

## Morphology and Taxonomy of the Japanese *Rhodymeniales* (2). Vegetative Anatomy and Reproductive Organs of *Lomentaria pinnata* (*Lomentariaceae*, *Rhodophyta*)

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Detailed morphological studies have been carried out on *Lomentaria pinnata* Segawa. This is the first report of male gametophytes and carposporophyte development for the species. The hollow thallus, spermatangia which are produced terminally on the mother cells, three-celled carpogonial branch, cystocarp protrudes on the thallus, tetrahedrally divided tetrasporangia, and tetrasporangia are formed in depressed sori, which satisfy the characteristics of the genus *Lomentaria*. While, the small cortical cells which form rosette-like appearance and the transverse septum occurs only at the base of the branches, which satisfy the characteristics of a separate genus *Chondrothamnion*. The breadth of thalli, branching times and presence of stoloniferous holdfast of *L. pinnata* are variable in their habitat. Comparisons of their type specimens confirm that *L. okamurai* is conspecific with *L. pinnata*. (Continued from J. Jpn. Bot. **83**: 11–19, 2008)

**Key words:** *Lomentaria okamurai*, *Lomentaria pinnata*, *Lomentariaceae*, morphology, *Rhodophyta*, *Rhodymeniales*, taxonomy.

The genus *Lomentaria* is characterized as follows: hollow thallus, three-celled carpogonial branch, mature cystocarp protrudes on the thallus, tetrahedrally divided tetrasporangia, and tetrasporangia formed in depressed sori (Lee 1978, Irvine and Guiry 1983, Womersley 1996, Yoshida 1998). Irvine and Guiry (1983) observed that *L. articulata* (Kützinger) Levring, the type species of the genus *Lomentaria*, has multilayered septum, whereas *L. clavellosa*

(Turner) Gaillon and *L. orcadensis* (Harvey) Collins have septa occurring only at the base of the branches. Guiry in Irvine and Guiry (1983) suggested these latter two species to be included in a separate genus, *Chondrothamnion* Kützinger (1843). Le Gall et al.'s (2008) molecular phylogenetic analyses using combined EF2 and LSU rRNA genes suggested that *L. catenata* Harvey is to be separated from *L. articulata*. However, further anatomical and phylogenetic

studies are needed to clarify taxonomic relationships among species of *Lomentaria*.

Okamura (1934a) reported *Lomentaria rosea* (Harvey) Thuret from Jogashima Island, Kanagawa Prefecture. Segawa (1948) later described it as a new species *L. okamurae* distinct from *L. rosea* because of its developed main axis, producing the small cells around the cortical cells, and tetrasporangial sori produced not only on the surface of main branches but also on the lateral branches (pinnate branches), and habitat in the intertidal zone rather than sublittoral zone. Although the name *L. okamurae* was published by Segawa (1948) without Latin description, Yoshida (1980) reassessed the name *L. okamurae* as to be validated by the ICBN, and added English description. On the other hand, Segawa (1938) described *L. pinnata* from Miyakejima Island. According to Segawa (1936, 1938) and Yoshida (1980), *L. okamurae* was distinct from *L. pinnata* because of its broader thallus, less than twice branched blade and the absence of stoloniferous holdfast. These features sometimes make represent morphological variations based on their ambiguousness.

Segawa (1936, as *L. rosea*) and Yoshida (1980) observed habit, vegetative anatomy, cystocarp and tetrasporangia of *L. okamurae*. Segawa (1938) observed habit, cystocarp and tetrasporangia of *L. pinnata*. The structure of male gametophytes and carposporophyte development of *L. okamurae* and *L. pinnata*, however, remain unknown. Recently, we collected *L. pinnata* including male and female gametophytes and tetrasporophytes from Sadamisaki, Ehime Prefecture, and describe here with the detailed morphological features. We also collected *L. pinnata* from Innoshima, Hiroshima Prefecture. The findings allow further examination of the circumscription and taxonomic position of *L. pinnata*.

### Materials and Methods

The collection data of all specimens examined are given in the species account.

Specimens were preserved in 10% formalin/seawater for anatomical observations. Voucher herbarium specimens were deposited at TNS. The specimens were sectioned with a freezing microtome, and the sections were stained with 1% erythrosin or 1% cotton blue, and mounted in 50% Karo light corn syrup. Drawings were made with a camera lucida.

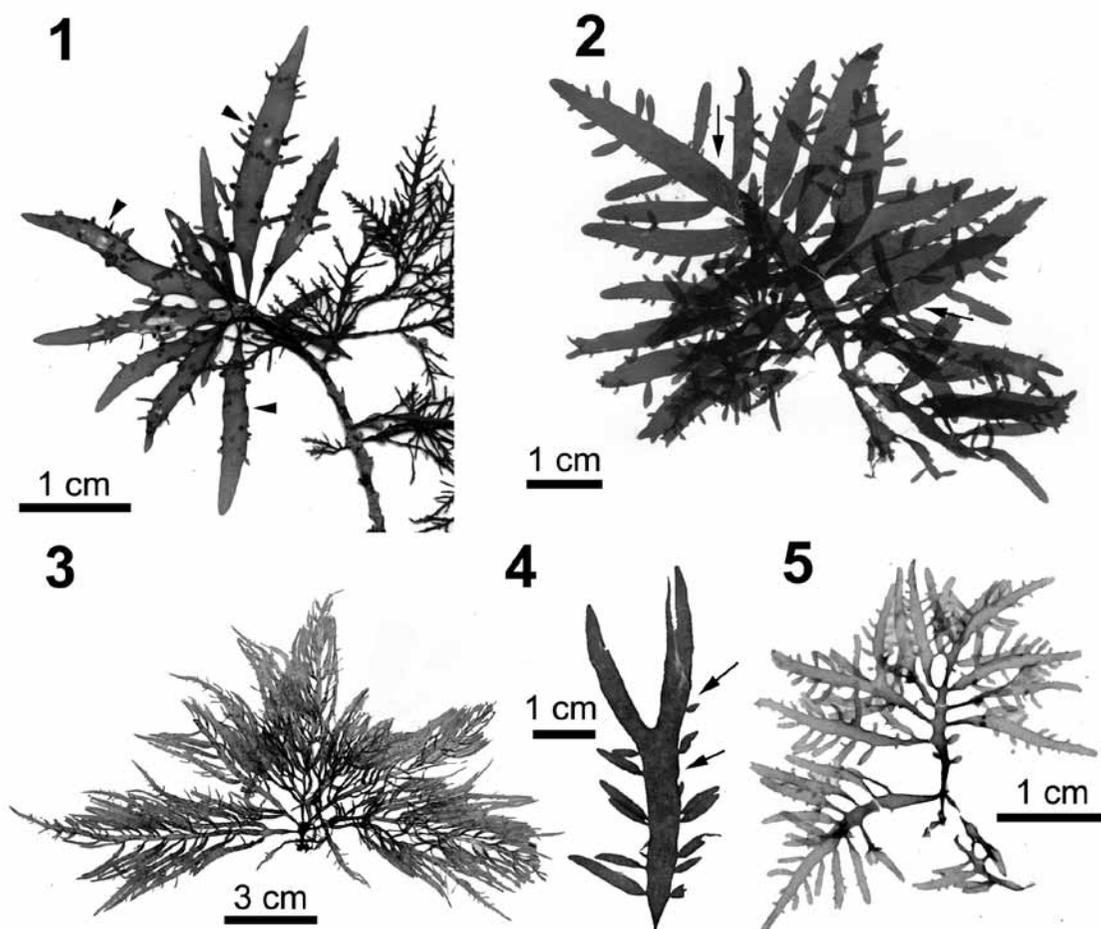
### Results

#### Habitat and habit (Figs. 1–8)

Plants grow on rocks or on the thallus of *Gelidium elegans* Kützinger or *Sargassum piluliferum* C. Agardh or on the leaves of *Zostera* spp. attaching by small discoid holdfast, 0.5 mm in diameter. The holdfast sometimes forms decumbent short rhizoidal stolon (Fig. 7). The thallus is erect, flaccid, flat, membranous, mucilaginous, yellowish to blight red, 2 to 4.5 cm, up to 9 cm in height, one to three times branched dichotomously with percurrent axes (Figs. 6–8). Lateral branches are more or less pinnately branched. The short branchlets are alternately or oppositely produced at the margins of lateral branches. The width of axes is variable within 1 to 6 mm. The branches are flat, spatulate, tapering to the obtuse apex, constricted at the base, 0.5 to 5 mm wide. The branchlets are flat, rarely constricted at the base, 1 to 5 mm long, 0.5 to 1 mm wide. The specimen was adhered to paper in drying.

#### Vegetative anatomy (Figs. 9–11)

The thallus is multiaxial, hollow, composed of one-layered cortex and one or two-layered medulla surrounding the central cavity (Fig. 9). Cortical cells are rectangular, uniform and regularly arranged, 20 to 43  $\mu\text{m}$  long, 12 to 31  $\mu\text{m}$  wide, 17 to 42  $\mu\text{m}$  thick, and cut off the small cortical cells around them. The small cortical cells are spherical to polygonal, 8 to 11  $\mu\text{m}$  long, 4 to 10  $\mu\text{m}$  wide. In surface view, the small cortical cells around cortical cells form rosette-like appearance (Fig. 10). Medullary cells are elongated rectangular, 16 to 38  $\mu\text{m}$  long,

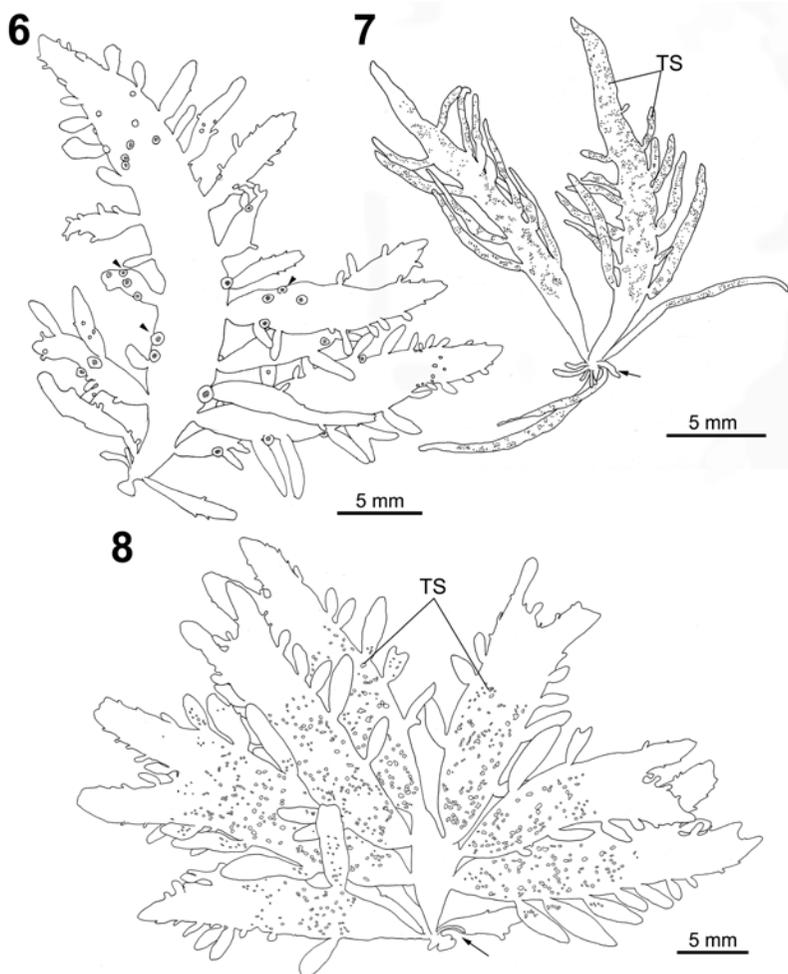


Figs. 1–3. *Lomentaria pinnata* Segawa: Herbarium specimens. 1. Cystocarpic plant from Okinoshima, Tateyama, Chiba Pref., 1 Mar. 2007 (TNS-AL-163994). Cystocarps (arrowheads) protrude from the surface of axes. 2. Tetrasporangial plant from Myojin, Ikata, Nishiuwa, Ehime Pref., 18 Feb. 2006 (TNS-AL-163991). Tetrasporangial sori (arrows) are scattered on the surface of axes and branches. 3. Tetrasporangial plant from Yaekojima, Innoshimaoohama, Onomichi, Hiroshima Pref., 9 Aug. 2006 (SAP 102114). The plant is branched three times. Fig. 4. *Lomentaria okamurae* Segawa: Toji, Shimoda, Shizuoka Pref., 22 Apr. 1937 (SAP 061724, holotype). Tetrasporangia (arrows) scattered on the surface of axes. Fig. 5. *Lomentaria pinnata* Segawa. Miyakejima, Tokyo Pref., Mar. 1936 (SAP 061739, holotype).

9 to 16  $\mu\text{m}$  wide. Innermost medullary cells (longitudinal filaments) longitudinally border the cortical cells, and solely bear secretory cells (gland cells). Secretory cells are spherical to pyriform, 8 to 15  $\mu\text{m}$  long, 6 to 13  $\mu\text{m}$  wide. The transverse septum occurs only at the base of the branch or branchlet (Fig. 11).

#### Male gametophyte (Fig. 12)

The gametophytes are dioecious. Spermatangia are developed in sori over the surface of upper parts of branches. Cortical cells cut off one to three spermatangial mother cells from their upper corners. Primary mother cells cut off laterally one to two secondary mother cells. Spermatangia are produced terminally on



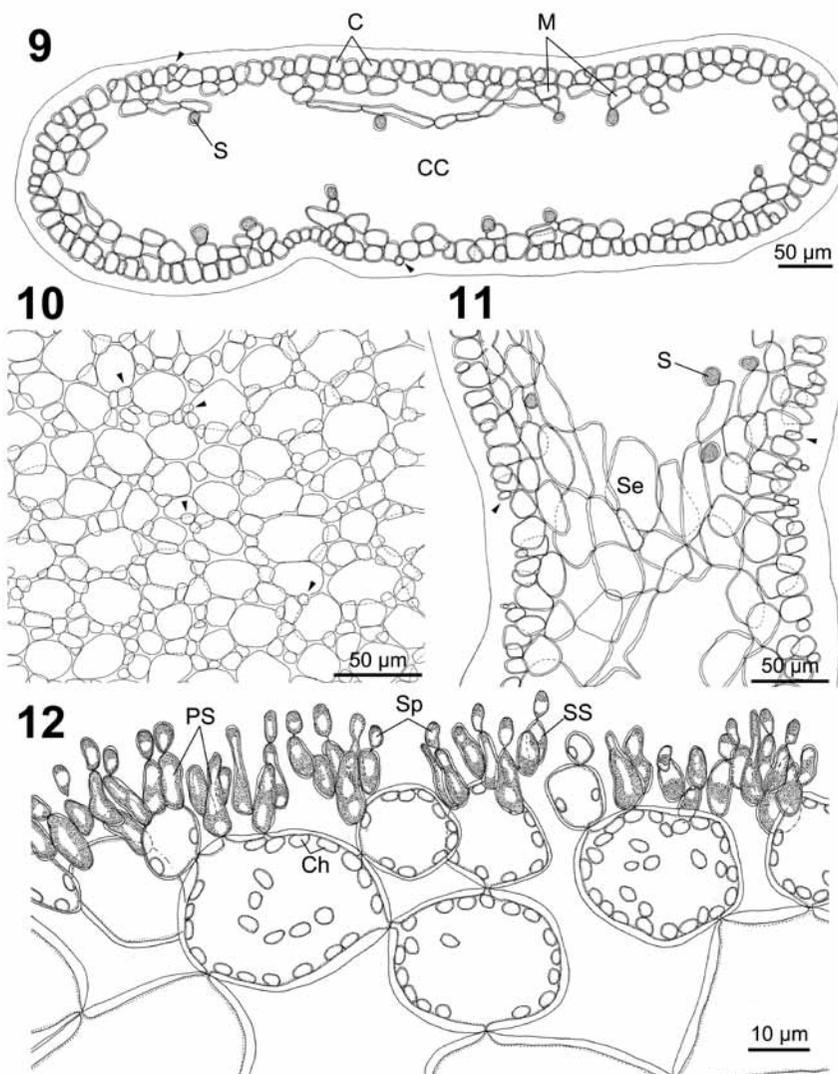
Figs. 6–8. *Lomentaria pinnata*: Habit. 6. Cystocarpic plant. Cystocarps (arrowheads) protrude from the surface of thallus, and are scattered on the axis and lateral branches. 7, 8. Tetrasporangial plants. Tetrasporangial sori (TS) are produced on the surface of axes, lateral branches and branchlets. 7. Small plant with narrow axes from Innoshimaoohama, Onomichi, Hiroshima Pref. Arrow indicates a short rhizoidal stolon produced from discoid holdfast. 8. Plant with broad axes from Myojin, Ikata, Nishiuwa, Ehime Pref.

both primary and secondary mother cells by centripetal constriction (Fig. 12). The primary mother cell rarely contains plastids, and is elongate rectangular or lanceolate with round apex, often slackly constricted at the center or upper part, 10 to 13  $\mu\text{m}$  long, 4 to 7  $\mu\text{m}$  wide. The secondary mother cell is smaller than the primary one, 7 to 13  $\mu\text{m}$  in long, 3  $\mu\text{m}$  wide. Mature spermatia lack plastids, and are elliptical

or orbicular, 4 to 5  $\mu\text{m}$  long, 2 to 3  $\mu\text{m}$  wide.

#### Female gametophyte (Figs. 1, 6, 13–18)

The procarp is composed of a three-celled carpogonial branch and a two-celled auxiliary cell branch (Figs. 13, 14). The supporting cell is uniform with a small cell cut off from cortical cell, 10 to 13  $\mu\text{m}$  long, 8 to 10  $\mu\text{m}$  wide. The first and second cell of carpogonial branch are

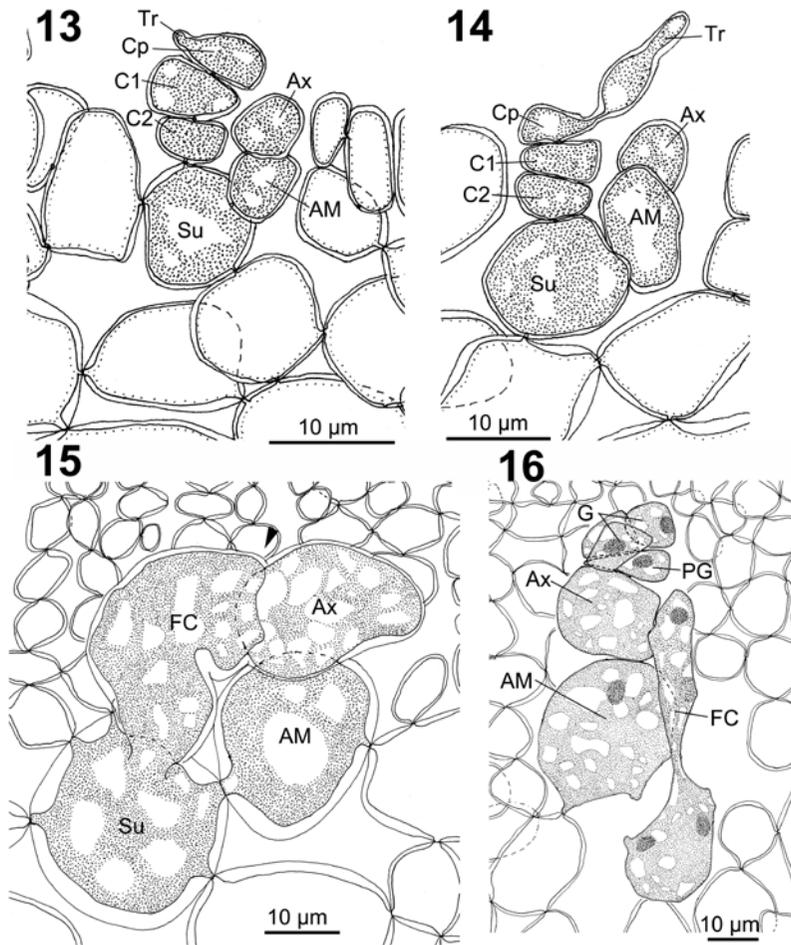


Figs. 9–12. *Lomentaria pinnata*. 9–11. Vegetative anatomies. 9. Transverse section of the thallus (S, secretory cell). The thallus is hollow, composed of one-layered cortex (C) and one or two-layered medulla (M) surrounding the central cavity (CC). 10. Surface view of thallus. The small cortical cells (arrowheads) around cortical cells form rosette-like appearance. 11. Longitudinal section at the base of branch. The transverse septum (Se) occurs only at the base of the branch. 12. Spermatangia (Sp) are produced terminally on both primary (PS) and secondary mother cells (SS) (Ch, chloroplast).

rectangular, 5 to 7  $\mu\text{m}$  long, 3 to 4  $\mu\text{m}$  wide. The carpogonium is conical, 7  $\mu\text{m}$  long, 4  $\mu\text{m}$  wide at the base, and contains distally a trichogyne. The trichogyne is club-shaped, protruded slantingly from the terminal of carpogonia. The

auxiliary mother cell is oblong, 6 to 11  $\mu\text{m}$  long, 4 to 7  $\mu\text{m}$  wide. The auxiliary cell is spherical to oval, 6  $\mu\text{m}$  long, 5  $\mu\text{m}$  wide.

Upon fertilization, the supporting cell, auxiliary mother cell and auxiliary cell enlarge,



Figs. 13–16. *Lomentaria pinnata*: Carposporophyte developments in young stage. 13, 14. The procarp is composed of a three-celled carpogonial branch and a two-celled auxiliary cell branch. AM. Auxiliary mother cell. Ax. Auxiliary cell. Cp. Carpogonium. C1–C2. The first to second cell of the carpogonial branch. Su. Supporting cell. Tr. Trichogyne. 15. Upon fertilization, the supporting cell, auxiliary mother cell and auxiliary cell enlarge, and the cells of the carpogonial branch fuse. Arrowhead indicates that the fused carpogonial branch (FC) directly contacts with the auxiliary cell. 16. The primary gonimoblast (PG) is cut off transversely from the auxiliary cell. Then the diploid nucleus migrates into the auxiliary cell, the carpogonial branch is fused with the supporting cell, and form a column-like fusion cell (G, gonimoblast filament).

and the cells of the carpogonial branch fuse. The fused carpogonial branch directly contacts the auxiliary cell (Fig. 15). The primary gonimoblast is cut off transversely from the auxiliary cell. Then the diploid nucleus migrates into the auxiliary cell, the carpogonial branch is fused with the supporting cell and form a column-like

fusion cell (Fig. 16), and the auxiliary mother cell is fused with the auxiliary cell and some vegetative cells around the procarp, forming a large trunk-like fusion cell (Figs. 17, 18).

The gonimoblast filaments develop outwardly from the fusion cell, forming a globose carposporophyte (Figs. 17, 18). As the

carposporophyte develops, the gonimoblast cells grow, and they are completely transformed into carposporangia.

The carposporophyte is covered with pericarp. Upon fertilization, the cortical cells around the procarp begin to divide, and elongate outwards.

Each sessile cystocarps protrude from the surface of thallus, and are scattered on the axes or lateral branch (Figs. 1, 6). Mature cystocarps are urceolate with an ostiole, 0.3 to 0.5 mm long, 0.5 to 0.8 mm wide.

### Tetrasporophyte (Figs. 2, 7, 8, 19)

The tetrasporophyte and gametophyte are isomorphic (*Polysiphonia*-type life history). Tetrasporangial sori are produced on the surface of axes, lateral branches and branchlets (Figs. 2, 7, 8). Tetrasporangia are terminally produced on cortical cells, tetrahedrally divided, and formed in the depressed sori (Fig. 19). Mature tetrasporangia are obovate, 112  $\mu\text{m}$  long, 94  $\mu\text{m}$  wide.

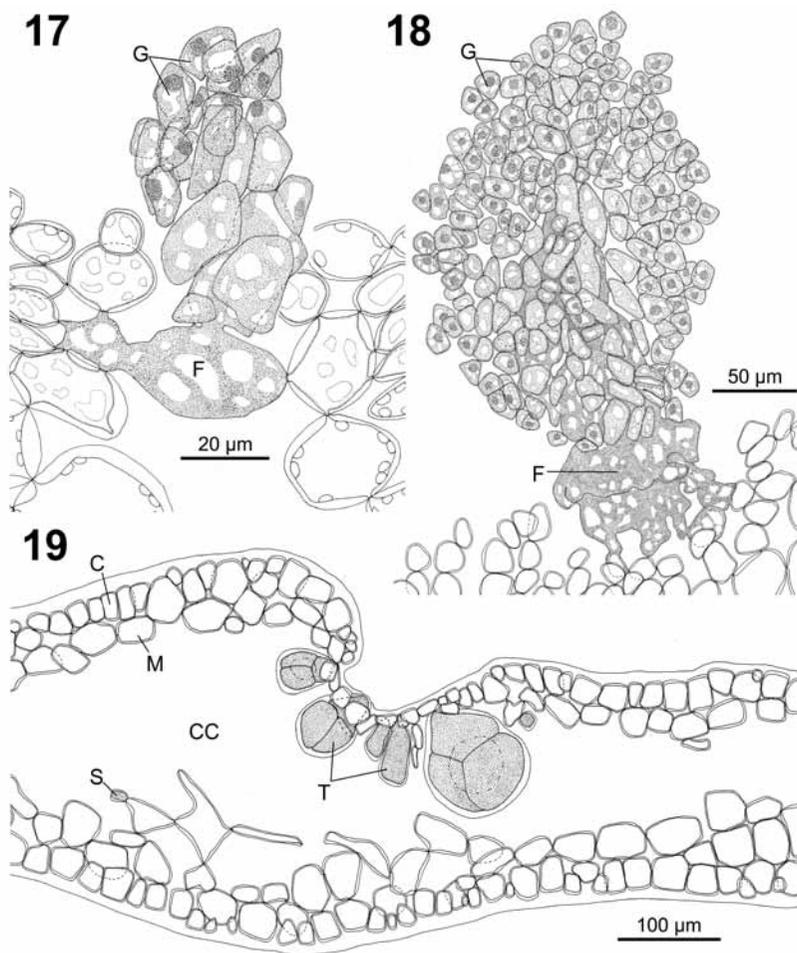
## Discussion

*Lomentaria pinnata* has hollow thallus, three-celled carpogonial branch, mature cystocarp protrudes on the thallus, tetrahedrally divided tetrasporangia, and tetrasporangia formed in depressed sori. These characteristics satisfy the characteristics of the genus *Lomentaria* (Lee 1978, Irvine and Guiry 1983, Womersley 1996 and Yoshida 1998). However, *L. articulata* the type species of genus *Lomentaria* and some other species such as *L. catenata* and *L. hakodatensis* have transverse septa constricting the medullary cavity at regular intervals (Lee 1978, Irvine and Guiry 1983). Others, such as *L. australis* (Womersley 1996), *L. clavellosa* and *L. orcadensis* (Irvine and Guiry 1983), *L. lubrica* (Suzuki and Yoshizaki 2008) and *L. pinnata* have septa borne only at the base of branches and branchlets. Guiry in Irvine and Guiry (1983) suggested removal of this latter series to a separate genus, *Chondrothamnion*

Kützing (1843). Furthermore, *rbcL* and combined SSU rRNA and *rbcL* analyses suggested that *L. pinnata* is strongly separated from *L. articulata* (Suzuki unpublished). In accordance with Guiry's opinion, *L. pinnata* should also be transferred to genus *Chondrothamnion*. Further study is required and should include *L. clavellosa* the type species of the genus *Chondrothamnion*.

Male gametophytes and carposporophyte development in *Lomentaria pinnata* are here reported for the first time for the species, while all others observed are in accordance with Segawa (1936, 1938) and Yoshida (1980). The development of spermatangia of *L. pinnata* is in accordance with those of *L. hakodatensis* (Tazawa 1975 and Lee 1978) and *L. lubrica* (Suzuki and Yoshizaki 2008). The structure of procarp and carposporophyte development are in accordance with those of *L. articulata* (Bliding 1928), *L. catenata* and *L. hakodatensis* (Lee 1978) and *L. lubrica* (Suzuki and Yoshizaki 2008).

According to Segawa (1936, 1938) and Yoshida (1980), *L. okamurae* was distinct from *L. pinnata* because of its broad thallus, less than twice branched blade and the absence of stoloniferous holdfast. However, these features represent morphological variations, which result in their ambiguousness of these two species (see Table 1). The materials from Hiroshima Prefecture often form narrow blades, twice to third branched (Fig. 3), and sometimes have stoloniferous holdfast (Fig. 7). These characteristics are corresponded to the type specimen (Fig. 5) and original description of *L. pinnata* (Segawa 1938), although Hiroshima's materials sometimes represent a form of broad blades without branching which correspond to *L. okamurae*. While, the materials from Ehime Prefecture which form broad blades without branching (Fig. 2) correspond to the type specimen (Fig. 4) and original description of *L. okamurae* (Yoshida 1980). Therefore, we consider *L. okamurae* and *L. pinnata* to be



Figs. 17–19. *Lomentaria pinnata*. 17, 18. Carposporophyte development. The auxiliary mother cell is fused with the auxiliary cell and some vegetative cells around the procarp, forming a large trunk-like fusion cell (F). The gonimoblast filaments (G) develop outwardly from the fusion cell, forming a globose carposporophyte. 19. Tetrasporangia (T) are terminally produced on cortical cells, tetrahedrally divided, formed in the depressed sori. C. Cortex. CC. Central cavity. M. Medulla. S. Secretory cell.

conspecific, and propose to include *L. okamurae* in *L. pinnata* as a synonym.

#### Taxonomic conclusion

***Lomentaria pinnata*** Segawa in Sci. Pap. Inst. Algol. Res., Hokkaido Univ. **2**: 148. f. 7 (1938) – Yoshida, Mar. Alg. Jpn. 838. pl. 3-78, f. B (1998).

*Lomentaria okamurae* Segawa, Kagaku:

231 (1948) – Yoshida in J. Jpn. Bot. **55**: 310. f. 1–4 (1980); Mar. Alg. Jpn. 838. pl. 3-78, f. A (1998).

*Lomentaria rosea* auct. non (Harvey) Thuret: Okamura in Shokubutsu oyobi Dobutsu **2**: 1725, f. 1 (1934); Bot. Mag. (Tokyo) **48**: 886 (1934) – Segawa in Sci. Pap. Inst. Algol. Res., Hokkaido Univ. **1**: 185. f. 6 (1936).

Japanese name: Hiroha-fushitsunagi.

Table 1. Comparison of main morphological characteristics between *Lomentaria okamurae* and *L. pinnata*

	<i>L. okamurae</i>	<i>L. okamurae</i>	<i>L. pinnata</i>	<i>L. pinnata</i>
Source	Type collection	Ehime Pref.	Hiroshima Pref.	Type collection
Holdfast	discoid without stolon	discoid with short stolon	discoid with short stolon	discoid with short stolon
Height	5 cm	4–5 cm	3–4.5(–7) cm	2–3 cm
Width of axis	3–4 mm	2–6 mm	1–1.5(–3) mm	1–1.5 mm
Branching time	0–1	0–1(–2)	1–3	2–3
Cortex	two-celled layer	two-celled layer	two-celled layer	—
Small cell	many	many	many	—
Spermatangium	—	same as <i>Lomentaria</i>	—	—
Carposporophyte development	—	<i>Lomentaria</i> -type	<i>Lomentaria</i> -type	—
References	Segawa (1936) Yoshida (1980)	present study	present study	Segawa (1938)

Type locality: Miyakejima Island, Tokyo Pref., Japan.

Geographical distribution: Japan: the central part of the Pacific coast of Honshu (Chiba Pref. to Mie Pref.), Niigata Pref. (Noda 1987), Toyama Pref. (Fujita 2001), Seto Inland Sea; South-west Asia: Philippine (Silva et al. 1987).

Specimens examined: Miyakejima, Tokyo Pref., Mar. 1936, S. Segawa (SAP 61739, holotype of *Lomentaria pinnata*); Touji, Shimoda, Shizuoka Pref., 22 Apr. 1937, tetrasporangial, S. Segawa (SAP 61724, holotype of *Lomentaria okamurae*); Hamajima, 34°18'N, 136°45'E, Shima, Mie Pref., 13 Mar. 1971, S. Hiraide (TNS-AL-163990); Myojin, 33°24'N, 132°07'E, Ikata, Nishiuwa, Ehime Pref., 18 Feb. 2006, M. Suzuki (TNS-AL-163992; spermatangial, TNS-AL-163991; tetrasporangial); Yaekojima, 34°20'N, 133°11'E, Innoshimaoohama, Onomichi, Hiroshima Pref., 9 Aug. 2006, tetrasporangial, Y. Yamagishi (TNS-AL-163993, SAP 102114); Okinoshima, 34°59'N 139°49'E, Tateyama, Chiba Pref., 1 Mar. 2007, cystocarpic, M. Suzuki (TNS-AL-163994).

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*okamurae* and *L. pinnata* at SAP. We thank two anonymous reviewers for valuable comments on this manuscript. We also thank Dr. Max H. Hommersand of The University of North Carolina at Chapel Hill and Dr. Lin Showe-Mei of National Taiwan Ocean University for improving this manuscript.

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日本産マサゴシバリ目の分類学的研究 (2). ヒロハフシツナギ (紅藻, フシツナギ科) の体構造と生殖器官

ヒロハフシツナギの体構造と生殖器官の詳細を観察した。本種の雄性配偶体と果孢子体形成過程は初報告である。本種の中空な体、雌雄生殖器官、四分孢子体の構造はフシツナギ属 *Lomentaria* の特徴に当てはまるが、本種は皮層細胞が周りに小細胞を生じ、枝の付け根を除き内腔を仕切る隔壁を持たず、これらの特徴は *Chondrothamnion* 属の特徴と一致する。*Lomentaria okamurae* と *L. pinnata* は、体の幅、分枝の回数、仮根枝の有無によって区別されてい

たが、これらの特徴は生育地によって変わることから、形態的な変異と考えられる。タイプ標本の比較を基に、*Lomentaria okamurae* を *L. pinnata* のシノニムとした。

*Lomentaria pinnata* の和名はヒメフシツナギであるが、精査した標本の多くが *L. okamurae* に相当したことから、*L. okamurae* の和名であるヒロハフシツナギを本種の和名とした。

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