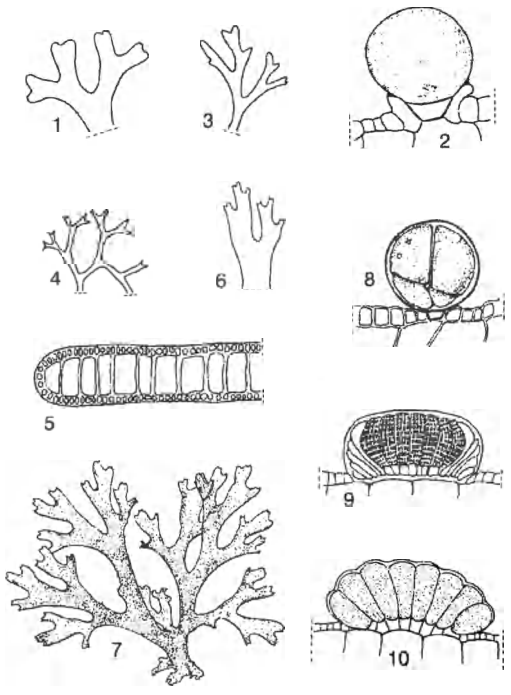
Origin and geographic distribution *Dictyota* is represented in most regions of the world, except around the poles. Species diversity is greater in the tropics than in temperate waters. The highest diversity of *Dictyota* is found in Australia. Approximately 40 different species names are recorded from the Indian Ocean, which however, can be reduced to 23 accepted species. Of those mentioned above, *D. dichotoma* is most often recorded as occurring on almost all coasts of South-East Asia, often together with its variety *intricata*. Because of taxonomic confusion, however, these distributional data (and those for *D. bartayresiana*) are not reliable. Most probably neither *D. dichotoma* var. *dichotoma* nor var. *intricata* do occur in South-East Asia.

Uses The thalli of several *Dictyota* are edible and used in Indonesia (Sulawesi), Malaysia and Thailand. In the Hawaiian Archipelago, *D. acutiloba* J. Agardh is cultivated in 'algal gardens' and sold on local markets. *Dictyota* is either eaten raw or cooked with coconut milk, pickled or preserved by smoke-drying and is very nutritious. Some *Dictyota* are known to have a somewhat bitter taste. Acetone extracts of '*Dictyota dichotoma*' in India showed synergism with a number of insecticides used to kill mosquito larvae. This synergism may be due to inhibition of some detoxifying enzymes in mosquito larvae by the algal extract. If this acetone extract can be combined with synthetic insecticides, it will result in reduced consumption of the latter, thus reducing aquatic pollution.

Properties Like most brown algae *Dictyota* contains alginic acid, an acid membrane mucilage with emulsifying, gelling and thickening properties which is very important on a world scale in a wide variety of industries. *D. bartayresiana* is known to contain a very high percentage of alginic acid: 17–18%. Unfortunately a high alginic acid content is not the only prerequisite for industrial utilization; the size and density of the crops are extremely important as well. Because of its relatively small size *Dictyota* is less attractive for commercial exploitation. The chemical composition of a *Dictyota* sp. identified as '*D. divaricata*' in the Arabian Gulf showed a very low protein content compared to similar studies of *Dictyota* spp. in different Indian Ocean localities: 1.7% of dry weight, compared to 19.8% in India. This may be due to the high salinity of the Arabian Gulf waters. *D. dichotoma* possesses a high folic acid content. Different experiments have proven that lipid-soluble extracts of several *Dictyota* possess antibiotic and antiviral substances (terpenes). The amount of these substances may vary from place to place and may depend on the season. *D. crenulata* J. Agardh was found to be active against a form of lymphocytic leukaemia and tumours. Other *Dictyota*, among which *D. dichotoma*, inhibit the growth of several human pathogenic and phytopathogenic fungi.

Description Thalli composed of dichotomously to irregularly branched straps, each with single lens-shaped apical cell; attachment by rhizoids or stolonoidal fibres. Branching by equal to unequal division of apical cell. One to several layers of large, thick-walled, medullary cells surrounded by single layer of small, pigmented cortical cells, iridescent or not – in dried specimens iridescence lost. Sori of hairs present or absent. Life cycle diplo-haplontic and isomorphic. Sporophyte forming unilocular tetrasporangia each containing 4 non-motile tetraspores; tetrasporangia grouped in sori or scattered over whole or parts of fronds. Gametophytes dioecious; oogonia and antheridia surrounded by one to several rows of paraphyses, grouped in sori.

- *D. bartayresiana*. Thalli erect, forming hemispherical tufts, 8–20 cm tall, attached by numerous patches of rhizoids, straw-coloured, never iridescent, texture somewhat crisp; individual straps up to 10–15 cm long, 5.7–7.3 mm wide, regularly dichotomously branched, branching angle 70–80°, interdichotomies short; margins smooth; surface proliferations absent; hair tufts common. Tetrasporangia scattered on both surfaces of straps, single, not surrounded by a ring of enlarged, sterile cells (involucrum). Gametangia unknown.
- *D. cervicornis*. Growth form very variable; thalli 10–15(–30) cm long, with or without well-developed base, attached by rhizoids, medium brown;



Dictyota. D. cervicornis Kütz. – 1, habit of apical portion of a thallus with truncate apices; 2, section through a young tetrasporangium with an one-celled stalk cell and an involucrum. D. friabilis Setch. – 3, habit of apical portion of a thallus with rounded apices. D. dichotoma (Huds.) J.V. Lamour. var. intricata (C. Agardh) Grev. – 4, habit of apical portion of a thallus with acute apices; 5, cross-section of a branch with one layer of large medulla cells surrounded by one layer of cortex cells. D. crispata J.V. Lamour. – 6, habit of an apical portion of a thallus with apiculate apices; 7, habit. D. bartayresiana auct. non J.V. Lamour. sensu Vickers – 8, section through a tetrasporangium with 4 tetraspores, an one-celled stalk cell and no involucrum. D. ciliolata Sond. ex Kütz. – 9, section of an antheridial sorus surrounded by paraphyses; 10, section of an oogonial sorus.

straps of whole thallus somewhat coarse, often with strongly elongated, linear interdichotomies in erect parts, average width 2.3–3.1 mm; apices truncate to rounded; branching regular dichotomous in lower and middle parts of thalli (branching angle 60–70°), apical parts typically cervicorn (branching angle 70–100°) or with recurved branches; margins smooth, sinuously curved; surface proliferations absent; hair tufts common. Tetrasporangia scattered over both surfaces of straps, not divided, mostly single, never in apical segments, surrounded by involucrum. Gametangia unknown.

– *D. ceylanica*. Growth form ascending, with very intricate appearance; thalli small, 4(–6) cm long, without conspicuous base, attached by rhizoids, medium to pale brown, blue to yellowish iridescent; straps procumbent, repent or erect, mostly filiform but extremely variable in width, (0.2–) 0.8–1.3(–5.8) mm broad; apices acute or rounded; branching mainly regularly dichotomous, branching angle broad divaricate (70–100°); margins smooth; surface proliferations absent, marginal proliferations common and obscuring the original branching pattern; hair tufts common. Tetrasporangia scattered over both surfaces of fronds, often forming a narrow, longitudinal line in the middle of the straps; sporangia rarely divided and not surrounded by involucrum. Only oogonial gametangia sori known, scattered on both surfaces of the straps, with a variable number of oogonia (12–58) per sorus.

– *D. ciliolata*. Growth form completely erect, 8–15 (–25) cm long, with conspicuous stupose holdfast giving rise to single frond of somewhat crisp texture, brown, often with broad transverse banding pattern of slightly iridescent zones alternating with non-iridescent zones; straps in whole thallus of same width, (1.5–) 3.7–9.1(–19.5) mm, width and height being highly variable between different specimens; apices regularly dichotomous or slightly irregularly dichotomous, never alternate, branching angle 35–50°; margins usually dentate, teeth slightly to prominently directed towards the apices, giving rise to marginal proliferations obscuring original branching pattern; surface proliferations absent; hair tufts common. Tetrasporangia scattered over both surfaces of fronds, sporangia without involucrum, divided sporangia frequently observed. Gametangia occasionally observed, evenly distributed over whole frond, also present in the apical segments; female gametangial sori with about 20 oogonia per sorus; male gametangial sori with about 25 oogonia per sorus, surrounded by 3–4 rows of unicellular paraphyses.

– *D. crispata*. Growth form ascending, 9–20(–30) cm long, with small prostrate base giving rise to several stiff, crisp, erect straps, harsh to the touch, brown to pale brown, not iridescent; average width between different specimens extremely variable, (1.0–)4.9–6.4(–22) mm, with anisoto-

mous dichotomous branching, branching angle 30–70°; margins smooth; surface proliferations common to abundant, marginal proliferations absent. Tetrasporangia scattered on both surfaces of straps, single or grouped in small, longitudinal sori often placed in apical segments, involucrum present, sporangia not divided. Both oogonia and antheridia (surrounded by 2–3 rows of pigmented paraphyses) in sori evenly distributed over whole surface of straps.

- *D. dichotoma* var. *dichotoma*. Extremely polymorphic, very difficult to characterize in a single description. Thalli erect, 10–35 cm tall, sometimes spirally twisted, medium brown; main straps 4–10 mm broad, usually with rounded apices; branching regularly dichotomous; margins smooth; proliferations on surface absent; hair tufts common. Tetrasporangia scattered over whole surface, except for a narrow, sterile marginal strip. Sporangia not surrounded by involucrum. Oogonia and antheridia common in Europe.
- *D. dichotoma* var. *intricata*. Similar to var. *dichotoma* but with characteristic long and narrow (1.1–1.8 mm broad) interdichotomies, with acute apices, proliferations on surface very common, often growing into new straps of similar shape. Tetrasporangia always single, dispersed over both surfaces of fronds, absent from apical segments.
- *D. friabilis*. Growth form completely procumbent, forming dense imbricate mats (up to 20–30 cm in diameter), composed of several layers of somewhat brittle (friable) straps, resulting in typical jigsaw aspect; thalli attached by marginal bundles of rhizoids arising from all parts, medium brown, pale bluish iridescent, often with conspicuous non-iridescent longitudinal stripes. Individual thalli small (3–5 cm long), straps with typical short and broad interdichotomies, 2.5–6.4(–11.0) mm broad, branching angle 60–110°; apices rounded to obtuse; margins smooth; marginal proliferations rare, surface proliferations absent; hair tufts common. Tetrasporangia scattered on upper surface of fronds, single, absent from apical segments, not surrounded by involucrum. Gametangia unknown.

Growth and development Most *Dictyota* seem to be common all the year round in the tropical seas. Because of the frequent occurrence of tetrasporangia one would expect an equal number of sporo- and gametophytes in a population. However, gametophytes are rarely found. This leads to the assumption that in many cases no meiosis occurs in the tetrasporangia and that the diploid spores develop to new sporophytes.

Other botanical information A high morphological variability makes identification of species of *Dictyota* very difficult. There has been persistent taxonomic confusion in both *D. bartayresiana* and *D. dichotoma*. Study of the type collections of species described by J.V. Lamouroux has revealed the genuine characters of *D. bartayresiana*. It is often confused with another pantropical species, which proved to be described by Lamouroux as *D. crispata*. Both species are common in South-East Asia.

D. dichotoma, the type species of the genus, is without doubt the most frequently reported species in the genus. It has been recorded in nearly every locality where *Dictyota* spp. occur. A combination of high morphological variability and a lack of distinctive characters makes it difficult to give an accurate and concise description. It has been separated from similar species in the Atlantic Ocean by means of chromosome counts and hybridization experiments. *D. dichotona* probably does not occur at all in South-East Asia. Specimens named as *D. dichotoma* var. *dichotoma* often belong to *D. crispata*, while specimens named as *D. dichotoma* var. *intricata* often belong to *D. ceylanica* or *D. ciliolata*.

In this notoriously variable genus misidentifications are very common. Specimens from the Philippines (and possibly also records from Peninsular Malaysia), identified as *D. dentata* J.V. Lamour. and *D. mertensii* (Mart.) Kütz., most probably belong to *D. crispata*.

Ecology *Dictyota* is very common in the Indo-Malaysian region. Each species is generally found in its own specific biotope; they are most abundant in shallow lagoons, separating the fringing reef from the coast. Healthy free-floating thalli of *D. bartayresiana* often thrive well among large seagrasses.

Propagation and planting There is no phycoculture of *Dictyota*.

Harvesting *Dictyota* is harvested by hand; attached as well as drifting specimens are collected.

Handling after harvest *Dictyota* is mainly used fresh or sun-dried.

Prospects *Dictyota* is only likely to be used in a restricted way for human food. It might become important as a component of insecticides against mosquito larvae and as a provider of fine chemicals and antibiotics.

Literature |1| Abbott, I.A., 1984. Limu. An ethnobotanical study of some Hawaiian seaweeds.

3rd Edition. Pacific Tropical Botanical Gardens, Lawai, Hawaii. 35 pp. |2| De Clerck, O., 1999. A revision of the genus Dictyota Lamouroux (Phaeophyta) in the Indian Ocean. Thesis Universiteit Gent, Belgium. 356 pp. + 3 append. |3| De Clerck, O. & Coppejans, E., 1997. The genus Dictyota (Dictyotaceae, Phaeophyta) from Indonesia in the Herbarium Weber-van Bosse, including the description of Dictyota canaliculata spec. nov. Blumea 42: 407–420. |4| Hörnig, I., Schnetter, R. & Prud'homme van Reine, W.F., 1992. The genus Dictyota (Phaeophyceae) in the North Atlantic. I. A new generic concept and new species. Nova Hedwigia 54: 45–62. |5| Subramonia Thangam, T. & Kathiresan, K., 1991. Mosquito larvicidal activity of marine plant extracts with synthetic insecticides. Botanica Marina 34: 537–539.

O. De Clerck, E. Coppejans & W.F. Prud'homme van Reine

Digenea simplex (Wulfen) C. Agardh

Spec. alg. 1: 389 (1822).

RHODOMELACEAE

$2n$ = unknown

Synonyms *Conferva simplex* Wulfen (1803), *Digenia wulfenii* Kütz. (1843), nom. illeg.

Vernacular names Philippines: bodo-bodo. Japan: kaininso, makuri. China: hairencao (when referring to medicine the name zhegucai is also used, but that is a misapplication of a name originally used for *Caloglossa leprieurii* (Mont.) G. Martens).

Origin and geographic distribution *D. simplex* is recorded from many localities in tropical and warm temperate areas. In South-East Asia it is only recorded from the Philippines (Luzon, Palawan), Indonesia (Tukangbesi Islands, east of Bitung, Sulawesi) and the northern coast of Papua New Guinea.

Uses *D. simplex* is mainly used as an anthelmintic medicine or vermifuge. Its use as a vermifuge was first described in Fujian Province (China) in 1530 A.D. It is the most efficient seaweed used in the treatment of *Ascaris* and *Oxyuris*, as well as whipworm (*Trichuris*) and tapeworm (*Taenia*) because it contains kainic acids. A single dose of 5–10 mg of α- kainic acid is capable of driving out *Ascaris* in adults and no unpleasant side effects have been observed. It can also be used together with santonin, where a synergetic action results in a marked increase of the ascaricidal effect. This algal compound is one of the few 'drugs from the sea' used in orthodox medicine. An extract of *D. simplex* from Asia is on the market under the names 'Helmia' and 'Digenea' for use in the treatment of worms. *D. simplex* also is a source of agar, but because of its small size and low agar content it is unlikely to gain any commercial importance.

Production and international trade The centre of collection of *D. simplex* is a very small area in the South China Sea, off the island of Pratas (= Donsha), Guandong Province (China), in an open lagoon of 16 km in diameter. About 300 t per year is produced there by some 45 divers. In addition to the Chinese production, almost the same amount of the alga used to be collected in southern Kyushu, Japan.

Properties *D. simplex* contains agar (10–15% of its dry weight) and kainic acids. Especially α-kainic acid is an effective anthelmintic agent, which is said to be about ten times stronger than santonin, a compound of the salt marsh plant *Artemisia maritima* L. Another anthelmintic agent from *D. simplex*, named α-allokainic acid, is only slightly anthelmintic.

Description Thalli erect, up to 10(–20) cm tall, dull brownish-red, cartilaginous, bushy, wiry below; main axes terete and heavily clothed with many radial, dichotomously branched, 3–15 mm long, stiff laterals; main axes without well-defined apical cell or polysiphonous structure. Medulla of large broadly parenchymatous cells; cortex of smaller cells; determinate lateral branchlets uncorticated, showing 6–10 pericentral cells with small deciduous trichoblasts at the apices. Life cycle diplo-haplontic and triphasic, isomorphic for tetrasporophytes and gametophytes. Tetraspores tetrahedral, in irregularly swollen, chiefly uncorticated upper parts of branchlets. Spermatangia in small ovoid disc clustered at tips of fertile branchlets; cystocarps ovoid, terminal and lateral on branchlets.

Ecology *D. simplex* is common and often abundant in the intertidal zone on rather exposed reefs and rocks. It is frequently much dwarfed and hardly more than 3–5 cm tall, but in sheltered spots it grows much larger, and is dredged to a depth of 20 m. It is a favoured support for many other algae and is commonly so heavily epiphytized that a dense colony of the dwarfed form may be completely concealed.

Propagation and planting *D. simplex* is not kept in phycoculture.

Diseases and pests *D. simplex* is usually heavily overgrown by epiphytes.