Bull. Natn. Sci. Mus., Tokyo, Ser. B, **23**(4), pp. 143–150, December 22, 1997

Reproductive Structures of *Dictyota linearis* (Dictyotales, Phaeophyceae) from Japan

Jiro Tanaka[1], Ayako Sano[1] and Taiju Kitayama[2]

[1] Department of Aquatic Biosciences, Tokyo University of Fisheries, 4–5–7, Konan, Minato-ku, Tokyo 108, Japan
[2] Department of Botany, National Science Museum, 4–1–1, Amakubo, Tsukuba 305, Japan

Abstract Sporophytes, and both female and male gametophytes of *Dictyota linearis* (C. Agardh) Greville were collected from the Japan Sea coast of Japan. Gametophytes are reported for the first time at the present study. Tetrasporangia, oogonia and antheridia are produced on both sides of the upper and middle parts of a blade. Tetrasporangia are produced separated from each other, and do not form a sorus. They are spherical and project on the cortical layer with a single stalk cell at the base. An oogonial sorus projects on the cortical layer with 1–2 layers of sterile cells in the peripheral area, and it is composed of 8–25 oogonia. Oogonium is long obovate with a single stalk cell at the base. An antheridial sorus is swollen above the cortex, and enclosed with 2–4 layers of sterile cells. Antheridium forms on a single basal stalk cell. Although tetrasporophyte and gametophytes are similar in external appearance when immature, they can be easily distinguished from each other by the shape and color of their sori when mature.

Keywords: antheridium, *Dictyota linearis*, Dictyotales, oogonium, Phaeophyceae, Reproductive structures, tetrasporangium.

The genus *Dictyota* can be clearly distinguished from the other genera of the Dictyotales, such as *Dilophus*, *Pachydictyon* and *Spatoglossum* by the combination of the following characteristics; the single layered medulla, the single layered cortex and one to two large meristematic cells at the apex of a blade. In the genus *Dictyota*, Yoshida *et al.* (1995) has documented 50 species from Japan and the adjacent waters. Gametophytes of many species of *Dictyota* are remained unknown in the literatures (Allender & Kraft, 1983; Noda, 1965; Okamura, 1936; Phillips, 1988; Womersley, 1987).

Okamura (1913) described *Dictyota linearis* based on the young sterile materials with a figure from the Seto Inland Sea and the Sado Island of the Japan Sea. Later, Noda (1965) reported sterile plants from the Sado Island. No other detailed study, particular with regard to the reproductive structures, had been undertaken on this species.

Materials and Methods

Collections of *Dictyota linearis* were made on the Japan Sea coast of Japan and the Pacific coast of central Japan. Collecting materials were made in the form of standard dry herbarium specimens. Thallus tissue was preserved in a solution of formalin, glycerine, ethanol and seawater (1 : 2 : 2 : 5), soon after the collection for detailed anatomical examination. Transverse sections were made from liquid-preserved specimens on a freezing microtome, stained with 1% aqueous aniline blue, and mounted in a 1 : 1 mixture of water and a corn sugar syrup as the semi-permanent slides. Differential interference contrast (DIC) optics (Nomarski apparatus, Nikon) were used for some photographs. These materials have been deposited in the Herbarium of Tokyo University of Fisheries (MTUF-AL) and the Herbarium of National Science Museum, Tokyo (TNS-AL).

Results

Dictyota linearis (C. Agardh) Greville, xliii. (1830); Okamura, Icon. Jap. Alg. 3: 29, pl. 107. (1913); Noda, Species Dictyotaceae Sado Isl. Japan Sea. p. 32. fig. 1 (6–8). (1965); Mar. alg. Japan Sea. p. 142, f. 115. (1987); Boergesen, Mar. alg. Canary Isl. II. p. 85. (1926); Takamatsu, Mar. alg. Japan Sea. p. 31. (1939); Ikoma, Mar. alg. southern Honshu Japan I. p. 28. (1956); Taylor, Mar. alg. E. Trop. Subtrop. Amer. p. 219. (1960); Earle, Phaeophyta E. Gulf of Mexico. p. 161, f. 52. (1969); Honda & Noda, Mar. alg. Toyama Bay. p. 8. (1970); Silva, Menez & Moe, Smithsonian contr. mar. sci. No. 27: 76.(1987).

Basionym: *Zonaria linearis* C. Agardh, Sp. Alg. I, p. 99, 134. (1820) (Type locality: Cadiz, Spain); De Toni, Syll. Alg. III, p. 275. (1895).

Japanese name: Ito-amiji.

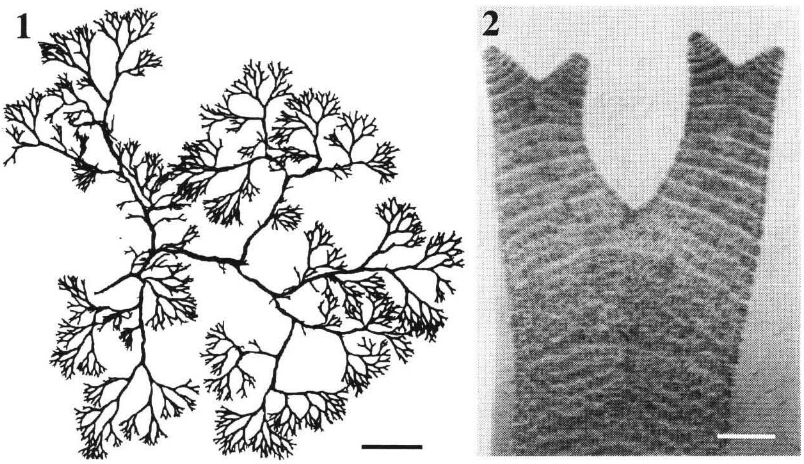
Distribution: Common in temperate to tropical regions in the world.

Local Distribution: the Japan Sea, the Seto Inland Sea, South-western Islands, Pacific coast of central Japan.

Specimens examined: Naikaifu, Sado Island, Niigata Pref., Aug. 8, 1995, coll. J. Tanaka (MTUF-AL-20068 tetrasporophyte; MTUF-AL-20069 female gametophyte; MTUF-AL-20070 male gametophyte; TNS-AL-44998 tetrasporophyte); Yaene, Hachijyo Island Tokyo, Feb. 15, 1990, coll. J. Tanaka (MTUF-AL-20071 sterile); Himi City, Toyama Pref., Oct. 11, 1990, coll. J. Tanaka (TNS-AL-44999 sterile).

Plants grow on *Sargassum* spp. and rocks at the subtidal zone in areas of weak wave action. Holdfast is made from a number of multicellular filamentous rhizoids. Erect thallus is light to medium brown in color, becoming darker when dried.

The blade is flat, dichotomously branched to produce many branches, twisted at each nodes, 10–20 cm and up to 30 cm in height (Fig. 1), gradually tapering towards from the basal part to the tip, 600–3000 μm at the lower part, 400–550 μm at the middle part and 300–350 μm at the tip in width. Ultimate branch is suddenly nar-



Figs. 1–2. *Dictyota linearis*. (MTUF-AL-20068) — 1. Whole thallus. scale bar: 1 cm. 2. Apical part of thallus, showing four growing tips. scale bar: 100 μm.

rowed to become sharp pointed at the apex (Fig. 2).

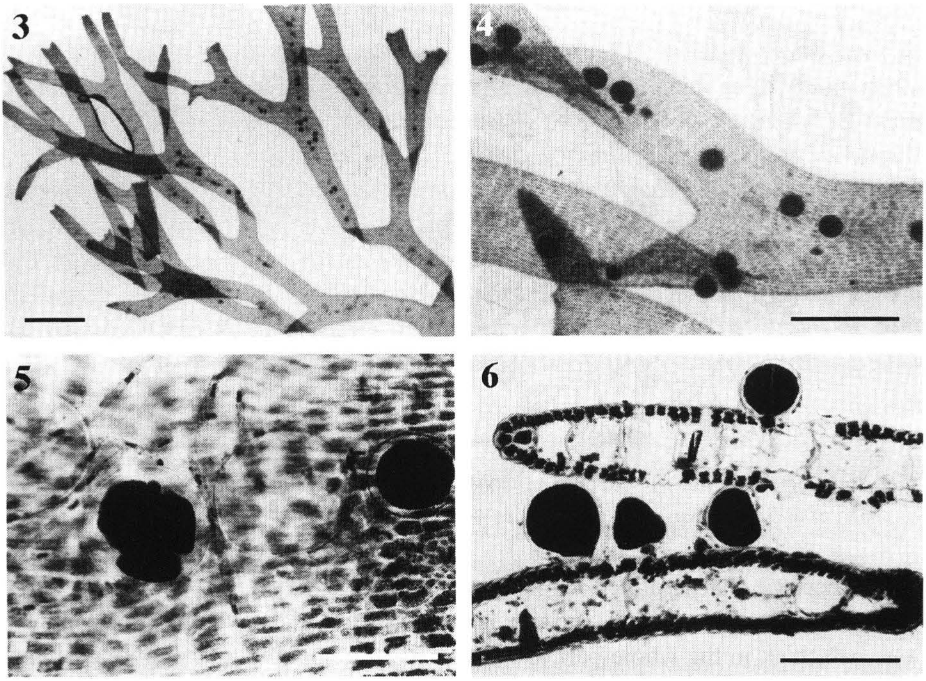
Blade is 40–70 μm thick with one layer of cortical cells and one medullary layer of one cell thick in the whole part. Cortical cell is long cubic in shape longitudinally arranged along the blade, 30–40 μm long, 12–15 μm in width and thickness, dark in color containing many discoid chloroplasts. Medullary cell is cubic, 70–80 μm long, 40–65 μm wide and 60–80 μm thick, almost colorless with a few plastids.

Hair pits arise abundantly from a central part of a blade, scattered throughout both surfaces of a blade especially when young. 30–50 colorless multicellular hairs arise from a hair pit.

A single meristematic cell is dome-shaped, 40–55 μm in diameter and 15–20 μm in height, is located at the apex of each blade, darker in color than the other vegetative cells (Fig. 2).

Three kinds of reproductive plants, that is, sporophyte, female and male gametophytes have similar appearances, and can not be distinguished from each other by their external appearances when immature. They commonly grow mixed in the same colony at the present sampling site in the Sado Island in summer (August), and the occurrence ratio (%) of sporophyte: female: male was 17 : 45 : 38 (n=58) there. Tetrasporangia are often scattered around the central part of a blade and rarely formed in a group (Figs. 3–4). Oogonia and antheridia are formed in sori on both surfaces of a blade in each plant. Each sorus is initially formed around a hair pit which become disappeared during the maturation, and is arranged in one or two rows along the central regions of a blade (Figs. 7 & 10).

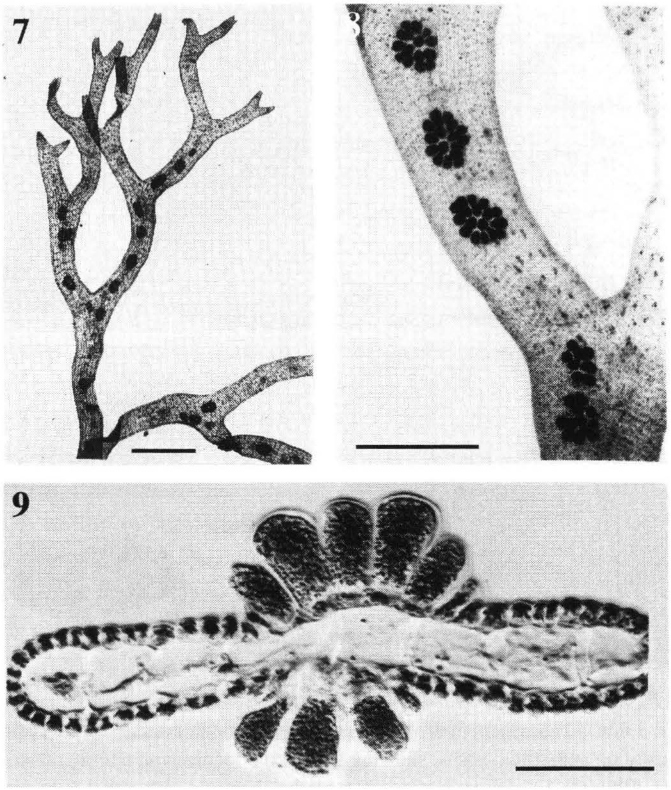
Development of tetrasporangia (Figs. 3–6). The initial cell of a tetrasporangium is produced from a cortical cell, and later differentiated into a tetrasporan-



Figs. 3–6. Tetrasporangial plant of *Dictyota linearis*. (MTUF-AL-20068) — 3. Upper part of thallus. scale bar: 1 mm. 4. Tetrasporangial sori arranged in both sides of a blade. scale bar: 500 μm. 5. Surface view of a blade, showing tetrasporangia and empty ones. scale bar: 100 μm. 6. Cross section of a blade, showing each tetrasporangium produced on a basal stalk cell. scale bar: 100 μm.

gial mother cell and a stalk cell at the base. Mature tetrasporangia are spherical in shape, 75–137 (average 102) μm in diameter, project above the cortex, borne on a single stalk cell which are disc shaped, 10–15 μm high and 30–40 μm in diameter (Fig. 6). Tetrasporangia often remain undivided in a sorus, and rarely divided tetrahedrally to form four spores (Fig. 5). After liberation of tetrasporangia and tetraspores, the sporangial walls remain attached to the stalk cells. Figure 5 shows two empty sporangia.

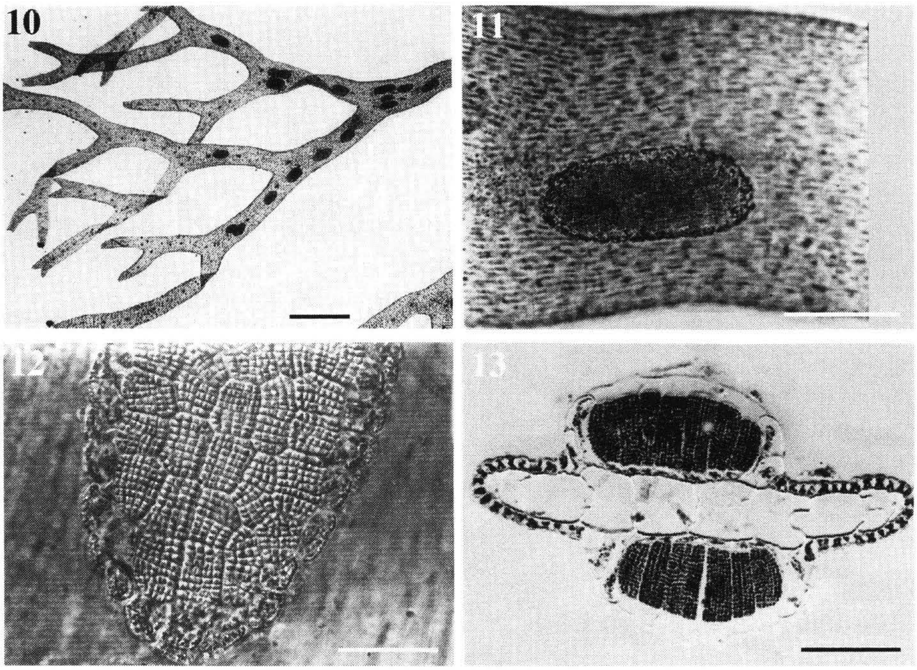
Development of oogonia (Figs. 7–9). Oogonial sori can be seen to be dark spots scattering throughout the upper and middle parts of a blade with the naked eyes (Fig. 7). They are slightly elliptical in outline, 131–418 (av. 280) μm long and 75–263 (av. 180) μm wide. 8–25 (av. 12.4) oogonia are compactly aggregated in a sorus (Fig. 8). Initial cell of an oogonium is produced from a cortical cell, and later differentiated into an oogonium and a stalk cell just before maturation. Mature oogonia project above the cortex, obovate, 38–63 (av. 51.9) μm in diameter and 63–88 (av. 75.3) μm high. Peripheral long cells around an sorus remain immature as sterile cells (Fig. 9).



Figs. 7–9. Female plant of *Dictyota linearis*. (MTUF-AL-20069) — 7. Upper part of thallus. scale bar: 1 mm. 8. Surface view of a blade, showing oogonial sori in a central part of a blade. scale bar: 500 μm. 9. Cross section of a blade, showing oogonial sori arranged in both sides on a blade, also showing peripheral sterile cells around a sorus and basal stalk cells. scale bar: 100 μm.

After liberation of oogonia, these sterile cells remain attached to the peripheral areas of a sorus.

Development of antheridia (Figs. 10–13). Antheridial sorus can be easily distinguished from the sori of the other reproductive thalli by its whitish color with the naked eyes. Their outlines are often long elliptical, 238–644 (av. 363) μm long and 113–213 (av. 159) μm wide (Figs. 10–11). An antheridial sorus projects above the cortex and is completely surrounded by the vegetative layers which are composed of the sterile cells (Fig. 12). Initial cell of an antheridium is produced by the elongation of a cortical cell, and later differentiated into an antheridium and a basal stalk cell. Mature antheridium is cylindrical, 63–82 (av. 71) μm high, and 22–31 μm in diameter, and divided into 32–64 tiers and 24–36 locules in each tier to produce 800–2000 antherozoids per each stalk cell. Stalk cells are disc-shaped, 12–16 μm high and 25–



Figs. 10–13. Male plant of *Dictyota linearis*. (MTUF-AL-20070) — 10. Upper part of thallus. scale bar: 1 mm. 11. Surface view of a blade, showing an antheridial sorus. scale bar: 500 μm. 12. A part of an antheridial sorus, showing antheridial locules and peripheral sterile cells layer. scale bar: 100 μm. 13. Cross section of a blade, showing antheridial sori arranged in both sides of a blade, and also showing peripheral sterile cells around and colorless covering cells over a sorus. scale bar: 100 μm.

35 μm wide (Fig. 13). A sorus is covered with a thin and colorless cortical layer until the liberation of antherizoids. After the liberation of antherizoids, stalk cells and peripheral sterile cell layer remain.

Discussion

Hörnig & Schnetter (1988) treated the taxon *Dictyota linearis* from the Mediterranean Sea as the synonym of *D. dichotoma* var. *intricata*. At the present study, the species epithet *D. linearis* would be tentatively used for the Japanese material because there is no information concerning the comparative morphology between the Mediterranean and the Japanese specimens.

Okamura (1913) collected and first described sterile plants of *Dictyota linearis* in Japan and later Noda (1965) reported sterile plants from the Sado Island in the Japan Sea. At present, from the same locality fertile plants which are sporophytes, and both male and female gametophytes were growing mixed in a colony of the collection site. In the present study *Dictyota linearis* was fully described with regard to all kinds of reproductive plants.

Tetrasporangium : The shapes of tetrasporangial sori are diversed among the members of *Dictyota*. Phillips (1988) reported that the elliptical sori of tetrasporangia in *Dictyota diemensis*, and that the tetrasporangia occurred singly or in groups of 2 or 3 and densely scattered over most of the thallus surface in *Dictyota dichotoma*. Foster *et al.* (1972) reported that the rounded and compactly aggregated sori in *D. binghamiae*. Whereas, tetrasporangia of *D. linearis* occur solely and arranged in one or two rows of the upper part of the thallus unlike the above mentioned species.

Phillips (1992) stated that the number of tetrasporangial stalk cells is important as a distinguishing characteristic among the *Dilophus* species which is the most related genus with *Dictyota*. *Dilophus fastigiatus*, *D. rubustus*, *D. mariginatus* have two stalk cells and *D. gunnianus* and *D. intermedius* have one stalk cell. Of the members of *Dictyota* known in the literature (Yabu, 1958; Foster *et al*, 1972), *D. dichotoma* and *D. binghamiae* have one stalk cell at the base of tetrasporangium as observed on *Dictyota linearis* at the present study.

Oogonium : *Dictyota* species have commonly the widely scatterred oogonial sori across the surface of a blade, such as *Dictyota diemensis*, *D. dichotoma* (Phillips, 1988) and *D. binghamiae* (Foster *et al*, 1972). Whereas in *D. linearis*, oogonial sorus are scattered linearly in one row on the surface of a blade as shown in Figs. 7–8. It is considered that the slender blade of *D. linearis* does not provide enough space for the formation of more oogonial sori, the same as the antheridial sorus.

Oogonial sorus is composed of less number of oogonia (8–25 per sorus) in *D. linearis* than 20–100 of *D. binghamiae* (Foster *et al*, 1972).

Antheridium : *Dictyota* species have the widely scatterred antheridial sori across the surface of a blade, such as *Dictyota diemensis* and *D. dichotoma* (Phillips, 1988). In *D. linearis*, antheridial sorus is arranged in one or two rows in the surface of a blade as shown in Fig. 10.

Matsunaga (1966) and Foster *et al.* (1972) described a single basal stalk cell in antheridium in *Dictyota dichotoma* and *D. binghamiae* respectively. In *D. linearis*, an antheridium is also borne on a single basal stalk cell.

Matsunaga (1966) gave a figure of the sterile cells in peripheral area of antheridial sorus of *Dictyota dichotoma* which were long and cylindrical ones attached to antheridial sorus. In *D. linearis*, an antheridial sorus is also surrounded by 2–3 layers of long unicellular sterile cells attached to a sorus as seen in Fig. 13. Furthermore *Dictyota linearis* has a thick colorless cover cells over a sorus (Fig. 13) as not seen in *D. dichotoma* and *D. binghamiae* (Foter *et al.*, 1972).

Acknowledgements

This study was supported by the research grant for 1997–1998 by the Showa

Seitoku Memorial Foundation to J. Tanaka, the first author.

References

Allender, B. M. & Kraft, G. T. 1983. The marine algae of Lord Howe Island (New South Wales): The Dictyotales and Cutleriales (Phaeophyta). *Brunonia*, **6**: 73–130.

Foster, M., Neushul, M. & Chi, E. Y. 1972. Growth and reproduction of *Dictyota binghamiae* J. G. Agardh. *Botanica Marina*, **15**: 96–101.

Hörnig, I. & Schnetter, R. 1988. Notes on *Dictyota dichotoma*, *D. menstrualis*, *D. indica* and *D. pulchella* spec. nova (Phaeophyta). *Phyton* (*Austria*), **28**: 277–291.

Matsunaga, K. 1966. On the male reproductive organ of *Dictyopteris divaricata* (Okamura) Okamura and *Dictyota dichotoma* Lamour. *Bull. Jap. Soc. Phycol.*, **14**: 8–11. (in Japanese)

Noda, M. 1965. The species of Dictyotaceae from Sado Island in the Japan Sea. *Sci. Rep. Niigata Univ. ser. D* (*Biol.*), **2**: 27–35.

Okamura, K. 1913. *Icones of Japanese algae. vol. 3. no. 2.* Maruzen. Tokyo. pp. 25–38.

Okamura, K. 1936. *Nippon Kaisoshi*. Uchida-roukakuho. Tokyo. 964 + 11pp.

Phillips, J. A. 1988. Reproduction in southern Australian species of the Dictyotales (Phaeophyta). *Botanica Marina*, **31**: 437–445.

Phillips, J. A. 1992. Taxonomy and reproduction in Australian species of *Dilophus* (Dictyotales, Phaeophyta). *Aust. Syst. Bot.*, **5**: 657–694.

Womersley, H. B. S. 1987. *The marine benthic flora of southern Australia Part II*. South Aust. Gov. Print. Division, Adelaide. 484 pp.

Yabu, H. 1958. On the nuclear division in tetrasporangia in *Dictyopteris divaricata* (Okamura) Okamura and *Dictyota dichotoma* Lamour. *Bull. Fac. Fish. Hokkaido Univ.*, **8**: 290–296. (in Japanese)

Yoshida, T., Yoshinaga, K. and Nakajima, Y. 1995. Check list of marine algae of Japan (revised in 1995). *Jpn. J. Phycol.* (*Sorui*), **43**: 115–171.