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## The genus *Prionitis* (Halymeniaceae, Rhodophyta) in Japan

Shigeo KAWAGUCHI\*

The vegetative morphology and reproductive development of nine members of the Halymeniaceae from Japan are described and illustrated. The nine species have in common a combination of the following characters: (1) absence of midribs, (2) the texture rigid cartilaginous, (3) the cortex and medulla compact, with the transitional region occupied by large, polygonal to rounded cells, (4) no refractive cells in the medulla, (5) reproductive structures confined to the ultimate or penultimate segments of main branches, and/or to the proliferous branchlets, or to the minute proliferations (sporophylls) and (6) auxiliary cell ampullae sparingly branched to the second order.

This combination of characters is consistent with *Prionitis lanceolata* (HARVEY) HARVEY (the type species of *Prionitis* J. AGARDH). Comparison is made to other related genera such as *Polyopes* J. AGARDH, *Cryptonemia* J. AGARDH, *Carpopeltis* SCHMITZ or *Grateloupia* C. AGARDH, and it is concluded that the genus *Prionitis* is distinct from these genera. The following nine species are therefore properly accommodated in the genus *Prionitis*: *P. patens* OKAMURA, *P. angusta* (HARVEY) OKAMURA, *P. elata* OKAMURA, *P. articulata* OKAMURA, *P. schmitziana* OKAMURA, *P. cornea* (OKAMURA) DAWSON, *P. divaricata* (OKAMURA) KAWAGUCHI comb. nov. [= *Carpopeltis divaricata* OKAMURA], *P. crispata* (OKAMURA) KAWAGUCHI comb. nov. [= *Carpopeltis crispata* OKAMURA], *P. ramosissima* (OKAMURA) KAWAGUCHI comb. nov. [= *Grateloupia ramosissima* OKAMURA]. Key to these species is provided.

The genus *Prionitis* J. AGARDH nom. cons. (1851, p. 185) includes approximately 30 species and varieties, mainly from the Pacific Ocean (CHIANG, 1970). In 1899, OKAMURA described five species of *Prionitis* from Japan: *P. patens* OKAMURA, *P. angusta* (HARVEY) OKAMURA, *P. elata* OKAMURA, *P. articulata* OKAMURA and *P. schmitziana* OKAMURA. Of these, *P. angusta*, *P. elata* and *P. articulata* were later transferred to *Carpopeltis* and *P. schmitziana* to *Cryptonemia* by OKAMURA (1909, 1910) on the basis of habit, substance or vegetative structure. Only one species, *P. patens* remained accredited to this genus from Japan and its adjacent waters.

*Prionitis* has been separated from other genera within the family Haly-

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meniaceae on one or more of the following characters: major branches without midribs and approximately the same breadth throughout; peglike or foliar proliferous branchlets produced from the margin or from the surfaces of the thallus; cortex and medulla compactly constructed, with the transitional region between them usually occupied by large rounded or polygonal cells; and reproductive structures confined to the ultimate segments and/or to the lateral proliferous branchlets, or to specially developed small proliferations called sporophylls (Cf. SCHMITZ & HAUPTFLEISH, 1897; OKAMURA, 1936; DAWSON, 1954; KYLIN, 1956; ABBOTT & HOLLENBERG, 1976). However, these characters are also found in certain species of *Carpopeltis* SCHMITZ, *Cryptonemia* J. AGARDH and *Polyopes* J. AGARDH, and the genus *Prionitis* is therefore not clearly differentiated from these genera.

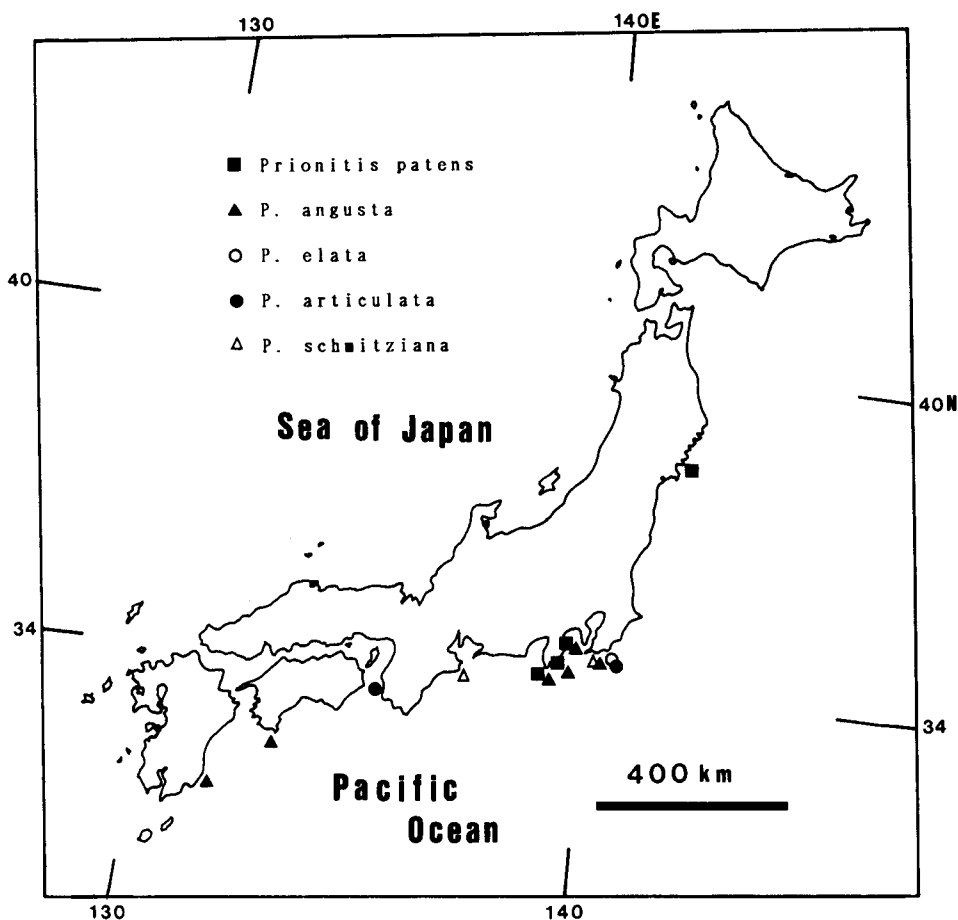


Fig. 1. Collection localities of *Prionitis* species.

The uncertainties surrounding the generic circumscription of *Prionitis* suggested the need for a critical re-examination of *Prionitis* and allied genera. SJOESTEDT (1926) and CHIANG (1970) published detailed morphological observations on the vegetative and reproductive structures of the type species *P. lanceolata* (HARVEY) HARVEY. In the present study, the Japanese species related to *Prionitis* have been vegetatively and reproductively examined in comparison with the type species, to contribute a better understanding of the genus. Nine species including the five species mentioned above, *Prionitis cornea* (OKAMURA) DAWSON, and the following three new combinations are treated below: *Prionitis divaricata* (OKAMURA) KAWAGUCHI, comb. nov. [*Carpopeltis divaricata* OKAMURA], *Prionitis crispata*

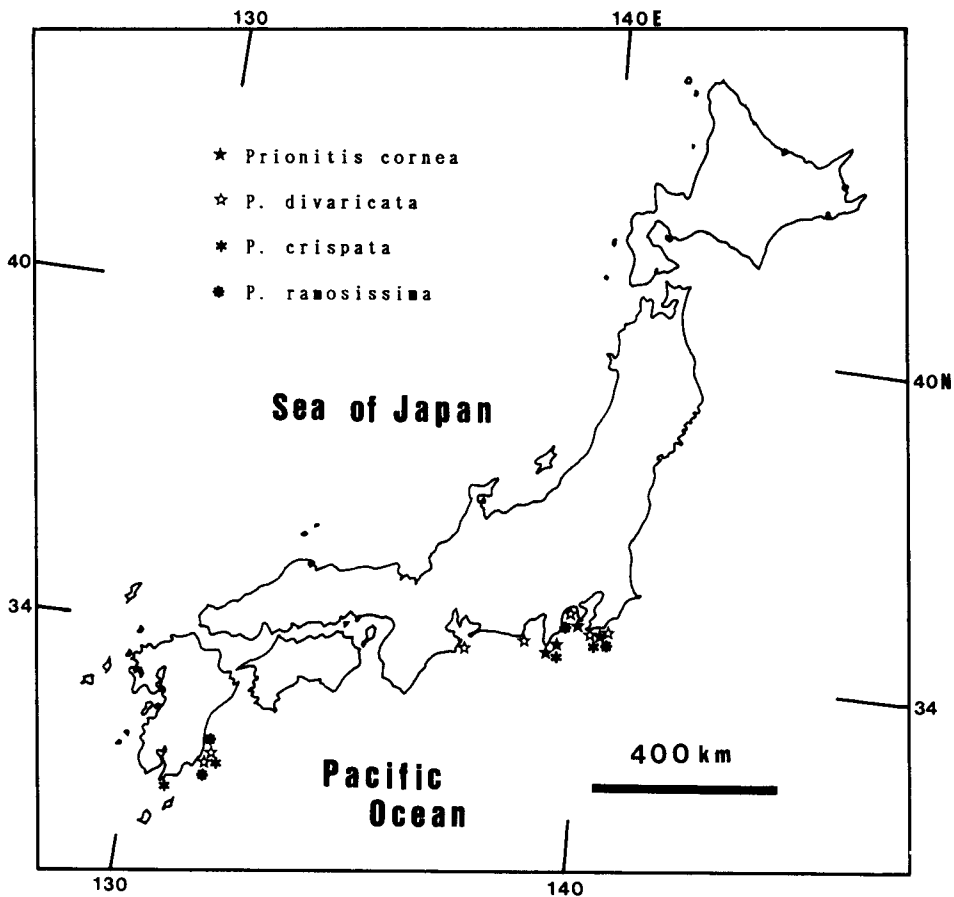


Fig. 2. Collection localities of *Prionitis* species (cont.).

(OKAMURA) KAWAGUCHI, comb. nov. [*Carpopeltis crispata* OKAMURA] and *Prionitis ramosissima* (OKAMURA) KAWAGUCHI, comb. nov. [*Grateloupia ramosissima* OKAMURA]. In addition, some comments on generic recognition of related genera, including *Carpopeltis*, *Cryptonemia*, *Polyopes* and *Grateloupia* are given.

### Materials and methods

Observations were made on either ca. 5 % formalin/seawater-preserved specimens or dried herbarium specimens. Dried specimens were resoaked in seawater or freshwater before sectioning. Sections were made by hand using a razor blade, then stained with 0.5 % (w/v) cotton blue in phenol/lactic acid/ glycerol/ water (1 : 1 : 1 : 1) solution, and mounted on slides in a glycerol-seawater mixture. Some reagents for squash preparation, such as NaOH, HCl or HNO<sub>3</sub>, were tried, but none were effective in softening the materials. The voucher specimens used in the present study are housed in the herbarium of the Department of Botany, Faculty of Science, Hokkaido University, Sapporo (SAP).

### Observations

#### *Prionitis patens* OKAMURA

Figs. 3-6

OKAMURA, 1899, p. 3, pl. 1, figs. 18-20, 1909, p. 73, 1936, p. 548. DE TONI, 1905, p. 1592.

Type : SAP (Okamura herb.)

Type locality : Mikawa, Aichi Prefecture

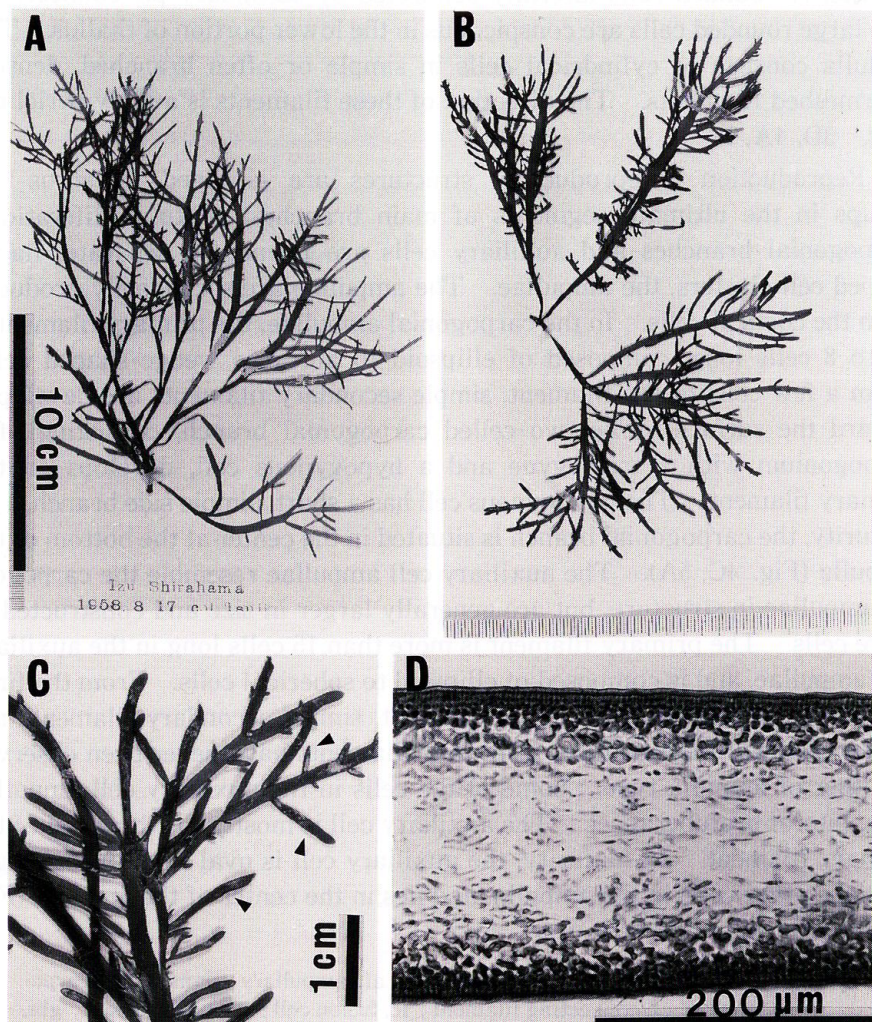
Distribution : Endemic

Japanese name : Hirakintoki

Materials examined : *Honshu* : cystocarpic, spermatangial, tetrasporangial, Shirahama, Shizuoka Prefecture, 17, viii, 1958, leg. Y. Tsuji, SAP 047388-94 ; tetrasporangial, Suzaki, Shizuoka Pref., 15, viii, 1958, leg. Y. Tsuji, SAP 047395-6 ; sterile, Shirahama, Shizuoka Pref., 21, v, 1966, leg. M. Yoshizaki, SAP 031307 ; sterile, Enoshima, Kanagawa Pref., 4, iv, 1926, leg. anonymous, SAP 20801 ; tetrasporangial, Yonezaki, Iwate Pref., 3, vi, 1954, leg. S. Kawashima, SAP 027843 (Fig. 1).

Vegetative structure --- The plant arises from a scutate holdfast through a short but rather thick cylindrical stipe, gradually expanding into a compressed, linear-lanceolate thallus, up to 20 cm high. The thallus branches in a dichotomous or at times trichotomous manner with patent axils and each segment, up to 7 mm wide, is generally slightly tapered at both ends.

Numerous proliferations are produced from the margin in a pinnate manner with patent axils. Some of the proliferations continue to grow into branchlets which are in turn beset with short proliferations, giving the branchlets almost the same appearance as the main branches. The apices are simply ligulate or bifurcate. The texture is cartilaginous and becomes firmer when dried. The color is usually purplish red or in some specimens reddish brown



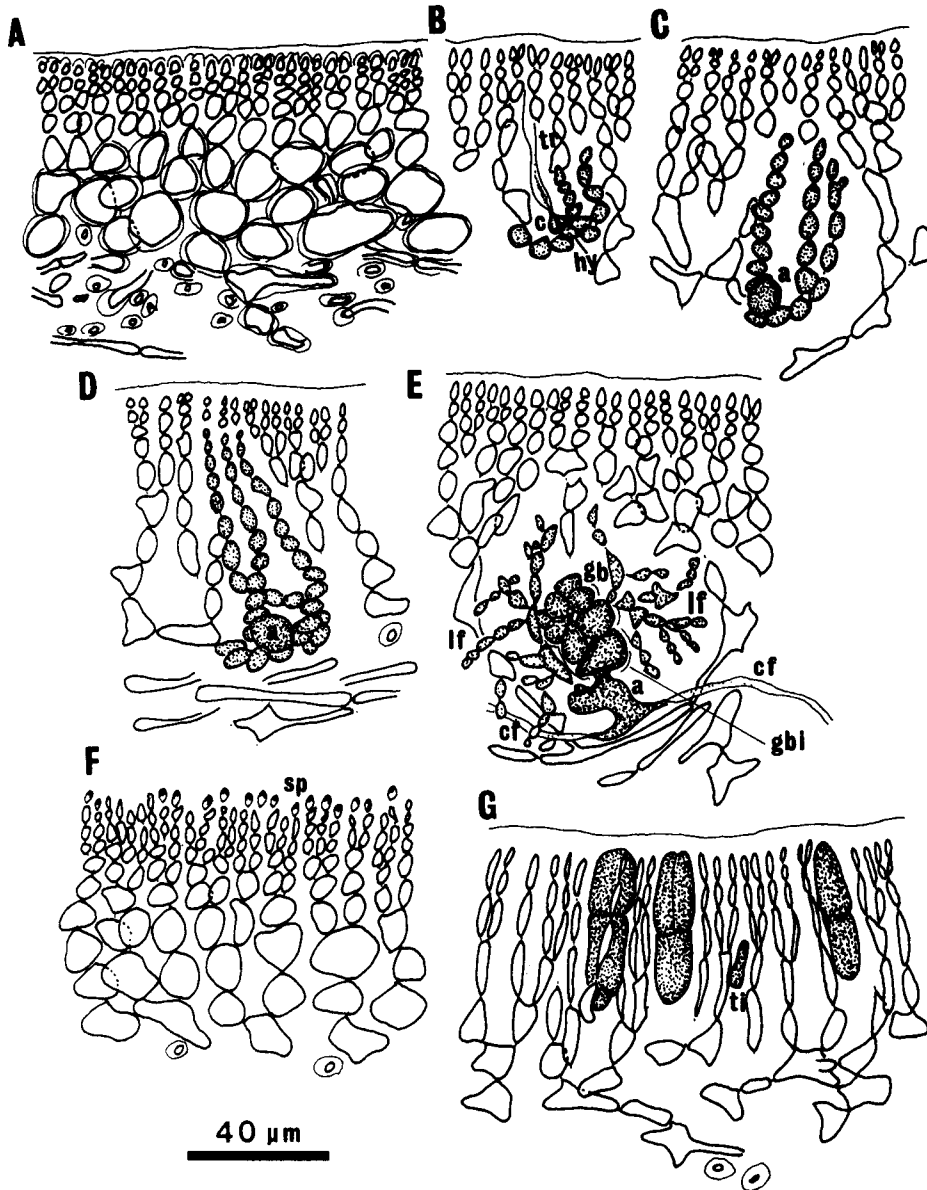
**Fig. 3.** *Prionitis patens* OKAMURA. A, B. Habit of dried tetrasporangial specimens showing patent branchlets (*Kawaguchi* 1003-4). C. Portion of B, showing proliferous short branchlets (arrowheads). D. Transverse section of upper portion of thallus. Scale in A applies to B.

(Fig. 3A-C).

The thallus in section is 250-500  $\mu\text{m}$  thick (gradually becoming thinner toward the apex) and is composed of cortical and medullary layers. The cortex consists of up to 15 cells and is separable into two layers. The outer cortex consists of 5-9 ellipsoid to somewhat cuboidal cells tightly packed in anticlinal rows. This layer connects to an inner cortex of larger, irregular, stellate, or rounded cells laterally connected by secondary pit-connections. The large rounded cells are conspicuous in the lower portion of thallus. The medulla consists of cylindrical cells in simple or often branched, densely intermeshed filaments. The direction of these filaments is mainly periclinal (Fig. 3D, 4A, B)

Reproduction --- Reproductive structures are confined to sorus-like groups in the ultimate segments of main branches, or to proliferations. Carpogonial branches and auxiliary cells are formed in separate, flask-shaped cell clusters, the ampullae. The ampullae are secondarily produced from the cortical cells. In the carpogonial ampullae, the primary filament is up to 8 cells long, composed of ellipsoid to at times wedge-shaped cells. From a few cells of the filament, simple secondary filaments are developed toward the surface. The two-celled carpogonial branch, consisting of a carpogonium with a trichogyne and a hypogynous cell, develops on the primary filament. The hypogynous cell has a short, simple side branch. At maturity, the carpogonial branch is situated in the center at the bottom of the ampulla (Fig. 4C, 5A). The auxiliary cell ampullae resemble the carpogonial ampullae in structure, but are generally larger in size and constructed of more cells. The primary filament is more than 15 cells long in the auxiliary cell ampullae, and is composed of ellipsoid to spherical cells. From the first, and one or two other cells of the filament, simple secondary filaments are produced toward the surface. Tertiary filaments have never been observed in either of ampulla type. Some of the cells in the auxiliary cell ampullae form lateral protuberances. The auxiliary cell is mostly the third cell of the primary filament. At maturity, the auxiliary cell is oval in shape, is larger than the other cells in the ampulla, and lies in the center of the ampulla (Fig.

Symbols used in figures: a, auxiliary cell; af, ampullary filament; c, carpogonium; cf, connecting filament; fc, fusion cell; gb, gonimoblast; gbi, gonimoblast initial cell; hy, hypogynous cell; lf, lateral filament produced from ampullary cell; pr, protuberance; sp, spermatium; ti, tetrasporangial initial; tr, trichogyne;



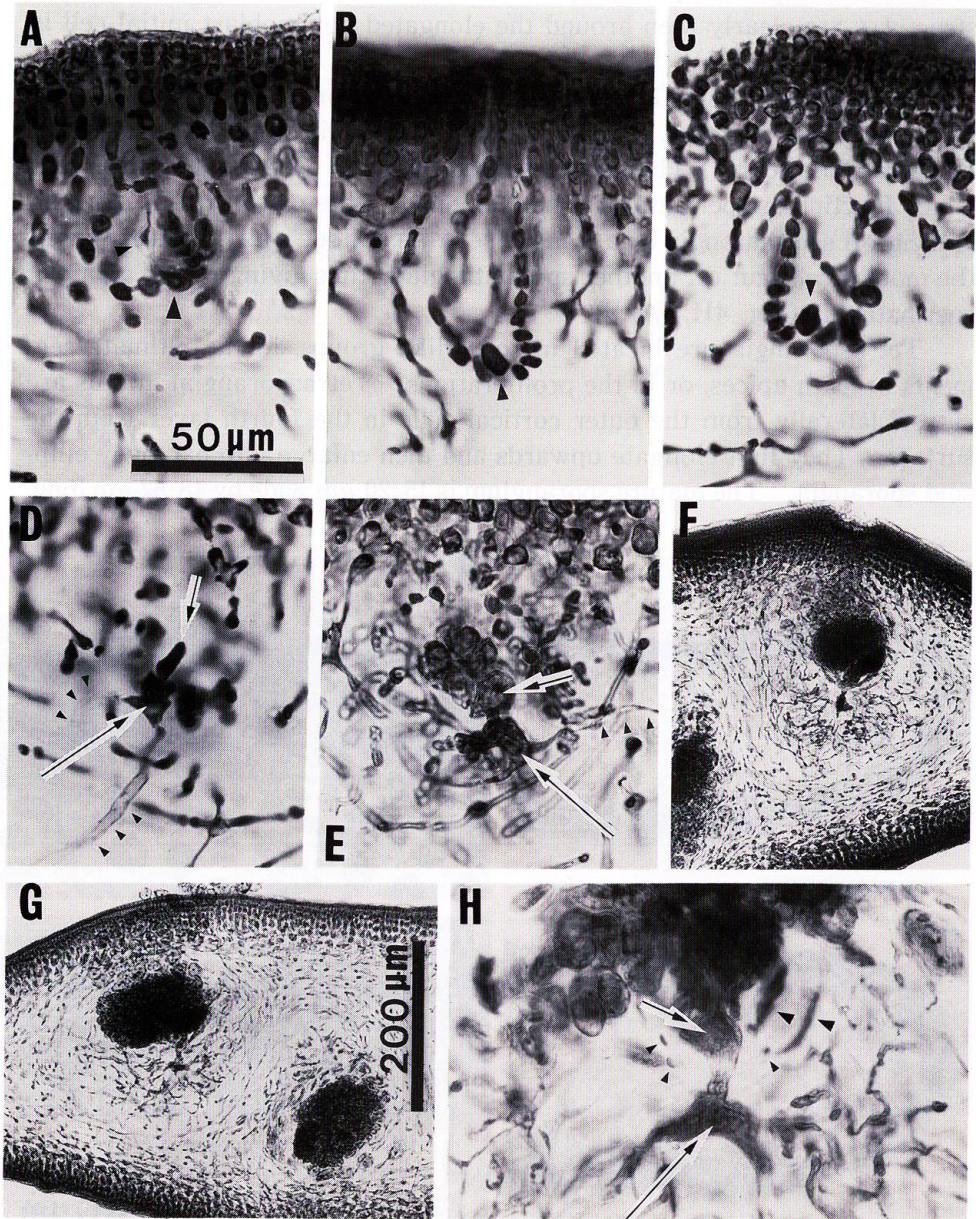
**Fig. 4.** *Prionitis patens* OKAMURA. A. Transverse section of middle portion of thallus. B. Carpoogonial ampulla. C, D. Auxiliary cell ampullae. E. Young stage in gonimoblast development. F. Spermatangia formation. G. Tetrasporangia formation.

4D, E, 5B, C).

Early stages of fertilization, from the attachment of spermatia to a trichogyne the cutting off of connecting filaments, were not traced with certainty. However, connecting filaments in contact with auxiliary cells were observed. After contact of a connecting filament with an auxiliary cell, but in most cases, a new connecting filament is produced from the opposite side of the auxiliary cell (Fig. 4E, 5E). Auxiliary cells, after slight elongation, cut off a gonimoblast initial cell toward the surface by a transverse septum (Fig. 5D). In some cases, successive gonimoblast cells were seen produced from the upper portion of the initial cell. The gonimoblast cells cut off from the initial cell in turn divide to form cells, which, except for these adjacent of the initial cell, develop into carposporangia. The sterile cells become elongated in the later stages. Presumed diploidization of the auxiliary cell also results in the promoting of lateral branches from the ampullary cells. As the carposporophyte develops, the lateral branches and the ampullary cells elongate to a great extent to surround it as an involucre (=pericarp or gonimocarp). Some neighboring vegetative cells or their derivatives partly contribute to the involucre formation, so that a rather thick pericarp surrounds the young carposporophyte. However, the cells of the pericarp subsequently become impoverished and only the remnants remain. The pericarp is thus considered to be poorly developed. The mature cystocarp is approximately spherical in shape, submerged in the thallus interior, and has a distinct pore at the top. At the bottom of the cystocarp, an irregularly-shaped cell is observed which is evidently due to the fusions between the auxiliary cell and neighboring ampullary cells (Fig. 5F, G).

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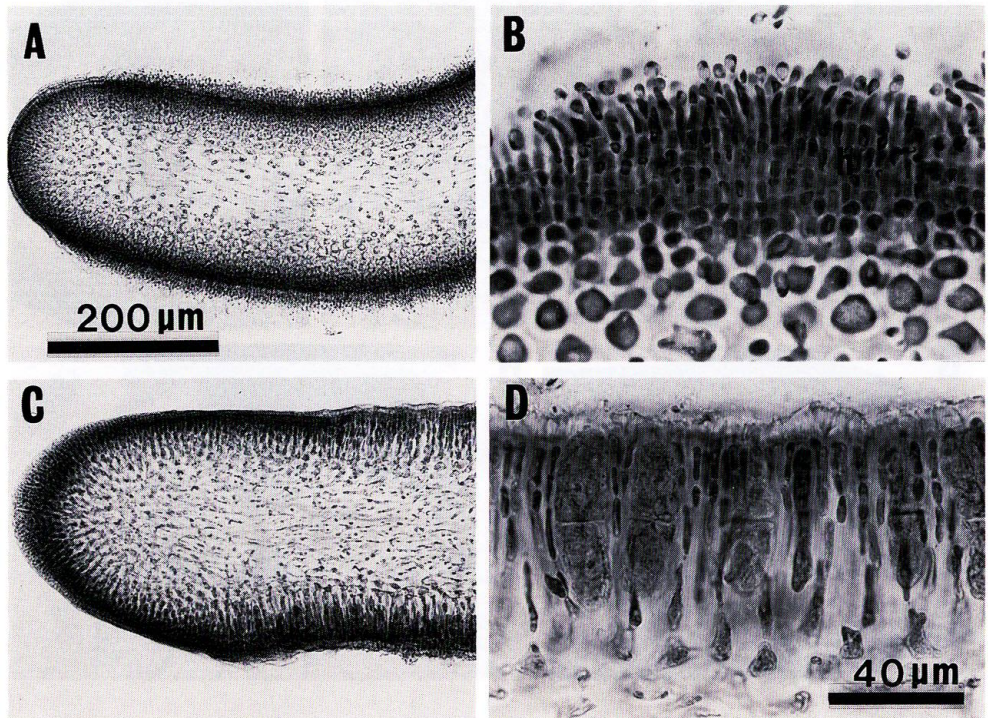
**Fig. 5.** *Prionitis patens* OKAMURA. A. Carpogonial ampulla, showing carpogonium (large arrowhead) and trichogyne (small arrowhead). B, C. Auxiliary cell ampullae. Arrowhead shows auxiliary cell positioned in the center at the bottom of the ampulla. D. Early stage of gonimoblast development showing gonimoblast initial cell (short arrow) just cut off from auxiliary cell (long arrow) in contact with connecting filament (arrowheads). Note that second connecting filament is cut off from the auxiliary cell. E. Young stage in gonimoblast development. Short arrow shows gonimoblast initial cell, long arrow fusion cell, and arrowheads connecting filament. F, G. Developed cystocarps. Note that pericarps are scarcely detectable. H. Portion of mature cystocarp, showing somewhat elongated gonimoblast initial cell (short arrow) with "rays" (large arrowhead) and ring-like structure (small arrowhead), and irregularly-shaped fusion cell (long arrow). Scale in A applies to B-E, H, and G to F.



Foliar radiating processes (apparently the same structure as "rays" reported in *Pachymenia* species by SIMONS & HEWITT, 1976, p. 25) and small ring-like structures are clearly seen around the elongated gonimoblast initial cell in old cystocarps (Fig. 5H).

Male plants are smaller in size and somewhat brighter in color than the other two kinds of plants. Spermatangia are found in the ultimate segments as sorus-like groups. They are produced from the outermost cortical cells which function as spermatangial mother cells. These mother cells elongate and cut off spermatangia by a transverse or an oblique well. In many cases, the mother cells cut off another spermatangium, thus giving rise to a pair of spermatangia (Fig. 4H, 6A, B).

Tetrasporangia are located in sorus-like groups, in the ultimate segments beneath apices, or in the proliferations. Tetrasporangial initials are cut off laterally from the outer cortical cells in the fourth layer from the surface. They first elongate upwards and then enlarge into narrowly ellipsoid sporangia. The mature sporangium is 15-20  $\mu\text{m}$  wide by 48-62  $\mu\text{m}$  long,



**Fig. 6.** *Prionitis patens* OKAMURA. A, B. Spermatangia formation. C, D. Tetrasporangia formation. Scale in A applies to C, and D to B.

submerged in the outer cortex, and cruciately or decussately divided (Fig. 4G, 6C, D).

Remarks --- *P. patens* has been reported from localities along the Pacific coast from northern to central Honshu (Fig. 1), growing on rocks in the upper subtidal zone. It was first described by OKAMURA (1899) from specimens collected at Aichi Prefecture. Since then, it has been consistently accredited to the genus *Prionitis*.

As is clear from the present study, the anatomical and reproductive features of this alga agree well with those of the type species *P. lanceolata* as shown by SJOESTEDT (1926) and CHIANG (1970). This alga is properly placed in the genus *Prionitis*.

### ***Prionitis angusta* (HARVEY) OKAMURA**

Figs. 7-10

OKAMURA, 1899, p. 4. ABBOTT & HOLLENBERG, 1976, p. 444.

Basionym: *Gymnogongrus ligulatus* var. *angustus* HARVEY, 1859, p. 332.

Synonyms: *Cryptonemia angusta* (HARVEY) OKAMURA, 1895, pl. 9, figs. 8-15; *Polyopes angustus* (HARVEY) DE TONI, 1905, p. 1596; *Carpopeltis angusta* (HARVEY) OKAMURA, 1909, p. 66, 1936, p. 551, TAZAWA, 1975, p. 120.

Type: TCD? (non vidi)

Type locality: Shimoda, Shizuoka Prefecture

Distribution: California, China, Korea, Japan.

Japanese name: Kintoki

Materials examined: *Kyushu*: cystocarpic, Meotoura, Miyazaki Pref., 3, vi, 1982, leg. S. Kawaguchi, SAP 047333. *Shikoku*: spermatangial, tetrasporangial, Tatsukushi, Kochi Pref., 7, vi, 1982, leg. S. Kawaguchi, SAP 047334, 047337. *Honshu*: spermatangial, Suzaki, Shizuoka Pref., 15, viii, 1958, leg. Y. Tsuji, SAP 047336; tetrasporangial, Tsumegizaki, Shizuoka Pref., 20, vi, 1982, leg. S. Kawaguchi, SAP 047332, 047339; sterile, Aburatsubo, Kanagawa Pref., 1, v, 1955, leg. Y. Tsuji, SAP 047335; tetrasporangial, Katsuura, Chiba Pref., 22, vi, 1982, leg. S. Kawaguchi, SAP 047338 (Fig. 1).

Vegetative structure --- The plant arises from a scutate holdfast through a short cylindrical stipe, gradually becoming slightly compressed above, repeatedly dichotomously branched, up to 30 cm high. The width of thallus is almost the same throughout, to 2 mm wide. The ramification is sometimes irregular, resulting in entangled branches. Slight constrictions are found in the thallus at irregular intervals. The apices are blunt and often bifurcate. Proliferations arise along the margin and from damaged apices. The proliferations are circular in shape and usually remain short in mature plants. In some cases, however, the proliferations grow into branchlets.

The texture is very rigid when fresh and becomes horny when dried. The color is blood red to purplish red, getting darker on drying (Fig. 7A,B).

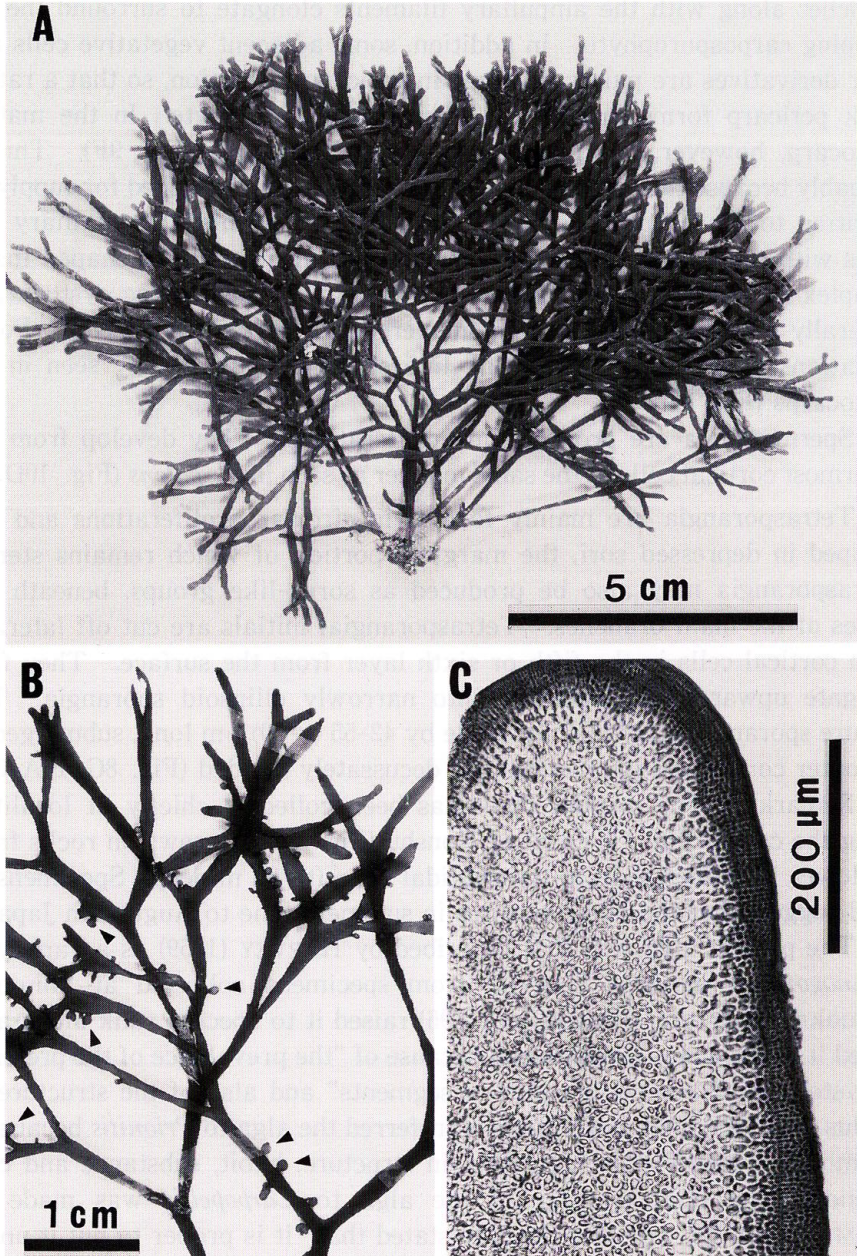
The thallus is up to 500  $\mu\text{m}$  thick, and is composed of a dense cortex and medulla. The cortex is about 10 cells thick in the upper portion of thallus, 20 cells or more below. Outer cortical cells are mostly cuboid and tightly packed in anticlinal rows 4–6 cells deep. This outer layer connects to an inner cortex, 4–5 cells deep, of large rounded cells laterally connected by secondary pit-connections. The medulla consists of short cylindrical cells which form simple or branched, densely interwoven filaments. These filaments are mainly periclinally and longitudinally oriented. Thus the medulla seems to consist of rounded cells in transverse section (Fig. 7C, 8A).

Reproduction --- Reproductive structures are mainly confined to small, circular proliferations, but are at times also found on the ultimate segments as sorus-like groups (Fig. 7B). Carpogonial branches and auxiliary cells are formed in ampullae secondarily developed from the cortical cells (Fig. 9A). In the carpogonial ampullae, the primary filament is composed of to 7 ellipsoid cells. From this filament, one or two, simple secondary filaments are produced. The two celled carpogonial branch develops on the primary filament. The hypogynous cell has a short side branch (Fig. 8B). In the auxiliary cell ampullae, the primary filament is up to 20 cells long, composed of ellipsoid to rounded cells decreasing in size distally. From the first, second or other cells of the filament, simple secondary filaments are developed. No tertiary filaments are seen in either type of ampulla. The auxiliary cell is usually the third or fourth cell of the primary filament, oval in shape, and larger than the other cells in the ampulla. It occupies a position in the center at the base of the ampulla as is the case with the carpogonial branch (Fig. 8D, E, 9B, C).

Early stages of fertilization were not observed. Several connecting filaments were observed to be cut off from a large, irregularly-shaped cell (Fig. 8C, 9D). This cell probably originated from fusions of the fertilized carpogonium with hypogynous cell and other cell(s) in the ampulla. Soon after being cut off, some connecting filaments stopped growth without elongation and in turn additional connecting filaments were cut off from the cells. Gonimoblast cells were observed developed from a gonimoblast initial

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**Fig. 7.** *Prionitis angusta* (HARVEY) OKAMURA. A. Habit of tetrasporangial specimen (SAP 047332). B. Detail of spermatangial specimen with circular proliferations (arrowheads) (SAP 047336). C. Transverse section of lower portion of thallus.



cell which was produced from the auxiliary cell presumably in contact with a connecting filament. In the course of gonimoblast development, the ampullary cells produce lateral, short branches (Fig. 8F). These lateral branches along with the ampullary filaments elongate to surround the developing carposporophyte. In addition, some adjacent vegetative cells and their derivatives are partly involved in pericarp formation, so that a rather thick pericarp forms around the young carposporophyte. In the mature cystocarp, however, the pericarp is poorly developed (Fig. 9F). This is probably because the cells forming a pericarp are impoverished for supplying nutrition to the carposporophyte. During these events, the auxiliary cell fuses with some adjacent ampullary cells and an irregularly-shaped fusion complex is formed at the base of a cystocarp. The mature cystocarp is generally spherical in shape, and submerged in the thallus interior. Foliar radiations ("rays") and small ring-like structures are clearly seen in old cystocarps (Fig. 9G).

Spermatangia are produced in proliferations. They develop from the outermost cortical cells in the same manner as seen in *P. patens* (Fig. 10D, E).

Tetrasporangia are mainly formed in circular proliferations and are grouped in depressed sori, the marginal portion of which remains sterile. Tetrasporangia may also be produced as sorus-like groups, beneath the apices of the main branches. Tetrasporangial initials are cut off laterally from cortical cells in the fifth or sixth layer from the surface. They first elongate upwards, then enlarge into narrowly ellipsoid sporangia. The mature sporangium is 12-17  $\mu\text{m}$  wide by 42-55 (-60)  $\mu\text{m}$  long, submerged in the outer cortex and is cruciately or decussately divided (Fig. 8G, 10A-C).

Remarks --- The present plant has been collected chiefly at localities along the central Pacific coast of Honshu (Fig. 1). It grows on rocks from the lower intertidal zone to the subtidal zone (to 32 m deep). Specimens at hand suggest that the plant matures in summer (June to August) in Japan.

The present alga was first described by HARVEY (1859) as a variety of *Gymnogongrus ligulatus* HARVEY from specimens collected at Shimoda, Shizuoka Prefecture. OKAMURA (1895) raised it to specific rank and transferred it to the genus *Cryptonemia* because of "the prevalence of the presence of cystocarps in lateral proliferous segments" and also of the structure of thallus. In 1899, OKAMURA again transferred the alga to *Prionitis* because it resembled *Prionitis elata* OKAMURA in structure, habit, substance and consistency. The final transfer of the alga to *Carpopeltis* was made by OKAMURA in 1910. At this time, he stated that "it is proper to put it under

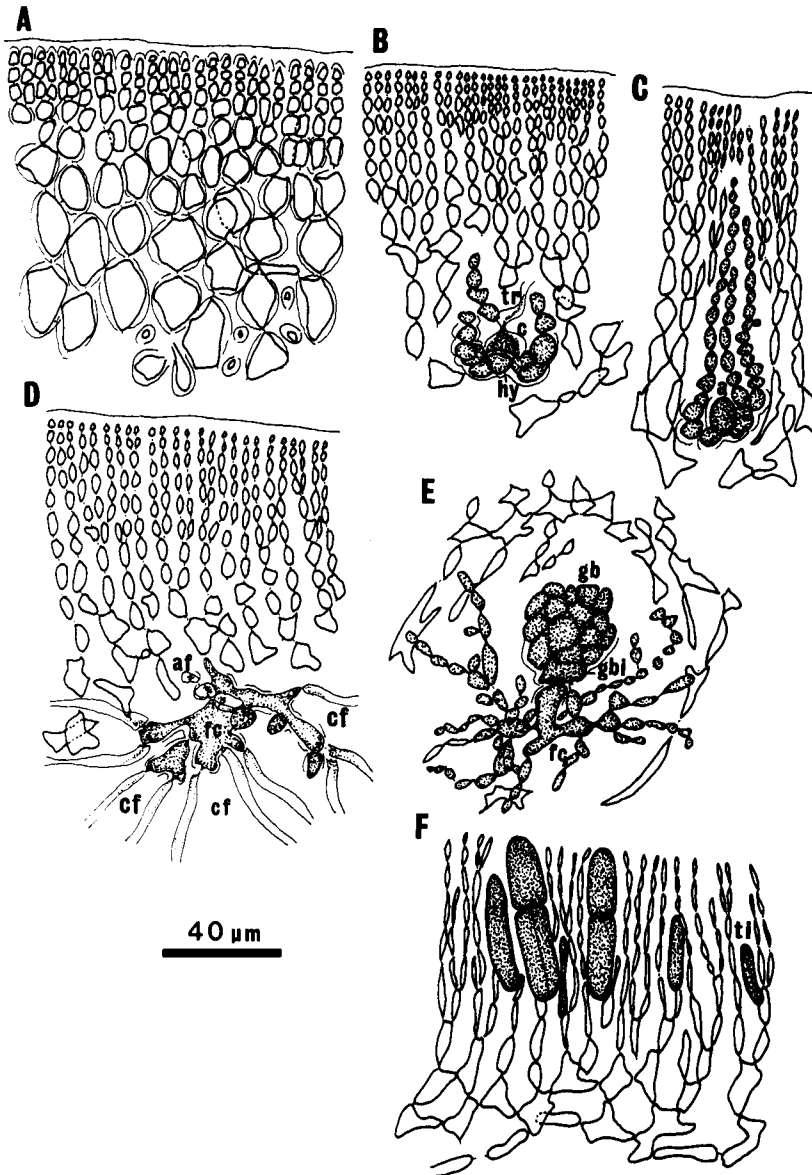
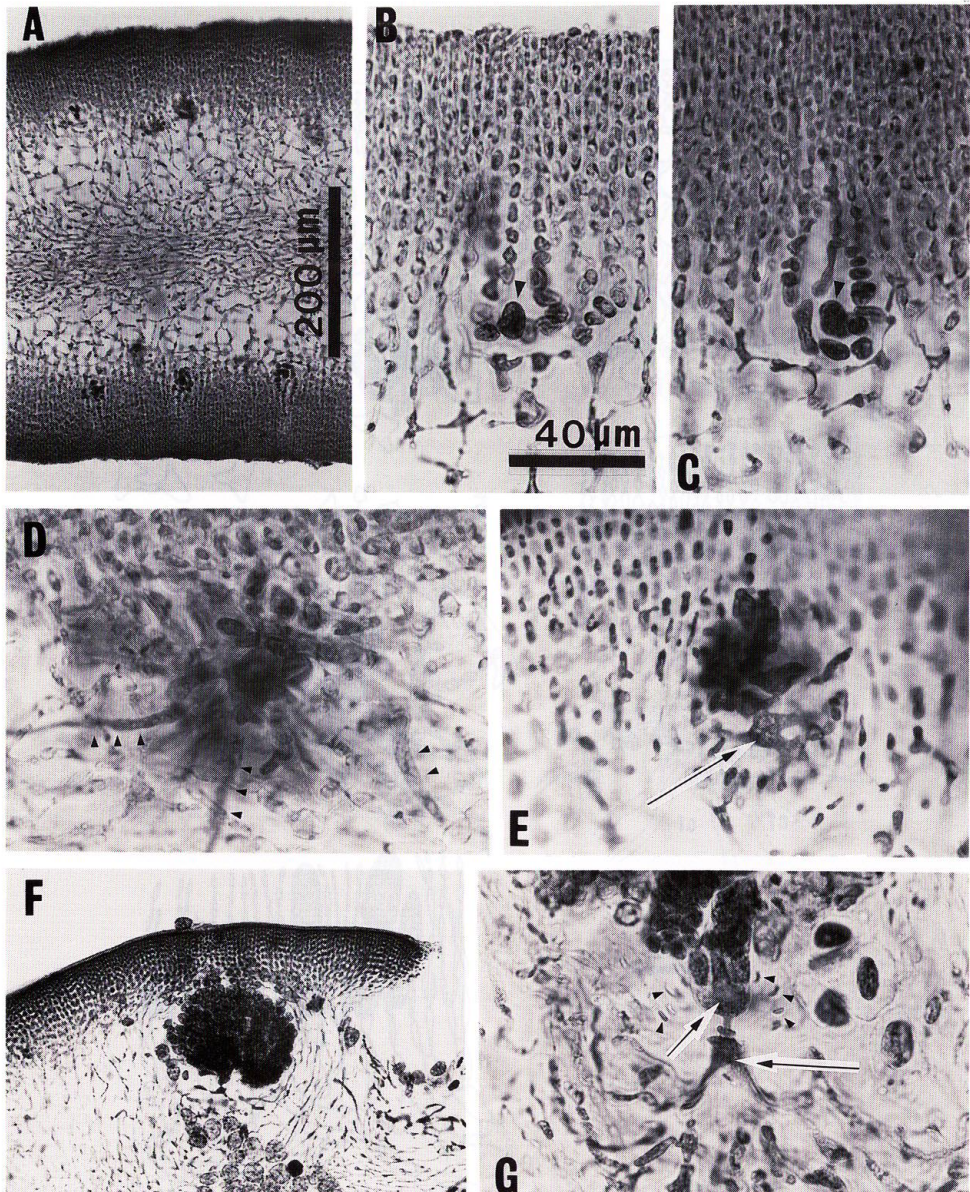
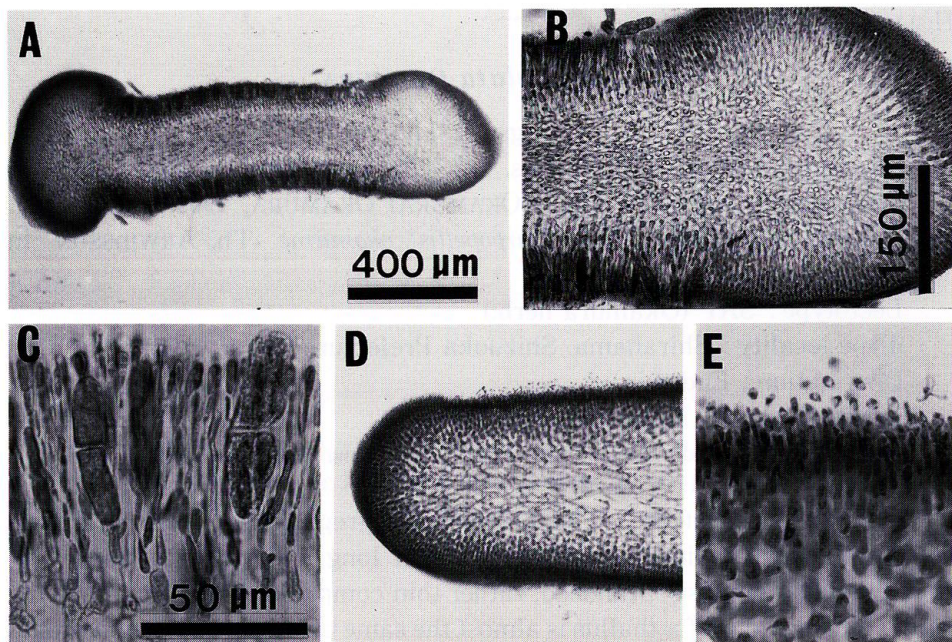


Fig. 8. *Prionitis angusta* (HARVEY) OKAMURA. A. Transverse section of middle portion of thallus. B. Carpogonial ampulla. C. Auxiliary cell ampulla. D. Connecting filaments (cf) produced from irregularly-shaped fusion cell (fc) and its derivative cells. Note that ampullary filament (af) is seen. E. Young stage in gonimoblast development. F. Tetrasporangia formation.



**Fig. 9.** *Prionitis angusta* (HARVEY) OKAMURA. A. Transverse section of proliferation bearing female reproductive structures. B, C. Auxiliary cell ampullae. D. Connecting filaments (arrowheads) produced from irregularly-shaped large cell. E. Early stage in gonimoblast development. Arrow shows fusion cell. F. Mature cystocarp with scarce pericarp. G. Basal portion of cystocarp. Long arrow shows fusion cell, short arrow gonimoblast initial and arrowheads ring-like structures. Scale in A applies also to F, and B to C-E and G.



**Fig. 10.** *Prionitis angusta* (HARVEY) OKAMURA. A. Tangential section of tetrasporangial proliferation. Note that tetrasporangia are formed in depression. B. Detail of marginal portion of tetrasporangial proliferation. C. Tetrasporangia formation. D. Tangential section of male proliferation. E. Spermatangia formation. Scale in B applies to D, and C to E.

the present genus from its often having thickened midrib in the lower portion of the frond and the character of fructified branchlets, having fruits of both kinds in roundish lateral branchlets as well as beneath apex of the terminal segments”.

However, no clear midribs were present in the materials at hand (in a few specimens only a faint thickening of the main branch was detected, though), and reproductive structures are mainly confined to the circular proliferations. Moreover, the auxiliary cell ampullae of this alga are sparingly branched to the second order. Comparing these aspects of morphology with those of the type species *P. lanceolata*, they suggest that the alga is more closely related to *Prionitis* than to any other genus within the Halymeniaceae. It is, however, unique among the members of *Prionitis* in having depressed tetrasporangial sori. It is most proper to put the present plant in the genus *Prionitis* as *P. angusta* (HARVEY) OKAMURA, in agreement with ABBOTT &

HOLLENBERG (1976, p. 444).

***Prionitis elata* OKAMURA**

Figs. 11-14

OKAMURA, 1899, p. 4, pl. 1, figs. 1-2. DE TONI, 1905, p. 1590.

Synonyms: *Carpopeltis elata* (OKAMURA) OKAMURA, 1909, nom. illeg. (non SCHMITZ), 1936, p. 553; *Carpopeltis okamurae* Th. ARWIDSSON in YAMADA, 1938, p. 124.

Lectotype: SAP (Okamura herb.)

Type locality: Shirahama, Shizuoka Prefecture

Distribution: Endemic

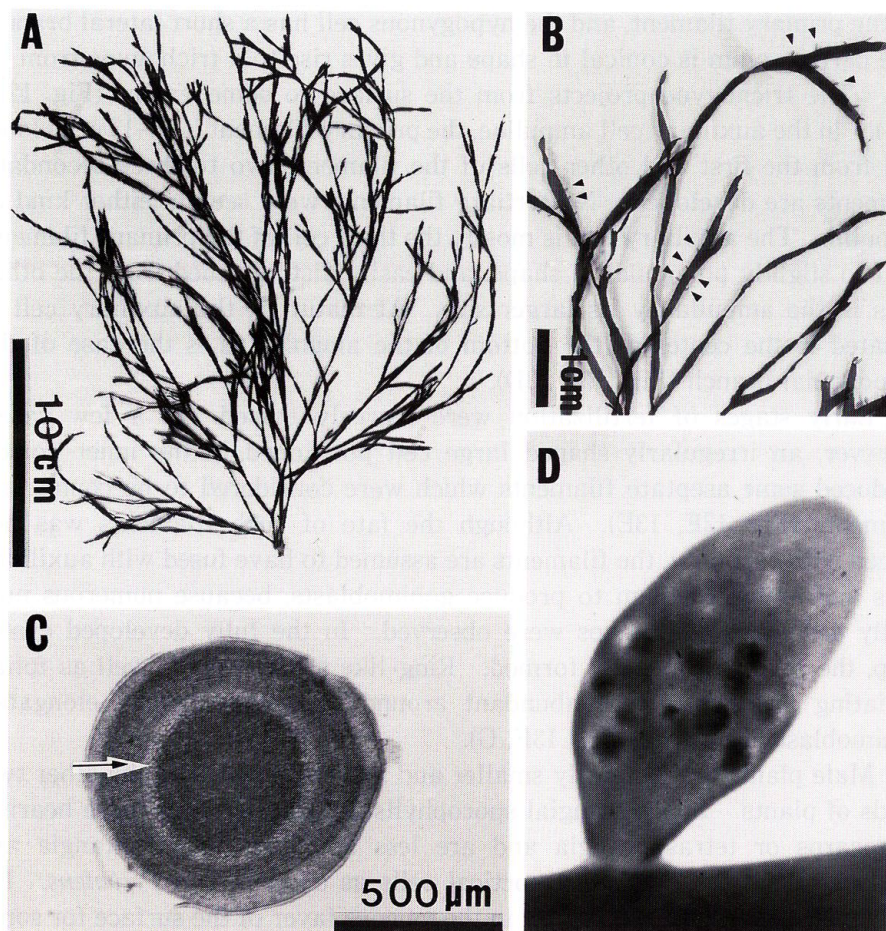
Japanese name: Naga-kintoki

Materials examined: *Honshu*: cystocarpic, spermatangial, tetrasporangial, Onjuku, Chiba Pref., 29, 30, xi, 1983, leg. M. Ohta, SAP 047340-6 (5-30 m deep) (Fig. 1).

Vegetative structure --- The plants arise gregariously from a scutate holdfast through cylindrical stipes to 1 cm long, expand into linear, repeatedly dichotomously branched, rather thin compressed thalli, up to 50 cm high. The breadth of a thallus is almost the same throughout, 1-2 mm broad. In each segment, faint constrictions are often found at irregular intervals. Apices are generally blunt and sometimes bifurcate. Proliferations arise along the margin and from the injured portions, but are rarely seen on the surfaces. The texture is cartilaginous and becomes rigid when dried. The color is blood red and remains unchanged on drying (Fig. 11A, B).

The thallus is up to 350  $\mu$ m thick, composed of cortical and medullary layers. The cortex consists of 6-10 cells. The outer cortex, 3-5 cells deep, consists of small, cuboid cells very tightly arranged in anticlinal rows. This layer changes rather abruptly into an inner cortex of larger, angular to rounded cells, tightly packed and laterally connected by secondary pit-connections (Fig. 12A-C). The abrupt transition from outer to inner cortex is particularly clear in the lower part of the thallus. The medulla consists of somewhat thick, cylindrical cells which form simple or branched filaments. These filaments are very densely interwoven and are mainly periclinally directed (Fig. 13A). The sections of a stipe show a few growth lines (probably of yearly basis) in the outer cortex (Fig. 11C).

Reproduction --- As few female specimens were available for study, insufficient observations could be made to clearly elucidate the developmental morphology of female reproductive structures. Female reproductive structures are formed in obovate or oblong sporophylls which are pale pink in color, taper at both ends, and are 1.5 mm long by 1 mm wide (Fig. 11B, D).



**Fig. 11.** *Prionitis elata* OKAMURA. A. Habit of spermatangial specimen (SAP 047346). B. Detail of branch showing specially developed small proliferation, i. e. sporophylls (arrowheads). C. Cross section of stipe with a few growth lines. Arrow shows inner cortical layer of large cells. D. Female sporophyll bearing cystocarps. Scale in C applies also to D.

Carpogonial branches and auxiliary cells are separately formed in ampullae accessorially developed from cortical cells (Fig. 13B). Both kinds of ampullae are similar in structure, but the auxiliary cell ampullae are generally larger in size. In the carpogonial ampullae, the primary filament is 7-8 cells long, and from the first and other cells of the filament, secondary filaments are produced toward the surface. The two-celled carpogonial branch develops

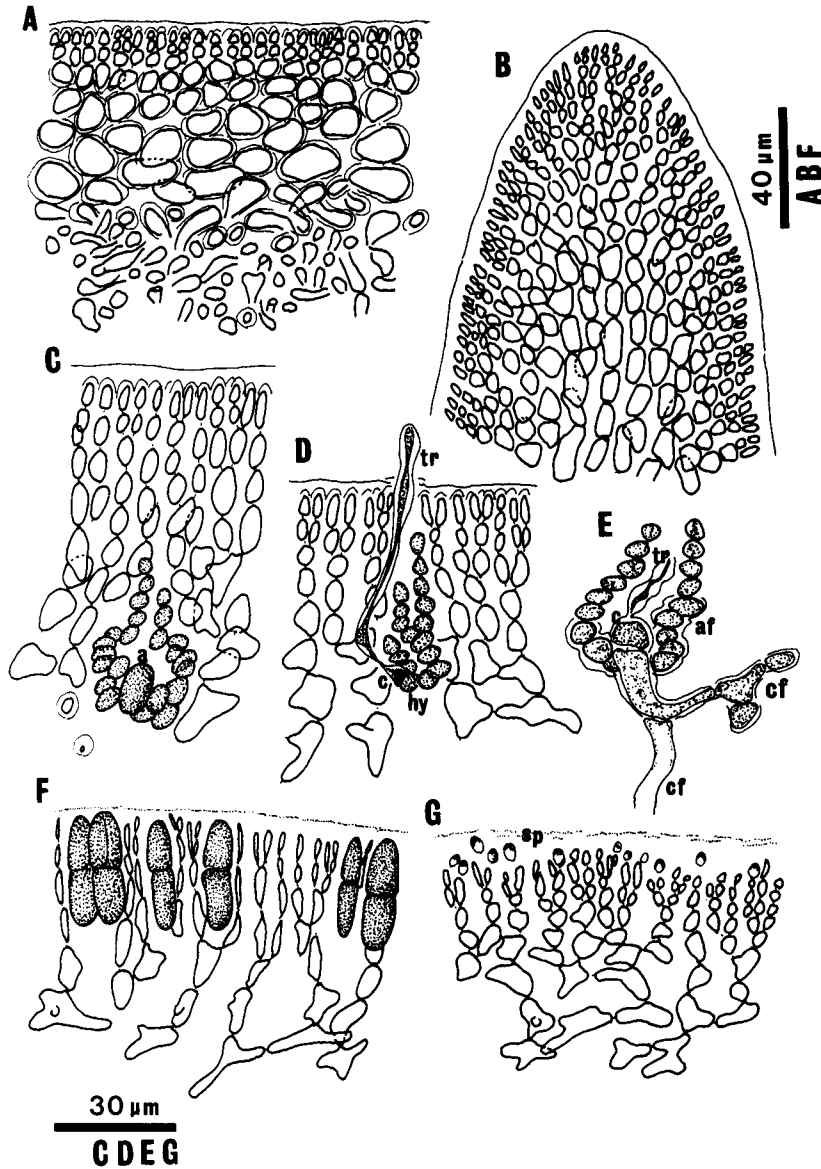
on the primary filament, and the hypogynous cell has a short lateral branch. The carpogonium is conical in shape and gives rise to a trichogyne from its top. The trichogyne projects from the surface to some extent (Fig. 12D, 13C). In the auxiliary cell ampullae, the primary filament is 10-12 cells long, and from the first and other cells of the filament, two to three secondary filaments are developed. No tertiary filaments were seen in either kind of ampulla. The auxiliary cell is mostly the third cell of the primary filament, oval to slightly polygonal in shape, and easily distinguished from the other cells in the ampulla by its larger size. At maturity, the auxiliary cell is situated in the center at the bottom of the ampulla as is the case of the carpogonial branch (Fig. 12F 13D).

Early stages of fertilization were scarcely traced. In a few cases, however, an irregularly-shaped large cell positioned in the inner cortex produced some aseptate filaments which were considered to be connecting filaments (Fig. 12E, 13E). Although the fate of such filaments was not traced with certainty, the filaments are assumed to have fused with auxiliary cells and activated them to produce gonimoblasts, because numerous normally developed cystocarps were observed. In the fully developed cystocarp, the pericarp is thinly formed. Ring-like structures, as well as foliar radiating processes, were abundant around the conspicuously elongated gonimoblast initial cell (Fig. 13F, G).

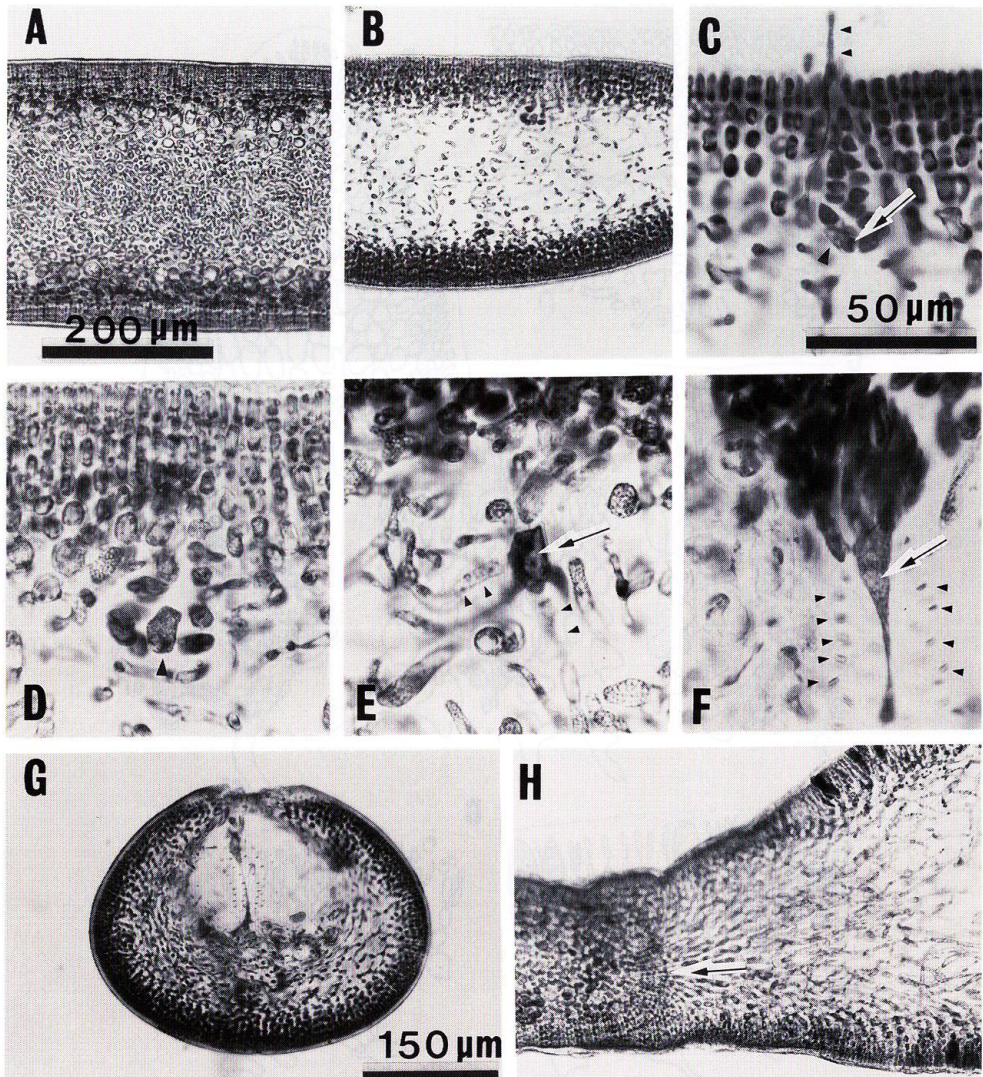
Male plants are generally smaller and less branched than the other two kinds of plants. Spermatangial sporophylls are smaller than those bearing cystocarps or tetrasporangia and are less abundant. Spermatangia are produced from the outermost cortical cells as described in *P. patens*. Liberated spermatia appear to rest in the mucous layer of the surface for some time (Fig. 12G, 14C, D).

Most of the specimens examined in the present study were tetrasporangial. Tetrasporangial sporophylls were similar in shape and size to female sporophylls (Fig. 13H). Tetrasporangial initials are cut off as a lateral cell from the cortical cells in the third or fourth layer from the surface. After elongation, the initials enlarge into narrowly ellipsoid cells, soon followed by a first transverse and successively by second and third divisions perpendicular to the first one. The cruciately or decussately divided sporangium is 13-15  $\mu\text{m}$  wide by 38-45  $\mu\text{m}$  long, submerged in the outer cortex (Fig. 12G, 14C, D).

Remarks --- *P. elata* has an apparently narrow range of distribution along the central Pacific coast of Honshu (Fig. 1). It has been found on rocks in the subtidal zone to 30 m deep. Judging from the growth lines



**Fig. 12.** *Prionitis elata* OKAMURA. A. Transverse section of middle portion of thallus. B. Longitudinal section of apical portion of thallus. C. Auxiliary cell ampulla. D. Carpogonial ampulla. E. Connecting filaments produced from cell with withered trichogyne. F. Tetrasporangia formation. G. Spermatangia formation.

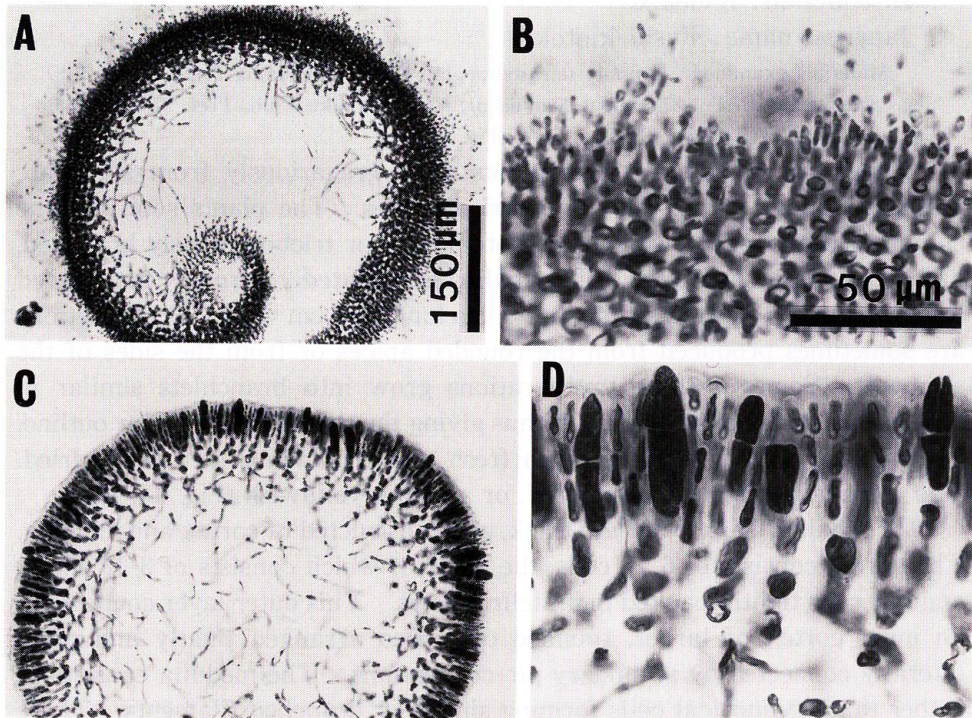


**Fig. 13.** *Prionitis elata* OKAMURA. A. Transverse section of lower part of thallus showing dense medulla and cortex. B. Transverse section of female sporophyll. C. Carpogonial ampulla. Arrow shows carpopogonium, and arrowheads trichogyne. D. Auxiliary cell ampulla. E. Connecting filaments (arrowheads) produced from large cell (arrow). F. Basal part of old cystocarp. Note that gonimoblast initial cell is conspicuously elongated and surrounded by numerous ring-like structures (arrowheads). G. Old cystocarp after liberation of carpospores. H. Transverse section of thallus through sporophyll bearing tetrasporangia. Note that cortex of main thallus (arrow) is clearly detectable. Scale in A applies also to B and H, and C to D-F.

(probably of yearly basis) in the outer cortex of the stipe, it is perennial.

This alga was first described by OKAMURA (1899) as a species of *Prionitis*. Later, OKAMURA (1909) transferred it to the genus *Carpopeltis*, overlooking the fact that *C. elata* had already been used by SCHMITZ for a species from Africa. At that time, OKAMURA stated that this species was similar to *Carpopeltis angusta* (HARVEY) OKAMURA in habit, substance and structure and he therefore transferred the species to *Carpopeltis*.

However, *C. angusta* is considered herein to be a species of *Prionitis*. In addition, features of this alga are more like *Prionitis* than any other genus. Such features are: (1) proliferations are numerous developed from the margin, (2) cortex and medulla are compactly constructed, (3) midribs are lacking, (4) reproductive structures are confined to the proliferations (sporo-



**Fig. 14.** *Prionitis elata* OKAMURA. A. Transverse section of male sporophyll. B. Spermatangia formation. C. Transverse section of tetrasporangial sporophyll. D. Tetrasporangia formation. Scale in A applies also to C, and B to D.

phylls) and (5) female reproductive structures are very similar to those of the type species *P. lanceolata*.

From the above, it is considered appropriate to place the alga in question in the genus *Prionitis*, and the binominal *P. elata* OKAMURA is therefore resurrected.

***Prionitis articulata* OKAMURA**

Figs. 15-17

OKAMURA, 1899, p. 5, pl. 1, figs. 3-4. DE TONI, 1905, p. 1590.

Synonym: *Carpopeltis articulata* (OKAMURA) OKAMURA, 1909, p. 70, 1936, p. 551.

Type: SAP (Okamura herb.)

Type locality: Iragozaki, Aichi prefecture

Distribution: Endemic

Japanese name: Fushi-kintoki

Materials examined: *Honshu*: tetrasporangial, Kata, Wakayama Pref., 21, x, 1918, leg. anonymous, SAP 20871 (about 20 m deep); sterile, Onjuku, Chiba Pref., 27, viii, 1984, leg. M. Ohta, SAP 047545 (25-32 m deep) (Fig. 1).

Vegetative structure --- The plants arise gregariously from a scutate holdfast through short, thick, cylindrical stipes. The plants soon become compressed above, a few times dichotomously or trichotomously branched, and grow up to 20 cm high. The thallus is repeatedly, strongly articulated into cuneate or ellipsoid segments 2-5 cm long by 1 cm wide. Proliferations are sometimes produced from the rounded apices or from the sides of the segments. Some of these proliferations grow into branchlets similar in appearance to the main branches, thus giving the thallus an irregular outline. The texture is cartilaginous when fresh and becomes firmer when dried. The color is generally purplish red, or at times yellowish (Fig. 15, 16).

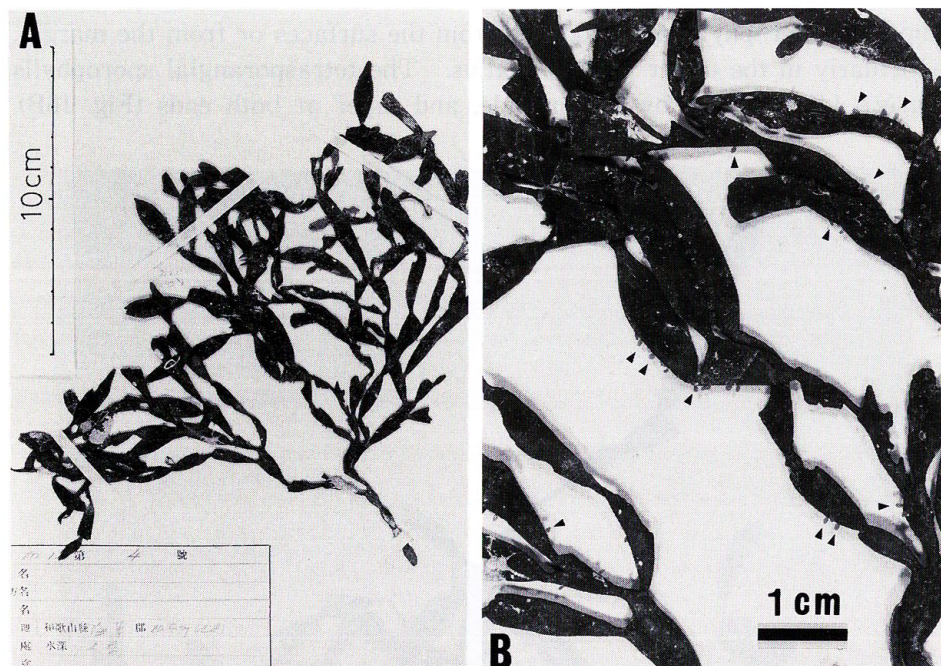
The thallus is up to 500  $\mu\text{m}$  thick, and constructed of cortex and medulla. The cortex consists of 6-18 cells, the outer of which consists of 3-10 small, angular cells tightly packed in anticlinal rows. This outer layer connects to an inner cortex of larger, rounded cells also arranged tightly and often laterally connected by secondary pit-connections. The medulla consists of rather thick cylindrical cells forming simple or branched filaments. These filaments are densely interwoven throughout the thallus and mainly periclinally directed (Fig. 17A, B). Sections of basal parts show growth lines in the outer cortex.

Reproduction --- Sexual plants were not available for study. Tetrasporangia are formed in sporophylls similar in shape to those of *P. elata*.

Numerous sporophylls are produced from the surfaces or from the margin, particularly in the upper part of thallus. The tetrasporangial sporophylls measure 1.5 mm long by 1 mm wide, and taper at both ends (Fig. 16B).



**Fig. 15.** *Prionitis articulata* OKAMURA. Habit of sterile specimen collected from 25-32 m deep (SAP 047545)



**Fig. 16.** *Prionitis articulata* OKAMURA. A. Habit of tetrasporangial specimen (SAP 20871). B. Detail of thallus showing tetrasporangial sporophylls (arrowheads) produced from the margin and the surfaces.

Tetrasporangial initials are cut off laterally from the cortical cells in the third layer from the surface. The mature sporangium is 10–15  $\mu\text{m}$  wide by 30–40  $\mu\text{m}$  long, narrowly ellipsoid in shape, submerged in the outer cortex, and cruciately or decussately divided (Fig. 17C, D).

Remarks --- This alga has been reported from localities along the central Pacific coast of Honshu (Fig. 1) and, from the literature, appears to have a narrow distribution range (Cf. SEGAWA, 1977). This alga grows on rocks at depths up to 32 m and has been only rarely collected.

This alga was first described as a species of *Prionitis*, *P. articulata* OKAMURA, by OKAMURA (1899) from a specimen collected at Irigozaki, Aichi Prefecture (central Honshu). Later, OKAMURA (1909) transferred it to *Carpopeltis* on the grounds that its allied species *P. elata* has been transferred to that genus. Since then this species has been accredited to *Carpopeltis* to date.

However, as stated earlier, *P. elata* belongs in *Prionitis*. In addition, features of the present plant, such as thallus structure and the presence of tetrasporangial sporophylls are similar to *P. elata*, as judged by OKAMURA

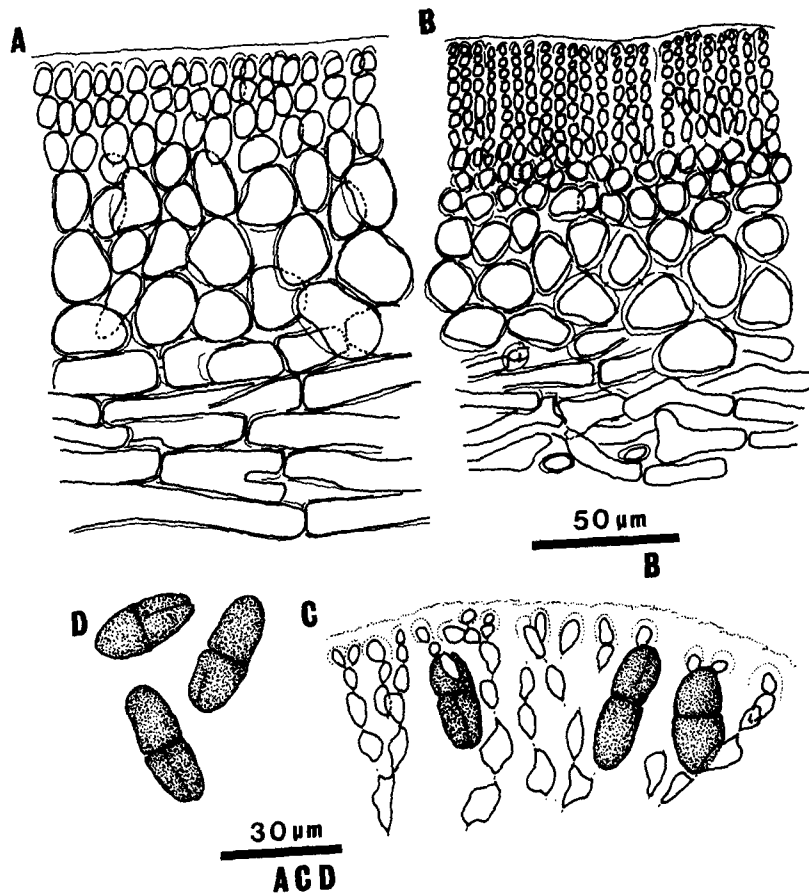


Fig. 17. *Prionitis articulata* OKAMURA. A. Longitudinal section of upper portion of thallus. B. Longitudinal section of middle portion of thallus. C. Transverse section of tetrasporangial sporophyll showing tetrasporangia formation. D. Almost mature tetrasporangia.

(1909), the binominal *P. articulata* OKAMURA therefore be resurrected.

***Prionitis schmitziana* OKAMURA**

Figs. 18-21

OKAMURA, 1899, p. 6. DE TONI, 1905, P. 1590.

Synonyms: *Cryptonemia schmitziana* (OKAMURA) OKAMURA, 1910, p. 77, 1936, p. 556; *Cryptonemia wilsonii*? (non J. AGARDH) OKAMURA, 1895, p. 8, pl. 9, figs. 16-22.

Type : SAP(Okamura herb.)

Type locality : Enoshima, Kanagawa Prefecture

Distribution : Endemic

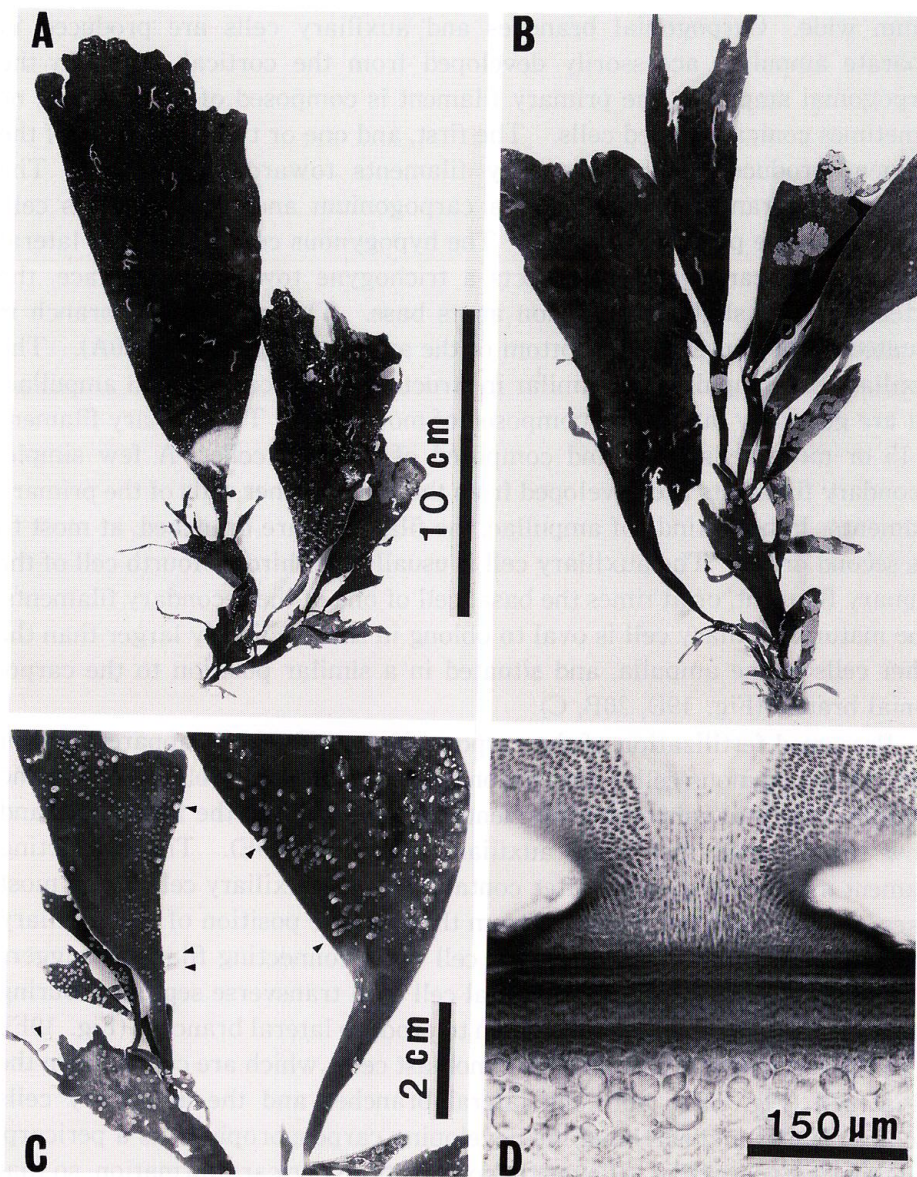
Japanese name : Ohba-kintoki

Materials examined : *Honshu* : sterile, Sugashima, Mie Pref. , 27, iv, 1955, leg. Y. Tsuji, SAP 047515; spermatangial, Shichirigahama, Kanagawa Pref. , 30, vi, 1981, leg. S. Kawaguchi, SAP 047510 (cast up ashore); tetrasporangial, Shichirigahama, Kanagawa Pref. , 16, x, 1981, leg. S. Kawaguchi, SAP 047512 (cast up ashore); cystocarpic, tetrasporangial, Shichirigahama, Kanagawa Pref. , 20, vi, 1983, leg. S. Kawaguchi, SAP 047511, 047513-4 (cast up ashore); spermatangial, tetrasporangial, Shichirigahama, Kanagawa Pref. , 22, vi, 1983, leg. S. Kawaguchi, SAP 047509, 047516 (cast up ashore); cystocarpic, Shichirigahama, Kanagawa Pref. , 20, vii, 1987, leg. S. Kawaguchi, *Kawaguchi* 1001-2 (cast up ashore) (Fig. 1).

Vegetative structure --- The plants arise singly or gregariously from a scutate holdfast through terete stipes. The plants gradually expand into membranous, lanceolate thalli with cuneate bases. This primary thallus, however, becomes split or eroded with age. In old plants, remnants of the primary thallus are thickened and narrow, assuming a stem-like appearance. Proliferations produced from the margin and the surfaces may grow into bladelets similar in shape to the primary thallus. This growth pattern can be repeated several times, so that aged plants usually have several orders of blades (Fig. 18A, B).

The thallus is up to 400  $\mu\text{m}$  thick, composed of cortex and medulla. The cortex consists of up to 10 cells in younger blades, and up to 15 cells in older blades. The outer cortex consists of small, angular cells very compactly arranged in anticlinal rows. This layer rather abruptly changes into a layer of larger, irregularly-shaped to rounded cells (inner cortex) also compactly arranged and laterally connected by secondary pit-connections. The medulla consists of simple or branched filaments of short, thick, cylindrical cells, and the filaments are very densely intermingled. The direction of these filaments is mainly periclinal. This three layer construction of thallus, i. e., outer cortex, inner cortex and medulla, is very conspicuous in this species and is maintained throughout a thallus, although the thickness of each layer decreases toward the apices (Fig. 19A). In some specimens, a few growth lines, probably of yearly origin, were observed in a thickened cortex (Fig. 18D). No highly refractive cells were observed in the material examined.

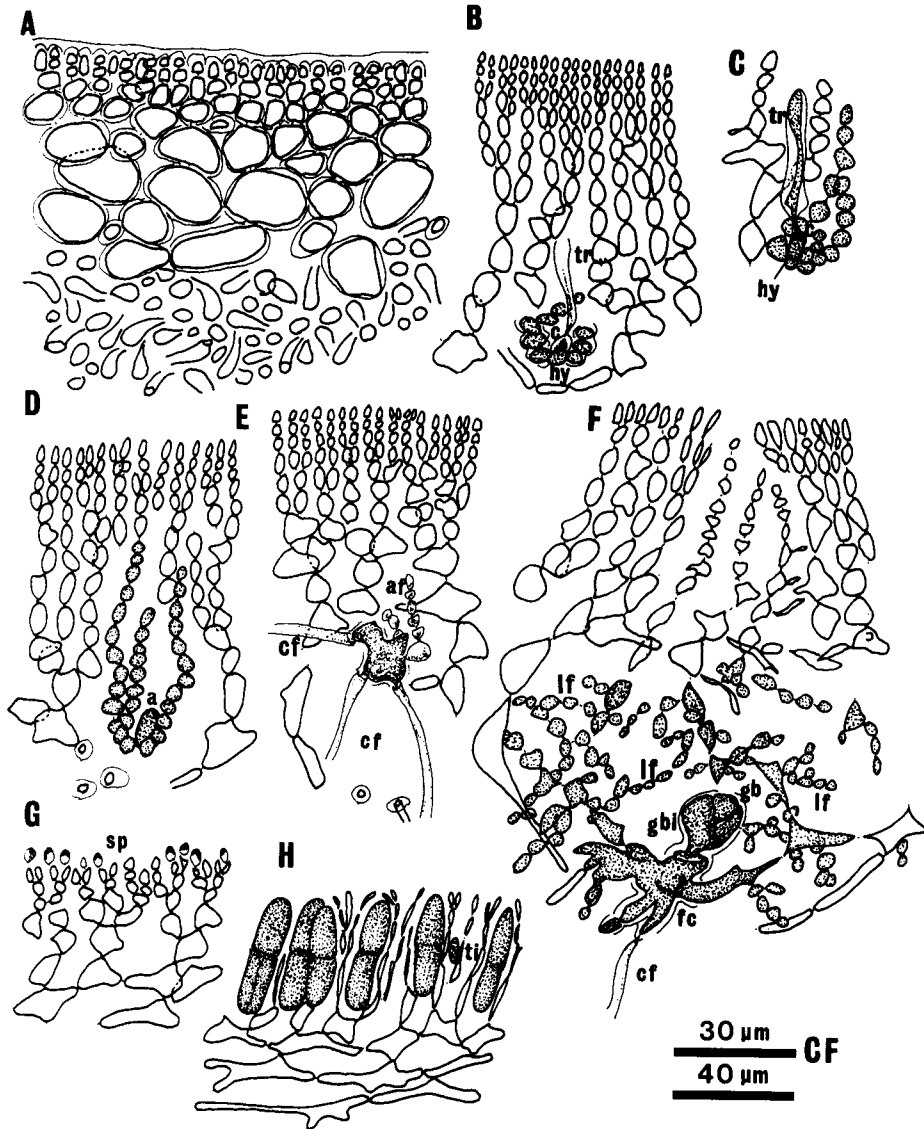
Reproduction --- Reproductive structures are confined to sporophylls produced from the surfaces and the margin of older blades. These sporophylls are generally pale in color, and detach readily when touched (Fig. 18C). Female sporophylls are obovate or oblong in shape, to 2 mm long and



**Fig. 18.** *Prionitis schmitziana* OKAMURA. A, B. Habit of cystocarpic liquid-preserved specimens (*Kawaguchi* 1001-2). C. Detail of thallus showing numerous sporophylls (arrowheads) produced from the margin and the surfaces. D. Transverse section of thallus through male sporophyll. Note that a few growth lines are seen in the cortex of main thallus. Scale in A applies to B.

1 mm wide. Carpogonial branches and auxiliary cells are produced in separate ampullae accessorially developed from the cortical cells. In the carpogonial ampullae, the primary filament is composed of 8-9 ellipsoid or sometimes conical-shaped cells. The first, and one or two other cells of the filament produce simple secondary filaments toward the surface. The carpogonial branch, consisting of a carpogonium and a hypogynous cell, develops on the primary filament. The hypogynous cell has a short lateral branch. The carpogonium projects a trichogyne toward the surface, the latter having a slight constriction at its base. The carpogonial branch is situated in the center at the bottom of the ampulla (Fig. 19B, C, 20A). The auxiliary cell ampullae are similar in structure to the carpogonial ampullae, but are generally larger and composed of more cells. The primary filament is 15 or more cells long, and composed of rounded cells. A few simple, secondary filaments are developed from the first or other cells of the primary filament. In both kinds of ampullae, the filaments are branched, at most to the second order. The auxiliary cell is usually the third or fourth cell of the primary filament, or at times the basal cell of one of the secondary filaments. The mature auxiliary cell is oval to oblong in shape, slightly larger than the other cells in the ampulla, and situated in a similar position to the carpogonial branch (Fig. 19D, 20B, C).

Presumed fertilization of the carpogonium results in its apparent fusion with the hypogynous cell. The fusion may involve other cell or cells in the ampulla. Several connecting filaments are cut off from the fusion cell, and grow toward, and fuse with, auxiliary cells (Fig. 19E). The connecting filament may cease to grow after contact with an auxiliary cell, but in most cases, another filament is cut off from the opposite position of the auxiliary cell. Diploidization of the auxiliary cell via a connecting filament triggers the cutting off of a gonimoblast initial cell by a transverse septum. During these events, the ampullary cells begin to produce lateral branches (Fig. 19F). With the successive divisions of gonimoblast cells, which are cut off from the initial cell (Fig. 20D), both the lateral branches and the ampullary cells become slender and surround the developing carposporophyte as a pericarp. Neighboring vegetative cells partly contribute to pericarp formation, so that a rather thick pericarp is seen in the young cystocarp. However, in the mature cystocarp, the pericarp is poorly developed (Fig. 20E). This is probably because the cells of the pericarp are impoverished for supplying nutrition. In the course of these events, the auxiliary cell fuses with adjacent ampullary cells to form an irregularly-shaped fusion cell at the base of the



**Fig. 19.** *Prionitis schmitziana* OKAMURA. A. Transverse section of young blade. Cortex is rather thinly constructed. B, C. Carpoogonial ampullae. D. Auxiliary cell ampulla. E. Connecting filaments produced from somewhat enlarged cell. F. Young stage in gonimoblast development. Note that ampullary cells produce lateral filaments (lf). G. Spermatangia formation. H. Tetrasporangia formation.

cystocarp. The mature cystocarp is spherical in shape, submerged in the thallus interior, and has a distinct pore at the top. "Rays" and ring-like structures are seen in old cystocarps (Fig. 20E, F).

Male sporophylls are smaller and softer than the other two kinds, and detach more easily than the other types when touched. Spermatangia are produced from the outermost cortical cells as in *P. patens* (Fig. 19G, 21A, B).

Tetrasporangial sporophylls are similar in shape but slightly thinner than female ones. Tetrasporangial initials are cut off laterally from the cortical cells in the third or fourth (rarely fifth) layer from the surface. The mature sporangium is narrowly ellipsoid in shape, 12-17  $\mu\text{m}$  wide by 38-45  $\mu\text{m}$  long in size, submerged in the outer cortex, and cruciately or decussately divided (Fig. 19H, 21C, D).

Remarks --- This alga has been reported from localities along the central Pacific coast of Honshu, particularly around the Kanto district (Fig. 1). Most specimens examined were collected from the drift and the plant's habitat is therefore unknown. The structure of the thallus, with several orders of blades in a single plant or growth lines in the cortex, suggests that it is perennial. From the collection data, the plants are known to mature from spring to summer (March to August).

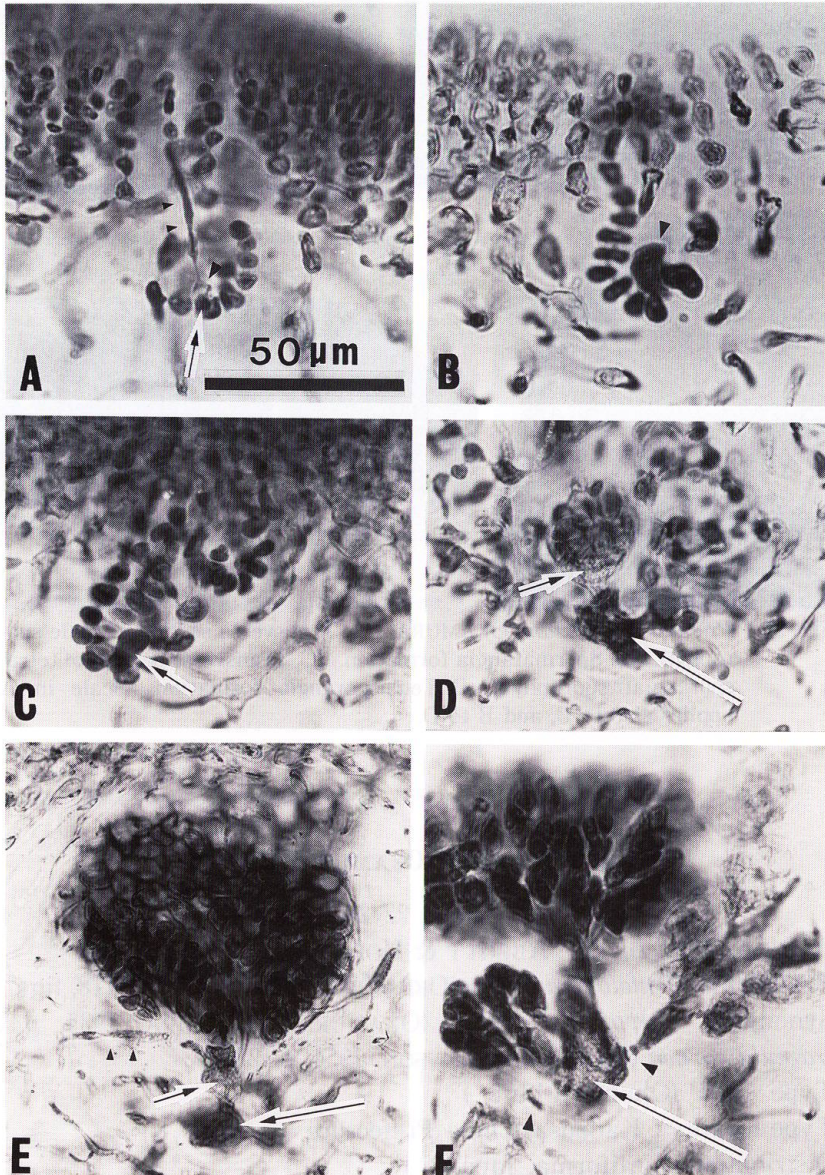
The species was originally described by OKAMURA (1899) as a species of *Prionitis* from specimens collected at Enoshima, Kanagawa Prefecture. Later, OKAMURA (1909) transferred it to the genus *Cryptonemia* because of "the leafy character of the frond and costa-like thickening of lower portion of older frond". Superficially this alga is reminiscent of certain members of *Cryptonemia* because of its rather thin, crispy, foliose blades and its basal structure. Closer examination, however, reveals that these similarities are very superficial, and most of the features seen in this alga align it more closely with *Prionitis* than *Cryptonemia*. Such features are: (1) the absence of midribs, (2) the compact construction of the cortex and medulla and absence of refractive cells in the medulla, (3) the reproductive structures

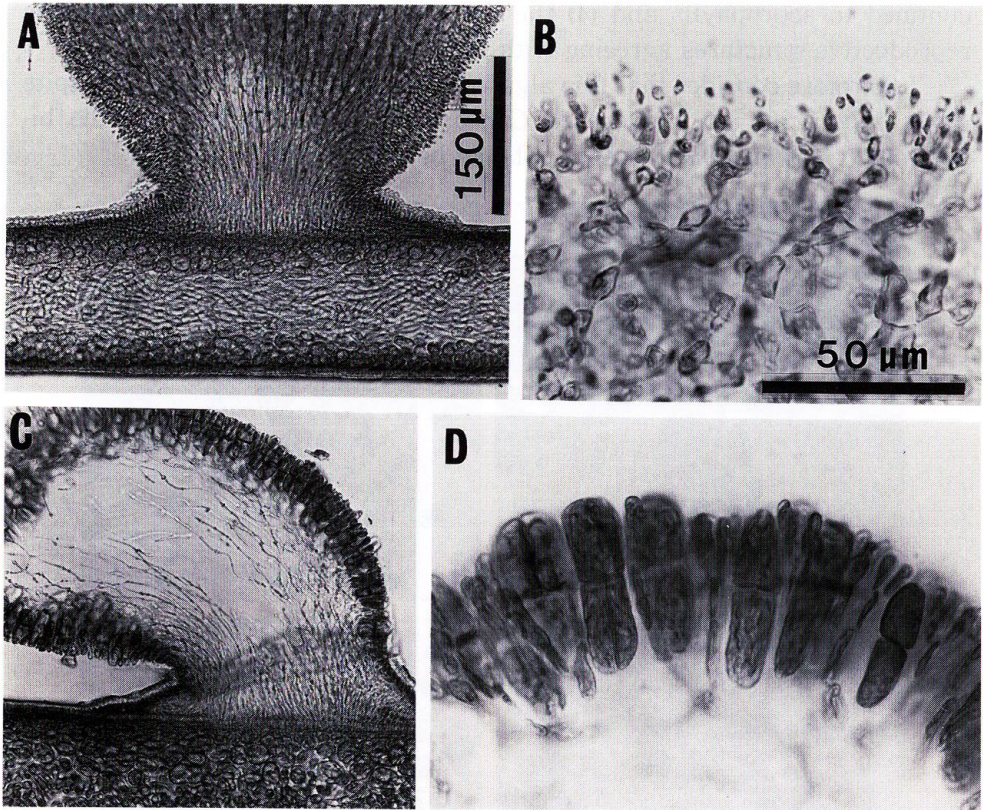
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**Fig. 20.** *Prionitis schmitziana* OKAMURA. A. Carpogonial ampulla. Arrow shows hypogynous cell, large arrowhead carpogonium and small arrowheads trichogyne. B, C. Auxiliary cell ampullae. D. Young stage in gonimoblast development. Short arrow shows gonimoblast initial cell and long arrow fusion cell. E. Mature cystocarp showing elongated gonimoblast initial (short arrow), fusion cell (long arrow) and "ray" (arrowheads). F. Detail of cystocarp. Arrow shows elongated gonimoblast initial and arrowhead ring-like structure. Scale in A applies also to B-F.

confined to sporophylls and (4) the developmental morphology of female reproductive structures agreeing with the type species *P. lanceolata*.

I therefore consider that this alga belongs in the genus *Prionitis*, in spite of its superficial resemblance to *Cryptonemia*, and conclude that the binominal *P. schmitziana* OKAMURA should be resurrected.





**Fig. 21.** *Prionitis schmitziana* OKAMURA. A. Transverse section of male sporophyll. B. Spermatangia formation. C. Transverse section of tetrasporangial sporophyll. D. Tetrasporangia formation. Scale in A applies also to C, and B to D.

***Prionitis cornea* (OKAMURA) DAWSON**

Figs. 22-25

DAWSON, 1958, p. 71. ABBOTT & HOLLENBERG, 1976, p. 445.

Basionym: *Grateloupia cornea* OKAMURA, 1913, p. 63, pl. 118, figs. 1-11.

Synonyms: *Carpopeltis cornea* (OKAMURA) OKAMURA, 1935, p. 2004;

*Zanardinula cornea* (OKAMURA) DAWSON, 1954, p. 282.

Type: SAP (Okamura herb. )

Type locality: Kadzusa, Chiba Prefecture

Distribution: California, Japan

## Japanese name : Tsuno-mukade

Materials examined ; *Honshu* : cystocarpic, Shirahama, Shizuoka Prefecture, 17, viii, 1958, leg. Y. Tsuji, SAP 097302-4 ; cystocarpic, Shimoda, Shizuoka Pref. , 19, vi, 1982, leg. S. Kawaguchi, SAP 047296, 047299 ; spermatangial, tetrasporangial, Tsumegizaki, Shizuoka Pref. , 20, vi, 1982, leg. S. Kawaguchi, SAP 047297-8, 047395-6 ; sterile, Jogashima, Kanagawa Pref. , 30, iv, 1955, leg. Y. Tsuji, SAP 047300 ; terasporangial, Onjuku, Chiba Pref. , 23, vi, 1982, leg. S. Kawaguchi, SAP 047301, 097309 (cast up ashore) (Fig. 2).

**Vegetative structure** --- The plants arise gregariously from a common callous holdfast through short cylindrical stipes, expanding slightly into linear, compressed blades. The thallus is repeatedly dichotomously branched and up to 30cm high. The breadth is almost the same throughout, to 2 mm broad. The apices are usually acute and bifurcate. Proliferations, often produced numerous along the margin, are constricted at the base, simple or sometimes bifurcate, and taper distally (Fig. 22A, B). The texture is somewhat cartilaginous when fresh and becomes rigid in drying. The color is bright red to purplish red.

The thallus is 400-600 $\mu$ m thick, composed of a cortex and medulla. The cortex is up to 17 cells thick in the lower thallus (in some cases, a few growth lines were observed) and 7-8 cells thick above. The cells of the outer cortex are cuboid to cylindrical in shape, and compactly arranged in anticlinal rows. Secondary pit-connections between adjacent cell rows are frequently observed in this layer (Fig. 23B). The outer cortex grades to an inner cortex of large, irregularly-shaped to rounded cells which in turn connects to a medullary layer of simple or branched, rather thick filaments mainly periclinally oriented. The medulla is very dense in the lower portion, but becomes less dense toward the apices (Fig. 23A, B, 24A).

**Reproduction** --- Reproductive structures are confined to sorus-like groups in the ultimate segments or, more often, to proliferations (Fig. 22C). Carpogonial branches and auxiliary cells are formed in separate ampullae accessorially produced from the cortical cells. In the carpogonial ampullae, the primary filament is composed of up to 11 ellipsoid to somewhat conical-shaped cells. From the filament, one or two (rarely three) simple secondary filaments are developed toward the surface. The carpogonial branch, consisting of a carpogonium and a hypogynous cell, develops on the primary filament (Fig. 23C, 24B). The auxiliary cell ampullae are similar in structure to the carpogonial ampullae, but generally larger in size and composed of more cells. The primary filament of the auxiliary cell ampullae is up to 13 cells long, and from the first or other cells of the filament one or two

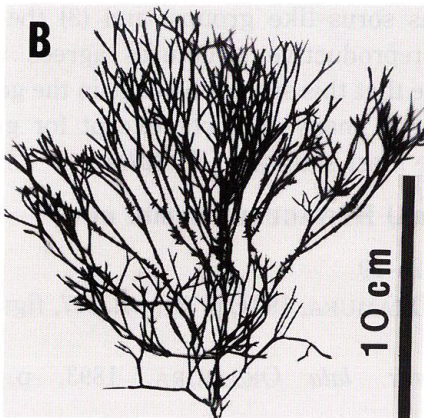
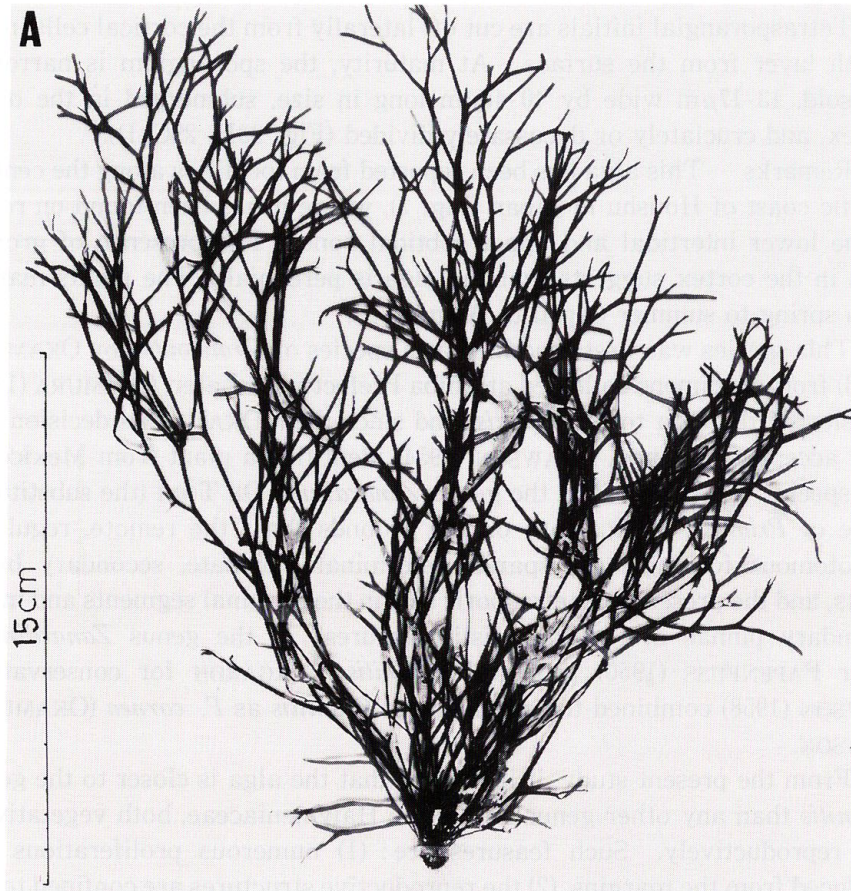
(rarely three) simple filaments are issued. No tertiary filaments were observed in either kind of ampulla. The auxiliary cell is usually the third cell of the primary filament, oval in shape, and easily recognized by its larger size (Fig. 23D, 24C).

Early stages of fertilization were not traced with certainty, although several connecting filaments were seen. These were produced from a large, irregularly-shaped cell (Fig. 23E), presumably the result of fusions between the carpogonium, the hypogynous cell and possibly some other cell in the ampulla. The ampullary cells surrounding the fusion cell become impoverished, so that their function seems to be to supply nutrition to the fusion cell. The connecting filaments grow toward auxiliary cells through the medulla. In one case, a connecting filament about to fuse with an auxiliary cell was observed (Fig. 24D). After contact with an auxiliary cell, another connecting filament is usually produced from the opposite side of the auxiliary cell. The auxiliary cell activated by a connecting filament cuts off a gonimoblast initial cell toward the surface by a concave wall. The gonimoblast initial cell cuts off cells and these cells in turn divide to form carposporangia (Fig. 23F, 24F, G). Some of the cells adjacent to the initial cell remain sterile. They become much elongated in the later stages of the cystocarp development. During these events, the ampullary cells produce lateral branches. As the carposporophyte develops further, these lateral branches, together with ampullary filaments, gradually elongate and surround it as a pericarp. Some vegetative cells are also involved in pericarp formation, and a rather thick pericarp forms around the young carposporophyte. However, in the mature cystocarp, a pericarp is scarcely detectable (Fig. 24H). This is probably because the cells of the pericarp become impoverished as they supply nutrition to the developing carposporophyte. The auxiliary cell partly fuses with some neighboring ampullary cells to form an irregularly-shaped fusion cell (Fig. 24I). The mature cystocarp is spherical to pear-shaped, submerged in the interior of thallus, and has a distinct ostiole. "Rays" and small ring-like structures were seen around the elongated gonimoblast initial cell in old cystocarps (Fig. 24I).

Spermatangia are formed from the outermost cortical cells as in *P.*

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**Fig. 22.** *Prionitis cornea* (OKAMURA) DAWSON. A. Habit of sterile specimen (SAP 047307). B. Habit of tetrasporangial specimen with numerous proliferations produced from the margin. (SAP 047297). C. Detail of proliferations (arrowheads) in B.



*patens*. Some liberated spermatia appear to remain embedded in the mucilaginous substance of the surface layer (Fig. 23G, 25A, B).

Tetrasporangial initials are cut off laterally from the cortical cells in the fourth layer from the surface. At maturity, the sporangium is narrowly ellipsoid, 13-17 $\mu$ m wide by 40-48 $\mu$ m long in size, submerged in the outer cortex, and cruciately or decussately divided (Fig. 23H, 25C, D).

Remarks --- This alga has been reported from localities along the central Pacific coast of Honshu in Japan (Fig. 2), where it has been found on rocks in the lower intertidal and upper subtidal zone. The presence of growth lines in the cortex suggests that the alga is perennial. The plants mature from spring to summer (April to August).

This species was first described as a species of *Grateloupia* by OKAMURA (1913) from specimens collected at Chiba Prefecture. Later, OKAMURA (1935) transferred the alga to *Carpopeltis*, and since then, OKAMURA's decision has been accepted in Japan. DAWSON (1954) identified a plant from Mexico as this species, but placed it in the genus *Zanardinula* DE TONI (the substituted name of *Prionitis* J. AGARDH) on the grounds that "the remote, regularly dichotomous forkings, the sparse, determinate, pinnate, secondary branchlets, and the presence of tetrasporic sori in the terminal segments and in the secondary pinnae are characteristic features" of the genus *Zanardinula*. After PAPPENFUSS (1950) proposed *Prionitis* J. AGARDH for conservation, DAWSON (1958) combined the species with *Prionitis* as *P. cornea* (OKAMURA) DAWSON.

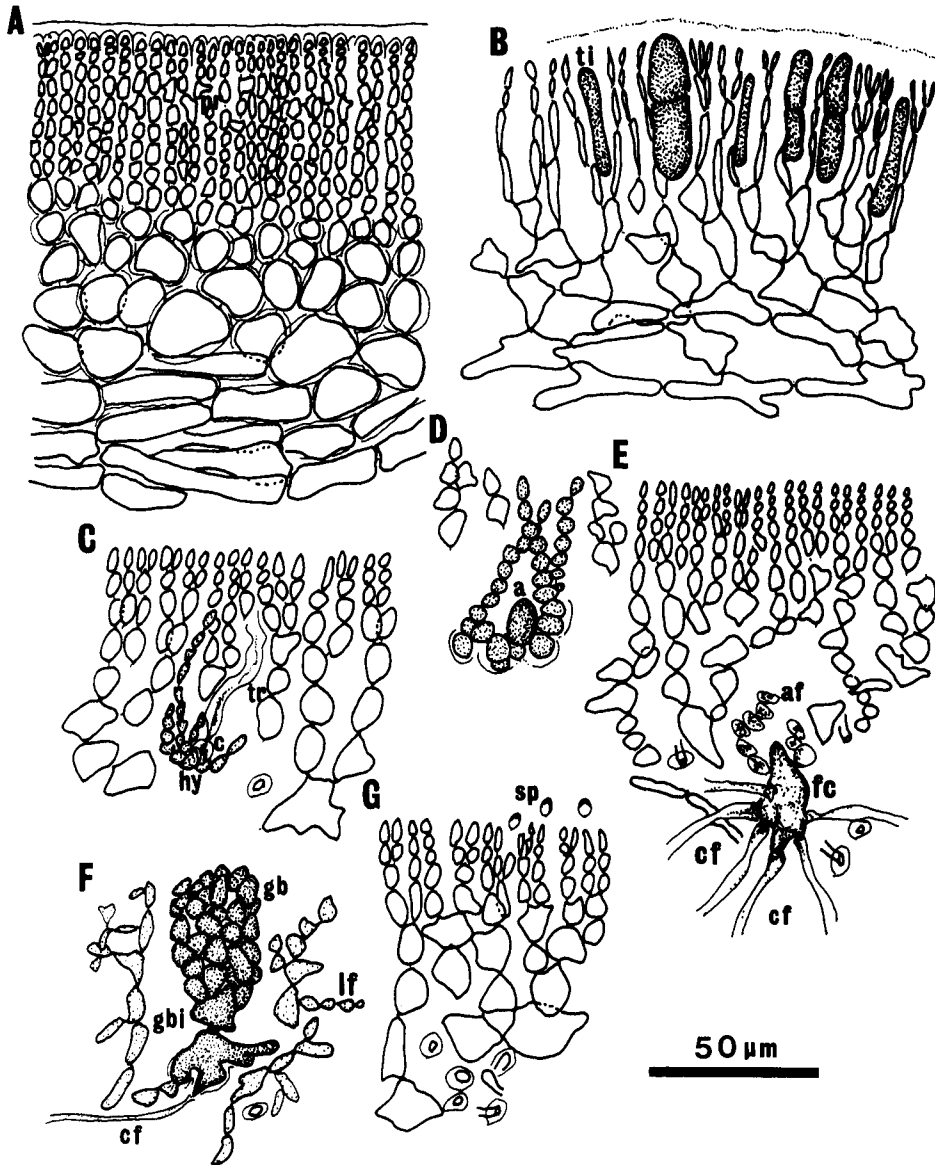
From the present study, it is evident that the alga is closer to the genus *Prionitis* than any other genus within the Halymeniaceae, both vegetatively and reproductively. Such features are: (1) numerous proliferations are produced from the margins, (2) the reproductive structures are confined to the ultimate segments or proliferations as sorus-like groups, and (3) the developmental morphology of female reproductive structures agrees with *Prionitis lanceolata*. I therefore conclude that this species belongs in the genus *Prionitis*, in agreement with DAWSON. In many respects, except for gross morphology, this species appears to be most similar to *P. patens*.

***Prionitis divaricata* (OKAMURA) KAWAGUCHI, comb. nov.**

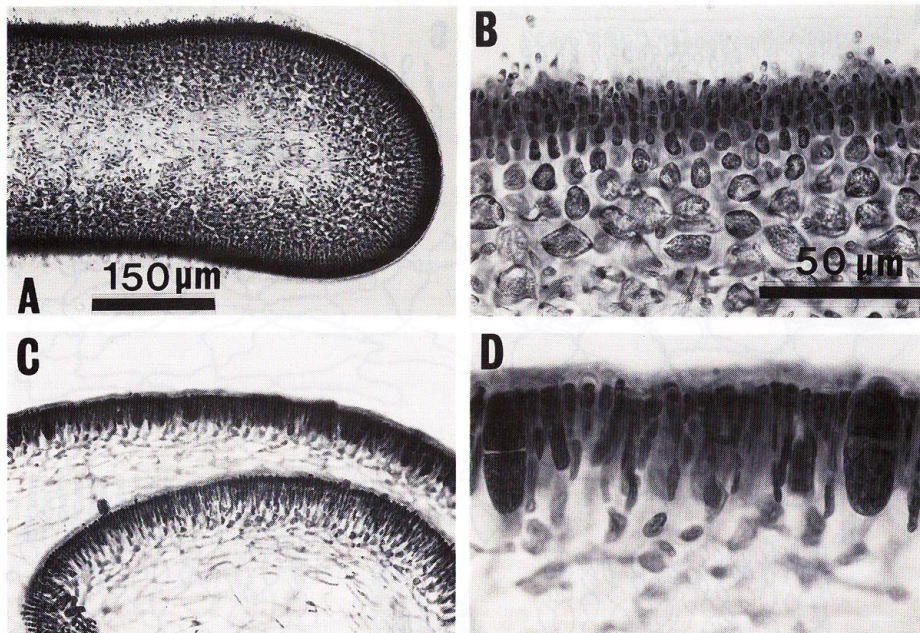
Figs. 26-29

Basionym: *Carpopeltis divaricata* OKAMURA, 1934, p. 31, pl. 317, figs. 1-5. TAZAWA, 1975, p. 121.

Synonyms: *Grateloupia affinis* var. *lata* OKAMURA, 1893, p. 101



**Fig. 23.** *Prionitis cornea* (OKAMURA) DAWSON. A. Longitudinal section of middle portion of thallus. Note that protuberances (pr) are seen in the outer cortex. B. Tetrasporangia formation. C. Carpogonial ampulla. D. Auxiliary cell ampulla. E. Connecting filaments (cf) produced from fusion cell (fc). F. Young stage in gonimoblast development. G. Spermatangia formation.



**Fig. 25.** *Prionitis cornea* (OKAMURA) DAWSON. A. Transverse section of proliferation bearing spermatangia. B. Spermatangia formation. C. Transverse section of proliferation bearing tetrasporangia. D. Tetrasporangia formation. Scale in A applies to C, and B to D.

(partim); *Grateloupia lata* OKAMURA, 1902, p. 87 (partim), 1916, p. 107; *Prionitis australis* (non J. AGARDH) ? YENDO, 1916, p. 263 (partim).

Type: SAP (Okamura herb.)

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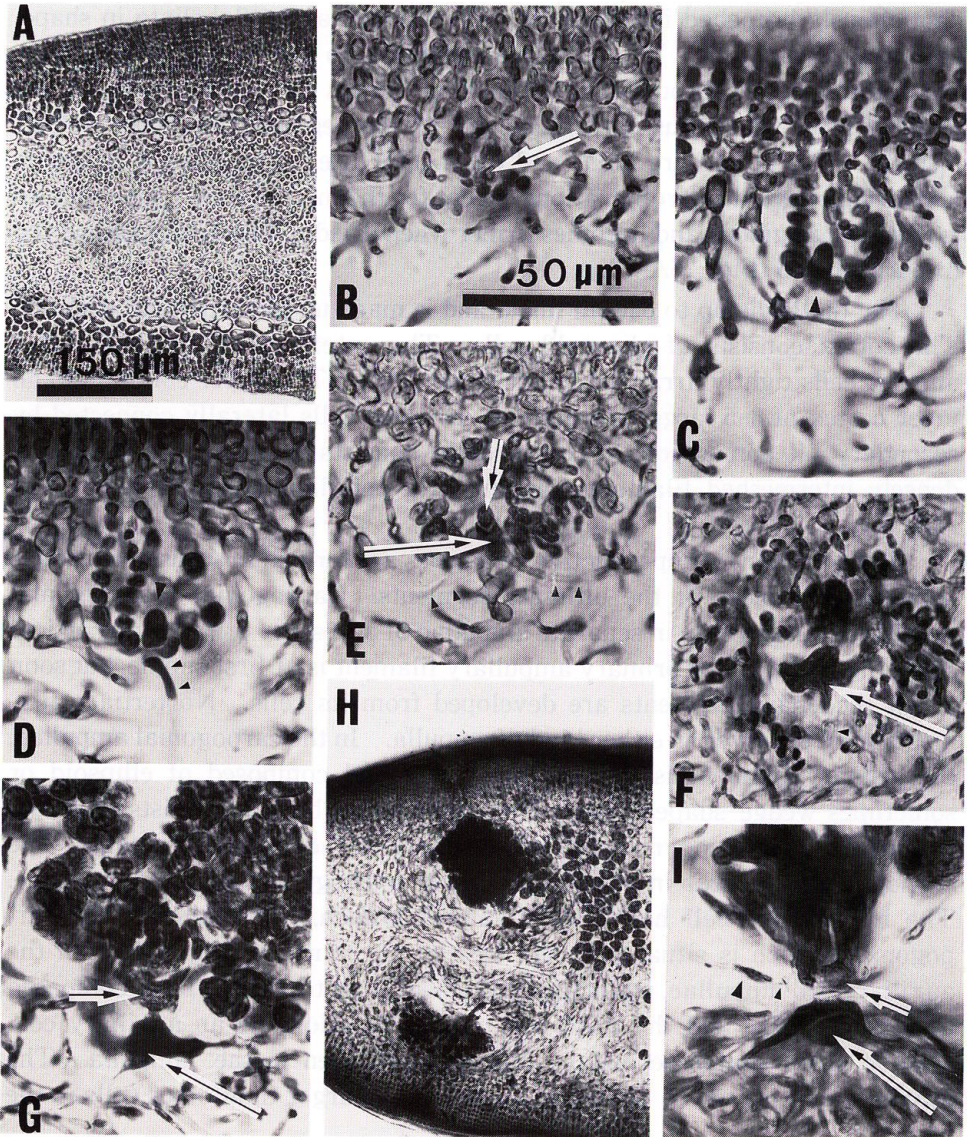
**Fig. 24.** *Prionitis cornea* (OKAMURA) DAWSON. A. Transverse section of lower portion of thallus. B. Carpogonial ampulla. Arrow shows carpogonium. C, D. Auxiliary cell ampullae. Large arrowhead shows auxiliary cell. Small arrowheads in D show connecting filament just about to fuse auxiliary cell. E. Early stage in gonimoblast development. Long arrow shows auxiliary cell and short arrow gonimoblast initial cell. Arrowheads show incoming and outgoing connecting filaments. F. Slightly advanced stage in gonimoblast development. Arrow shows fusion cell and arrowhead connecting filament. G. Basal portion of mature cystocarp showing gonimoblast initial (short arrow) and fusion cell (long arrow). H. Mature cystocarps embedded deep in the thallus. I. Basal portion of old cystocarp showing "ray" (large arrowhead), ring-like structure (small arrowhead), gonimoblast initial (short arrow) and fusion cell (long arrow). Scale in A applies to H, and B to C-G and I.

Type locality : Moroiso, Kanagawa Prefecture

Distribution : Endemic

Japanese name : Hitotsumatsu

Materials examined : *Kyushu* : sterile, Uto, Miyazaki Prefecture, 16, vi, 1983, leg. S. Kawaguchi, SAP 047372; sterile, Meotoura, Miyazaki Pref. , 3, vi, 1982, leg. S. Kawaguchi, SAP 047373. *Honshu* : sterile, Sugashima, Mie Pref. , 27, iv, 1957, leg. Y.

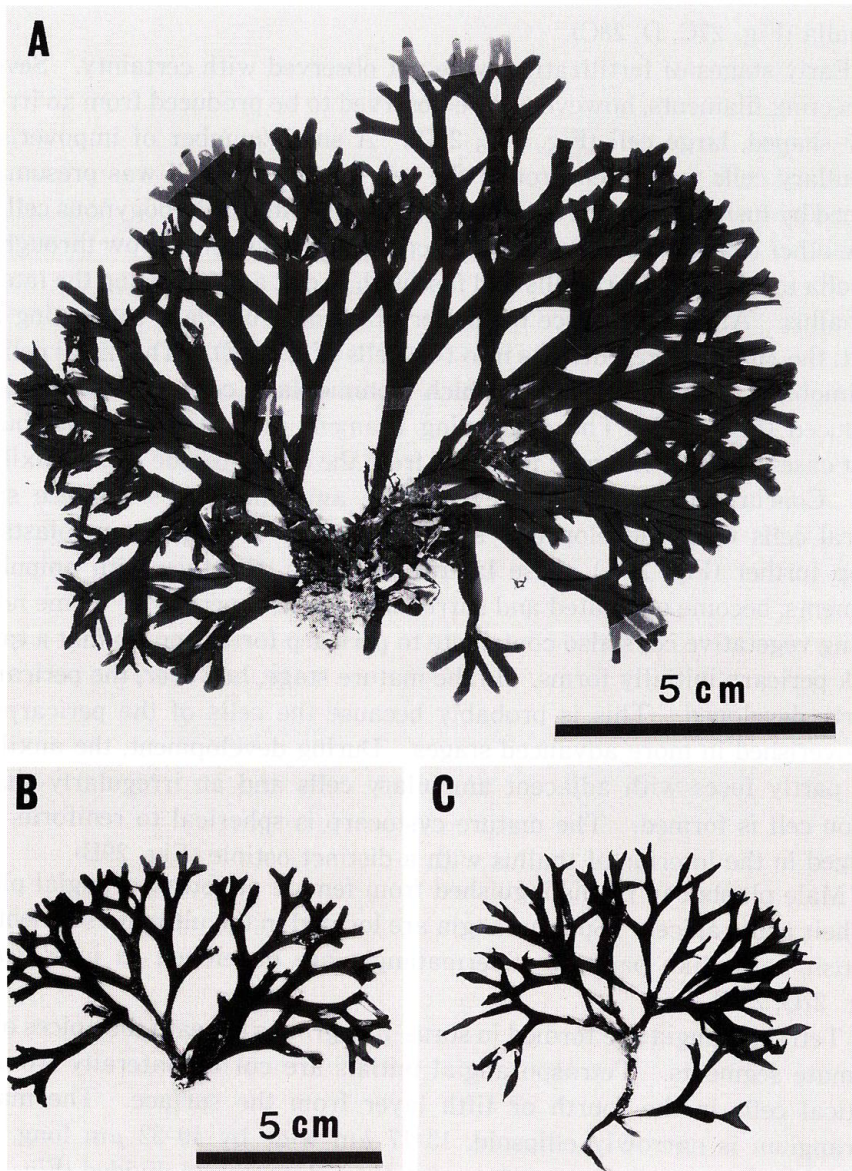


Tsuji, SAP 047366; sterile, Omaezaki, Shizuoka Pref., 27, iii, 1982, leg. M. Masuda, SAP 047371; cystocarpic, spermatangial, tetrasporangial, Shichirigahama, Kanagawa Pref., 21, vi, 1982, leg. S. Kawaguchi, SAP 047368-70 (all cast up ashore); tetrasporangial, Futomi, Chiba Pref., 23, vi, 1982, leg. S. Kawaguchi, SAP 047374; sterile, Katsuura, Chiba Pref., 22, vi, 1982, leg. S. Kawaguchi, SAP 047367 (Fig. 2).

**Vegetative structure** --- The plants arise singly or sometimes gregariously from a discoid holdfast through short cylindrical stipes. The plants soon expand into compressed thalli with a cuneate base, repeatedly dichotomously branched in one plane with rounded axils, flabellate in shape, and up to 15 cm high. The segments are linear, to 8 mm broad, and almost the same breadth throughout. Branching occurs more frequently in the upper portion of thallus, so that length of the segments becomes shorter distally. The apices are blunt and often bifurcate. The margin is entire, and usually devoid of proliferations except for the injured ends. The texture is rigid cartilaginous and becomes firmer when dried. The color is blood red to purplish red (Fig. 26A-C).

The thallus is up to 650  $\mu$ m thick, and is made up of cortex and medulla. The cortex consists of about 10 cells. The outer cortex consists of 5-7 angular cells tightly arranged in anticlinal rows. This layer connects to an inner cortex of 3-5 large, polygonal to rounded cells laterally connected by secondary pit-connections. The medulla consists of simple or branched, densely intermeshed filaments running in a periclinal direction (Fig. 27A, 28A).

**Reproduction** --- Reproductive structures are formed in sorus-like groups between the apices of the ultimate segments. Carpogonial branches and auxiliary cells develop in separate ampullae of accessory origin from cortical cells (Fig. 28B). The primary ampullary filament is at first simple, but soon a few secondary filaments are developed from its cells. No tertiary filaments were observed in either kind of ampulla. In the carpogonial ampullae, the primary filament is up to 7 cells long and composed of ellipsoid or sometimes wedge-shaped cells. The carpogonial branch consists of a carpogonium and a hypogynous cell and develops on the primary filament. The carpogonium, conical in shape, projects a trichogyne toward the surface. The hypogynous cell has a short lateral branch. At maturity, the carpogonial branch is situated at the base of the ampulla (Fig. 27B). In the auxiliary cell ampullae, the primary filament is up to 13 cells long, composed of rounded cells, and the third cell usually functions as an auxiliary cell. Two or three simple secondary filaments are seen in the ampulla. The auxiliary cell is oval to oblong in shape and is larger than other cells in the



**Fig. 26.** *Prionitis divaricata* (OKAMURA) KAWAGUCHI. A. Habit of tetrasporangial specimen (SAP 047370). B. Habit of cystocarpic specimen (SAP 047368). C. Habit of spermatangial specimen (SAP 047369). Scale in B applies also to C.

ampulla (Fig. 27C, D, 28C).

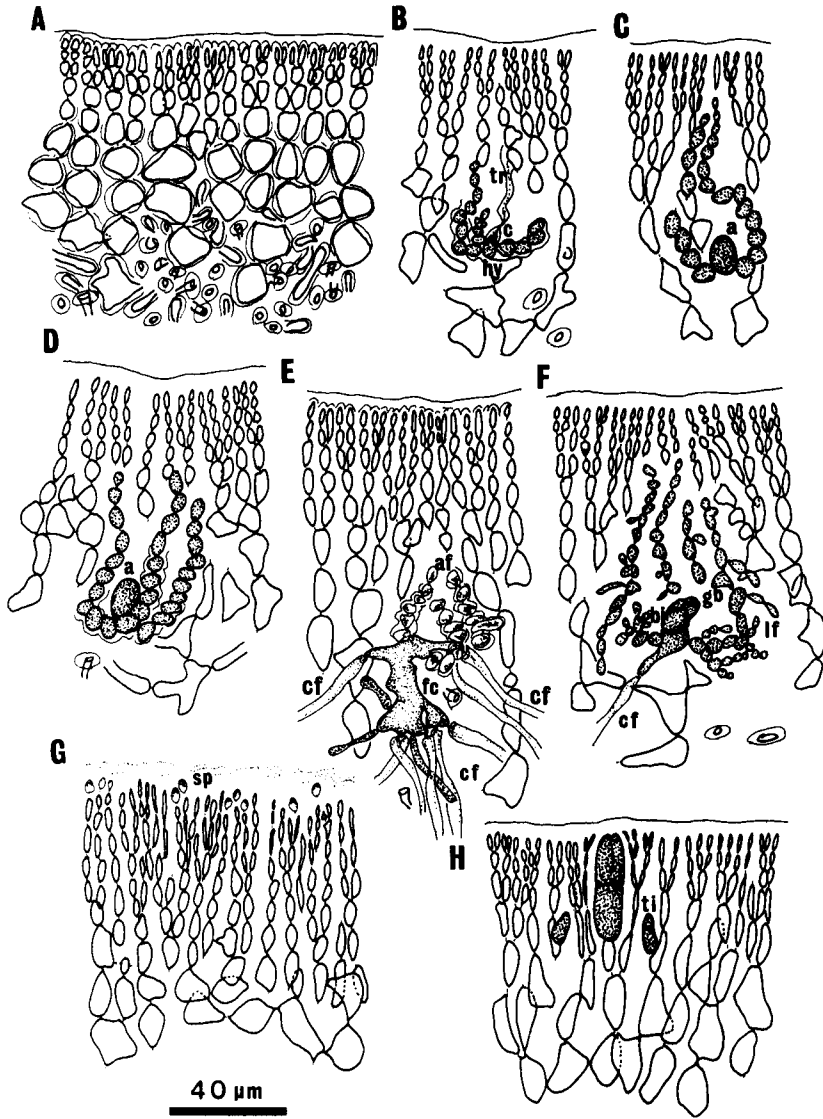
Early stages of fertilization were not observed with certainty. Several connecting filaments, however, were observed to be produced from an irregularly-shaped, large cell (Fig. 27E, 28D). A small number of impoverished ampullary cells were seen around the cell, so that the cell was presumably formed by fusions of the fertilized carpogonium with the hypogynous cell and some other cells in the ampulla. The connecting filaments grow through the medulla toward auxiliary cells and fuse with one at a point facing the interior of thallus. After acceptance of the fertilized nucleus via a connecting filament, the auxiliary cell divides into two cells (Fig. 28E). The distal cell is a gonimoblast initial cell from which gonimoblast cells are successively produced (Fig. 27E). The connecting filament may stop growing, but in most cases, another filament is cut off from the opposite side of the auxiliary cell. Concurrently with these events, the ampullary cells produce small lateral cells which develop into short filaments. As the gonimoblasts develop further (Fig. 29A), these lateral filaments, together with ampullary filaments, become elongated and surround them as a pericarp. Some neighboring vegetative cells also contribute to pericarp formation, so that a rather thick pericarp initially forms. In the mature stage, however, the pericarp is poorly developed. This is probably because the cells of the pericarp are impoverished in more advanced stages. During development, the auxiliary cell partly fuses with adjacent ampullary cells and an irregularly-shaped fusion cell is formed. The mature cystocarp is spherical to reniform, submerged in the interior of thallus with a distinct ostiole (Fig. 29B).

Male plants can be distinguished from female or tetrasporangial plants by their acute apices. Spermatangia are located in the ultimate segments as whitish, sorus-like patches. Spermatangia are developed as in *P. patens* (Fig. 27G, 29C).

Tetrasporangia are formed in sorus-like groups beneath the apices of the ultimate segments. Tetrasporangial initials are cut off laterally from the cortical cells in the fourth or fifth layer from the surface. The mature sporangium is narrowly ellipsoid, 13-17  $\mu\text{m}$  wide by 40-52  $\mu\text{m}$  long, submerged in the outer cortex, and cruciately or decussately divided (Fig. 27H, 29D, E).

Remarks --- This alga has been reported from localities along the Pacific coast of Honshu, Shikoku and Kyushu (Fig. 2). It has been found on rocks in the lower intertidal zone, particularly at places exposed to wave action.

This alga was first included in the species *Carpopeltis flabellata* auct.



**Fig. 27.** *Prionitis divaricata* (OKAMURA) KAWAGUCHI. A. Transverse section of middle portion of thallus. B. Caropogonial ampulla. C, D. Auxiliary cell ampullae. E. Connecting filaments (cf) produced from irregularly-shaped fusion cell (fc). F. Young stage in gonimoblast development. Note that lateral filaments (lf) are produced from ampullary cells. G. Spermatangia formation. H. Tetrasporangia formation.

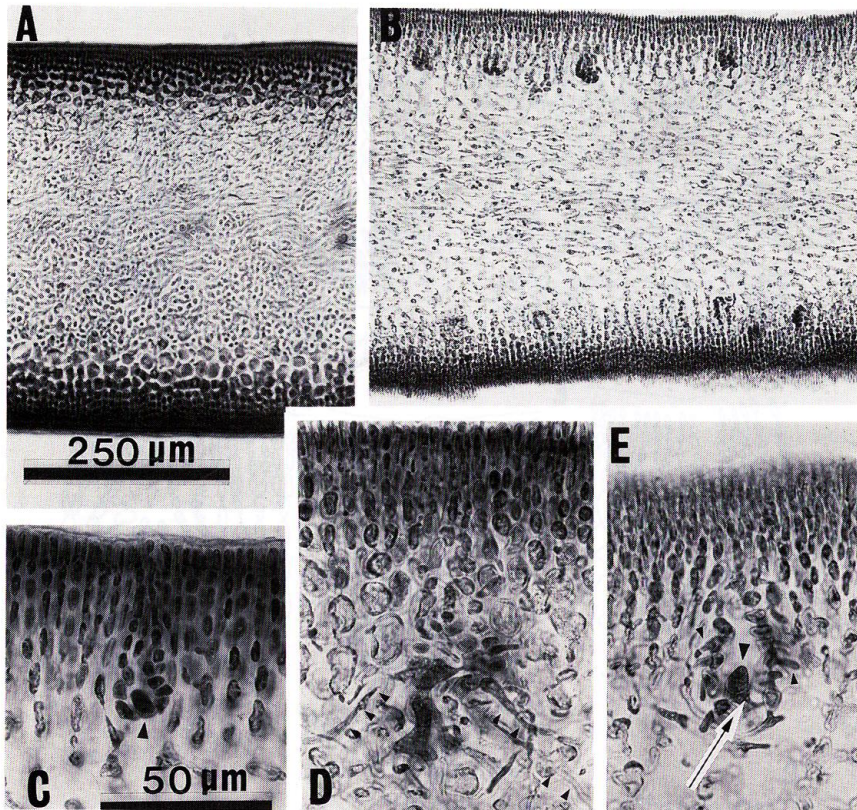


Fig. 28. *Prionitis divaricata* (OKAMURA) KAWAGUCHI. A. Transverse section of middle portion of thallus. B. Transverse section of apical portion of thallus showing female reproductive structures. C. Auxiliary cell ampulla. D. Connecting filaments (arrowheads) produced from irregular-shaped cell. E. Early stage in gonimoblast development. Note that gonimoblast initial (arrowhead) has just been produced from auxiliary cell (arrow). Scale in A applies also to B, and C to D and E.

OKAMURA, a species now known as *Carpopeltis prolifera* (HARIOT) KAWAGUCHI et MASUDA (KAWAGUCHI & MASUDA, 1984). In 1934, OKAMURA recognized the alga as a distinct species, *C. divaricata* OKAMURA, and this has been accepted since (Cf. SEGAWA, 1957).

From the present study, it is now known that this species shares taxonomically important vegetative and reproductive features with the members of the genus *Prionitis*. Such features are: (1) absence of mid-ribs, (2) the cells of the inner cortical cells irregular to rounded, (3) reproductive structures

confined in sorus-like groups in the ultimate segments and (4) the developmental morphology of female reproductive structures in agreement with the type species *P. lanceolata*.

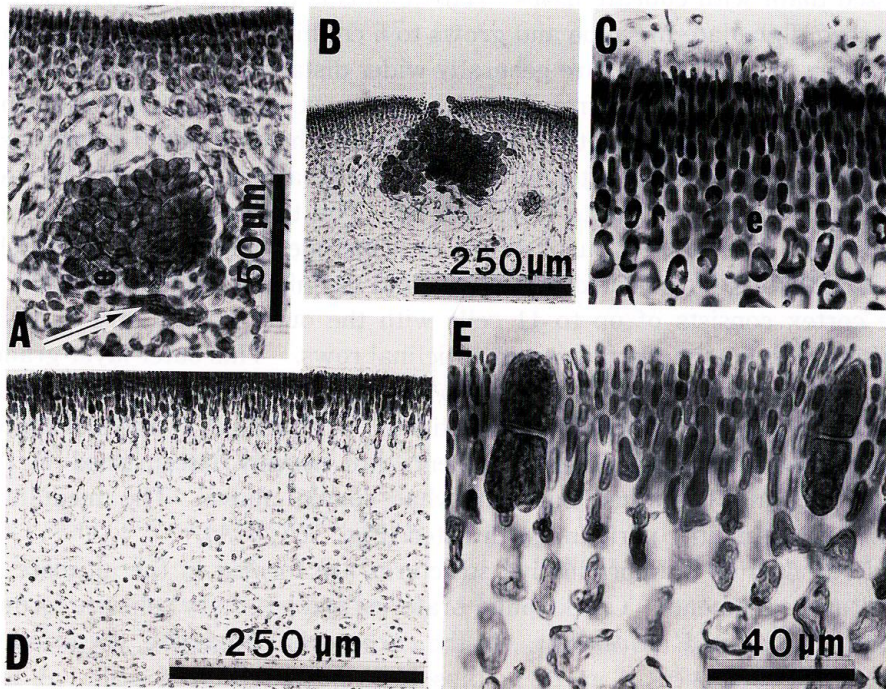
Although it often lacks proliferations, the alga therefore falls within the circumscription of *Prionitis*, and the following new combination is proposed: *Prionitis divaricata* (OKAMURA) KAWAGUCHI, comb. nov. [basonym: *Carpopeltis divaricata* OKAMURA, 1934: 31]

*P. divaricata* seems to be similar in gross morphology to *P. australis* J. AGARDH from California (Cf. ABBOTT & HOLLENBERG, 1976, p. 444, fig. 394).

***Prionitis crispata* (OKAMURA) KAWAGUCHI, comb. nov.**

Figs. 30-33

Basionym: *Carpopeltis crispata* OKAMURA, 1934, p. 32, pl. 317, figs. 6-11.



**Fig. 29.** *Prionitis divaricata* (OKAMURA) KAWAGUCHI. A. Advanced stage in gonimoblast development. Arrow shows fusion cell. B. Mature cystocarp with distinct ostiole. Note that pericarp is scarcely developed. C. Spermatangia formation. D. Transverse section of apical portion of tetrasporangial plant. E. Tetrasporangia formation. Scale in E applies to C.

Synonyms : *Grateloupia affinis* var. *lata* OKAMURA, 1893, p. 101 (partim); *Grateloupia lata* OKAMURA, 1902, p. 87 (partim), 1916, p. 107; *Prionitis australis* (non J. AGARDH) ? YENDO, 1916, p. 263 (partim).

Type : SAP (Okamura herb.)

Type locality : Moroiso, Kanagawa Prefecture

Distribution : Endemic

Japanese name : Tosakamatsu

Materials examined : *Kyushu* : spermatangial, Nango, Miyazaki Prefecture, 25, v, 1982, leg. S. Kawaguchi, SAP 047385; cystocarpic, spermatangial, tetrasporangial, Ohdomari, Kagoshima Pref., 14, vi, 1983, leg. S. Kawaguchi, SAP 047382-4 (all cast up ashore). *Honshu* : cystocarpic, tetrasporangial, Shimoda, Shizuoka Pref., 19, vi, 1982, leg. S. Kawaguchi, SAP 047386-7; tetrasporangial, Futomi, Chiba Pref., 23, vi, 1982, leg. S. Kawaguchi, SAP 047381 (Fig. 2).

Vegetative structure --- The plants arise gregariously from a callous holdfast through short cylindrical stipes, and gradually expand into compressed thalli with cuneate bases. The thallus is repeatedly dichotomously branched, flabellate in shape and grows to 6 cm high. Segments vary from 2 to 8 mm in breadth, and are generally wider distally. The apical portions are crowded with short, narrow branches. In most cases, the upper segments are strongly crispate, so that the thallus assumes a hemispherical appearance. The apices are blunt and often bifurcate. Proliferations are rarely observed except for the injured parts (Fig. 30A-C). The texture is somewhat cartilaginous. The color is purplish red, or sometimes greenish, or yellowish.

The thallus, constructed of a cortex and medulla, is up to 500  $\mu\text{m}$  thick. The cortex consists of up to 11 cells with the outer cortex of 4-6 small, ellipsoid cells compactly aligned in anticlinal rows. This outer layer grades to an inner cortex of larger, stellate to rounded cells, laterally connected to adjacent cells by secondary pit-connections. The medulla consists of simple or branched filaments. These filaments are densely intermeshed in the lower portion of thallus, but somewhat sparse above. The medullary filaments are mainly periclinally directed (Fig. 31A, 32A).

Reproduction --- Reproductive structures are formed in the ultimate or penultimate segments. Carpogonial branches and auxiliary cells are formed in ampullae as in *P. divaricata*. In the carpogonial ampullae, the primary filament is composed of up to 7 ellipsoid to conical-shaped cells. A few simple, secondary filaments are produced from the filament. The carpogonial branch develops on the primary filament and consists of a carpogonium and a hypogynous cell. The carpogonium projects a trichogyne toward the surface. The hypogynous cell has a short lateral branch (Fig.

31C, 32B). In the auxiliary cell ampullae, the primary filament consists of up to 15 rounded cells. From the first, second or other cells of the filament, two to three simple secondary filaments arise upwards. No tertiary filaments are seen in either kind of ampulla. The auxiliary cell is generally the second or third cell of the primary filament. The mature auxiliary cell is oval in shape and larger than the other ampullary cells. It occupies a similar position to the carpogonial branch in the ampulla (Fig. 31B, 32C).

Early stages of fertilization were not observed clearly, except that several connecting filaments were produced from an irregularly-shaped, large cell (Fig. 31D). The cell is apparently due to fusions of the fertilized carpogonium with a cell or cells in the ampulla. Stages in the development of gonimoblasts were as described for *P. divaricata* (Fig. 32D-F). The mature cystocarp is submerged in the interior of thallus, spherical in shape and has a poorly developed pericarp. It has a distinct ostiole (Fig. 33A). An irregularly-shaped fusion cell, of the auxiliary cell and adjacent ampullary cells, is formed below the gonimoblast (Fig. 33B).

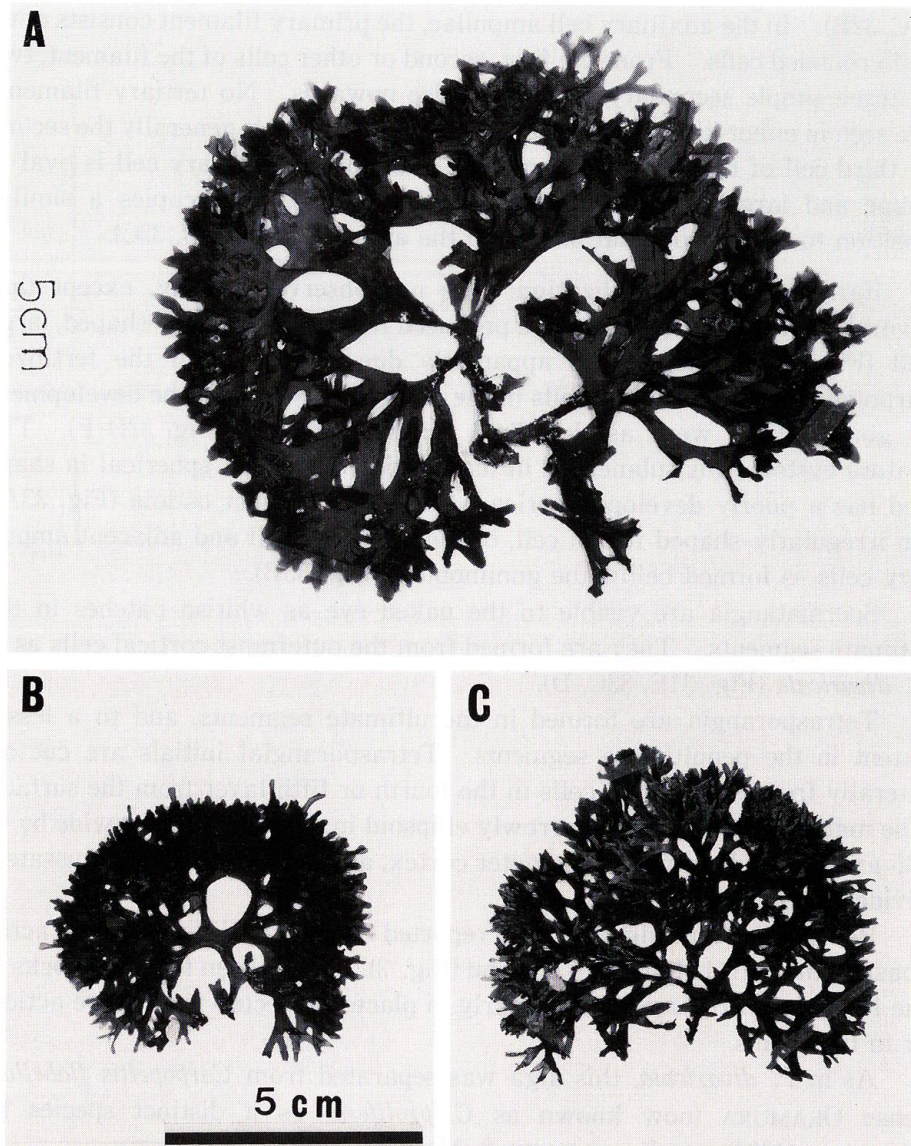
Spermatangia are visible to the naked eye as whitish patches in the ultimate segments. They are formed from the outermost cortical cells as in *P. divaricata* (Fig. 31E, 33C, D).

Tetrasporangia are formed in the ultimate segments, and to a lesser extent in the penultimate segments. Tetrasporangial initials are cut off laterally from the cortical cells in the fourth or fifth layer from the surface. The mature sporangium is narrowly ellipsoid in shape, 11-12  $\mu\text{m}$  wide by 42-45  $\mu\text{m}$  long, submerged in the outer cortex, and is cruciately or decussately divided (Fig. 31F, 33E, F).

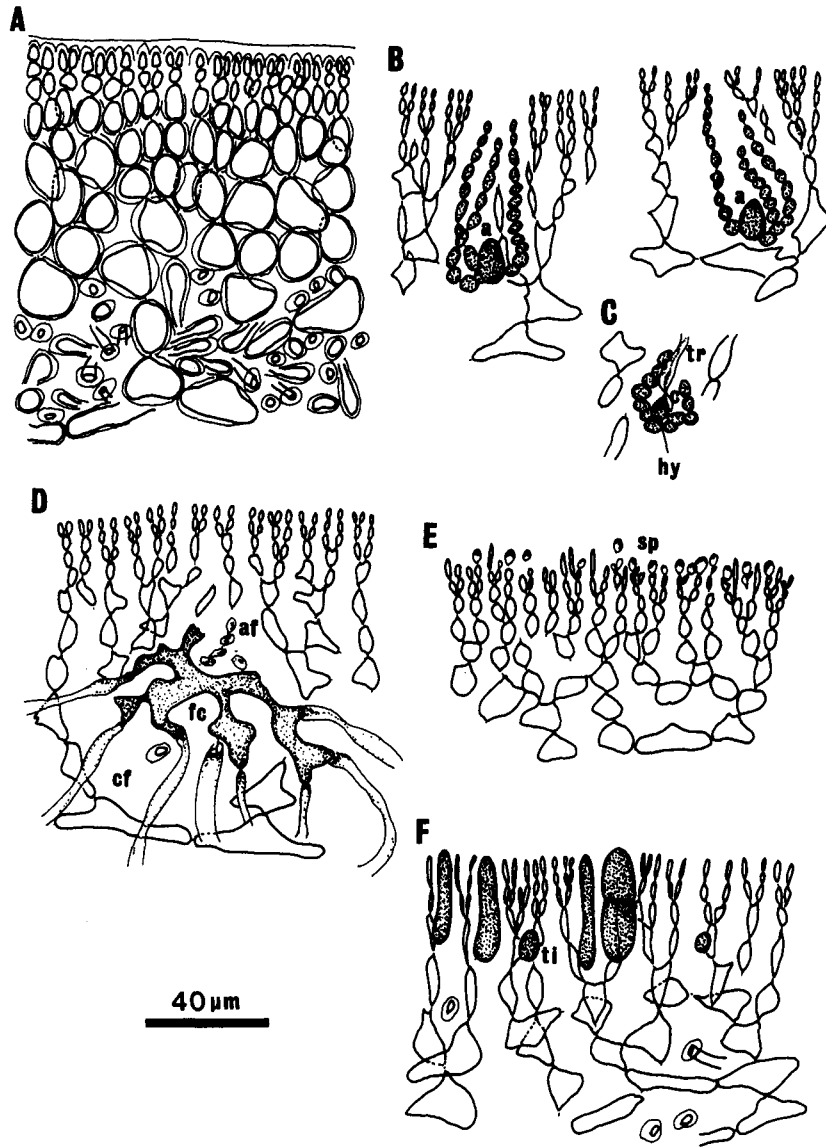
Remarks --- This alga has been reported from localities along the Pacific coast from central Honshu to Kyushu (Fig. 2). It has been found on rocks in the lower intertidal zone, particularly in places protected from wave action, or in tide-pools.

As in *P. divaricata*, this alga was separated from *Carpopeltis flabellata* sensu OKAMURA (now known as *C. prolifera*) as a distinct species by OKAMURA (1934) (see KAWAGUCHI & MASUDA, 1984).

The structure of the thallus and developmental morphology of female reproductive structures of this species agree well with *P. lanceolata*. The alga is similar to *P. divaricata* in reproduction, but differs from the latter in habit, thallus size and habitat. This species is therefore transferred to the genus *Prionitis* and the following new combination is proposed: *Prionitis crispata* (OKAMURA) KAWAGUCHI, comb. nov. [basonym: *Carpopeltis cri-*



**Fig. 30.** *Prionitis crispata* (OKAMURA) KAWAGUCHI. A. Habit of tetrasporangial specimen (SAP 047387). B. Habit of spermatangial specimen (SAP 047386). C. Habit of cystocarpic specimen (SAP 047386). Scale in B applies to C.



**Fig. 31.** *Prionitis crispata* (OKAMURA) KAWAGUCHI. A. Transverse section of middle portion of thallus. B. Auxiliary cell ampullae. C. Carogonial ampulla. D. Connecting filaments (cf) produced from irregular-shaped fusion cell (fc). E. Spermatangia formation. F. Tetrasporangia formation.

*spata* OKAMURA, 1934 : 32].

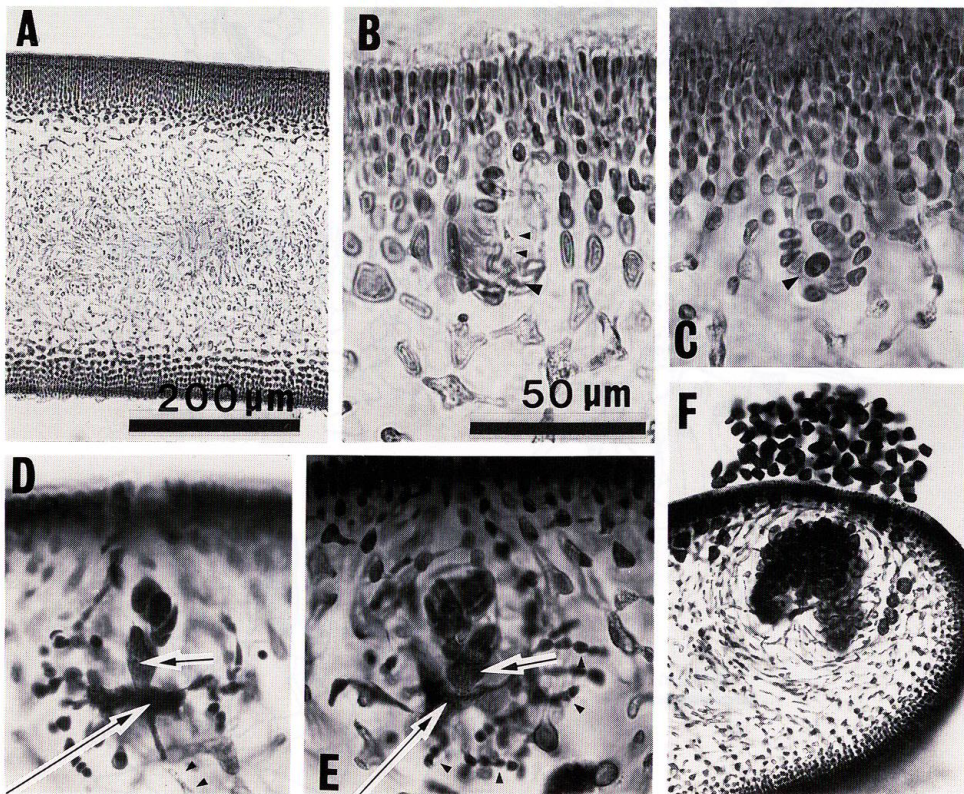
***Prionitis ramosissima* (OKAMURA) KAWAGUCHI, comb. nov.**

Figs. 34-36

Basionym: *Grateloupia ramosissima* OKAMURA, 1913, p. 60, pl. 118, figs. 1-11, 1936, p. 542. DAWSON, 1954a, p. 432.

Lectotype: SAP (Okamura herb.)

Type locality: Nemoto, Chiba Prefecture



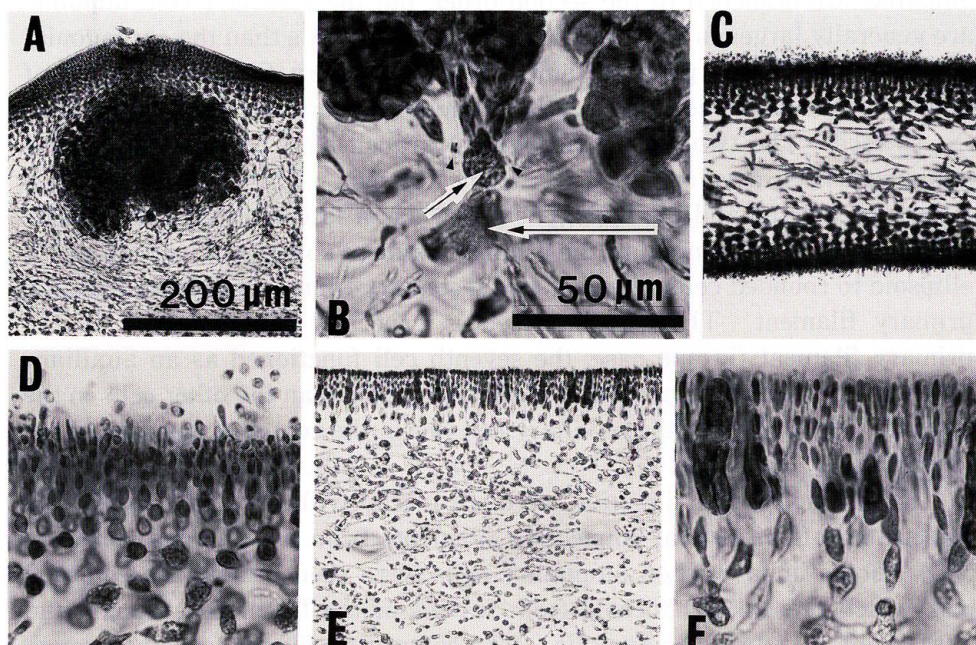
**Fig. 32.** *Prionitis crispata* (OKAMURA) KAWAGUCHI. A. Transverse section of lower portion of thallus. B. Carpogonial ampulla. Large arrowhead shows carpogonium and small arrowheads trichogyne. C. Auxiliary cell ampulla. D. Early stage in gonimoblast development. Long arrow shows fusion cell, short arrow gonimoblast initial, and arrowheads connecting filament. E. Slightly advanced stage, showing lateral filaments (arrowhead) produced from ampullary cells. F. Mature cystocarp. Scale in A applies to F, and B to C-E.

Distribution: Viet Nam, Japan

Japanese name: Suji-mukadenori

Materials examined: *Kyushu*: tetrasporangial, Meotoura, Miyazaki Prefecture, 3, vi, 1982, leg. S. Kawaguchi, SAP 047356-7; tetrasporangial, Aoshima, Miyazaki Pref., 11, vi, 1983, leg. S. Kawaguchi, SAP 047363-5. *Honshu*: cystocarpic, spermatangial, Shichirigahama, Kanagawa Pref., 20, vi, 1983, leg. S. Kawaguchi, SAP 047358-61 (all cast up ashore); sterile, Futomi, Chiba Pref., 23, vi, 1982, leg. S. Kawaguchi, SAP 047362 (Fig. 2).

Vegetative structure --- The plants arise gregariously from a scutate holdfast, terete below and slightly compressed above, simple or sometimes a few times irregularly dichotomously branched, and up to 30 cm high. The thallus is of similar breadth throughout, to 1.5 mm in diameter, usually with pointed apices. Numerous proliferations, tapering at both ends, are produced in various directions from the thallus. Some of the proliferations continue to grow into branchlets beset again with short proliferations and



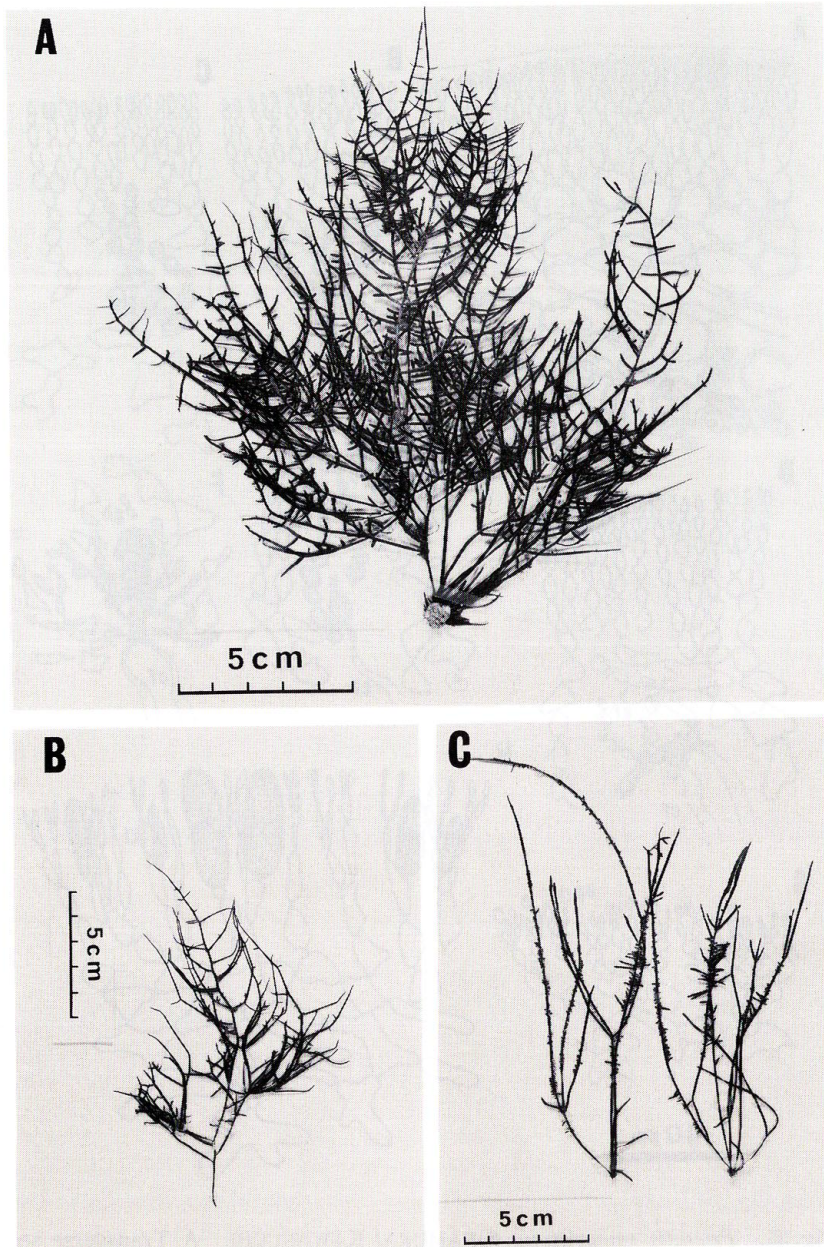
**Fig. 33.** *Prionitis crispata* (OKAMURA) KAWAGUCHI. A. Mature cystocarp with ostiole. B. Basal part of mature cystocarp. Long arrow shows fusion cell, short arrow gonimoblast initial and arrowhead ring-like structure. C. Transverse section of male plant. D. Spermatangia formation. E. Transverse section of tetrasporangial plant. F. Tetrasporangia formation. Scale in A applies to C and E, and B to D and F.

these may obscure the main branch (Fig. 34A-C). The color is dark red to brownish red, or at times greenish to yellowish. The texture is cartilaginous, and becomes firmer in drying.

The thallus is up to 1.5 mm thick, made up of cortical and medullary layers. The cortex is 10-20 cells thick. The outer cortex consists of 4-8 small, ellipsoid to angular cells tightly packed in anticlinal rows. This layer grades to, or rather abruptly connects to, an inner cortex of larger, rounded cells, often laterally connected by secondary pit-connections. The medulla consists of densely intermeshed, somewhat slender filaments. The filaments are simple or branched, and are generally periclinally oriented (Fig. 35A, 36A).

Reproduction --- Reproductive structures are confined to the short proliferations. Carpogonial branches and auxiliary cells are produced in separate ampullae, accessorially produced from the cortical cells. Both types of ampullae are branched to the second order, but the auxiliary cell ampullae are generally larger in size and composed of more cells than the carpogonial ampullae. In the carpogonial ampullae, the primary filament consists of about 10 cells with one or two cells developing secondary filaments toward the surface. The two-celled carpogonial branch of a carpogonium and a hypogynous cell develops on the primary filament. The carpogonium projects a trichogyne and the hypogynous cell has a lateral branch (Fig. 35B). In the auxiliary cell ampullae, the primary filament consists of up to 16 small, ellipsoid to rounded cells. One or two secondary filaments develop from the primary filament. The auxiliary cell is generally the third cell of the primary filament (in one case, the seventh cell functioned as an auxiliary cell), oval to oblong in shape, and is slightly larger than the other cells in the ampulla. At maturity, the auxiliary cell lies in the center at the base of the ampulla (Fig. 35C, 36B).

Early stages of fertilization were not traced with certainty, except for the cutting off of several connecting filaments from an enlarged cell (Fig. 35D). Some impoverished ampullary cells were seen around the enlarged cell, which presumably formed from fusions of the fertilized carpogonium with a cell or cells in the ampulla. The connecting filaments grow through the medulla and fuse with an auxiliary cell at a point facing the interior of thallus (Fig. 35E). Presumed diploidization of the auxiliary cell, besides promoting lateral filaments from the ampullary cells, results in the production of a gonimoblast initial cell by a concave, transverse septum. From the initial cell, gonimoblast cells are successively produced and these cells in



**Fig. 34.** *Prionitis ramosissima* (OKAMURA) KAWAGUCHI. A. Habit of cystocarpic specimen with crowded branches (SAP 047361). B. Habit of spermatangial specimen (SAP 047360). C. Habit of tetrasporangial specimen with few branches (SAP 047369).

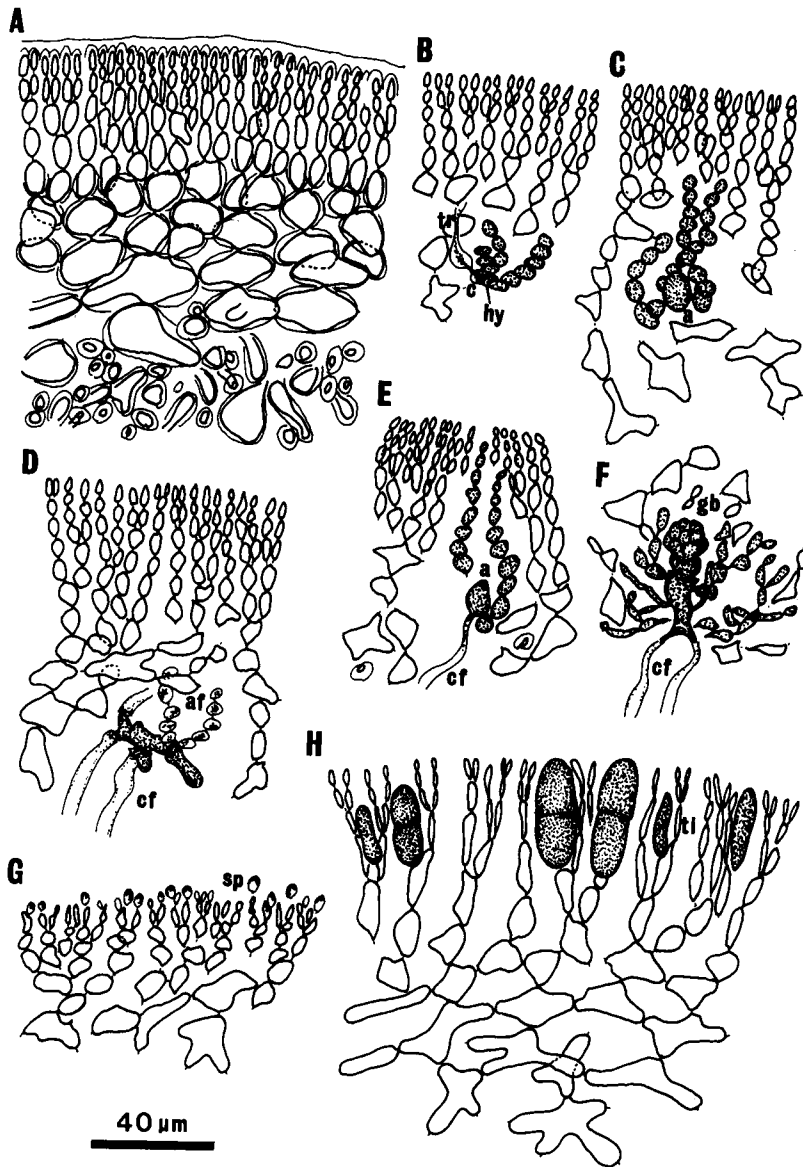
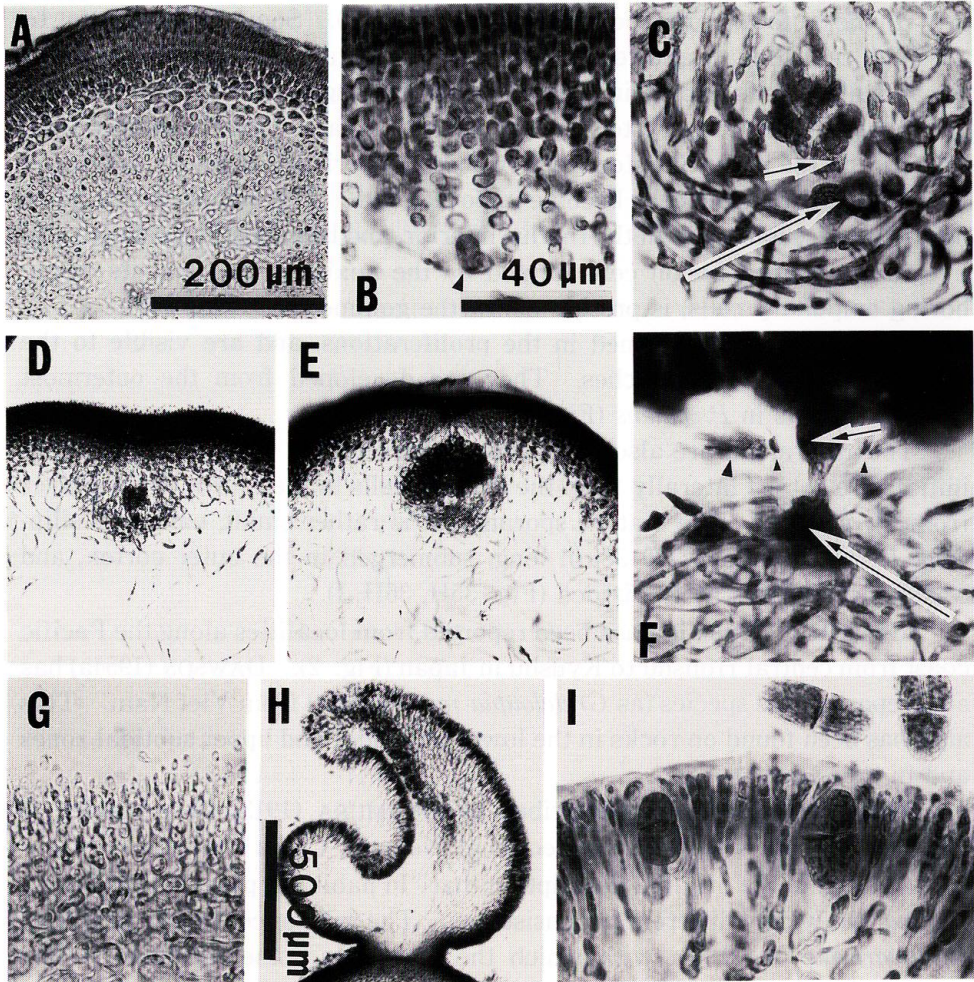


Fig. 35. *Prionitis ramosissima* (OKAMURA) KAWAGUCHI. A. Transverse section of middle portion of thallus. B. Carpogonial ampulla. C. Auxiliary cell ampulla. D. Connecting filaments produced from slightly enlarged cell. E. Contact of connecting filament with auxiliary cell. F. Young stage in gonimoblast development. G. Spermatangia formation. H. Tetrasporangia formation.



**Fig. 36.** *Prionitis ramosissima* (OKAMURA) KAWAGUCHI. A. Transverse section of lower portion of thallus. A single growth line is seen in the cortex. B. Auxiliary cell ampulla. C. Young stage in gonimoblast development. Long arrow shows fusion cell and short arrow gonimoblast initial. D, E. Advanced stages in gonimoblast development. Thick pericarpic tissue is seen around the lower portion of gonimoblast. F. Basal part of mature cystocarp. Long arrow shows fusion cell, short arrow elongated gonimoblast initial, large arrowhead "ray" and small arrowhead ring-like structure. G. Spermatangia formation. H. Transverse section through tetrasporangial proliferation. I. Tetrasporangia formation. Scale in A applies to D and E, and B to C, F, G and I.

turn divide to form carposporangia (Fig. 35F, 36C). Some cells adjacent to the initial cell elongate and remain sterile. As the carposporophyte develops, the ampullary cells and their lateral filaments elongate and surround it as a pericarp. In the young cystocarp, the pericarp is rather well developed (Fig. 36D, E). In the mature cystocarp, however, the pericarp is poorly developed because the pericarpic cells become impoverished. The mature cystocarp is pear-shaped, submerged in the thallus interior, and has a distinct ostiole. An irregularly-shaped fusion cell, formed by the auxiliary cell and its neighboring ampullary cells, is present below the gonimoblast (Fig. 36F).

Spermatangia are formed in the proliferations, and are visible to the naked eye as whitish patches. They are developed from the outermost cortical cells as in *P. patens* (Fig. 35G, 36G).

Tetrasporangia are also formed in proliferations. The tetrasporangial initials are cut off laterally from the cortical cells in the fourth or fifth layer from the surface. The mature sporangium is rather small, narrowly ellipsoid, 15-20 $\mu$ m wide by 30-38 $\mu$ m long, submerged in the outer cortex, and cruciately or decussately divided (Fig. 35H, 36H, I).

Remarks --- This alga has been reported from localities along the Pacific coast from central Honshu to Kyushu in Japan (Fig. 2). DAWSON (1954a) has also reported this species (as *Grateloupia ramosissima*) from Viet Nam. This alga has been found on rocks in the lower intertidal and upper subtidal zones and in tide-pools.

This species was first described by OKAMURA (1913) as a species of *Grateloupia* from a specimen collected at Nemoto, Chiba Prefecture. OKAMURA stated in the original description that "In habit the plant is allied to *G. filicina*, but widely different in consistence. The substance is more firm than *G. divaricata* OKAMURA with which the plant has some affinities". The present plant has some similarities to *G. divaricata* (Cf. OKAMURA, 1895, figs. 1-2), but differs in having a very rigid texture, compact cortex, large and rounded inner cortical cells and reproductive structures confined to the proliferations. These features suggest that the present plant is more closely related to the genus *Prionitis* than to *Grateloupia*, a genus which tends to include lubricous plants with scattered reproductive structures (Cf. KRAFT, 1977).

I therefore conclude that the present plant should be transferred to genus *Prionitis* as *P. ramosissima* (OKAMURA) KAWAGUCHI, comb. nov. [basionym *Grateloupia ramosissima* OKAMURA, 1913: 60].

### Discussion

In addition to the characters currently accepted for the family Halymeniaceae (Cf. SCHMITZ & HAUPTFLEISH, 1897, KYLIN, 1956, as Grateloupiaceae), the species treated in the present study have the following characters in common: (1) absence of midribs, (2) rigid cartilaginous texture, (3) compact cortex and medulla with the transitional region occupied by large, polygonal to rounded cells, (4) no refractive cells in the medulla, (5) reproductive structures confined to the ultimate or penultimate segments of main branches, and/or to the proliferous branchlets, or to the specially developed, small proliferations (sporophylls) and (6) auxiliary cell ampullae sparingly branched at most to the second order.

This combination of characters is consistent with *Prionitis lanceolata* (HARVEY) HARVEY (the type species of *Prionitis*) as described by SJOESTEDT (1926) and CHIANG (1970), although individual characters may occur in other genera such as *Carpopeltis*, *Cryptonemia*, *Polyopes* or *Grateloupia*. However, the genus *Cryptonemia*, to some members of which *P. schmitziana* is superficially similar, differs from *Prionitis* in having highly refractive stellate (or ganglionic) cells in the medulla and auxiliary cell ampullae profusely branched to the third or fourth order (Cf. ABBOTT, 1967; CHIANG, 1970; GUIRY & IRVINE, 1974; SCOTT *et al.*, 1982). The genus *Polyopes* is also easily separated from *Prionitis* as it has densely branched (to the fourth or fifth order) auxiliary cell ampullae and elevated tetrasporangial sori (nemathecia) (Cf. CHIANG, 1970).

CHIANG (1970) studied several specimens of the type species of the genus *Carpopeltis*, *C. phyllophora* (HOOKER et HARVEY) SCHMITZ. He observed *C. phyllophora* to have a conspicuous midrib, rather thin medullary layer ( $1/3$ – $1/8$  of thickness of thallus) and to produce cystocarps in terminal sori. However, as the specimens lacked early stages in the ontogeny of the cystocarp and only mature cystocarps were observed, CHIANG (1970) concluded that "the systematic position of *Carpopeltis* is uncertain". ABBOTT and HOLLENBERG (1976), in describing *Carpopeltis bushiae* (FARLOW) KYLIN from California, added a comment that "development of the female reproductive structures leading to formation of the gonimoblast in *Carpopeltis* is uncertain, and these structures have never been studied in either of the western N. American species attributed to this genus; thus their systematic position must remain uncertain until such studies are made".

Recently, I examined some voucher herbarium specimens of *C. phyllophora* on loan from the University of Melbourne (MELU), which included

female and tetrasporangial materials. A careful examination of these specimens revealed the following: *C. phyllophora* possesses a very thin thallus (to 200  $\mu$ m thick in a specimen 17cm high), conspicuous midribs (in section some growth lines probably of yearly basis were found in the cortex), a well developed inner cortical layer composed of large rounded cells and a rather thin medullary layer of sparsely intermeshed filaments. The reproductive structures are formed in the ultimate segments, just beneath the apices, as clearly delimited sori and the portions bearing tetrasporangia become much broader. Auxiliary cell ampullae are profusely branched, reminiscent of those seen in *Cryptonemia* (this aspect of morphology in *C. phyllophora* needs to be verified). Spermatangia are found in plants bearing cystocarps suggesting that the species is monoecious (KAWAGUCHI, unpubl. ).

As I could not clearly follow the developmental morphology of female reproductive structures of *C. phyllophora*, the generic status of *Carpopeltis* must remain uncertain. Nevertheless, the features of *C. phyllophora* mentioned above appear to be remarkably distinct from those of *P. lanceolata* and those of the Japanese species treated in the present study.

The genus *Grateloupia* should be included in the comparison because of its similarity to *Prionitis* in ampullar structure. According to the currently accepted circumscription of the genus *Grateloupia* (Cf. KRAFT, 1977), it has lubricous texture, stellate and secondarily-connected inner cortical layer, lax medulla and scattered reproductive structures, whilst *Prionitis* has rigid texture, compact cortex and medulla and reproductive structures confined to certain portions of thallus, particularly in the proliferations. It appears that these differences serve to distinguish *Prionitis* from *Grateloupia*, in spite of their similarity in ampulla structure. Table 1 shows comparative features of the genera mentioned above.

"Ray" structures, i. e., foliar radiating processes surrounding the stalk and sides of the gonimoblast initial (SIMONS & HEWITT, 1976), were found in most species treated in the present study. The "rays" are undoubtedly the remnants of sterile, gonimoblast cells near the initial, and the structures were found in certain members of *Grateloupia* and also in *Polyopes* from Japan (KAWAGUCHI, unpubl. ). Although SIMONS and HEWITT (1976) considered the presence or not of "ray", parallel with the presence or not of pericarpic ostiole, as of importance in separating *Pachymenia* from *Aeodes* from South Africa, the taxonomic significance of such features should be downgraded among other genera within this family. "Ringlike" structures mentioned by me in the present study are the remnants of the pit-connections between the gonimoblast initial and the gonimoblast cells produced from it.

Overall, it is concluded that *P. patens* and other Japanese species considered in this study belong in the genus *Prionitis* and that this genus is distinct from other genera of the Halymeniaceae.

**Table 1.** Comparative features of *Prionitis*, *Cryptonemia*, *Polyopes*, *Carpopeltis* and *Grateloupia*. Data largely extracted from SJOESTEDT (1926), DAWSON (1954), BALAKRISHNAN (1961), KAWABATA (1962), CHIANG (1970), GUIRY & IRVINE (1974), ABBOTT & HOLLENBERG (1976), SCOTT *et al.* (1982) and KAWAGUCHI (unpubl.).

	<i>Prionitis</i>	<i>Cryptonemia</i>	<i>Polyopes</i>	<i>Carpopeltis</i> *	<i>Grateloupia</i>
Texture of blade	rigid or cartilaginous	membranous to firm and crisp	rigid	membranous to cartilaginous	lubricous to leathery
Cortical cells	great variation-15-20 layers	4-8	10-15	4-6	great variation 5-20
Thickness of thallus ( $\mu\text{m}$ )	great variation 250-1000	150-300	<2000	<200	great variation 300-2000
Number of medullary filaments	many	somewhat many	many	few	few to many
Direction of medullary filaments	periclinal	periclinal	periclinal	periclinal	periclinal (anticlinal)**
Refractive cell	-	+	-	-	-(+)**
Midrib	-	+ (-)**	-	+	-
Position of tetrasporangium	confined (soral aggregation)	scattered or confined	confined (nemathecia)	confined (soral aggregations)	scattered
Auxiliary cell ampulla	sparingly branched to 2nd order	profusely branched to 3rd or 4th order	very profusely branched to 5th order	profusely branched(?)	sparingly branched to 2nd order
Pericarp	thin	thin	somewhat thick	somewhat thick	thin or thick
Size of tetrasporangium ( $\mu\text{m}$ )	great variation 10-20 $\times$ 30-62	very small 7-10 $\times$ 15-25	10-13 $\times$ 30-40	not given	great variation 8-25 $\times$ 20-63

\* Data on only *C. phyllophora* (type species).

\*\* Rare case shown in blank.

**Key to the species of *Prionitis* from Japan**

- 1 . Reproductive structures developed in the ultimate segments of the thallus and proliferations.....2
- 1 . Reproductive structures confined to small, specially developed proliferations (sporophylls) .....7
  - 2 . Thallus cylindrical to somewhat compressed, to 3 mm in width, simple or dichotomously branched .....3
  - 2 . Thallus compressed or flat, regularly or irregularly dichotomously branched, beset with proliferations .....4
- 3 . Thallus cylindrical, simple or a few times dichotomously branched, beset with numerous proliferations tapering at both ends ....*P. ramosissima*
- 3 . Thallus cylindrical to compressed, repeatedly dichotomously branched, with slight constrictions at irregular intervals; reproductive structures mainly formed in small, circular proliferations .....*P. angusta*
  - 4 . Thallus with proliferations from margin .....5
  - 4 . Thallus without proliferations .....6
- 5 . Thallus repeatedly dichotomously branched, to 3 mm in width, ending in bifurcate apices .....*P. cornea*
- 5 . Thallus irregularly branched with patent axils, to 8 mm in width, with numerous pinnately arranged proliferous branchlets .....*P. patens*
  - 6 . Thallus up to 12 cm in height, dichotomously branched in one plane .....*P. divaricata*
  - 6 . Thallus densely gregarious, less than 6 cm in height; upper portion of thallus strongly crisped, often having a spherical to hemispherical outline .....*P. crispata*
- 7 . Thallus flat, broadly lanceolate, up to 5 cm in width, simple or irregularly lobed; new blades proliferously developed from margin or surfaces .....*P. schmitziana*
- 7 . Thallus compressed, less than 1 cm in width, dichotomously branched .....8
  - 8 . Thallus narrow, to 2-3 mm in width, repeatedly dichotomously branched .....*P. elata*
  - 8 . Thallus strongly articulated, internodes narrowly ellipsoid, to 1 cm in width .....*P. articulata*

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