# Culture Studies on *Caulerpa* (Caulerpales, Chlorophyceae) III. Reproduction, Development and Morphological Variation of Laboratory-cultured *C. racemosa* var. *peltata*

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Reproduction, development and morphological variation of the marine green alga Caulerpa racemosa var. peltata from the southern part of Japan were studied in culture in the laboratory. Anisogamous biflagellate male and female gametes were produced monoeciously and copulated with each other. Settled zygotes became spherical and increased in volume. After five weeks, they formed two germ tubes which extended in opposite directions. Both germ tubes became elongated and branched, resulting in the formation of creeping, filamentous, protonema-like plants. These plants formed primary shoots which differentiated into creeping rhizomes and upright axes. Each upright axis successively formed ramuli and developed into an assimilator. The morphology of assimilators, i.e., shape and arrangement of ramuli, varied with culture conditions. The effects of temperature and light intensity on the formation of assimilators were investigated with 25 combinations of 5 temperatures (20.0-30.0 C) and 5 light intensities (0.5-8.0 klux). The morphological plasticity of this alga is identical to that of Caulerpa racemosa var. laetevirens, which was previously described by the present authors. Thus, apparently, the plasticity of this taxon is correlated with environmental factors. It appears, moreover, that C. racemosa var. peltata and C. racemosa var. laetevirens are ecophenes (ecads) of a single species.

Key words: Caulerpa racemosa var. laetevirens — Caulerpa racemosa var. peltata — Chlorophyceae — Development — Morphological Variation — Reproduction

The coenocytic siphonous marine green alga, *Caulerpa racemosa* (Forssk.) J. Agardh, is widely distributed in tropical and temperate waters and exhibits a remarkably high degree of morphological variation. More than sixteen varieties and twelve forms have been recognized (Weber-van Bosse, 1898; Børgesen, 1907, 1925; Taylor, 1928, 1950, 1960; Gilbert, 1942; Eubank, 1946; Egerod, 1975). The plant is characterized as having a prostrate cylindrical rhizome with branched filamentous rhizoids and erect assimilators. The assimilator is an upright axis bearing one or more ramuli. Many forms that are intermediate or transitional between *C. racemosa* var. *peltata* and

other taxa, e.g., C. racemosa var. laetevirens, C. racemosa var. chemnitzia, and C. racemosa var. turbinata, have often been found in the field (Weber-van Bosse, 1898; Børgesen, 1925; Gilbert, 1942; Peterson, 1972). Moreover, there are morphologically complex plants which have, in different portions of the same thallus, characteristics of more than two taxa (Tandy, 1934; Gilbert, 1942; Eubank, 1946; Ohba and Enomoto, 1987).

We studied the life history of *Caulerpa racemosa* var. *laetevirens* in culture and reported that there was a correlation between morphological variation and environmental factors (Enomoto and Ohba, 1987; Ohba and Enomoto, 1987). An unialgal culture experiment using various combinations of temperature and light intensity revealed that well-developed assimilators take the *laetevirens*-type shape when cultured at low temperatures (20.0, 22.5 C) under high light intensities (5.0, 8.0 klux), and the *peltata*-type shape when cultured at both low and high temperatures (20.0-30.0 C) under low light intensities (0.5, 1.5 klux). These results indicate that *C. racemosa* var. *laetevirens* and var. *peltata* are probably morphological variations of a single species (Ohba and Enomoto, 1987). To confirm this hypothesis, we designed an experiment in which three strains of wild *C. racemosa* var. *peltata* were used as mother plants in culture. The present report includes descriptions of the mode of reproduction and development, and life history of this taxon.

#### Materials and Methods

Three strains of *Caulerpa racemosa* var. *peltata* were collected from shaded rocks between the lowest tidal mark and a depth of 5 m at Muroto-misaki (33N, 134E) on Shikoku Island and at Ayamaru-misaki and Ushuku (28N, 130E) on Amami-ôshima Island in May or June between 1982 and 1989. The plants were kept at 25 C under 1.0-3.0 klux with 14L/10D. The procedures for pre-culture of wild plants and isolation of zygotes are described in a previous paper (Enomoto and Ohba, 1987).

For analysis of effects of temperature and light intensity on morphological variation, cross-gradient culture experiments were carried out. In the present experiments, 25 sets of culture conditions were obtained by combinations of 5 temperatures (20.0, 22.5, 25.0, 27.5 and 30.0 C) and 5 light intensities (0.5, 1.5, 3.0, 5.0 and 8.0 klux)\*. These combinations are represented by numbers and letters and schematically shown in Fig. 1. Toshiba daylight fluorescent lamps (6100 K; FL40SD-SDL) were used as the light source. A photoperiod of 14L/10D (06:00-20:00 light / 20:00-06:00 dark) was employed. Zygotes derived from the same plant were cultured at 25 C under 1.5 klux with 14L/10D. After about two months, zygotes grew to filamentous germlings (protonema-like plants) which were about 10 mm in length. Then each

<sup>\*</sup> Conversion of the light intensity (lux) from a white fluorescent tube into photon flux density  $(\mu \text{ mol } m^{-2} \text{ s}^{-1})$  was performed by the method of Lüning (1981) as follows:

 $<sup>1 \</sup>text{ lux} \simeq 0.02 \ \mu \text{ mol } \text{ m}^{-2} \text{ s}^{-1} = 0.02 \ \mu \text{ E} \text{ m}^{-2} \text{ s}^{-1}$ 

Estimates of the light intensities used in the present experiment are 10, 30, 60, 100 and 160  $\mu$  mol m<sup>-2</sup> s<sup>-1</sup> (= $\mu$ E m<sup>-2</sup> s<sup>-1</sup>).

germling was transferred to a glass vessel (90 mm in diameter, 90 mm in height) that contained 350 ml of Provasoli's ES medium (prepared as described by McLachlan, 1973). Three vessels were exposed to each set of conditions mentioned above. The medium was changed every two weeks. After 4 months, the assimilators of the germlings were analyzed morphologically. Crossgradient culture experiments were carried out using germlings derived from the same plant at the same time. Cultures were not axenic, but they were strictly unialgal.

#### Results

#### Field observations and morphology





In Japan, Caulerpa racemosa var. peltata is distributed from Yonakuni-jima Island (24N, 123E) to Tateyama in Chiba Prefecture (35N, 140E) on the Pacific coast, and to the Oki Islands (36N, 133E) in the Sea of Japan (Okamura, 1930, 1936; Yamada and Tanaka, 1938; Kajimura, 1976; Ohba and Aruga, 1982). It is usually found on shady rocks, in hollows, on the undersurfaces of overhanging rocks, and among branches of corals in shallow water, or on unshaded rocks below a depth of 5 m. Morphologically complex plants are often found; peltata-type assimilators are produced on rhizomes in the shade, whereas laetevirens-type assimilators are produced on the same rhizomes exposed to the sun. The peltata-type assimilator consists of an upright axis with shield-form ramuli whose heads are discoidal, while the laetevirenstype assimilator consists of an upright axis with cylindrical ramuli whose heads are obtuse. Intermediate-type assimilators can be found on the same rhizomes at the interface between sun and shade, when plants grow in hollows or on the undersurfaces of overhanging rocks in shallow water.

The morphological characteristics of the wild plants from Ayamaru-misaki, Ushuku and Muroto-misaki (Fig. 2) were almost the same as those described by Eubank (1946). The rhizome was cylindrical, irregularly branched and intricate, 1.0-2.5 mm in diameter, 10-50 cm or more in length, and had *peltata*-type assimilators. The upright axis was cylindrical, simple or branched, 5-15(-25) mm in height, bearing 1-20 ramuli. The ramulus is in the form of a shield with an entire or dentate discoidal head, 1.0-3.0 mm in length, 2.0-7.0 mm in diameter at its discoidal head, and 0.4-1.0 mm in diameter at its stipe.



Figs. 2-17. Reproduction and development of *C. racemosa* var. *peltata.* 2. Wild vegetative plant. 3. Fertile plant with protoplasmic networks, one day before liberation of gametes. 4. Protoplasmic network in a fertile assimilator. 5. Liberation tube (arrow) on a ramulus stipe. 6. Liberation tubes (arrows) on a rhizome. 7. Male gamete. 8. Female gametes, each with a stigma. 9. Male gamete (single arrowhead), female gametes (double arrowheads) and planozygotes (arrows). 10. Planozygote. 11. Settled zygotes, 3 hr after copulation. 12. Spherical body after 17 days. 13. Spherical body after 32 days. 14. Primary germ tube formation, after 35 days. 15. 40-day-old germling extending a primary germ tube. 16. 46-day-old germling, each with a narrow primary germ tube (arrowheads) and a thick secondary germ tube (arrows). 17. 65-day-old germling with two lower thin filaments and one upper thick filament. Arrow indicates the original spherical body. Scale bars: Figs. 2-3, 10 mm; Fig. 4, 500  $\mu$ m; Figs. 5-6, 17, 1 mm; Figs. 7-12, 10  $\mu$ m; Figs. 13-16, 100  $\mu$ m.

## Formation and liberation of gametes

Within about one month after the start of pre-culture, vegetative plants from the field (Fig. 2) became fertile. First signs of maturation were recognized in the evening, three days before the liberation of gametes; the disappearance of homogeneously distributed protoplasm occurred throughout the thallus. Subsequently protoplasmic masses gradually accumulated (Fig. 3) and formed an irregular network by the evening of the day before liberation of gametes (Fig. 4). At that time, the upper portion of the protoplasmic network in each ramulus changed in color from green to dark yellowish green, while the networks in lower portions of ramuli, upright axes and rhizomes remained green. The female gametes with a reddish stigma were formed in the dark yellowish green portion of the plant and the male gametes without a stigma were formed in the green portion. The plants were monoecious.

In the evening of the second day before release of gametes, discharge tubes began to form at the margins of ramulus heads and stipes, at the apex of upright axes, and on the upper surfaces of rhizomes. In the evening of the day before release of gametes, each tube was a simple cylinder,  $150-200-250 \ \mu m$  in diameter and  $1.3-1.5-2.0 \ mm$  in length (Figs. 5, 6). No trabecula was observed in any liberation tube. Release of gametes always took place about 1 hr after the start of illumination in the early morning (around 07:00). Dark-green viscous material containing numerous gametes was released through discharge tubes and precipitated on the bottom of the vessel. After release of gametes, the mother plant lost its contents and faded completely. The plants were holocarpic. Numerous gametes swam out from the viscous material when the medium was gently agitated.

The biflagellate male gametes were relatively small, being 5.2-7.0  $\mu$ m long and 2.2-3.0  $\mu$ m wide (Fig. 7), while the biflagellate female gametes were larger, being 5.8-8.5  $\mu$ m long and 2.7-3.3  $\mu$ m wide (Fig. 8). The flagellum was 8.9-10.0  $\mu$ m in length. The gametes were teardrop-shaped, being pointed at the anterior and rounded at the posterior. They exhibited a weak positive phototactic response.

## Formation of zygotes

After conjugation of male with female gametes, quadriflagellate heart-shaped planozygotes were visible, each with two chloroplasts and a stigma (Figs. 9, 10). These planozygotes then changed to a teardrop shape of 7.5-8.7  $\mu$ m long and 3.9-5.6  $\mu$ m wide, and exhibited a weak negative phototactic response. After swimming actively for a while, they settled on the substratum and became spherical (Fig. 11). Twenty-four hr after settling, the spherical zygotes, 4.1-5.6  $\mu$ m in diameter, still had two chloroplasts and a stigma, but were surrounded by a thin cell wall.

Twenty-four hr after release of gametes, male and female gametes that had not conjugated became spheres of  $2.0-3.5 \ \mu m$  in diameter that rested on the substratum, but they all died within a few days. No parthenogenetic reproduction was observed.

# Germination and development of zygotes

The spherical bodies that developed from the settled zygotes continued to increase in volume for about a month. Seventeen days after the settling of zygotes, the



enlarged spherical bodies had a diameter of  $25-30 \ \mu$ m with many chloroplasts (Fig. 12). After 32 days, they had attained a diameter of  $100-120 \ \mu$ m and each had 300-400 chloroplasts (Fig. 13). After 35 days, they began to produce a primary germ tube,  $25-42 \ \mu$ m in diameter, on the side away from the light (Figs. 14, 15). A few primary germ tubes were sometimes produced from a spherical body. About 10 days later, a secondary germ tube,  $64-88 \ \mu$ m in diameter, appeared on the opposite side (Fig. 16), and then protoplasmic streaming was observed in germlings. Primary and secondary germ tubes gradually differentiated into thinner prostrate filaments and thicker erect filaments, respectively (Fig. 17).

About one month after the formation of germ tubes, germlings developed into prostrate, filamentous protonema-like plants (Fig. 18). After about 45 days, prostrate young plants produced primary shoots of  $300-400 \ \mu$ m in diameter on their creeping filaments (Fig. 19). Most of these shoots developed either directly into assimilators or into creeping rhizomes that later produced assimilators. At 25.0 C under 1.5 klux, assimilators began to form on the rhizome; a shield-form ramulus was found near the apex of an upright axis (Fig. 20). Young plants continued to elongate their rhizomes which gave rise to many assimilators and rhizoids (Fig. 21). The assimilator consisted of an upright axis with one ramulus arising from near its apex. After 3 months, the morphology of well-developed plant was similar to that of the mother plant in having shield-form ramuli (Fig. 22).

When zygotes were inoculated at high density in the vessel, they developed into tufty, sometimes branched, filamentous plants which were similar in morphology to vegetative thalli of *Derbesia* or *Chlorodesmis* (Fig. 23).

About 5 months after the beginning of germ-tube formation, germlings developed into mature plants and became fertile. They repeated the processes of formation and release of gametes and developmental sequences of zygotes in the same manner as those described above.

# Temperature and light intensity cross-gradient experiments

The thalli cultured under 25 different sets of conditions grew sufficiently to allow morphological analysis to be made after four months (Figs. 24-26). The gross morphology of assimilators varied with different culture conditions. Two morphological aspects of the assimilators were compared: (1) shapes of ramuli and (2) arrangement of ramuli on upright axes. In all cases, the upright axes and rhizomes were cylindri-

<sup>Figs. 18-25. Development of C. racemosa var. peltata.
18. Protonema-like plant, 30 days after formation of germ tubes.
19. Primary shoots (arrowheads) arising from creeping filaments, after 45 days.
20-22. Plants with peltata-type ramuli, cultured at 25.0 C under 1.5 klux.
20. After 2 months. Arrowhead indicates the apex of an upright axis.
21. After 75 days. Arrowheads indicate the apex of an upright axis.
22. After 3 months.
23. Tufty filamentous plant, cultured at 25.0 C under 1.5 klux, after 2 months.
24. A plant with</sup> *laetevirens*-type assimilators, cultured at 20.0 C under 8.0 klux, after 5 months.
25. A plant with intermediate-type assimilators, cultured at 20.0 C under 8.0 klux, after 5 months.



Fig. 26 Morphogenetic responses of *C. racemosa* var. *peltata* to various temperatures and light intensities. Scale bar: 2 mm. Refer to Fig. 1 for explanation of symbols.

	A	В	С	D	E		Assimilator form
Light intensity (klux) 20 0.2 0.8 0.9	L C P	L C P	тм	Т <sub>м</sub>	тм	5	L : laetevirens-type I : intermediate-type P : peltata-type Ramulus shape C : cylindrical T : trumpet-form S : shield-form Arrangement P : peltata-type
	L C P	T P	Тм	тм	тм	4	
	L C P	I T D	Тм	тм	тм	3	
	T D	Р	Р	Р "	Тм	2	
	Р	<b>Р</b> ѕм	<b>Р</b> ѕм	Р	Р	D : distichous M : monostichous	
	20.0	22.5	25.0	27.5	30.0		

Fig. 27. Schematic representation of the morphogenetic responses to the cross-gradients of temperature and light intensity that are shown in Fig. 26.

cal. Since there is no morphological difference among the three strains, morphology of the Ushuku strain only is described in detail.

Three types of assimilator were recognized under the 25 different culture conditions: *peltata*-type; *laetevirens*-type; and a type that was intermediate between the *peltata*-type and the *laetevirens*-type. The formation of assimilators was inhibited at 30.0 C, some assimilators being dwarfed.

1) Peltata-type [Fig. 26 and Fig. 27 P(S, M)]:

This type of assimilator developed under 8 combinations of low to high temperature and low light intensity : A(1), B(1, 2), C(1, 2), D(1, 2), E(1). The ramuli showed a shield form with flat discoidal heads and were arranged in a monostichous pattern (solitary or secund) on the upright axis. The overall appearance of well-developed assimilators was similar to that of the mother plants in having shield-form ramuli. 2) Laetevirens-type [Fig. 26 and Fig. 27 L(C P)]:

This type of assimilator developed under 4 combinations of low temperature and high light intensity: A(3, 4, 5) and B(5). The ramuli showed a cylindrical form with obtuse heads and were arranged in a polystichous pattern (tristichous, decussate, or spiroscalate phyllotaxis) on the upright axis. The overall appearance of well-developed assimilators was the same as that of *C. racemosa* var. *laetevirens*.

3) Intermediate-type:

The ramuli showed a trumpet form with obconical heads. The arrangement of the ramuli on the upright axes or the rhizomes varied with the culture conditions, allowing the differentiation of three kinds of intermediate-type assimilators, as follows:

(a) Intermediate-type assimilator with a polystichous arrangement of ramuli [Fig. 27 I(T P)]. This type developed under only one combination of relatively low temperature and high light intensity, namely, B(4).

(b) Intermediate-type assimilator with a distichous (opposite or alternate) arrangement of ramuli [Fig. 26 and Fig. 27 I(T D)]. This type developed under two combinations of low temperature and moderate light intensity, namely, A(2) and B(3).

(c) Intermediate-type assimilator with a monostichous arrangement of ramuli [Fig. 26 and Fig. 27 I(T M)]. This type developed under 10 combinations of moderate to high temperature and moderate to high light intensity, namely, C(3, 4, 5), D(3, 4, 5), E(2, 3, 4, 5).

### Discussion

The occurrence of many intermediate or transitional growth forms of Caulerpa racemosa has caused taxonomic confusion. Results from transplant experiments with Caulerpa in the field led Tandy (1934) to suggest that C. peltata and C. fastigiata might be only ecological forms of C. racemosa. Gilbert (1942) reported many forms that appeared to be intermediate between C. peltata and C. racemosa. Eubank (1946) proposed that C. peltata should be considered as a variety of C. racemosa because of the presence of various transitional forms and of morphologically complex plants. Peterson (1972) stated that the ability of C. racemosa to change its growth form in altered light environments provided evidence for an environmental effect on morphological variability, and he suggested that the varieties of C. racemosa, such as var. peltata (Lamx.) Eubank and var. lamourouxii (Turn.) W.-v. Bosse, should be considered to be ecological phenotypes. Calvert (1976) found that when several taxa of wild Caulerpa plants, which possessed a radial arrangement of newly formed ramuli changed to bilateral.

Studies of *C. racemosa* var. *laetevirens* in culture, using germlings derived from the zygotes of wild plants, revealed that *laetevirens*-type assimilators, which are identical to those present on the mother plants, developed under conditions of low temperatures (20.0, 22.5 C) and high light intensities (5.0, 8.0 klux), while *peltata*-type assimilators were formed at low and high temperatures (20.0-30.0 C) and low light intensities (0.5, 1.5 klux) (Ohba and Enomoto, 1987). Assimilators intermediate between these two types were formed under the other sets of conditions.

The results of the present cross-gradient culture experiment using germlings derived from wild specimens of *C. racemosa* var. *peltata* support the hypothesis that the morphological plasticity of *Caulerpa* is correlated with environmental factors, such as temperature and light intensity. The *peltata*-type assimilators found on the mother plants were formed at low and high temperatures (20.0-30.0 C) and low light intensities (0.5, 1.5 klux), whereas the *laetevirens*-type assimilators were formed at low temperatures (20.0, 22.5 C) and high light intensities (3.0-8.0 klux). Intermediate-type assimilators were formed at low temperatures are sthose of our previous studies summarized above.

We have observed a correlation between the type of assimilator and light intensity

in nature in Japan. Plants with only *peltata*-type assimilators grow on shaded rocks or in deep water while plants with only *laetevirens*-type assimilators grow on sunny rocks in shallow water. An individual plant that extends from a shaded to a sunny habitat is often morphologically complex, with *peltata*-type assimilators produced in the shade, *laetevirens*-type assimilators produced in the sun, and intermediate-type assimilators produced at the interface between sun and shade.

The present observations concerning the process of formation of gametes, the sizes of male and female gametes, the germination process of zygotes, the developmental sequences of germlings, and the process of assimilator formation correspond closely to those made with *C. racemosa* var. *laetevirens* (Enomoto and Ohba, 1987).

From these results it appears that C. racemosa var. peltata (Lamx.) Eubank and C. racemosa var. laetevirens (Mont.) Weber-van Bosse are ecophenes (ecads) of a single taxon of Caulerpa. Moreover, these results suggest that C. racemosa var. chemnitzia and C. racemosa var. turbinata, which are often reported as forms intermediate between C. racemosa var. peltata and C. racemosa var. laetevirens, may be ecophenes of the same taxon.

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#### References

- BØRGESEN, F. 1907. An ecological and systematic account of the Caulerpas of the Danish West Indies. Kgl. Danske Vidensk. Selsk. Skrifter, Ser. 7, 4: 337-392.
- ------. 1925. Marine algae from the Canary Islands. I. Chlorophyceae. Kgl. Danske Vidensk. Selsk., Biol. Medd. 5(3): 1-123.
- CALVERT, H.E. 1976. Culture studies on some Florida species of *Caulerpa*: morphological responses to reduced illumination. Br. Phycol. J. 11: 203-214.
- EGEROD, L. 1975. Marine algae of the Andaman Sea coast of Thailand : Chlorophyceae. Bot. Mar. 18 : 41-66.
- ENOMOTO, S. AND H. OHBA. 1987. Culture studies on *Caulerpa* (Caulerpales, Chlorophyceae) I. Reproduction and development of *C. racemosa* var. *laetevirens*. Jpn. J. Phycol. **35**: 167-177.
- EUBANK, L.L. 1946. Hawaiian representatives of the genus Caulerpa. Univ. Calif. Publ. Bot. 18: 409-432.
- GILBERT, W.J. 1942. Notes on *Caulerpa* from Java and the Philippines. Pap. Mich. Acad. Sci., Arts & Letters 27: 7-26.
- KAJIMURA, M. 1976. On swarmer production in Caulerpa peltata var. peltata from the Oki Islands, Shimane Prefecture. Bull. Jpn. Soc. Phycol. 24: 25-28 (in Japanese with English abstract).
- LÜNING, K. 1981. Light. In C.S. LOBBAN AND M.J. WYNNE, ed., The Biology of Seaweeds, pp. 326-355. Blackwell Sci. Publ.,
- McLachilan, J. 1973. Growth media-marine. In J.R. STEIN, ed., Handbook of Phycological Methods : Culture Methods and Growth Measurements, pp. 25-51. Cambridge Univ. Press, Cambridge.

- OHBA, H. AND Y. ARUGA. 1982. Seaweeds from Ishigaki Island and adjacent islets in Yaeyama Islands, southern Japan. Jpn. J. Phycol. 30: 325-331 (in Japanese with English abstract).
- AND S. ENOMOTO. 1987. Culture studies on Caulerpa (Caulerpales, Chlorophyceae) II.
   Morphological variation of C. racemosa var. laetevirens under various culture conditions.
   Jpn. J. Phycol. 35: 178-188.
- OKAMURA, K. 1930. On the algae from the Island Hatidyo. Rec. Oceanogr. Wk. Japan 2: 92-110, pls. 6-10.
- -----. 1936. Nihon kaisô-shi (Algae of Japan). Uchida Rokakuho, Tokyo (in Japanese).
- PETERSON, R.D. 1972. Effects of light intensity on the morphology and productivity of Caulerpa racemosa (Forsskal) J. Agardh. Micronesica 8: 63-86.
- TANDY, G. 1934. Experimental taxonomy in marine algae, with special reference to Caulerpa. Proc. Linn. Soc. London 146: 63-64.
- TAYLOR, W.R. 1928. The marine algae of Florida with special reference to the Dry Tortugas. Carnegie Inst. Wash. Publ. No. 379: 1-219, pls. 1-37.
- ———. 1950. Plants of Bikini and other northern Marshall Islands. Univ. Michigan Press, Ann Arbor.
- ———. 1960. Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas. Univ. Michigan Press, Ann Arbor.
- WEBER-VAN BOSSE, A. 1898. Monographie des Caulerpes. Ann. Jardin Bot. Buitenzorg 15: 243-401, pls. 20-34.
- YAMADA, Y. AND T. TANAKA. 1938. The marine algae from the Island of Yonakuni. Sci. Pap. Inst. Algol. Res., Fac. Sci., Hokkaido Imp. Univ. 2: 55-86.

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