STUDIES ON JAPANESE SPECIES OF *LAURENCIA*, WITH SPECIAL REFERENCE TO THEIR COMPARATIVE MORPHOLOGY

by

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I. Introduction

Since the genus *Laurenica* was established by Lamouroux in 1813, many species have been reported by a number of authors, among whom J. Agardh (1841, 1863, 1876 & 1892), Greville (1830), Harvey (1847–49, 1853, 1854, 1855 & 1858–63), Kützing (1849 & 1865) and Setchell & Gardner (1924 & 1930) may be worth mentioning. A systematic arrangement of those species was proposed by Yamada who in 1931 divided them into four sections, after adding many new species. Yamada's division of the sections is based on the following characteristics: 1) the species with cortical cells elongated radially and arranged like palisade cells in the cross sections of branchlet are grouped in Section Palisadae; 2) among the species with no such elongated cortical cells, those which have a compressed frond are grouped in Section Pinnatifidae; 3) among the species with neither elongated cortical cells nor compressed frond, those which have abundant lenticular thickenings in the walls of the medullary cells are grouped in Section Forsterianae, and 4) those which have very few, if any, or no such lenticular thickenings are grouped in Section Cartilagineae. Other characteristics used by Yamada to distinguish the species from each other are as follows: 1) the cortical cells near the end of the ultimate branchlet which are or are not projecting; 2) the stichidial branchlets which are either simple or compound; 3) presence or absence of the percurrent main axis, and other characteristics such as mode of branching, the margins of the frond which are or are not undulate, size, texture and colour of the frond, nature of the ultimate branchlets, etc.

After the publication of Yamada's work, a number of new species were added by authors such as Børgesen (1932, 1934, 1937, 1938, 1945 & 1954), Cribb (1958), Dawson (1944, 1944a, 1945, 1954, 1958 & 1963), Dawson, Neushul & Wildman (1960), Hollenberg (in Smith & Hollenberg, 1943), Howe (1934), Howe & Taylor (1931), Kylin (1938 & 1941), Stechell & Gardner (1937), Taylor (1945 & 1947) and Tseng (1943). Two new species were also added from Japan by Yamada himself (1932; in Yamada & Segawa, 1953).

A detailed anatomical study of this genus was first made by Falkenberg (1901) on five species, viz., *Laurencia obtusa* (Hudson) Lamouroux, *Laurencia paniculata* (Agradh) J. Agardh, *Laurencia papillosa* (Forskaal) Greville, *Laurenica pinnatifida* (Gmelin) Lamouroux and *Laurencia clavata* Sonder. Of these species, *Laurencia pinnatifida* was also used by Kylin (1923) in his thorough study of the reproductive organs and vegetative structure.

Among the twenty one species ever reported to occur in Japan and the surrounding vicinity (cf. Yamada in Okamura, 1936), twenty species are known from the present territory of Japan (cf. Yamada, 1931 & 1932; Yamada in Okamura, 1936; Yamada & Segawa, 1953). Thirteen of these twenty species have been established as new to science by Yamada on the basis of the Japanese

Table 1. Phases of life-history arranged in opposition to the name of species of *Laurencia* known from the present territory of Japan, one in boldface being new to Japan, and the status of our knowledge of them indicated by the name of authors who reported the respective phase in a given species.

Species	Phases of life-history and authors who reported them		
	Antheridial	Cystocarpic	Tetrasporangial
L. capituliformis	Saito in the present paper	Saito in the present paper	Yamada, 1931; Yamada in Okamura, 1936; Saito in the present paper
L. cartilaginea	Saito in the present paper	Saito in the present paper	Yamada, 1931; Yamada in Okamura, 1936; Saito in the present paper
L. intermedia	Saito, 1961 & in the present paper	Saito, 1961 & in the present paper	Yamada, 1931; Yamada in Okamura, 1936; Saito, 1961 & in the present paper
L. nipponica	Saito, 1960 & in the present paper	Inagaki, 1933; Iwamoto, 1960; Saito, 1960 & in the present paper	Yamada, 1931; Yamada in Okamura, 1936; Inagaki, 1933; Iwamoto, 1960; Saito, 1960 & in the present paper
L. obtusa	Saito in the present paper	Yamada in Okamura, 1936; Saito in the present paper	Yamada in Okamura, 1936; Inagaki, 1933; Saito in the present paper
L. okamurai	Saito, 1965 & in the present paper	Saito, 1965 & in the present paper	Yamada, 1931; Yamada in Okamura, 1936; Saito, 1965 & in the present paper
L. venusta	Saito, 1964 & in the present paper	Saito, 1964 & in the present paper	Yamada, 1931; Yamada in Okamura, 1936; Saito, 1964 & in the present paper
L. glandulifera		Inagaki, 1933	Yamada in Okamura, 1936; Inagaki, 1933
L. grevilleana		Okamura, 1922; Yamada in Okamura, 1936	Okamura, 1922; Yamada in Okamura, 1936
L. pinnata		Okamura, 1922	Okamura, 1922; Yamada, 1931
L. undulata		Yamada, 1931; Yamada in Okamura, 1936	Saito in the present paper
L. yendoi		Yamada, 1931; Yamada in Okamura, 1936	Yamada, 1931; Yamada in Okamura, 1936
L. amabilis			Yamada & Segawa, 1953
L. composita			Yamada, 1931; Yamada in Okamura, 1936
L. hamata			Yamada, 1932; Yamada in Okamura, 1936
L. heteroclada			Yamada in Okamura, 1936
L. intricata			Saito in the present paper
L. japonica			Yamada, 1931; Yamada in Okamura, 1936
L. ceylanica			
L. majuscula			
L. papillosa			

materials. Eleven of these thirteen species were described from the tetrasporiferous plants, one from the female plant, and the remaining one from both tetrasporiferous and female plants. On the other hand, among the seven exotic species which were reported by Yamada (1931 & in Okamura, 1936) to occur in Japan, three have been known to be represented in Japan by both tetrasporiferous and cystocarpiferous plants, one by the tetrasporiferous alone, and the remaining three only by the sterile, as shown in Table 1. Thus the current knowledge of the Japanese species of *Laurencia*, especially concerning their reproductive organs, is rather incomplete, and the systematic relationships of most of the species, especially of the Japanese ones, are left uncertain awaiting a thorough study of their morphology.

Therefore, I have engaged for these several years in the morphological studies of this genus. Some of the results so far obtained have been provisionally reported (Saito, 1960, 1961, 1964 & 1965). Here I wish to publish the more recent results of my studies enumerating ten Japanese species of *Laurencia*, including one species new to Japan, which have been studied morphologically with the materials I have collected. Of these ten species, seven were studied with the male, female and tetrasporiferous plants, two with the tetrasporiferous, and the remaining one with the sterile. Comparing these results with those of the previous workers, I concluded that it would be reasonable to divide the genus *Laurencia* into two subgenera.

I wish to express my sincere thanks to my teacher, Emer. Professor Jun Tokida, for his kindness in giving me guidance and encouragement throughout the present study, and for reading and criticizing the manuscript. My cordial thanks are also due to Emer. Professor Yukio Yamada, Faculty of Science, Hokkaido University, who gave me valuable suggestions for the identification of some species. To Professor Tadashi Tamura and Professor Hidejiro Niiyama of our Faculty of Fisheries, Professor Mitsuzo Noda of Niigata University, Professor Maxwell S. Doty of the University of Hawaii, Dr. Isabella A. Abbott of Hopkins Marine Station of Stanford University I am much indebted for their kind encouragement and valuable advice. I am also much obliged to Messers. Hikoei Ohmi, Tomitaro Masaki, Hiroshi Yabu, Hirotoshi Yamamoto, Takashi Kaneko and Hitoshi Kito of our Faculty of Fisheries for their support and assistance.

II. Materials and Method

Most of the materials used for the present study were collected by myself in the following localities.

Hokkaido: Oshoro, Shiribeshi Province; Esashi, Hiyama Province; Matsumae, Moheji, Anama, Cape Tachimachi and Kinaoshi, Oshima Province; Muroran,

Iburi Province; and Akkeshi, Kushiro Province.

Japan Sea coast of Honshu: Gozu, near Naoetsu, Nou and vicinity, Echigo Province; and Shichirui, Idzumo Province.

Pacific coast of Honshu: Cape Nojimazaki and Cape Sunozaki, Awa Province; Hassei, near Aburatsubo, Sagami Province; and Shirahama, Kii Province.

The collected materials were fixed and preserved in 4–10 per cent formalin seawater solution, and from some of these preserved materials were prepared the herbarium specimens for a study of the external structure. The microscope preparations were made from hand and paraffin sections, or by the smear method. In the paraffin method, sections were cut 6–10μ in thickness and stained with Heidenhain's iron-alum haematoxylin or Meyer's carm-alum for the study of the nucleus and with anilin blue or lactic blue for the study of the cytoplasm. Most of the studies of the internal structure were carried out with the preparations by the paraffin method. Hand sections stained with lactic blue or anilin blue were also used to supplement the paraffin method for the study of the vegetative structure. The smear method was employed exclusively for the study of the antheridium and the trichoblast by staining them with aceto-carmin.

III. Descriptions of the Species

1. *Laurencia obtusa* (Hudson) Lamouroux

Plates I & II, Text-figs. 1–5

Lamouroux, 1813, p. 42; Greville, 1830, p. 110; Harvey, 1848, pl. 148; Kützing, 1849, p. 854; 1865, pls. 54 & 55; J. Agardh, 1863, p. 750; 1876, p. 653; De Toni, 1903, p. 791; Taylor, 1928, p. 180, pl. 33, fig. 3; 1960, p. 626; Yamada, 1931, p. 222; Yamada in Okamura, 1936, p. 858; Inagaki, 1933, p. 57; Takamatsu, 1936, p. 38; 1938, p. 66; 1938a, p. 135, 1939, p. 76; Cribb, 1958, p. 173, pl. 9, fig. 3; Tokida & Masaki, 1959, p. 191; Kanamori, 1965, p. 65; Noda, 1967, p. 43.

Fucus obtusus Hudson, 1778, p. 586.

Japanese name. Magire-sozo (Okamura).

Specimens examined. Growing on rocks in the littoral zone. Moheji, near Hakodate, Hokkaido, 16 August (♂♀⊕), 11 Spetember (♂♀⊕), 28 September (♂♀⊕) 1962; 1 August (♂ & sterile), 27 August (♂♀⊕), 13 September (♂♀⊕) 1963; 10 August 1964 (♂♀⊕). All of the specimens were collected by Y. Saito.

Distribution. Very widely distributed in the world, although only the following few localities have been reported in Japan to contain this species: Oshoro, Shiribeshi Province, Hokkaido (Inagaki, 1933; Yamada in Okamura, 1936; Tokida & Masaki, 1959); Uzen Province (Takamatsu, 1939; Kanaomori, 1965); Ugo, Mutsu, Rikuchu and Rikuzen Provinces, Northeastern Honshu (Takamatsu, 1936, 1938, 1938a & 1939); Sado Island (Noda, 1967).

It was reported by Yamada (in Okamura, 1936) that the specimen which had been illustrated by Okamura (1922) in his Icones of Japanese Algae, vol. 4, pl. 193 as *Laurencia obtusa* (Hudson) Lamouroux appeared to be one of his new species, *Laurencia okamurai* Yamada. Therefore, the first convincing record of the present species in Japan was attributed to the work of Inagaki (1933). Yamada (in Okamura, 1936) was of the opinion, however, that the occurrence of *Laurencia obtusa* in Japan was doubtful and that most of the specimens referred to by Japanese workers as *Laurencia obtusa* might be identical to *Laurencia okamurai* Yamada or *Laurencia nipponica* Yamada. Takamatsu (1936, 1938, 1938a & 1939) reported *Laurencia obtusa* from several localities in Northeastern Honshu, Japan, but he named them "Mitsude-sozo" instead of "Magire-sozo", probably according to Okamura (1922), who also referred to his "Mitsude-sozo" as *Laurencia obtusa*.

I collected many specimens at Moheji, Hokkaido, which were definitely referable to the present species. The following descriptions are based on these specimens.

The fronds are erect, with several erect axes tufted below, standing on a discoid base. Basal stoloniferous branches are absent (Pl. I, Figs. 1–3, Pl. II, Fig. 1). The erect axes are cylindrical, 850–2150μ in diameter, 3.5–16.7 cm. high (7.2 cm. high on the average among 130 individuals) and paniculately branched. The branching is alternate, opposite or subverticillate; the branches are 610–850μ in diameter and the ultimate sterile branchlet 260–330μ in diameter. The fronds are generally purplish pink or brown and sometimes dark purple in colour, fleshy and

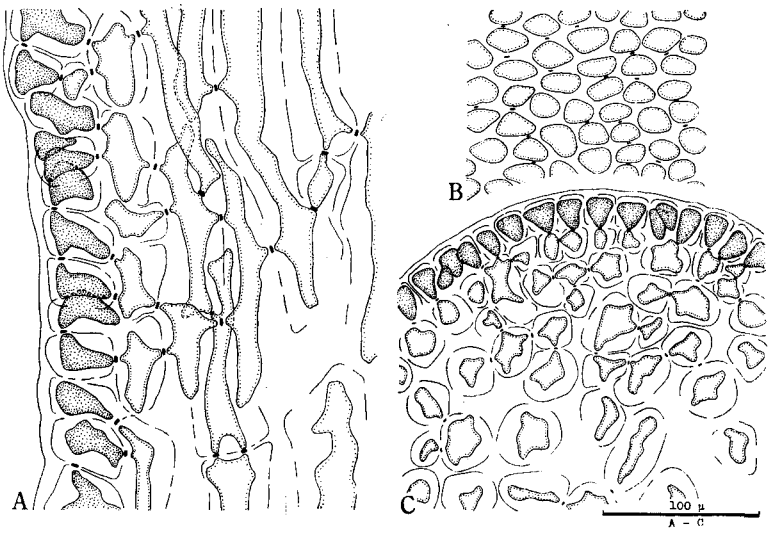

Fig. 1. *Laurencia obtusa* (Hudson) Lamouroux
A, Longitudinal section through a branch. **B**, Surface view of the cortical cell arrangement in the upper part of the ultimate branchlet. **C**, Transverse section through a branchlet.

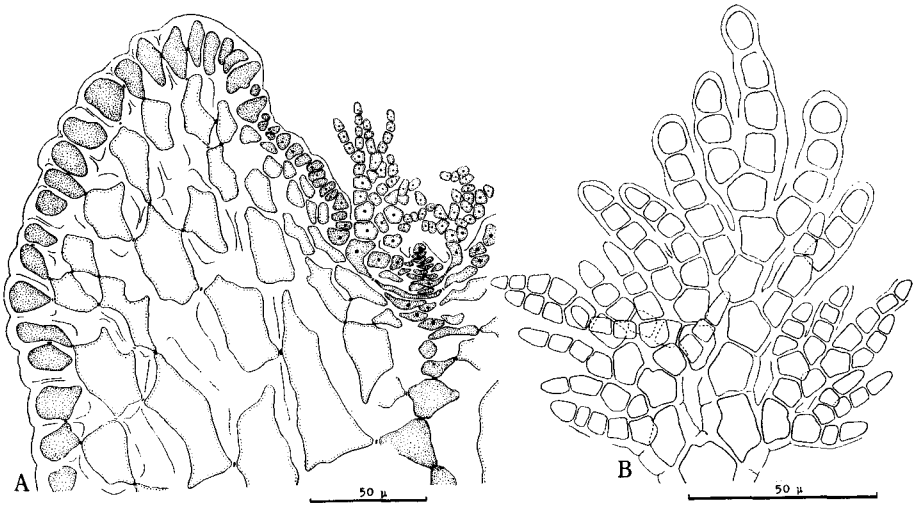

Fig. 2. *Laurencia obtusa* (Hudson) Lamouroux
A, Part of median longitudinal section through the apical portion of a branchlet.
B, A young trichoblast.

soft in texture, and adhere well to paper when dried. In a surface view, the cortical cells in the main axis are irregularly arranged and 27–62μ broad, while in the apical portion of the ultimate branchlet they are nearly round, slightly elongated laterally and 9–25μ long by 18–26μ broad (Text-fig. 1, B); in some specimens the cortical cells in the main axis are elongated and filamentous, up to 140μ long by 5–11μ broad and sometimes branched. The cortical cells in a transverse section are neither elongated radially nor arranged like palisade and 18–24μ high by 13–22μ broad in the ultimate branchlet (Text-fig. 1, C); they are slightly projected above the frond surface as seen in a longitudinal section (Text-fig. 2, A, Text-fig. 5, B). There are no lenticular thickneings in the walls of the medullary cells (Text-fig. 1, C). The apical cell of the ultimate branchlet is situated at the bottom of the apical depression, and it cuts off, by oblique walls, wedge-shaped segments which form the axial cell-row. All of the cells in the branchlet, including those of the trichoblast and of the young reproductive organs, are linked directly to the axial cells or indirectly by the pericentral cells (Pl. II, Figs. 6–8, 11 & 12, Text-fig. 2, A, Text-fig. 3, A, Text-fig. 5, A). Longitudinal secondary pit-connections among the cortical cells are present (Text-fig. 1, A, Text-fig. 2, A) and are observable in a surface view of the branchlet (Text-fig. 1, B). The trichoblast arises from a young pericentral cell near the growing apex, and is gradually displaced toward the periphery of the apical depression with the advance of growth, branching dichotomo-alternately (Text-fig. 2, A & B, Text-fig. 5, A).

The terminal portion of an ultimate branchlet in the male plant is characteristically broad, clavate or somewhat horn-shaped, 390–1100μ in diameter (Pl. II,

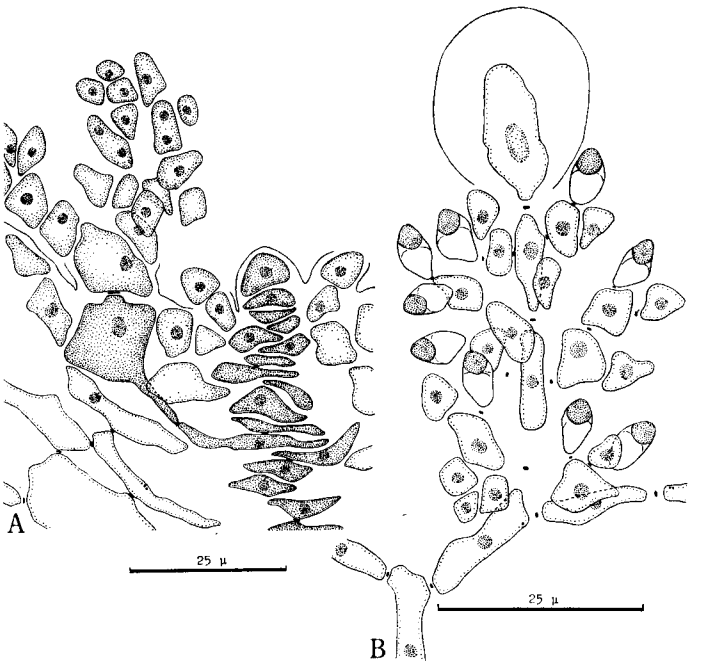

Fig. 3. *Laurencia obtusa* (Hudson) Lamouroux
A, Part of the apical portion of a median longitudinal section through the antheridial receptacle, showing the growing point and an antheridium-initial.
B, Apical portion of a mature antheridium in a smeared preparation.

Fig. 2), and bears one to four antheridial depressions, 160–310μ deep and 2.2–2.7 times as broad as the depth, which are furnished with many fertile and sterile trichoblasts (Pl. II, Fig. 8). The fertile trichoblast, or antheridium, arises from a young pericentral cell near the growing apex (Pl. II, Fig. 11, Text-fig. 3, A) and consists of a dichotomo-alternately branched central axis and four pericentral cells, or spermatangial mother-cells, on each axial cell (Text-fig. 3, B). Each mother-cell gives rise to 1–4 ovoid spermatangia, 6.6–8.4μ long by 3.5–5.1μ in diameter, each of which contains a large nucleus at its apex (Pl. II, Fig. 10, Text-fig. 3, B). A pericentral cell from a lower segment of the axis usually produces a corymbose branch and a tuft of spermatangia. The terminal cell of the axis of a fertile trichoblast is vesicular and ovoid, up to 32μ long by 25μ in diameter (Pl. II, Fig. 10, Text-fig. 3, B).

The ultimate branchlets in the female plant are cylindrical while sterile, but they become clavate with the development of the procarps and cystocarps (Pl. II, Fig. 5). The initial cell of the procarp arises from a pericentral cell of the fertile branchlet and acts as the fertile central cell of the procarp. This fertile cell is linked to the axial cell of the branchlet through the pericentral cell which gradually becomes elongated and filamentous below, with the growth of the branchlet tissues

(Pl. II, Fig. 12). The fertile central cell cuts off a few pericentral cells, of which the innermost one becomes the supporting cell bearing a four-celled carpogonial branch. The number of pericentral cells of the fertile central cell was not counted exactly. The carpogonial branch is curved to embrace the supporting cell (Pl. II, Fig. 13, Text-fig. 4, A). The supporting cell also cuts off downwards a few sterile cells. It was not clear whether or not the sterile cells were in two groups. These sterile cells are later divided into a number of cells which contribute to the growth of the gonimoblast by supplying nutrients. After fertilization a large auxiliary cell cuts off from the supporting cell on the upper side (Text-fig. 4, B) and fuses directly with the carpogonium. Subsequently the supporting cell fuses with the fertilized auxiliary cell forming a fusion-cell. This fusion-cell gives rise to a process, the first gonimoblast initial, toward one of the above mentioned sterile cells situated nearby and fuse with it (Text-fig. 4, C). The fusion-cell continues to fuse with other sterile cells and with the surrounding cells including the central cell and the gonimbolast cells which were formed during earlier stages of gonimbolast development, and becomes large and irregular in shape (Pl. II, Fig. 14, Text-fig. 4, D & E). The pericarp originates from the pericentral cells of the fertile central cell of the procarp. Before or after fertilization, the procarp is covered by a young pericarp, but the carpogonial branch is still naked on its inner side (Pl. II, Fig. 13, Text-fig. 4, A). With the growth of the branchlet, the developing procarp is gradually displaced toward the periphery of the apical depression, and some cortical cells of the branchlet contribute to the growth of the outer portion of the pericarp (Pl. II, Fig. 14, Text-fig. 4, D). Thus the developing pericarp consists of cells of two different origins. The ripe cystocarp, ovoid in shape and up to 840μ in diameter, is situated on the lateral surface of the branchlet (Pl. II, Fig. 5) and provided with a carpostome. The cystocarpic cavity is filled with a mucilaginous substance which stains well with iron-alum haematoxylin. The innermost cells of the pericarp having originated from the pericentral cells of the fertile central cell of the procarp, become markedly thin and filamentous in shape, and protoplasmic in content, as a result of their probable function to supply nutrition to the gonimoblast through the fusion-cell. The terminal cells of the gonimoblast increase in size and become carpospores (Pl. II, Fig. 15, Text-fig. 4, E).

The ultimate branchlets in the tetrasporophyte are converted into stichidia. The stichidia are cylindrical, 380–460μ in diameter, and beset with many dark purplish spots or tetrasporangia scattered over their lateral surfaces. After the shedding of the spores, these spots become colourless, and the stichidia look undulate on the surface (Pl. II, Figs. 3 & 4). The tetrasporangium originates from a pericentral cell near the growing apex in the apical depression of a branchlet. The fertile pericentral cell cuts off a sporangium and a cover-cell, and becomes elongated and filamentous below with the growth of the branchlet tissues (Pl. II, Fig. 7, Pl. Text-fig. 5, A). The fertile pericentral cell is also linked by means of secondary

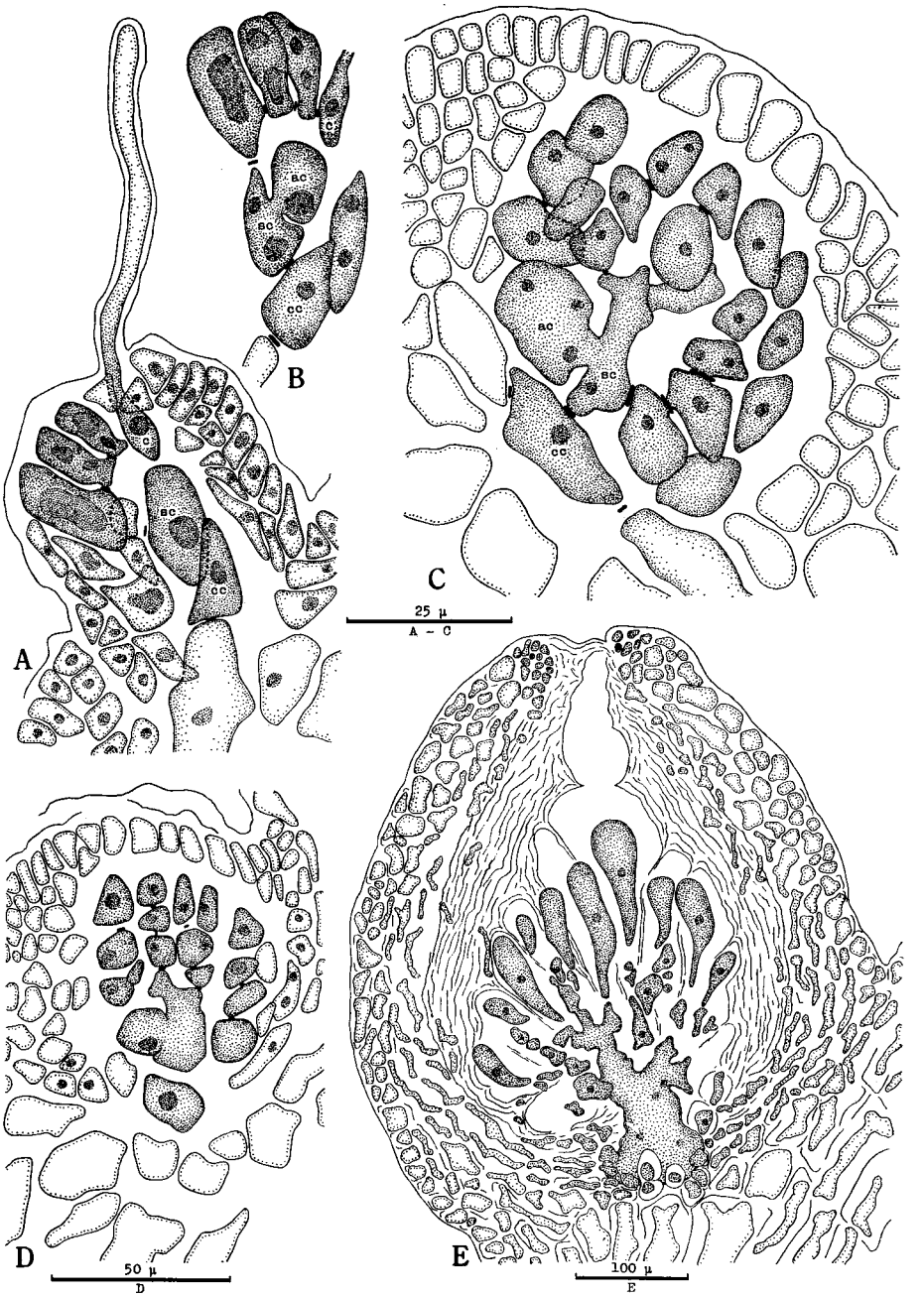

Fig. 4. *Laurencia obtusa* (Hudson) Lamouroux

A, Longitudinal section through a procarp which is ready for fertilization (cf. Pl. II, Fig. 13). **B,** Division of auxiliary cell from supporting cell, in longitudinal section through a procarp just after fertilization. **C & D,** Longitudinal section through a young cystocarp, showing the various developmental stages of fusion-cell and gonimoblast. **E,** Median longitudinal section through a ripe cystocarp. ac: auxiliary cell. c: carpogonium. cc: central cell. sc: supporting cell.

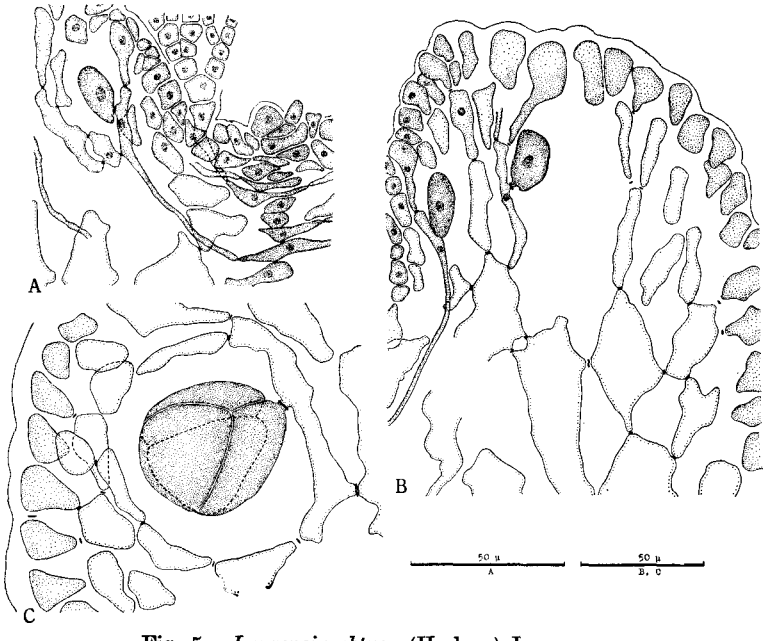

Fig. 5. *Laurencia obtusa* (Hudson) Lamouroux
A, Part of apical porition of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on the elongated pericentral cell which is connected to the axial cell. **B,** Ditto, showing more developed tetrasporangia at the periphery of the apical depression. **C,** Ditto, showing a divided tetrasporangium on the lateral side of an inner cortical cell at the lateral side of a stichidial branchlet.

pit-connections with some of the subcortical cells which have been derived from the divisions of other pericentral cells. The cover-cell cut from the fertile pericentral cell covers the sporangium from the inside, and other cover-cells which have originated from the subcortical cells cover it laterally from the outside (Text-fig. 4, A & B). The elongated pericentral cell is later divided into several segments (Text-fig. 4, B). The first nuclear division of the sporangium can be observed while the sporangium is at the periphery of the apical depression, whereas the second division can be observed when the sporangium is not in the depression but on the lateral surface of the stichidial branchlet. Longitudinal growth of the stichidial branchlet is not suppressed by the formation of many sporangia. Thus the mature tetrasporangia are on the lateral surface of the stichidium and arranged parallel to its central axis as seen in a longitudinal section (Pl. II, Fig. 6). The sporangium is divided tetrahedrally (Pl. II, Fig. 6, Text-fig. 4, C).

2. ***Laurencia intricata*** Lamouroux

Plate III, Figs. 1–3, Plate IV, Figs. 1–4, Text-figs. 6 & 7

Lamouroux, 1813, p. 43, pl. 3, figs. 8 & 9; J. Agardh, 1863, p. 750; 1876, p. 649; De Toni, 1903, p. 786; Taylor, 1960, p. 626.

Chondria intricata Montagne, 1842, p. 41.

Laurencia obtusa (Hudson) Lamouroux var. *intricata* (Lamouroux) Yamada, 1931, p. 225.

Japanese name. Motsure-sozo (Saito, nov. nom.).

Specimens examined. Growing on rocks or epiphytic on Sargassum spp. in the littoral zone. *Hokkaido*: Moheji, near Hakodate, 11 September 1962 (⊕); 27 August (⊕), 5 September (⊕ & sterile), 30 September (⊕) 1963. *Japan Sea coast of Honshu*: Nou and vicinity, Echigo Province, 19 August 1961 (⊕); Shichirui, Idzumo Province, 21 June 1964 (⊕). All of these specimens were collected by Y. Saito.

Distribution. *CUBA* (Montagne, 1842) and its adjacent area (Taylor, 1960).

The present species is reported here to be new to Japan. The following description of the tetrasporiferous plant is based on the specimens from Moheji, Hokkaido.

Forming a mat-like clump on some species of *Sargassum* or on rocks, the fronds are densely tufted below with entangled and coalescing basal stoloniferous branches (Pl. III, Figs. 1 & 2), about 3.5–10.5 cm. high (5.7 cm. high on the average among the 44 fully grown individuals examined), fleshy in texture, purplish pink in colour while young, becoming greenish when old, but usually pink at the apices, and adhere to paper when dried. The main axis is not percurrent. The main branches are 920–1110μ in diameter, irregularly branched near the base, somewhat paniculate upward, branching in upper portions alternately, oppositely or subverticillately; the secondary branches are 540–850μ in diameter, and the ultimate sterile branchlets are 290–400μ in diameter. The cortical cells in the main and the secondary branches are slightly elongated longitudinally in a surface view, and 28–50μ long by 19–30μ broad (Text-fig. 6, B), while those in the ultimate branchlet are nearly roundish or slightly elongated laterally, 10–25μ long in a longitudinal direction and 12–27μ broad (Text-fig. 6, A). Although the cortical cells in a cross section are neither elongated radially nor arranged like palisade cells, they are 14–25μ long radially and 12–22μ broad in the ultimate branchlet (Text-fig. 6, D), and slightly projected above the frond surface (Pl. IV, Figs. 1 & 2). The lenticular thickenings in the medullary cell walls are absent (Text-fig. 6, D). The apical cell of the ultimate branchlet at the bottom of the apical depression cuts off, by oblique walls, wedge-shaped segments which form the axial cell-row. All of the cells including those of the trichoblasts and the tetrasporangium initials in the branchlet are linked directly to the axial cells or indirectly to them by the pericentral cells (Pl. IV, Figs. 1–4, Text-fig. 7, A). The trichoblast arises from a young pericentral cell near the growing apex; it branches dichotomo-alternately and is gradually displaced toward the periphery of the apical depression with the advance of growth (Pl. IV, Fig. 2). The cortical cells of the branch are observed to have the secondary pit-connections in both longitudinal

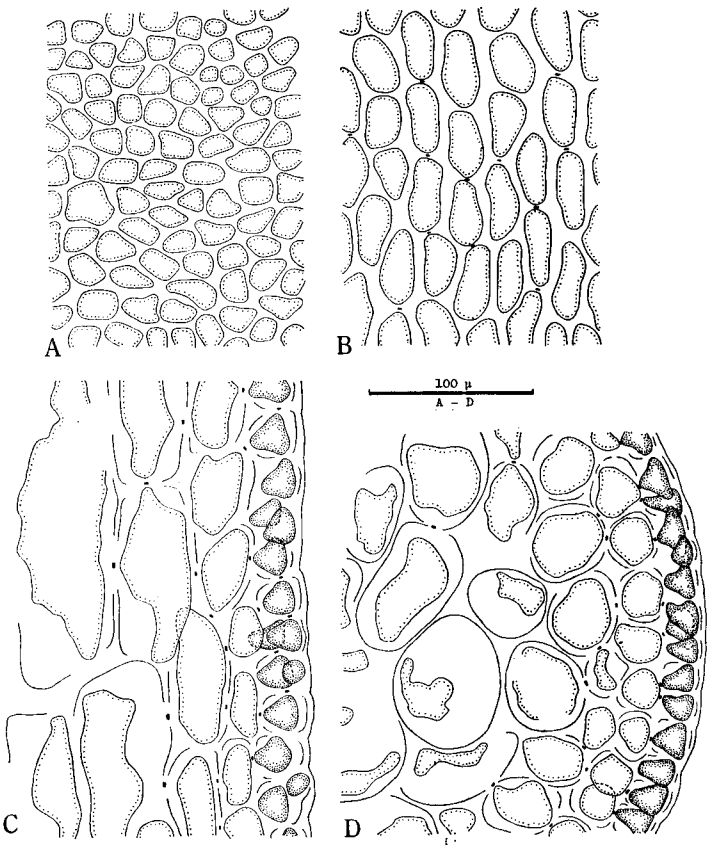

Fig. 6. *Laurencia intricata* Lamouroux
A & B, Surface view showing the cortical cell arrangement in the ultimate branchlet (**A**) and in the branch (**B**). **C,** Longitudinal section of a branch. **D,** Transverse section of a branchlet.

section (Text-fig. 6, C) and surface view (Text-fig. 6, B).

The ultimate branchlets are converted into stichidia. The stichidia are cylindrical, 380–440μ in diameter, and beset with many dark purplish spots or tetrasporangia scattered over their lateral surfaces. After the shedding of the spores, these spots become colourless and the stichidia look undulate on the surface (Pl. III, Fig. 3). The tetrasporangium originates from a pericentral cell near the growing apex in the apical depression of a branchlet. The fertile pericentral cell cuts off a sproangium and a cover-cell, and then becomes elongated and filamentous below with the growth of the branchlet tissues (Pl. IV, Figs. 3 & 4). The fertile pericentral cell is also linked by means of the secondary pit-connections with some of the subcortical cells which have been derived from the divisions of the other pericentral cells lying beneath it (Text-fig. 7, B). The cover-cell cut off from the fertile pericentral cell covers the sporangium from the inside, while other cover-

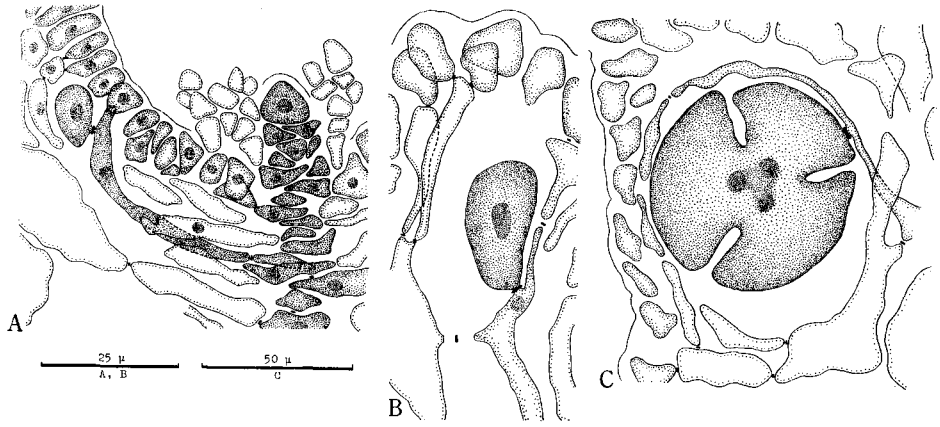

Fig. 7. *Laurencia intricata* Lamouroux

A, Part of apical portion of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on an elongated pericentral cell which is connected to an axial cell (cf. Pl. IV, Fig. 3). **B**, Ditto, showing a more developed tetrasporangium at the periphery of the apical depression. **C**, Ditto, showing a divided tetrasporangium at the lateral portion of the stichidial branchlet.

cells which originate from the subcortical cells cover it laterally from the outside (Text-fig. 7, B). The elongated pericentral cell is later divided into several segments. The first nuclear division of the sporagnium can be observed while the sporagnium is at the periphery of the apical depression, whereas the second division can be observed when the sporangium is not in the depression but on the lateral surface of the stichidial branchlet. Many sporangia are born in the stichidial branchlet, but the longitudinal growth of the latter is not suppressed. Thus the mature tetrasporangia are arranged on the upper lateral of the stichidium, parallel to its central axis as seen in a longitudinal section (Pl. IV, Fig. 1). The sporangium is divided tetrahedrally (Pl. IV, Fig. 1, Text-fig. 7, C).

3. *Laurencia venusta* Yamada
Plates V & VI, Text-figs. 8–14

Yamada, 1931, p. 203, pl. 6, fig. a, text-fig. H; Yamada in Okamura, 1936, p. 854; Okamura, 1931, p. 116; Takamatsu, 1939, p. 76; pl. 13, fig. 2; Saito, 1956, p. 106; 1964, p. 69, pls. 1–8; Cribb, 1958, p. 168, pl. 5, fig. 11; Kang, 1966, p. 105.

Japanese name. Hime-sozo (Yamada).

Specimens examined. Growing on rocks in the lower littoral zone. *Hokkaido*: Moheji, near Hakodate, 27 August (♀⊕), 5 September (⊕), 13 September (♂♀⊕), 30 September (⊕) 1963, Y. Saito. *Kyushu*: Takarashima Island, one of the Tokara Islands, 30 May 1953 (⊕), E. Ogata.

Distribution. *JAPAN. Hokkaido*: Oshima Province (Saito, 1964). *Japan*

Sea coast of Honshu: Tsugaru & Ugo Provinces, Tobishima Island (Takamatsu, 1939); Echigo Province (Saito, 1956). *Kyushu*: Satsuma & Hizen Provinces, Goto Islands & Koshikijima Island (Yamada, 1931). *KOREA* (Kang, 1966). *FORMOSA* (Okamura, 1931). *AUSTRALIA* (Cribb, 1958).

The present species was established by Yamada (1931) on the basis of the tetrasporiferous specimens from Kyushu, Japan. The male plant was first reported by Cribb (1958) from Australia. I collected a few male and female plants together with many tetrasporiferous specimens at Moheji, Hokkaido. Morphological studies on them were reported in an earlier paper (Saito, 1964). Here I will again give a description of the species but supplementing it with results of more recent studies.

The fronds are erect, up to nearly 10 cm. high, with several erect axes densely tufted below with entangled, more or less coalesced, basal branches (Pl. V, Figs. 2–4). They are purplish red, sometimes slightly greenish in colour, cartilaginous but not so rigid in texture, and adhere to paper upon drying. The erect axes are cylindrical, 690–920μ in diameter, 2.2–9.6 cm. high (4.16 cm. high on the average among 63 individuals), and paniculately branched. The branching is alternate, opposite or verticillate; the branches are 540–620μ in diameter with the ultimate sterile branchlets 310–460μ in diameter. The cortical cells, 25–39(–52)μ long radially and 33–50(–58)μ wide, are not elongated longitudinally in a surface view (Text-fig. 8, A) nor elongated radially or arranged like palisade cells in the transverse section of a branchlet (Text-fig. 8, B). The cortical cells in the terminal portion of the ultimate branchlet are more or less flattened laterally, so that they seen arranged somewhat like palisade cells in a longitudinal section, but are not projected above the frond surface (Text-fig. 9). The lenticular thickenings of the medullary cell walls are abundant not only in the older but also in the younger tissues of the ultimate branchlet (Pl. VI, Figs. 4 & 7–9, Text-fig. 8, B, Text-figs. 9, 10 & 13). The apical cell of the ultimate branchlet at the bottom of its apical depres-

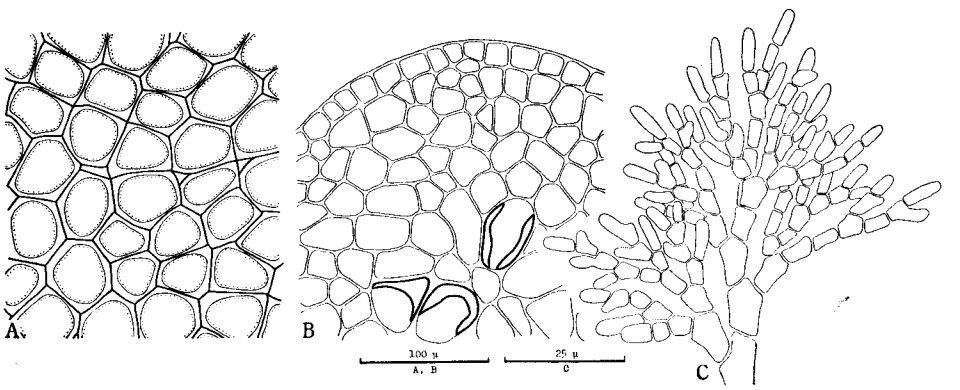

Fig. 8. *Laurencia venusta* Yamada
A, Surface view of main axis. **B**, Transverse section of a branchlet. **C**, A young trichoblast.

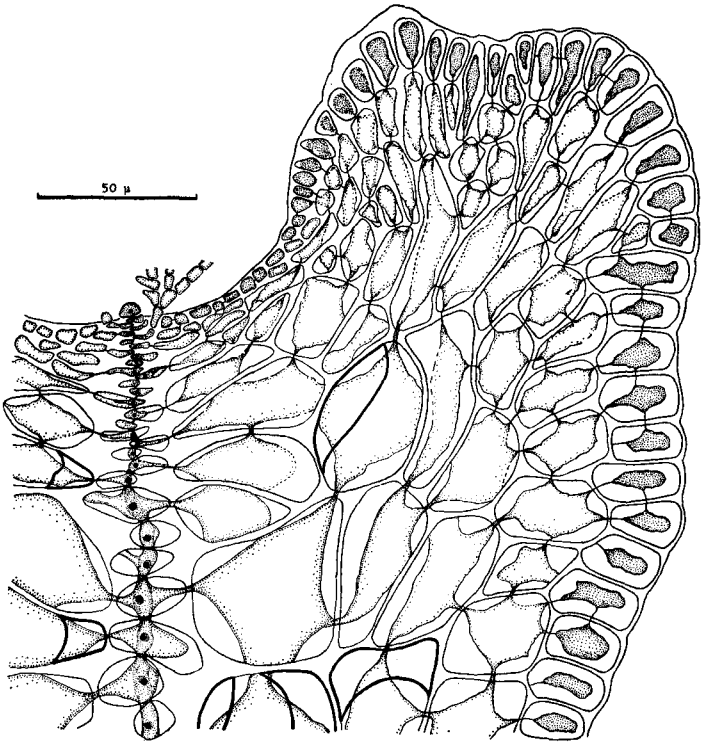

Fig. 9. *Laurencia venusta* Yamada
Part of median longitudinal section through a sterile branchlet.

sion cuts off, by oblique walls, wedge-shaped segments which form the axial cell-row. All of the cells in the branchlet including those of the trichoblasts and of the young reproductive organs are linked directly to the axial cells or indirectly through the pericentral cells (Pl. VI, Figs. 6, 7, 9 & 10, Text-figs. 9 & 10, Text-fig. 11, A, Text-fig. 12, A). Longitudinal secondary pit-connections among the cortical cells are present (Text-fig. 9). The trichoblast which arose from a young pericentral cell near the apical cell is gradually displaced toward the periphery of the apical depression with the advance of growth, branching dichotomo-alternately and sometimes trichotomously or oppositely (Text-fig. 8, C).

The male plant in my collection is represented by a single fragmentary specimen, about 4 cm. in length, the upper half of which is shown in Pl. V, Fig. 1. One of the branches bearing many antheridial branchlets or receptacles on the lower half of this specimen is shown in Pl. VI, Fig. 2. The terminal portion of the antheridial branchlets is characteristically broad, attaining 340–910μ in diameter, and bears one to three, or more, depressions, 75–160μ in depth, 2.7–2.9 times as broad as it is deep and furnished with many fertile and sterile trichoblasts (Pl. VI, Fig. 4, Text-fig. 10). The fertile trichoblast, or antheridium, also

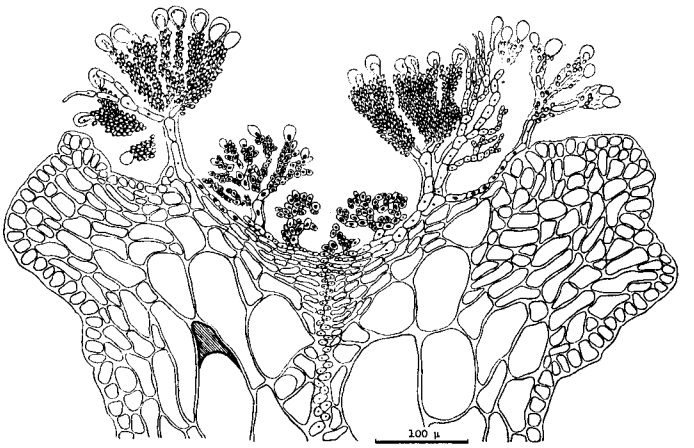

Fig. 10. *Laurencia venusta* Yamada
Median longitudinal section through an antheridial receptacle (cf. Pl. VI, Fig. 4).

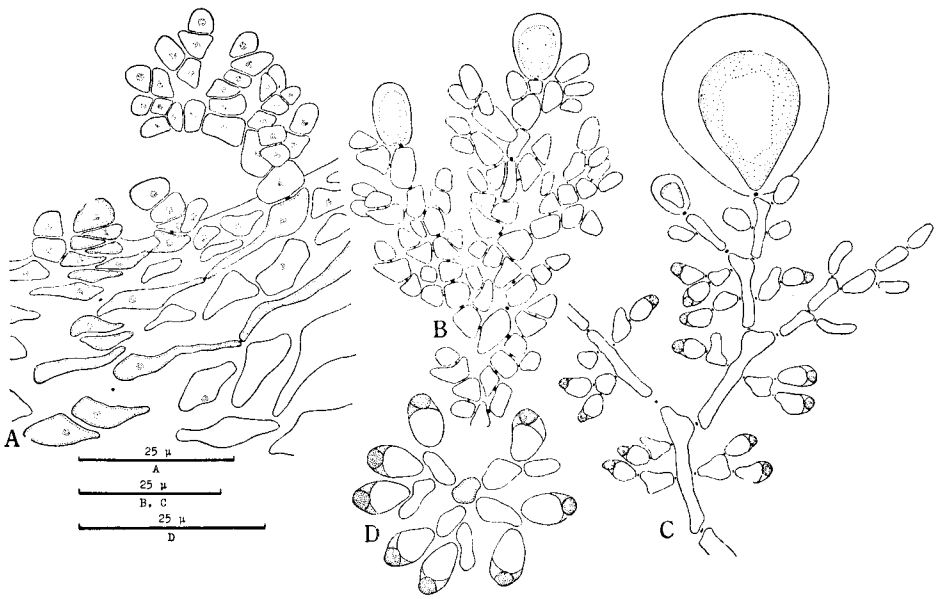

Fig. 11. *Laurencia venusta* Yamada
A, Part of median longitudinal section through an antheridial receptacle, showing the growing point and an antheridium-initial. **B** & **C**, Apical portion of a young (**B**) and a mature (**C**) antheridium in a smeared preparation. **D**, Transverse section through an antheridium.

arises from a young pericentral cell near the growing apex and consists of a dichotomo-alternately brnached central axis and four pericentral cells, or spermatangial mother-cells, on each axial cell (Text-fig. 11, B-D). Sometimes the axial cell cuts off one more set of spermatangial mother-cells (Text-fig. 11, C).

Each mother-cell gives rise to 2–3(–4) ovoid spermatangia, 7.8–9.7μ long by 4.7–5.6μ in diameter, which contain a large nucleus at their apices. The terminal cells of the fertile trichoblasts are vesicular in appearance, ovoid in shape and often very large, up to 36μ long by 31μ in diameter (Pl. VI, Figs. 4 & 5, Text-fig. 10, Text-fig. 11, B & C).

In the female plant, the ultimate branchlets are slender while sterile, but their terminal portions become thickened and fist-shaped with the development of the procarps and cystocarps (Pl. VI, Figs. 1 & 7). The initial cell of a procarp arises from a pericentral cell and acts as the fertile central cell of the procarp. This fertile cell is linked to the axial cell of the brnachlet by the pericentral cell which gradually becomes elongated and filamentous below with the growth of the branchlet tissues (Text-fig. 12, A). The fertile central cell cuts off some pericentral cells of which inner one becomes the supporting cell which cuts off a four-celled carpogonial branch. The carpogonial branch is curved so as to embrace the supporting cell (Pl. VI, Fig. 6, Text-fig. 12, B). The number of pericentral cells of the fertile central cell was not counted exactly, but seems to be four. The supporting cell also cuts off several sterile cells on the inside and somewhat downwards, but it cannot be established whether they are in two groups. These sterile cells later divide into more cells which contribute to the growth of the gonimoblast by supplying nutri-

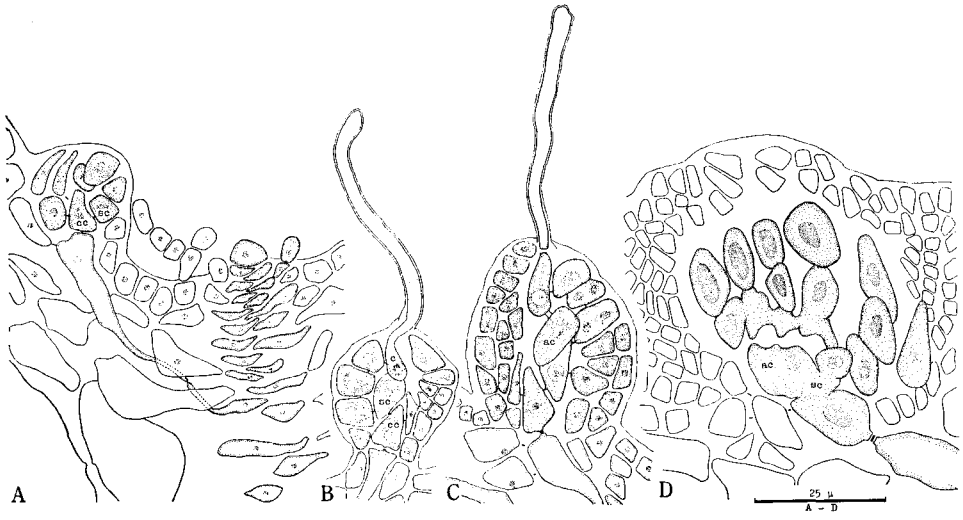

Fig. 12. *Laurencia venusta* Yamada

A, Part of median longitudinal section through a fertile branchlet of a female plant, showing the growing point and a young procarp on an elongated pericentral cell. **B**, Longitudinal section through a procarp which is ready for fertilization (cf. Pl. VI, Fig. 6). **C**, Longitudinal section through a procarp just after fertilization. **D**, Longitudinal section through a young cystocarp, showing fusion-cell and initial stage of gonimoblast development. ac: auxiliary cell. c: carpogonium. cc: central cell. sc: supporting cell.

tion. After fertilization a large auxiliary cell is cut off from the supporting cell on the upper side (Text-fig. 12, C), and the auxiliary cell fuses directly with the carpogonium which has already been cut off from the trichogyne (Text-fig. 12, C). Subsequently the supporting cell fuses with the fertilized auxiliary cell forming a fusion-cell. This fusion-cell gives rise to a process, the first gonimoblast cell, toward one of the above mentioned sterile cells situated nearby and soon they fuse with each other (Text-fig. 12, C & D). The fusion-cell gradually increases in size by coalescing with the surrounding cells including the central cell, the pericentral cell which forms the inner part of the pericarp, the sterile cells, and the older gonimoblast cells. The pericarp originates from the pericentral cells of the fertile central cell of the procarp. Before and after fertilization, the procarp is covered by a young pericarp, but the carpogonial branch is still naked on its inner side (Pl. VI, Fig. 6, Text-fig. 12, B & C). With the growth of the branchlet, the developing procarp is gradually displaced toward the periphery of the apical depression, and some cortical cells of the branchlet contribute to the growth of the outer portion of the pericarp (Pl. VI, Fig. 7). Thus the fully developed pericarp consists of cells of two different origins. The ripe cystocarp, ovoid in shape and up to 870μ in diameter, is situated on the lateral surface of the branchlet (Pl. VI, Fig. 1) and is

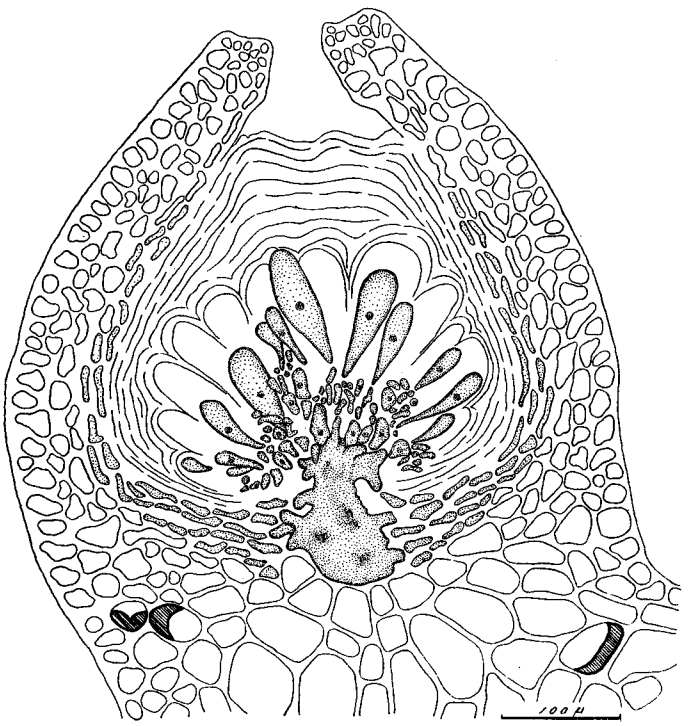

Fig. 13. *Laurencia venusta* Yamada
Median longitudinal section through a ripe cystocarp.

provided with a carpostome. The cystocarpic cavity is filled with a mucilaginous substance which stains well with both iron-alum haematoxylin and carm-alum. The innermost cells of the pericarp which originated from the pericentral cells of the fertile central cell of the procarp become markedly thin and filamentous in shape, and dense in content, indicating that they probably supplied nutrition to the gonimoblast through the fusion-cell. The terminal cells of the gonimoblast increase in size and become carpospores (Pl. VI, Figs. 7 & 8, Text-fig. 13).

The ultimate branchlets in the tetrasporophyte are converted into stichidia. The stichidia are cylindrical, 450–520μ in diameter, and beset in the apical portion with many dark purplish spots or tetrasporangia which are scattered over their surfaces. After the shedding of the spores, these spots become colourless and the stichidia look undulate on the surface (Pl. VI, Figs. 3 & 9). The tetrasporangium originates from a pericentral cell near the growing apex in the apical depression of a branchlet. The fertile pericentral cell, which has cut off a sproangium and a cover-cell, becomes elongated and filamentous below with the growth of the branchlet tissues (Pl. VI, Fig. 10, Text-fig. 14, A). The fertile pericentral cell is also linked by means of secondary pit-connections to some of the subcortical cells situated near the sporangium. The fertile pericentral cell is later divided into several segments. The first nuclear division of the sporangium can be observed while the sporangium is at the periphery of the apical depression, whereas the second division can be observed when the sporangium is not in the depression but on the lateral surface of the stichidial branchlet (Pl. VI, Fig. 9, Text-fig. 14, B). The longitudinal growth of the stichidial branchlet is not suppressed by the formation of many sporangia. Thus the mature sproangia are on the lateral surface of the stichidium and arranged

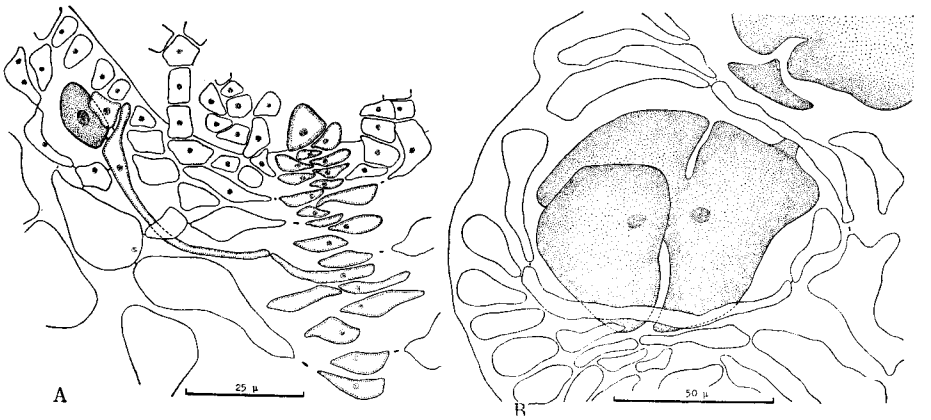

Fig. 14. *Laurencia venusta* Yamada
A, Part of median longitudinal section through a stichidial branchlet, showing the growing point and a tetrasporangium-initial on an elongated pericentral cell. B, Ditto, showing a divided tetrasporangium on the lateral side of the stichidium.

parallel to the central axis as seen in a longitudinal section (Pl. VI, Fig. 9). The sporangium is divided tetrahedrally (Text-fig. 14, B).

The above description is essentially identical to that given by Yamada (1931) except that there is a small difference in the mode of branching. The specimens from southern Japan studied by Yamada show secund branching, especially on the curved branch. In the specimens from Moheji, Hokkaido, such a mode of branching is rather rare. However, this difference seems to me to be a variation of no critical value induced by a change in habitat. The specimens illustrated by Takamatsu (1939) and those from Echigo Province in my collection seem to show the same mode of branching as the specimens from Moheji, Hokkaido.

4. *Laurencia okamurai* Yamada

Plates VII-IX, Text-figs. 15–21

Yamada, 1931, p. 206, pl. 7, text-figs. J & K; Yamada in Okamura, 1936, p. 856; Higashi, 1935, p. 154; 1936, p. 298; Takamatsu, 1938, p. 66; 1939, p. 76; Hasegawa, 1949, p. 70; Ohshima, 1950, p. 150; Tanaka, 1950, p. 11; Imahori & Searashi, 1955, p. 73; Kawashima, 1955, p. 34; Saito, 1956, p. 106; 1965, p. 207, pls. 1–9; Hirose, 1957, p. 103; 1958, p. 268; Segawa & Ichiki, 1959, p. 112; Segawa & Kamura, 1960, p. 61; Segawa & Yoshida, 1961, p. 19; Noda, 1964, p. 73; 1966, p. 80; 1967, p. 44; Noda & Kang, 1964, p. 43; Kang, 1965, p. 57; 1966, p. 105; Kanamori, 1965, p. 64; Kida, 1965, p. 17.

Japanese name. Mitsude-sozo (Okamura).

Specimens examined. Growing on rocks in the lower littoral and upper sublittoral zones. *Hokkaido*: Oshoro, Shiribeshi Province, 19 July 1962 (sterile); 29 July 1963 (sterile); 20 July 1964 (sterile); Esashi, Hiyama Province, 31 July 1963 (⊕); Matsumae, Oshima Province, 3 August 1962 (♂♀⊕), 23 July 1963 (♂♀⊕), 29 July 1964 (♂♀⊕); Moheji, near Hakodate, Oshima Province, 16 August (♂♀⊕), 11 September (♀⊕), 28 September (♀⊕) 1962; 27 August (♂♀⊕), 5 September (♂♀⊕), 13 September (♂♀⊕) 1963; 10 August 1964 (♂♀⊕). *Japan Sea coast of Honshu*: Nou, Echigo Province, 23 July 1960 (♀⊕); Shichirui, Idzumo Province, 21 June 1964 (sterile). All of these specimens were collected by Y. Saito.

Distribution. *JAPAN*. *Hokkaido*: Shiribeshi, Hiyama & Oshima Provinces (Saito, 1965); Okushiri Island (Hasegawa, 1949). *Japan Sea coast of Honshu*: Mutsu Province (Takamatsu, 1938); Ugo Province (Takamatsu, 1939); Uzen Province (Higashi, 1936; Takamatsu, 1939; Kanamori, 1965); Echigo Province (Saito, 1956 & 1965); Sado Island (Noda, 1967); Toyama Bay (Ohshima, 1950); Noto Province (Imahori & Searashi, 1955); Echizen Province (Higashi, 1936); Tajima Province (Hirose, 1958); Idzumo Province (Saito, 1965); Nagato Province (Yamada, 1931). *Pacific coast of Honshu*: Rikuchu Province (Kawashima, 1955); Iwaki Province (Noda, 1964); Awa & Sagami Provinces (Higashi, 1935); Kii Province (Yamada,

1931). *Kyushu*: Hizen, Satsuma & Bungo Provinces (Yamada, 1931); Higo Province (Segawa & Ichiki, 1959; Segawa & Yoshida, 1961); Mage Island (Tanaka, 1950). *Shikoku*: Shiaku Islands (Hirose, 1957); Deba-jima Island (Yamada, 1931). *RYUKYU* (Segawa & Kamura, 1960). *KOREA* (Noda & Kang, 1964; Noda, 1966; Kang, 1965 & 1966). *CHINA* (Yamada, 1931).

The present species was established by Yamada (1931) on the basis of the tetrasporiferous specimens from southern Japan and China. According to the reports by the above listed workers, this species is distributed all around the coast of Japan. However, there had been no information on the sexual plants before my discovery of them in 1960 and 1962. The female plant was first collected in 1960 at Nou, Echigo Province, and the male plant in 1962 at Matsumae and Moheji, Hokkaido. Morphological studies on both sexual and asexual plants from Moheji were reported in my earlier paper (1965). Here I will again give a full description of the species but supplementing it with the results of more recent studies.

The fronds are erect, nearly 20 cm. high, with several erect axes densely tufted below with entangled and somewhat coalesced basal branches (Pl. VII, Pl. VIII, Fig. 4). They are generally purplish green although sometimes dark purple in colour, fleshy to cartilaginous but not rigid in texture, and adhere to paper when dried. The erect axes are cylindrical, 820–1230μ in diameter, 4.8–18.8 cm. high (10.1 cm.

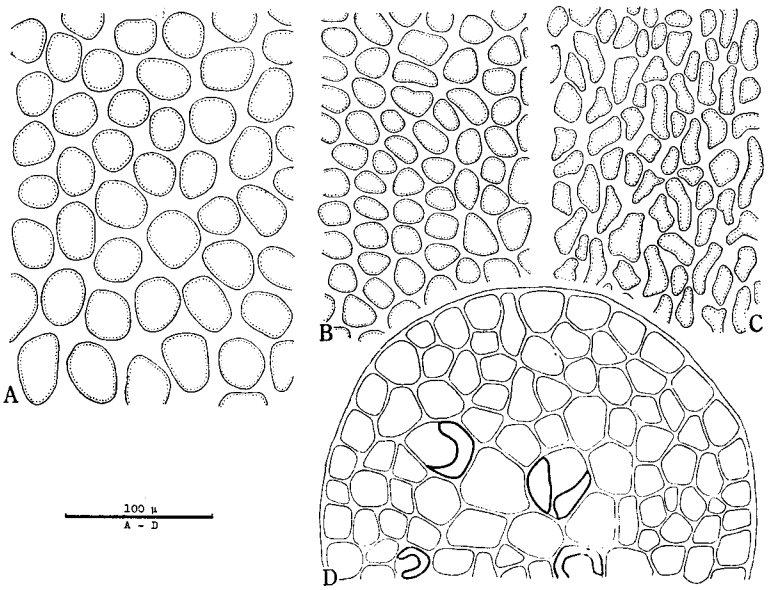

Fig. 15. *Laurencia okamurai* Yamada
A–C, Surface view showing the cortical cell arrangement in the upper part of the branch (**A**), in the upper part of the ultimate branchlet (**B**) and in the main axis (**C**). **D**, Transverse section of a branchlet.

high on the average of 77 individuals examined), and paniculately branched. The branching is alternate, opposite or verticillate; the branches are 630–800μ in diameter. In a surface view, the cortical cells in the main axis are irregularly elongated longitudinally, 11–16μ wide and about 1.6–4.3 times as long as the width (Text-fig. 15, C). In the basal portion of a branch they are slightly elongated longitudinally and somewhat larger, 26–35μ wide and 1.3–2.2 times as long as the width, in the upper part of a branch they are nearly spherical, about 23–32μ in diameter (Text-fig. 15, A), and in the apical portion of an ultimate branchlet they are small, roundish and slightly elongated laterally (Text-fig. 15, B). The cortical cells, in a transverse section, are neither elongated radially nor arranged like palisade cells, 20–32(–44)μ long radially, and (14–)24–37μ wide (Text-fig. 15, D); and in a longitudinal section they are not projected above the frond surface (Text-fig. 16, A), and are occasionally connected to each other by longitudinal secondary pit-connections (Text-fig. 16, A). Lenticular thickenings of the cell walls are present in the medulla (Text-fig. 15, D), especially abundant at the base of the cystocarps (Pl. IX, Fig. 10, Text-fig. 20) and at the forked portions of the frond, but rather rare in the younger tissues such as the apical portion of an ultimate branchlet. The apical cell of the ultimate branchlet is situated at the bottom of the apical depression, and it cuts off, by oblique walls, wedge-shaped segments which form the axial cell-row. All of the cells in the branchlet including those of the trichoblast and of the young reproductive organs are linked directly to the axial

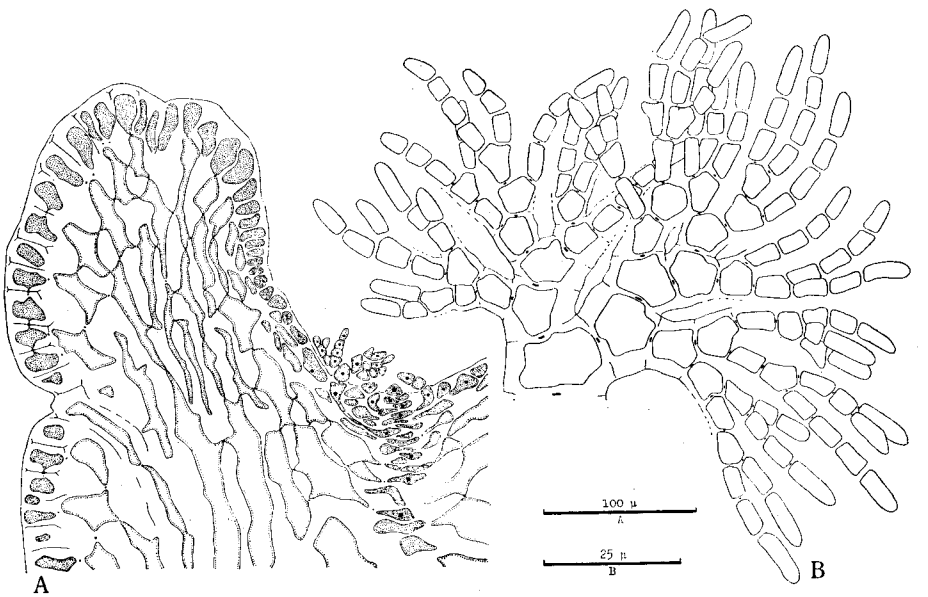

Fig. 16. *Laurencia okamurai* Yamada
A, Part of median longitudinal section through the apical portion of a sterile branchlet. **B**, A young trichoblast.

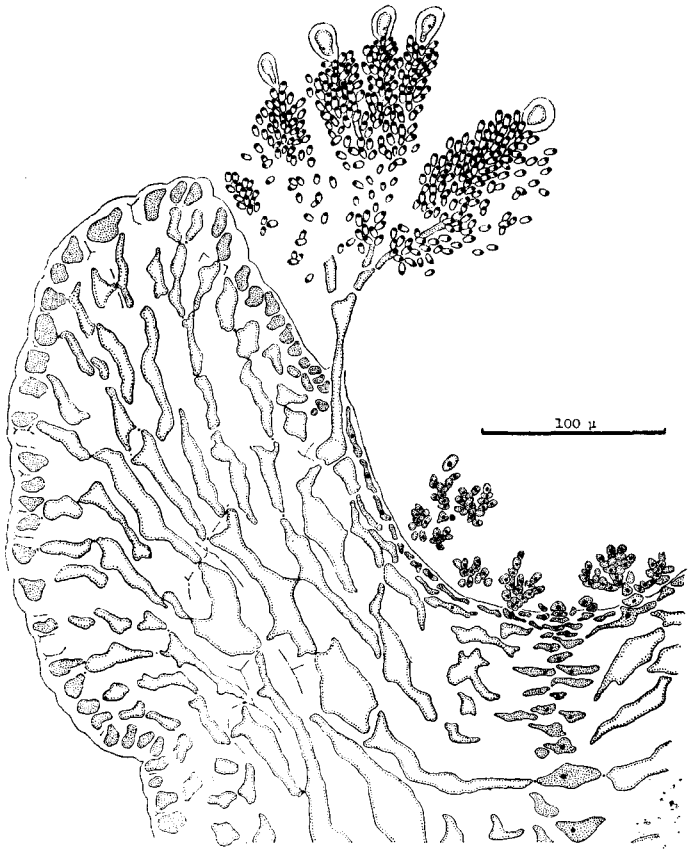

Fig. 17. *Laurencia okamurai* Yamada
Part of median longitudinal section through an antheridial receptacle

cells or indirectly through the pericentral cells (Pl. IX, Figs. 1, 2, 5, 9, 11 & 12, Text-fig. 16, A, Text-fig. 17, Text-fig. 19, A, Text-fig. 21, A). The trichoblast which arose from a young pericentral cell near the apical cell is gradually displaced toward the periphery of the apical depression with the advance of growth, branching dichotomo-alternately (Text-fig. 16, A & B).

The terminal portion of an ultimate branchlet in the male plant is characteristically broad, attaining 400–940μ in diameter (Pl. VIII, Fig. 3), and bears one to three or more antheridial depressions which are 140–290μ in depth, 1.26–1.35 times as broad as it is deep and furnished with many fertile and sterile trichoblasts (Pl. IX, Fig. 1, Text-fig. 17). The fertile trichoblast, or antheridium, arises from a young pericentral cell near the apical cell (Pl. IX, Fig. 2) and consists of a dichotomo-alternately branched axis and four pericentral cells, or spermatangial mother-cells, on each axial cell (Text-fig. 18, A & C). Each mother-cell gives rise to 1–3 (or more) oviod spermatangia, 6.9–9.7μ long by 4.2–5.6μ in diameter, each of which

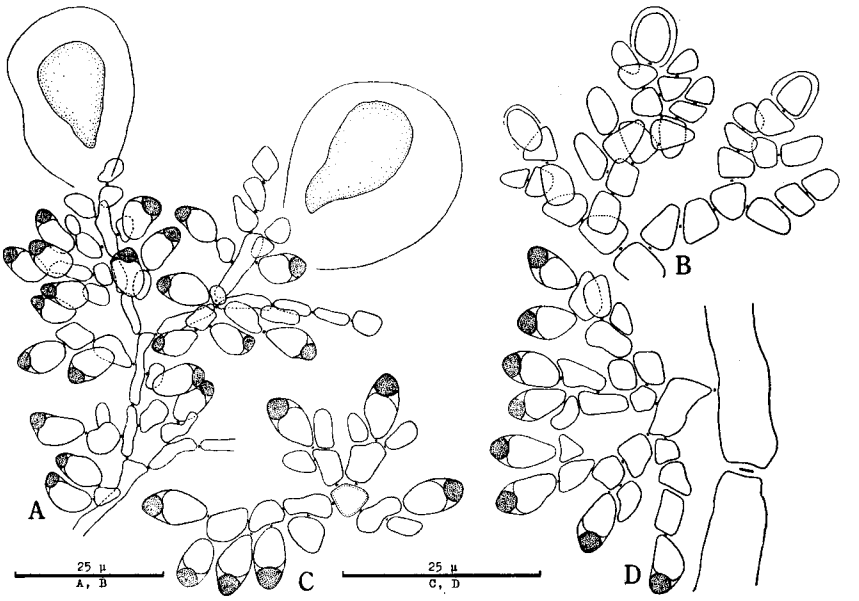

Fig. 18. *Laurencia okamurai* Yamada
A & B, Apical porition of a mature (**A**) and a young (**B**) antheridium in a smeared preparation. **C,** Transverse section of an antheridium. **D,** A tuft of spermatangia from the lower portion of a mature antheridium in a smeared preparation.

contains a large nucleus at its apex (Pl. IX, Figs. 3 & 4, Text-fig. 18, A, C & D). Some of the axial cells are occasionally found to give rise directly to a spermatangium (Text-fig. 18, A). A pericentral cell from a lower segment of the axis usually produces a corymbose branch and a tuft of spermatangia (Text-fig. 18, D). The terminal cell of the axis of the fertile trichoblast is vesicular in appearance, ovoid in shape, and often very large, up to 42μ long by 35μ in diameter (Pl. IX, Figs. 4 & 5, Text-fig. 17, Text-fig. 18, A).

The ultimate branchlets in the female plant are cylindrical while sterile, but they become clavate with the development of the procarps and cystocarps (Pl. VIII, Fig. 2, Pl. IX, Fig. 9). The initial cell of the procarp arises from a percientral cell of the fertile branchlet and acts as the fertile central cell of the procarp. This fertile cell is linked to the axial cell of the branchlet through a pericentral cell which gradually becomes elongated and filamentous below, with the growth of the branchlet tissues (Pl. IX, Fig. 5, Text-fig. 19, A). The fertile central cell cuts off the supporting cell of the carpogonial branch on the inside, i.e. toward the growing point of the branchlet, as one of the four pericentral cells. The four-celled carpogonial branch is formed on the inside of the supporting cell together with some sterile cells. The carpogonial branch is curved so as to embrace the supporting cell (Pl. IX, Figs. 5 & 6, Text-fig. 19, A & B). The sterile cells formed together with the

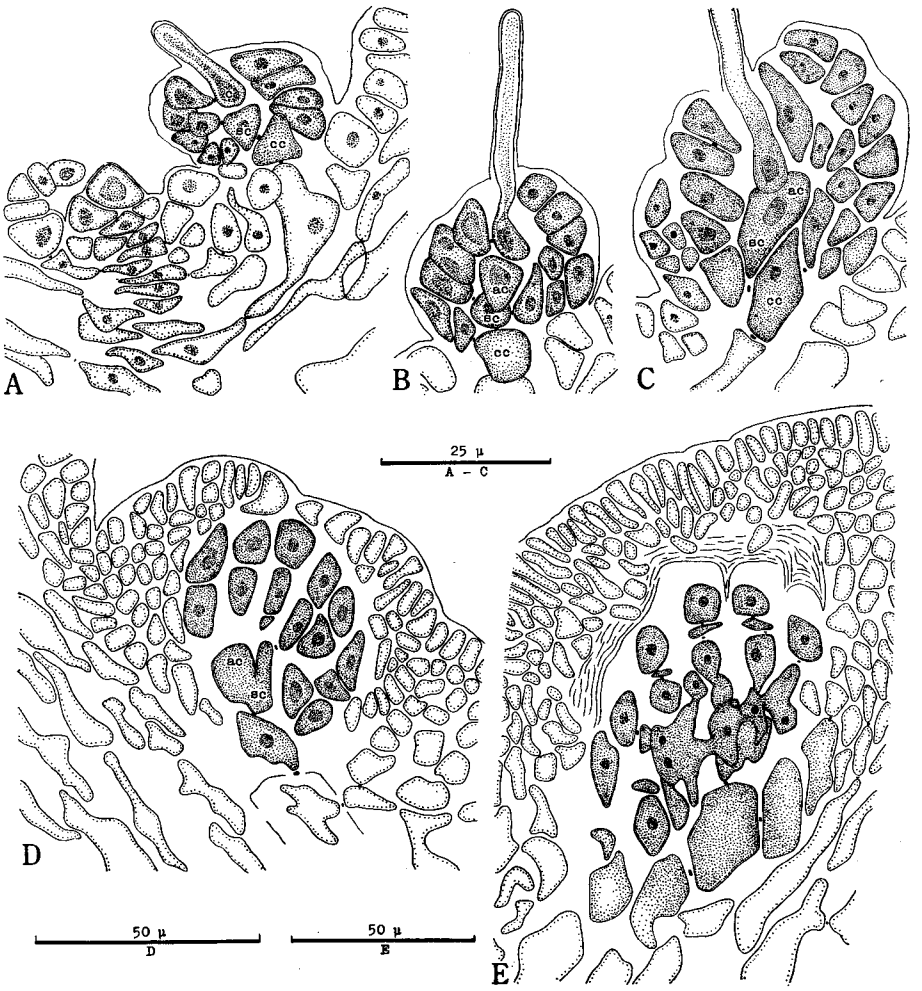

Fig. 19. *Laurencia okamurai* Yamada

A, Part of median longitudinal section through a fertile branchlet of a female plant, showing a procarp ready for fertilization, attached to the top of the elongated pericentral cell (cf. Pl. IX, Fig. 5). **B**, Longitudinal section through a procarp after fertilization, showing the auxiliary cell formed on the supporting cell (cf. Pl. IX, Fig. 6). **C**, Longitudinal section through a procarp after fertilization, showing the fusion between the supporting cell and the auxiliary cell. **D**, Longitudinal section through a more developed procarp, showing the initial stage of the fusion-cell formation (cf. Pl. IX, Fig. 7). **E**, Longitudinal section through a young cystocarp, showing the gonimoblast development. ac: auxiliary cell. c: carpogonium. cc: central cell. sc: supporting cell.

carpogonial branch divide into many sterile cells which later contribute to the growth of the gonimoblast by supplying nutrition. After fertilization a large auxiliary cell is cut off from the supporting cell on the upper side (Pl. IX, Fig. 6, Text-fig. 19, B) and fuses directly with the carpogonium. Then the supporting

cell fuses with the fertilized auxiliary cell to form a fusion-cell (Text-fig. 19, C). The fusion-cell gives rise to a process, the first gonimoblast-initial, toward the nearest of the above mentioned sterile cells and after a little while they fuse with each other. The fusion-cell continues to fuse with other sterile cells and also with the surrounding cells including the central cell and the gonimoblast cells formed in earlier stages of its growth, and becomes larger and irregular in shape (Pl. IX, Figs. 7–9, Text-fig. 19, D & E, Text-fig. 20). The pericarp originates from three pericentral cells derived from the divisions of the fertile central cell of the procarp. Before or just after fertilization, the procarp is covered by a young pericarp, but the carpogonial branch is still naked on its inner side (Pl. IX, Figs. 1 & 2, Text-fig. 19, A & B). With the growth of the fertile branchlet, the developing procarp is gradually displaced toward the periphery of the apical depression, and some cortical cells of the branchlet contribute to the growth of the pericarp (Pl. IX, Fig. 9). Thus the developed pericarp consists of cells of two different origins. The ripe cystocarp, ovoid in shape and up to 820μ in diameter, is situated on the

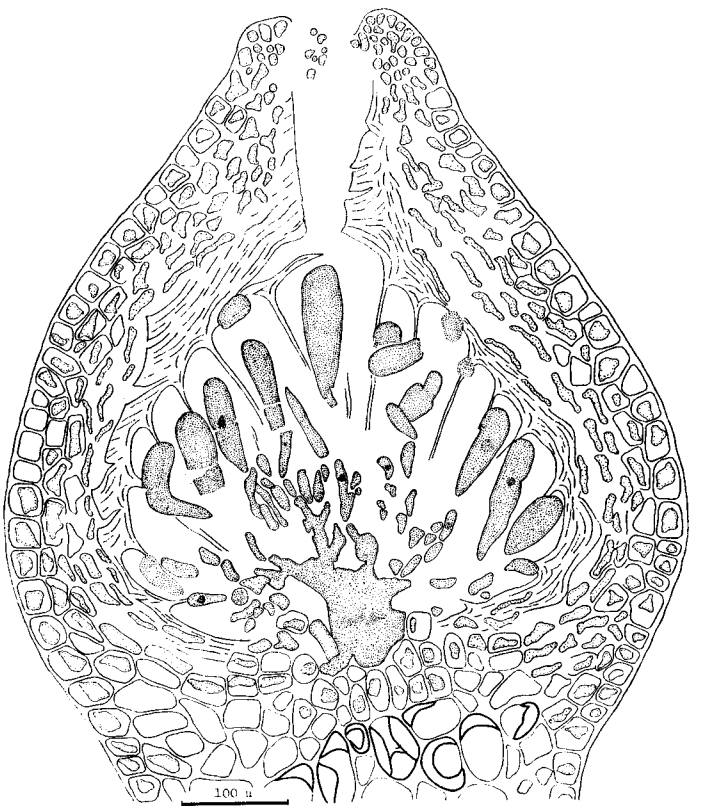

Fig. 20. *Laurencia okamurai* Yamada
Median longitudinal section through a mature cystocarp.

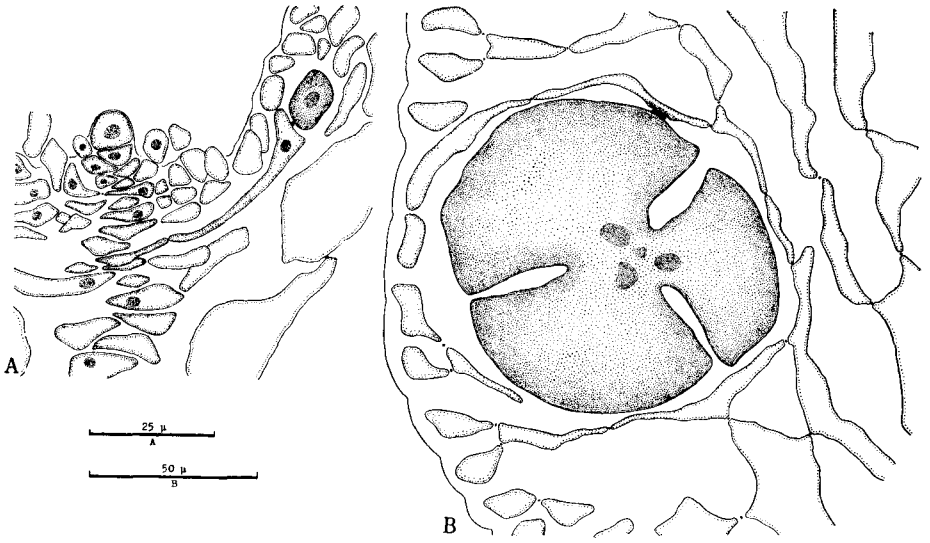

Fig. 21. *Laurencia okamurai* Yamada
A, Part of median longitudinal section through a stichidial branchlet, showing a tetrasproangium-initial on the elongated pericentral cell which is connected to the elongated axial cell (cf. Pl. IX, Fig. 11). **B**, Ditto, showing a divided tetrasporangium on the lateral side of the stichidial branchlet.

lateral surface of the branchlet (Pl. VIII, Fig. 2) and is provided with a carpostome. The cystocarpic cavity is filled with a stratified mucilaginous substance which stains well with iron-alum haematoxylin. The innermost cells of the pericarp which originated from the pericentral cells of the fertile central cell of the procarp become markedly thin and filamentous in shape, and dense in content, indicating that they probably supplied nutrition to the gonimoblast through the fusion-cell. The terminal cells of the gonimoblast enlarge and become carpospores (Pl. IX, Fig. 10, Text-fig. 20).

The ultimate branchlets in the tetrasporophyte are converted into stichidia. The stichidia are cylindrical and 450–550μ in diameter. The tetrasporangium originates from a pericentral cell near the growing apex in the apical depression of the branchlet. The fertile pericentral cell cuts off a sporangium and a cover-cell, and then becomes elongated and filamentous below with the growth of the branchlet tissues (Pl. IX, Fig. 11, Text-fig. 21, A). The fertile pericentral cell is also linked by means of secondary pit-connections to some of the subcortical cells which have been derived from the divisions of other pericentral cells lying beneath it. The cover-cell which has been cut from the fertile pericentral cell covers the sporangium from the inside, and other cover-cells which originated from the subcortical cells cover it from the outside and on the lateral side. The elongated pericentral cell is later divided into several segments. The longitudinal growth

of a stichidial branchlet is continued after the formation of the sporangia. Thus the stichidia is beset in the upper portion with many dark purplish spots or tetrasporangia scattered over its lateral surface (Pl. VIII, Fig. 1) and arranged, in the longitudinal section, parallel to the central axis of the stichidium (Pl. IX, Fig. 12). After the shedding of the spores, these spots become colourless and the stichidia look undulate on the surface (Pl. VIII, Fig. 1). The first nuclear division of the sporangium can be observed while the sporangium is at the periphery of the apical depression, whereas the second division can be observed when the sporangium is not in the depression but on the lateral side of the stichidial branchlet. The sporangium is divided tetrahedrally (Text-fig. 21, B).

5. *Laurencia nipponica* Yamada

Plates X & XI, Text-figs. 22–29

Yamada, 1931, p. 209, pl. 9; Yamada in Okamura, 1936, p. 855, fig. 400; Inagaki, 1933, p. 56, fig. 24; Higashi, 1936, p. 297; Takamatsu, 1938, p. 65; 1939, p. 75; Nagai, 1941, p. 229; Hasegawa, 1949, p. 70 (f. *orientalis*); Moritake, 1949, p. 25; Ohshima, 1950, p. 148, fig. 121; Tokida, 1954, p. 216; Tokida & Masaki, 1959, p. 191; Imahori & Searashi, 1955, p. 72; Saito, 1956, p. 106; 1960, p. 85, pl. 1, text-figs. 1 & 2; Iwamoto, 1960, p. 42, pl. 10, figs. A-C; Kato & Kato, 1963, p. 69; Kanamori, 1965, p. 64; Noda, 1966, p. 80; 1967, p. 43; Kang, 1966, p. 105.

Laurencia glandulifera (non Kützing) Saito, 1956, p. 106.

Japanese name. Ura-sozo (Yamada).

Specimens examined. Growing on rocks in the lower littoral and upper sublittoral zones. *Hokkado*: Oshoro, Shiribeshi Province, 19 July 1962 (♂♀⊕), 29 July 1963 (♂♀⊕), 20 July 1964 (♂♀⊕); Esashi, Hiyama Province, 31 July 1963 (⊕); Matsumae, Oshima Province, 23 April 1963 (sterile); Cape Shirakami, Oshima Province, 11 May 1963 (♂ & sterile), H. Yamamoto; Moheji, near Hakodate, Oshima Province, 2 July 1962 (♀⊕); 12 April (sterile), 25 April (♀ & sterile), 8 May (♂ & sterile), 13 June (♂♀⊕) 1963; 19 March (sterile), 27 April (♂ & sterile), 18 May (♂⊕), 2 June (♂♀⊕), 20 July (♂♀⊕) 1964; Cape Tachimachi, Hakodate, 9 May (♂ & sterile), 12 June (♂ & sterile) 1963; Kinaoshi, Oshima Province, 8 June 1963 (♂ & sterile), 1 July 1965 (♂ & sterile); vicinity of Institute of Algological Research, Hokkaido Univ. (Muroran), 24 September 1962 (♂♀⊕), 8 September 1964 (♂♀⊕); vicinity of Akkeshi Marine Biological Station, 22 July 1963 (♂♀⊕). *Japan Sea coast of Honshu*: Gozu, near Naoetsu, Echigo Province, 2 August 1957 (⊕), 2 May 1960 (♂♀⊕); Nou and vicinity, Echigo Province, 9 May (⊕), 17 May (♂♀⊕) 1956; 10 June 1958 (⊕); 30 April 1960 (⊕); 16 May (♂♀⊕), 26 May (⊕) 1961; 20 May 1963 (♂♀⊕). All of these specimens except those from Cape Shirakami were collected by Y. Saito.

Distribution. *JAPAN*. *Hokkaido*: Rishiri Island (Yamada, 1931; Yamada in Okamura, 1936, as locality of f. *orientalis*); Shiribeshi Province (Inagaki, 1933;

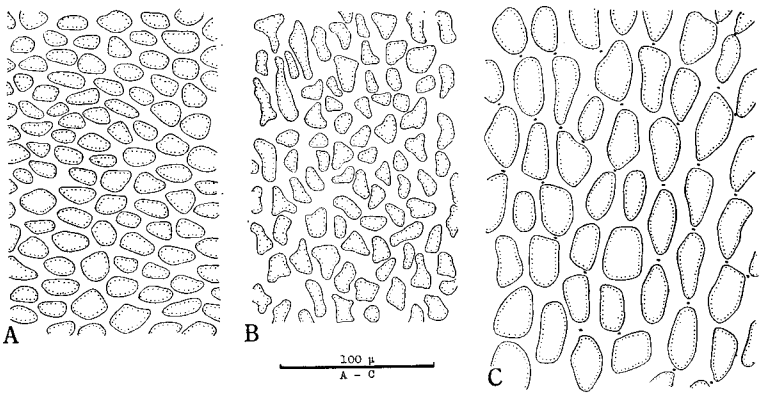

Fig. 22. *Laurencia nipponica* Yamada
Surface view showing the cortical cell arrangement in the upper part of the ultimate branchlet (**A**), in the main axis (**B**) and in the basal part of the branch (**C**).

Yamada in Okamura, 1936; Tokida & Masaki, 1959); Okushiri Island (Hasegawa, 1949, as locality of f. *orientalis*); Oshima Province (Moritake, 1949); Nemuro Province (Yamada, 1931; Yamada in Okamura, 1936, as locality of f. *orientalis*); Kitamai Province (Iwamoto, 1960). *Japan Sea coast of Honshu*: Tsugaru Province, Ugo Province and Tobishima Island (Takamatsu, 1938 & 1939); Uzen Province (Higashi, 1936); Echigo Province (Yamada, 1931; Yamada in Okamura, 1936; Higashi, 1936; Saito, 1956 & 1960); Sado Island (Noda, 1967); Toyama Bay (Ohshima, 1950); Noto Province (Imahori & Searashi, 1955); Inaba Province (Yamada, 1931; Yamada in Okamura, 1936; Higashi, 1936); Nagato Province (Yamada, 1931; Yamada in Okamura, 1936). *SAGHALIEN* (Tokida, 1954). *KURILE ISLANDS* (Nagai, 1941). *KOREA* (Kang, 1966). *CHINA* (Yamada, 1931; Yamada in Okamura, 1936; Noda, 1966).

The present species was established by Yamada (1931) on the basis of the tetrasporiferous specimens from Japan Sea coast of Honshu and from China. The female plant was reported from Oshoro (Inagaki, 1933) and Lake Saroma (Iwamoto, 1960), Hokkaido. I collected it, together with the male and tetrasporiferous plants at Nou, Echigo Province, the type locality of the present species and reported my observations on them in 1960. However, the female materials at that time were unfortunately too old to observe cystocarpic development. I later made detailed observations with the specimens collected at Oshoro and Moheji, Hokkaido.

The fronds are erect, up to nearly 40 cm. high,with several erect axes tufted below with entangled rhizoidal branches (Pl. X, figs. 1–3 & 5). They are generally purplish red, orange or brown in colour, somewhat cartilaginous but not so rigid in texture, and adhere to paper when dried except for very old individuals. The erect axes are cylindrical, 1350–2600μ in diameter, 12.5–37.5 cm. high (20.4 cm. high on the average among 110 individuals), and paniculately branched. The branching is

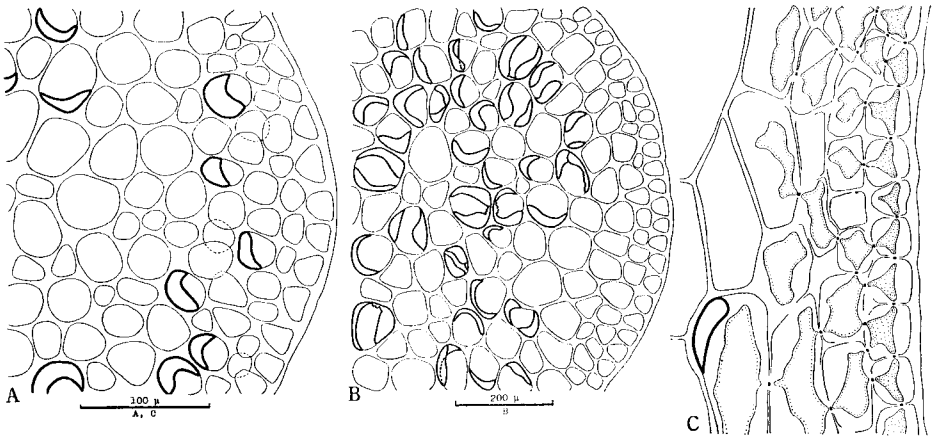

Fig. 23. *Laurencia nipponica* Yamada
A & B, Transverse section of a branchlet (**A**) and of a forked portion of a main axis (**B**). **C,** Longitudinal section of a branch.

alternate, opposite or verticillate; the branches are 720–1210μ in diameter with the ultimate sterile branchlets being 270–390μ in diameter. In a surface view, the cortical cells in the main axis are arranged somewhat irregularly, longitudinally elongated, 8–17μ wide and about 1.4–5.2 times as long as the width (Text-fig. 22, B), while those in the basal portion of the branch are arranged longitudinally, slightly elongated, 18–33μ wide and 1.4–2.6 times as long as the width (Text-fig. 22, C). In the upper part of a branch, the cortical cells seen from the surface are nearly round and about 24–34μ in diameter, but in the apical portion of an ultimate branchlet they are small, roundish and slightly elongated laterally (Text-fig. 22, A). In a longitudinal section, the cortical cells are not projected above the frond surface, even at the apical portion of an ultimate branchlet (Text-fig. 23, C, Text-fig. 24, B). Longitudinal secondary pit-connections among the cortical cells are present (Text-fig. 23, C, Text-fig. 24, B), and can also be seen in a surface view of a branch (Text-fig. 22, C). In a transverse section of the frond, the cortical cells, 14–27μ long by 19–30μ wide in an ultimate branchlet (Text-fig. 23, A), are neither elongated radially nor arranged like palisade cells. Lenticular thickenings of the cell walls are present in the medulla (Text-fig. 23, A-C, Text-fig. 28); they are especially abundant at the forked portion of the frond (Text-fig. 23, B), but rather rare in younger tissues such as the apical portion of an ultimate branchlet. The apical cell of the ultimate branchlet is situated at the bottom of the apical depression, and it cuts off, by oblique walls, wedge-shaped segments which form the axial cell-row. All of the cells in the branchlet including those of the trichoblasts and of the young reproductive organs are linked directly to the axial cells or indirectly through the pericentral cells (Pl. XI, Figs. 5, 6, 9, 14 & 15, Text-fig. 24, B, Text-fig. 25, A, Text-fig. 26, A, Text-fig. 29, A). The trichoblast arising from a young

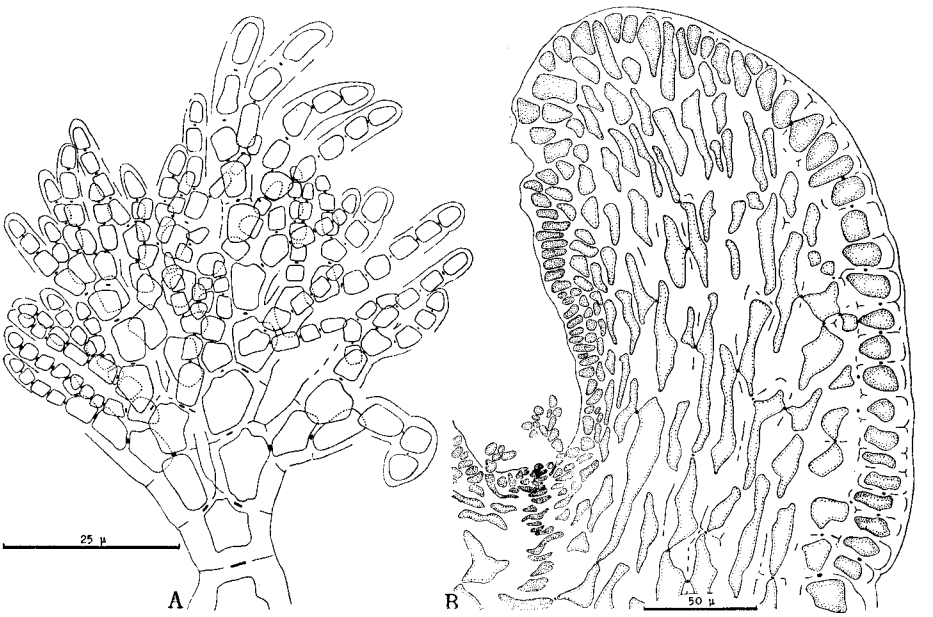

Fig. 24. *Laurencia nipponica* Yamada
A, A young trichoblast. **B**, Part of apical portion of median longitudinal section through a sterile branchlet.

pericentral cell near the apical cell, is gradually displaced toward the periphery of the apical depression with the advance of growth, and branches dichotomo-alternately (Text-fig. 24, A).

The terminal portion of the ultimate branchlet in the male plant is characteristically broad, 410–1120μ in diameter, up to 2440μ long when fully grown, and cylindrically thick (Pl. XI, Figs. 1 & 2). It generally bears a single antheridial depression, 154-220μ deep and 2.1–2.3 times as wide as it is deep, and is furnished with many fertile and sterile trichoblasts (Pl. XI, Fig. 5). The fertile trichoblast, or antheridium, arises from a young pericentral cell near the apical cell (Pl. XI, Fig. 6, Text-fig. 25, A) and consists of a dichotomo-alternately branched central axis and four pericentral cells, or spermatangial mother-cells, on each axial cell (Pl. XI, Figs. 7 & 8, Text-fig. 25, B & C). Each mother-cell gives rise to 1—3 (or more) ovoid spermatangia, 7.7–9.8μ long by 4.8–6.9μ in diameter, which contain a large nucleus. The position of the nucleus in the spermatangium is not limited to its apex as found in other species but it occurs in other places as well (Text-fig. 25, C). Some of the axial cells are occasionally found to give rise directly to a spermatangium as a pericentral cell. A pericentral cell from a lower segment of the axis usually produces a cormybose branch and a tuft of spermatangia. The terminal cell of the axis of the fertile trichoblast is vesicular in appearance, ovoid in shape, and often very large, up to 44μ long by 35μ in diameter (Pl. XI, Fig. 8, Text-fig. 25, C).

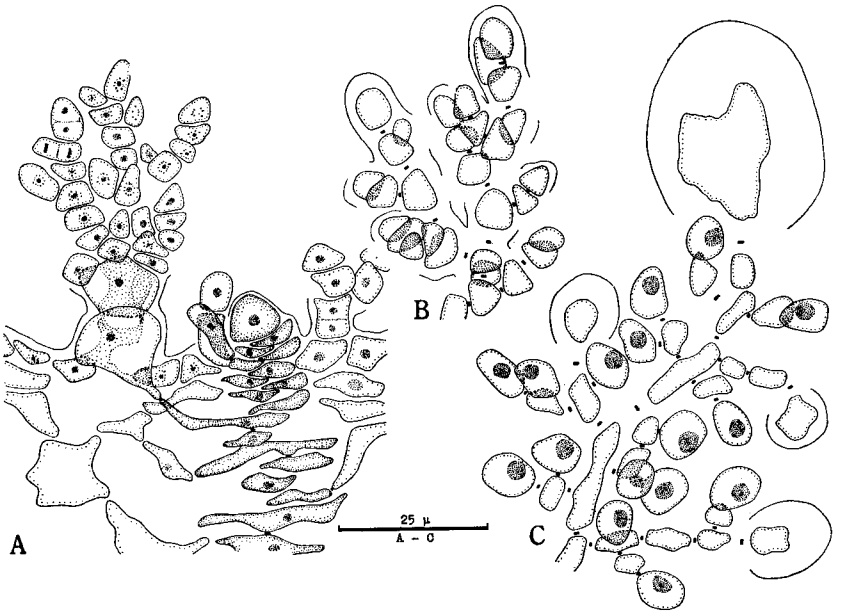

Fig. 25. *Laurencia nipponica* Yamada
A, Part of median longitudinal section through an antheridial receptacle, showing the growing point and an antheridium-initial (cf. Pl. XI, Fig. 6). **B** & **C**, Apical portion of a young (**B**) and mature (**C**) antheridium from a smeared preparation.

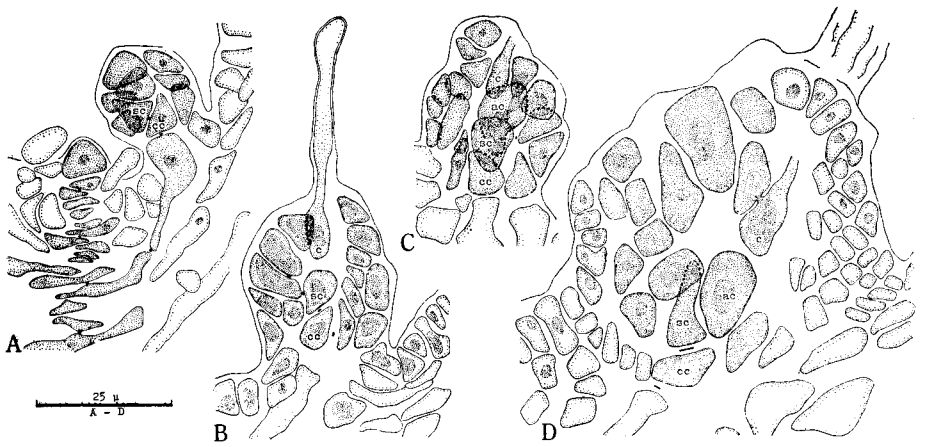

Fig. 26. *Laurencia nipponica* Yamada
A, Part of median longitudinal section through a fertile branchlet of a female plant, showing a procarp attached to the top of the elongated pericentral cell which is connected to the elongated axial cell (cf. Pl. XI, Fig. 9). **B**, Longitudinal section through a procarp ready for fertilization (cf. Pl. XI, Fig. 10). **C**, Longitudinal section through a procarp after fertilization, showing the auxiliary cell formed on the supporting cell (cf. Pl. XI, Fig. 11). **D**, Longitudinal section through a more developed procarp. ac: auxiliary cell. c: carpogonium. cc: central cell. sc: supporting cell.

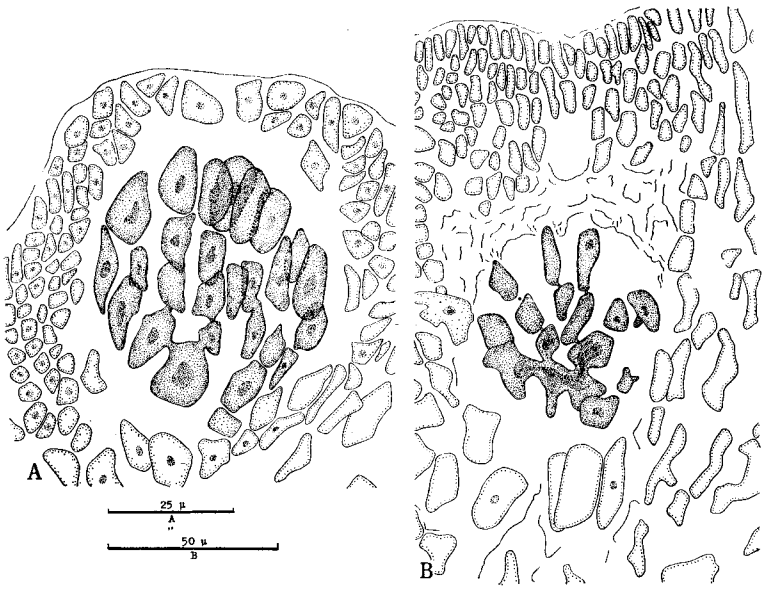

Fig. 27. *Laurencia nipponica* Yamada
A, Longitudinal section through a young procarp, showing an early stage of fusion-cell formation. B, Longitudinal section through a more developed young cystocarp, showing an early stage of gonimbolast formation (cf. Pl. XI, Fig. 12).

The ultimate branchlets in the female plant are cylindrical while sterile, but they become clavate with the development of the procarps and the cystocarps (Pl. XI, Fig. 3). The initial cell of the procarp arises from a pericentral cell of the fertile branchlet and functions as the fertile central cell of the procarp. This fertile cell is linked to the axial cell of the branchlet through a pericentral cell which graudally becomes elongated and filamentous below with the growth of the branchlet tissues (Pl. XI, Fig. 9, Text-fig. 26, A). The fertile central cell cuts off the supporting cell of the carpogonial branch on the inside, i.e. toward the growing point of the branchlet, as one of the four pericentral cells (Pl. XI, Fig. 9, Text-fig. 26, A). The four-celled carpogonial branch is formed on the supporting cell which also cuts off sterile cells (Pl. XI, Figs. 9–11, Text-fig. 26, A-C). These sterile cells later divide into several cells which contribute to the growth of the gonimoblast. The carpogonial branch is curved so as to embrace the supporting cell (Pl. XI, Fig. 10, Text-fig. 26, B). After fertilization a large auxiliary cell cuts off from the supporting cell on the upper side (Pl. XI, Fig. 11, Text-fig. 26, C) and fuses with the carpogonium. The supporting cell then fuses with the fertilzied auxiliary cell to form a fusion-cell (Text-fig. 26, C & D). No connecting cell is formed from the carpogonium to fuse with the auxiliary cell. The fusion-cell gives rise to a process, the first gonimbolast-initial, toward the nearest of the above mentioned sterile cells and after a little while they fuse with each other. The fusion-

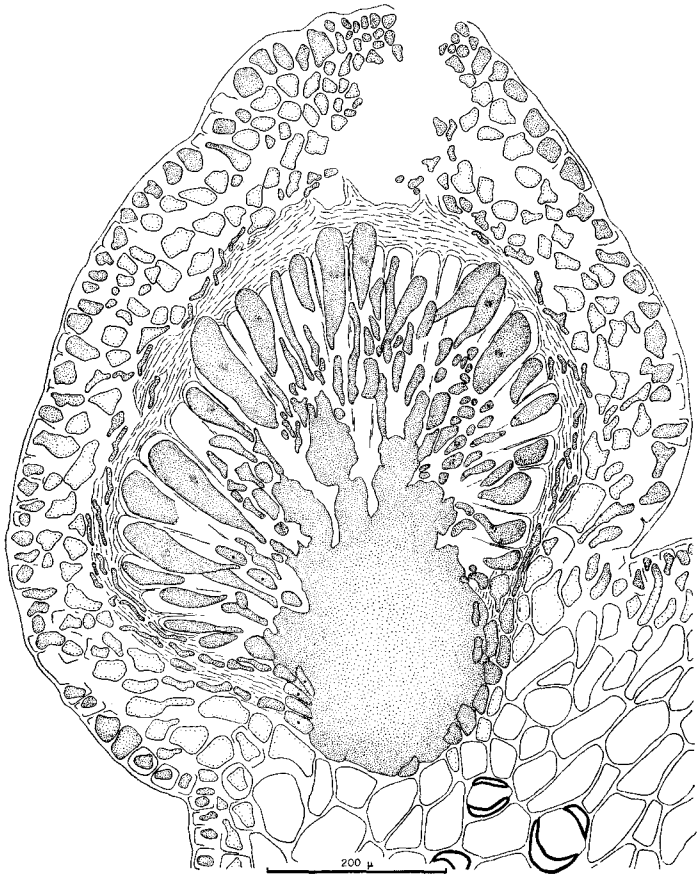

Fig. 28. *Laurencia nipponica* Yamada
Median longitudinal section through a ripe cystocarp.

cell continues to fuse with other sterile cells and also with the surrounding cells including the central cell and the gonimoblast cells formed during earlier developmental stages, and becomes large and irregular in shape (Pl. XI, Fig. 12, Text-fig. 27, A & B, Text-fig. 28). The pericarp originates from the pericentral cells of the fertile central cell of the procarp. Before or after fertilization, the procarp is partly covered by a young pericarp, but the carpogonial branch is still naked on the inside (Pl. XI, Fig. 10, Text-fig. 26, B). With the advance of growth of the branchlet, the developing procarp is gradually displaced toward the periphery of the apical depression, and some cortical cells of the branchlet contribute to the growth of the outer portion of the pericarp. Thus the fully developed pericarp consists of cells of two different origins. The ripe cystocarp, ovoid in shape and up to 860μ in diameter, is situated on the lateral surface of the branchlet and provided with a carpostome (Pl. XI, Figs. 3 & 13, Text-fig. 28). The cystocarpic

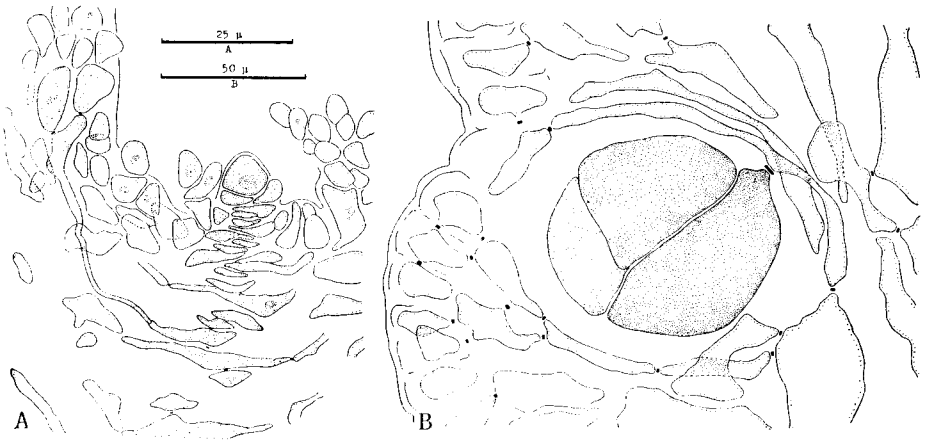

Fig. 29. *Laurencia nipponica* Yamada
A, Part of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on the elongated pericentral cell which is connected to the elongated axial cell (cf. Pl. XI, Fig. 14). B, Ditto, showing a divided tetrasporangium on the lateral side of the stichidial branchlet.

cavity is filled with a mucilaginous substance which stains well with iron-alum haematoxylin. The innermost cells of the pericarp become markedly thin and filamentous in shape, and dense in content, indicating that they have probably supplied nutrition to the gonimoblast through the fusion-cell. The terminal cells of the gonimoblast enlarge and become carpospores (Pl. XI, Fig. 13, Text-fig. 28).

The ultimate branchlets in the tetrasporophyte are converted into stichidia. The stichidia are cylindrical, 410–560μ in diameter, and are beset in the upper portion with many dark purplish spots or tetrasporangia scattered over their surfaces. After the shedding of the spores, these spots become colourless and the stichidia look undulate on the surface (Pl. XI, Fig. 4). The tetrasporangium originates from a pericentral cell near the growing apex in the apical depression of a branchlet. The fertile pericentral cell cuts off a sporangium and a cover-cell, and then becomes elongated and filamentous below with the growth of the branchlet tissues (Pl. XI, Fig. 14, Text-fig. 29, A). The fertile pericentral cell is also linked by means of secondary pit-connections to some of the subcortical cells which have been derived from the divisions of the other pericentral cell lying beneath it. The cover-cell cut from the fertile pericentral cell covers the sporangium from the inside, and the other cover-cells which originate from the subcortical cells cover it from the outside and on the lateral side (Text-fig. 29, B). The elongated fertile pericentral cell is later divided into several segments. The first nuclear division of the sporangium is at the periphery of the apical depression, whereas the second division can be observed when the sporangium is not in the depression but on the lateral side of the stichidial branchlet (Pl. XI, Fig. 15). Although many sporangia

are formed in a stichidial branchlet, the longitudinal growth of the branchlet is not suppressed. Thus the mature tetrasporangia are formed on the lateral side of the stichidium and arranged parallel to the central axis as seen in longitudinal section (Pl. XI, Fig. 15). The division of the sporangium is tetrahedral (Text-fig. 29, B).

6. *Laurencia pinnata* Yamada

Plate IV, Figs. 8 & 9, Text-fig. 30

Yamada, 1931, p. 242, pl. 28; Yamada in Okamura, 1936, p. 859; Higashi, 1935, p. 157; 1936, p. 298; Segawa, 1936, p. 196; Segawa & Ichiki, 1959, p. 112; Segawa & Kamura, 1960, p. 62; Takamatsu, 1938, p. 66; Hasegawa, 1949, p. 70; Moritake, 1949, p. 25; Ohshima, 1950, p. 149; Imahori & Searashi, 1955, p. 72; Kawashima, 1955, p. 34; Saito, 1956, p. 106; Kida, 1964, p. 234; 1965, p. 17; Noda, 1964, p. 73; 1966, p. 81; 1967, p. 44; Noda & Kang, 1964, p. 43; Kang, 1965, p. 57; 1966, p. 107; Kanamori, 1965, p. 65.

Laurencia pinnatifida (non Lamouroux) Okamura, 1922, p. 174 & 181, pl. 192.

Japanese name. Hane-sozo (Okamura).

Specimens examined. Growing on rocks in the lower littoral and sublittoral zones. *Hokkaido*: Matsumae, 7 April 1962, H. Yamamoto; 23 April 1963, Y. Saito; Cape Shirakami, 11 May 1963, H. Yamamoto; Sumiyoshi, Hakodate (washed ashore), 16 April 1965, T. Kaneko. *Japan Sea coast of Honshu*: Nou and vicinity, Echigo Province, 10 June 1954, 1 July 1955, 16, 17 & 22 June 1956, Y. Saito. All of these specimens are sterile.

Distribution. *JAPAN*. *Hokkaido*: Okushiri Island (Hasegawa, 1949); Hakodate (Harvey, fide Yamada, 1931; Moritake, 1949). *Japan Sea coast of Honshu*: Mutsu Province (Takamatsu, 1938); Uzen Province (Kanamori, 1965); Echigo Province (Saito, 1956; Noda, 1967): Etchu Province (Higashi, 1936; Ohshima, 1950); Noto Province (Imahori & Searashi, 1955). *Pacific coast of Honshu*: Rikuchu Province (Kawashima, 1955); Iwaki Province (Noda, 1964); Sagami Province (Yamada, 1931; Higashi, 1935). *Kyushu*: Higo Province (Segawa & Ichiki, 1959); Amami Island (Kida, 1964). *Shikoku*: Okinoshima Island (Kida, 1965). *RYUKYU* (Segawa & Kamura, 1960). *KOREA* (Noda & Kang, 1964; Noda, 1966; Kang, 1965 & 1966).

The present species was established by Yamada (1931) on the basis of the tetrasproiferous specimens from Enoshima, Japan. Until then, this plant passed among us under the name of *Laurencia pinnatifida* following Harvey who referred the specimens collected at Hakodate by C. Wright, to that species.

The fronds are erect, forming a clump with several erect main branches with no entangled nor coalescing portions. They are purplish pink or orange in colour, fleshy and soft in texture, and adhere to paper when dried. Main axes are present in some specimens. These main branches or axes stand on a discoid base and are

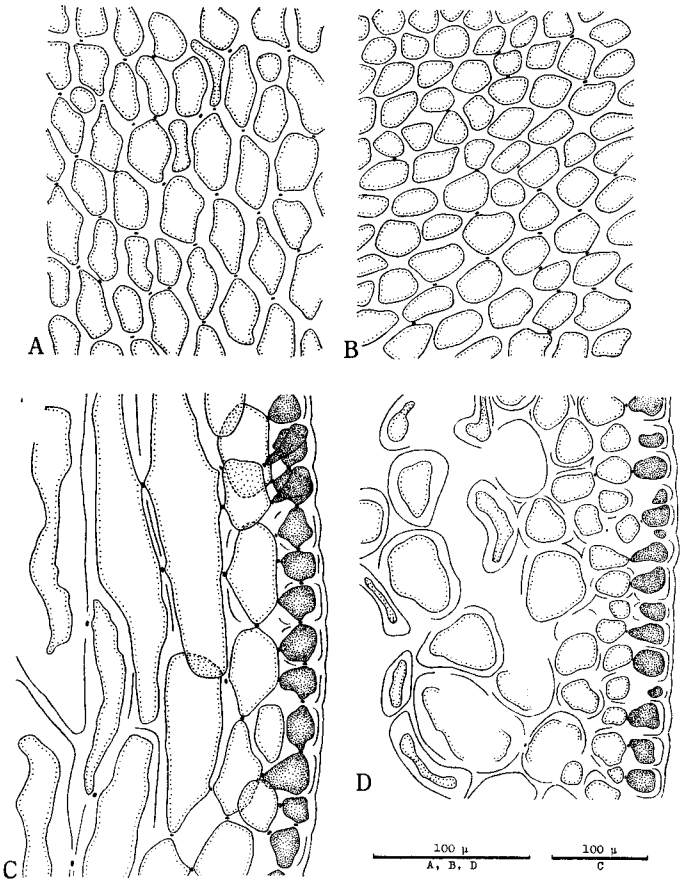

Fig. 30. *Laurencia pinnata* Yamada
A & B, Surface view showing the cortical cell arrangement in the secondary branch (**A**) and in the ultimate branchlet (**B**). **C**, Longitudinal section of a branch. **D**, Transverse section of a branchlet.

3–7.5 cm. high and are pinnately branched, cylindrical and 900–1150μ in diameter near the base. They are soon compressed and up to 4700μ wide in upper portions. The branches are distichous on the margins, and suboppositely alterante (Pl. IV, Figs. 8 & 9). The cortical cells in a surface view are somewhat elongated longitudinally, 18–35μ long by 10–17μ wide in the main branches. They are also elongated longitudinally, 30–54μ long by (8–)18–27μ wide in the secondary branches (Text-fig. 30, A), and slightly elongated laterally, 18–26μ long by 21–30μ wide in the apical portion of the branchlets (Text-fig. 30, B). In a transverse section of the branches, the cortical cells are neither elongated radially nor arranged like palisade cells, but in a longitudinal section of the apical portion of the branchlets, they are slightly elongated and arranged somewhat like palisade cells, barely projecting above the frond surface. Lenticular thickenings in the

walls of the medullary cells are absent (Text-fig. 30, C & D). The apical cell of the ultimate branchlet is situated at the bottom of the apical depression, and it cuts off, by oblique walls, wedge-shaped segments which form the axial cell-row. All of the cells in the branchlet, including those of the trichoblast, are linked directly to the axial cells, or indirectly by way of the pericentral cells. Longitudinal secondary pit-connections among the cortical cells are present (Text-fig. 30, C).

The above description is based on the sterile specimens from Matsumae, Hokkaido. It generally agrees with the description given by Yamada (1931). Unfortunately, I did not collect any fertile specimens. Okamura's illustration of a branch bearing some stichidial branchlets clearly shows that the tetrasporangia of the present species are scattered on the lateral side of the stichidium. Thus the tetrasporangia must be arranged parallel to the central axis in the longitudinal section of a stichidium.

7. ***Laurencia intermedia*** Yamada

Plates XII & XIII, Text-figs. 31–35

Yamada, 1931, p. 191, pl. 1, fig. c, pl. 2; Yamada in Okamura, 1936, p. 853, fig. 399; Higashi, 1935, p. 157; 1936, p. 298; Segawa, 1934, p. 88; Segawa & Ichiki, 1959, p. 111; Segawa & Yoshida, 1961, p. 19; Moritake, 1949, p. 25; Ohshima, 1950, p. 147, fig. 120; Saito, 1956, p. 106; 1961, p. 42, figs. 1–4; Hirose, 1958, p. 268; Noda, 1964, p. 73; 1966, p. 80; 1967, p. 43; Noda & Kang, 1964, p. 43; Kang, 1965, p. 57; 1966, p. 105.

Japanese name: Kuro-sozo (Yamada).

Specimens examined. Growing on rocks in the lower littoral and upper sublittoral zones. *Hokkaido*: Oshoro, Shiribeshi Province, 19 July (♂ & sterile), 22 September (♂ ♀ ⊕) 1962; 29 July 1963 (♂ & sterile); 20 July 1964 (♂ ♀ ⊕); Moheji, near Hakodate, Oshima Province, 2 July (sterile), 16 August (♂ ♀ ⊕), 11 September (⊕), 28 September (⊕) 1962; 12 April (sterile), 25 April (sterile), 16 May (sterile), 5 September (⊕) 1963; 10 August 1964 (♂ ♀ ⊕). *Japan Sea coast of Honshu*: Gozu, near Naoetsu, Echigo Province, 2 August 1957 (⊕); Nou and vicinity, Echigo Province, 4 September 1954 (⊕); 22 April (sterile), 22 June (sterile) 1956; 26 June (⊕), 23 July (⊕), 19 August (♂ ♀ ⊕), 29 August (♂ ♀ ⊕) 1960; 29 April (sterile), 19 August (♀ ⊕) 1961. *Pacific coast of Honshu*: Hassei, near Aburatsubo, Sagami Province, 26 May 1963 (♂ & sterile). All of these specimens were collected by Y. Saito.

Distribution. *JAPAN*. *Hokkaido*: Oshima Province (Moritake, 1949). *Japan Sea coast of Honshu*: Echigo Province (Saito, 1956 & 1961); Sado Island (Noda, 1967); Etchu Province (Higashi, 1936; Ohshima, 1950); Tajima Province (Hirose, 1958). *Pacific coast of Honshu*: Iwaki Province (Noda, 1964); Sagami Province (Yamada, 1931; Yamada in Okamura, 1936; Higashi, 1935); Idzu Province (Segawa, 1935). *Kyushu*: Higo Province (Segawa & Ichiki, 1959; Segawa &

Yoshida, 1961). *KOREA* (Noda & Kang, 1964; Noda, 1966; Kang, 1965 & 1966).

The present species was established by Yamada (1931) on the basis of the tetrasporiferous specimens from Enoshima, Japan. According to the workers listed above, this species is widely distributed in Japan. The sexual plants were first collected by myself at Nou and its vicinity as reported previously (Saito, 1961). A more detailed description is given here on the basis of the specimens from Moheji, Hokkaido.

The fronds are erect, with several erect axes loosely tufted below with somewhat entangled and slightly coalesced stoloniferous branches (Pl. XII, Figs. 1–4). Generally dark purple in colour but becoming black in drying, they are sometimes greenish when young and yellowish when old. They are cartilaginous and rigid in texture, and never adhere to paper when dried. The main axes are cylindrical, 960–1150μ in diameter near the base and 1900–2900μ in diameter in the middle porition. They are 4.4–13 cm. high (9.0 cm. high on the average among 50 individuals), paniculately branched, and sometimes not percurrent but divided one or more times. The branching is opposite, subverticillate or alternate; the branches are 1110–2040μ in diameter with the ultimate sterile branchlets 270–620μ in diameter. In a surface view, the cortical cells in the main axis are usually hexagonal, 12–17μ long by 14–19μ broad (Text-fig. 31, A), while those in the branch are longitudinally elongated, 35–62μ long by 16–27μ broad (Text-fig. 31, B). The cortical cells in the apical portion of the ultimate branchlet are roundish and elongated laterally, 10–16μ long by 13–22μ broad (Text-fig. 31, C). In a transverse section of the frond, the cortical cells are elongated radially and arranged like palisade cells, 26–37μ long by 10–18μ broad (Text-fig. 31, E). Lenticular thickenings of the medullary cell walls are absent. The apical cell of the ultimate branchlet is situated at the bottom of the apical depression, and it cuts off, by oblique walls, wedge-shaped segments which form the axial cell-row. All of the cells in the branchlet, including those of the trichoblasts and of the young reproductive organs, are linked directly to the axial cells or indirectly through the pericentral cells (Pl. XIII, Figs. 1, 2, 8 & 10–13). The cortical cells are never connected to each other by secondary pit-connections either longitudinally or laterally (Text-fig. 31, D & E). The trichoblast arises from a young pericentral cell near the growing apex, and is gradually displaced toward the periphery of the apical depression with the advance of growth, branching dichtomo-alternately (Pl. XIII, Fig. 14).

The terminal portion of the ultimate branchlet in the male plant is characteristically thick, attaining 770–1660μ in diameter (Pl. XII, Figs. 4 & 7), and bears one to three or more antheridial depressions, 140–520μ deep, and 2.1–2.7 times as broad as it is deep. These antheridial depressions are furnished with many fertile and sterile trichoblasts (Pl. XIII, Fig. 1). The fertile trichoblast, or antheridium, originates from a young pericentral cell near the growing apex (Pl. XIII, Fig. 2) and consists of dichotomo-alternately branched axial cells and four pericentral cells, or

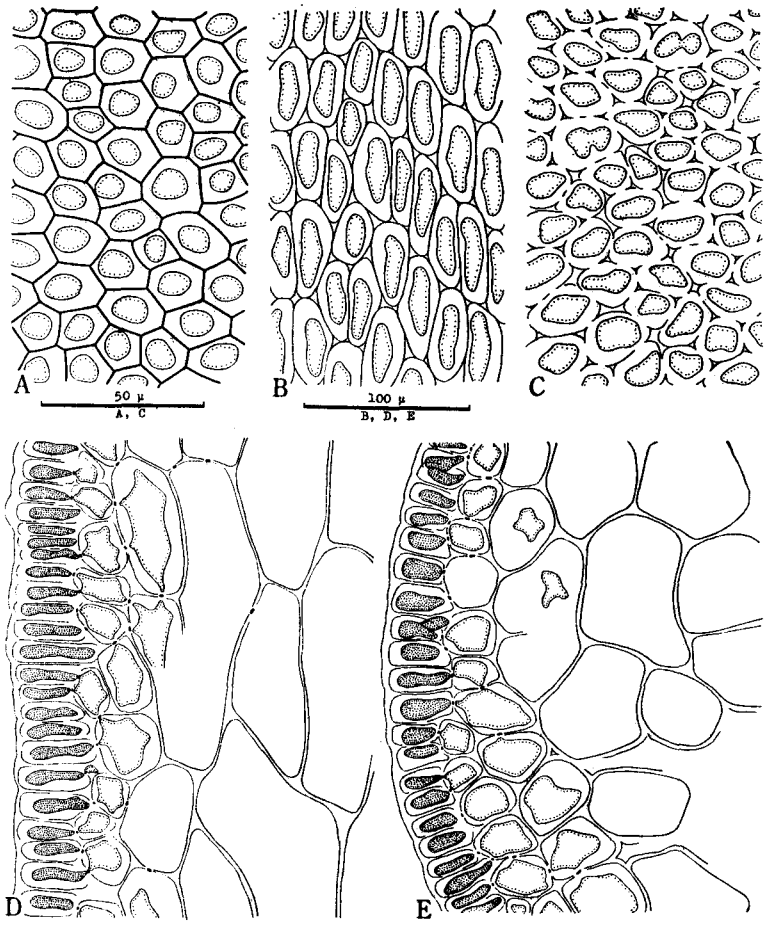

Fig. 31. *Laurencia intermedia* Yamada
A-C, Surface view showing the cortical cell arrangement in the main axis (**A**), a branch (**B**) and in the upper part of an ultimate branchlet (**C**). **D**, Longitudial section of an ultimate branchlet. **E**, Transverse section of an ultimate branchlet.

spermatangial mother-cells, on each axial cell (Text-fig. 32, A-C). Each mother-cell gives rise to 1–3 (or more) ovoid spermatangia, 8.8–12.2μ long by 4.6–6.3μ in diameter, which contain a large nucleus at their apices (Pl. XIII, Fig. 4, Text-fig. 31, A-C). A pericentral cell from a lower segment of the axis usually produces a corymbose branch and a tuft of spermatangia. The terminal cell of the axis of a fertile trichoblast is vesicular in appearance, ovoid in shape, and often very large, up to 50μ long by 42μ in diameter (Pl. XIII, Fig. 4, Text-fig. 32, A & B).

The ultimate branchlets in the female plant are cylindrical while sterile, but they become clavate with the development of the procarps and cystocarps (Pl. XII, Fig. 5). The initial cell of the procarp arises from a pericentral cell of the fertile

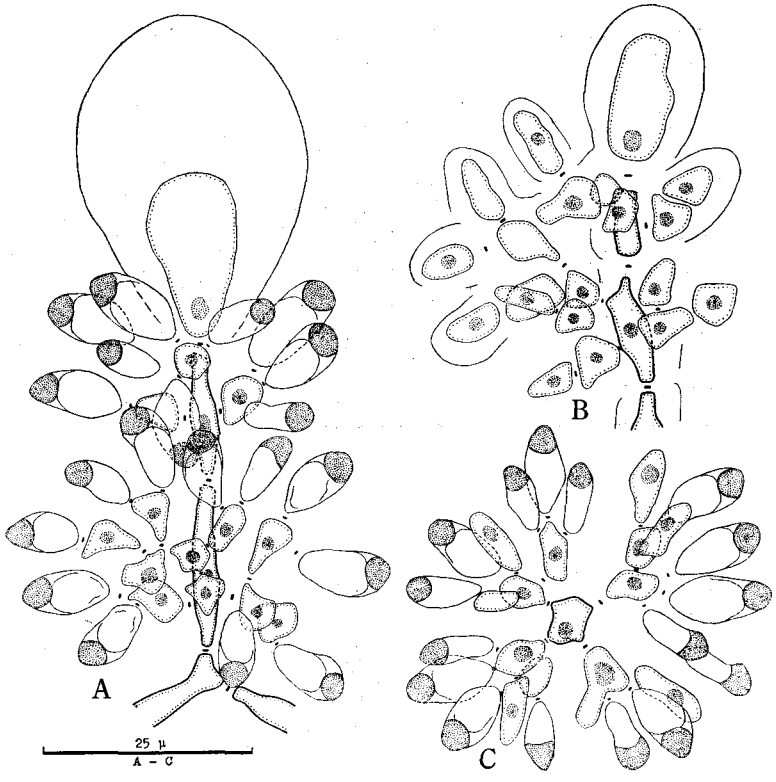

Fig. 32. *Laurencia intermedia* Yamada
A & **B**, Apical portion of a mature (**A**) and a young (**B**) antheridium from a smeared preparation. **C**, Transverse section through a mature antheridium.

branchlet and acts as the fertile central cell of the procarp. This fertile cell is linked to the axial cell of the branchlet through the pericentral cell which gradually becomes elongated and filamentous below, with the growth of the branchlet tissues. The fertile central cell cuts off the supporting cell of the carpogonial branch on the inside, i.e. toward the growing point of the branchlet, as one of the four pericentral cells. The four-celled carpogonial branch is formed adaxially on the supporting cell, together with some sterile cells. The carpogonial branch is curved so as to embrace the supporting cell (Pl. XIII, Fig. 5, Text-fig. 33, A). Eaeh sterile cell formed at the same time as the carpogonial branch is divided into several cells which generally contribute to the growth of the gonimoblast. After fertilization a large auxiliary cell cuts off from the supporting cell on the upper side (Pl. XIII, Fig. 6, Text-fig. 33, B) and fuses with the carpogonium. The supporting cell then fuses with the fertilized auxiliary cell to form a fusion-cell (Pl. XIII, Figs. 6 & 7, Text-fig. 33, B & C). No connecting cell is formed to bridge the carpogonium with the auxiliary cell. The fusion-cell gives rise to a process, the first gonimoblast cell, toward the above mentioned sterile cell which is situated nearby, and later they

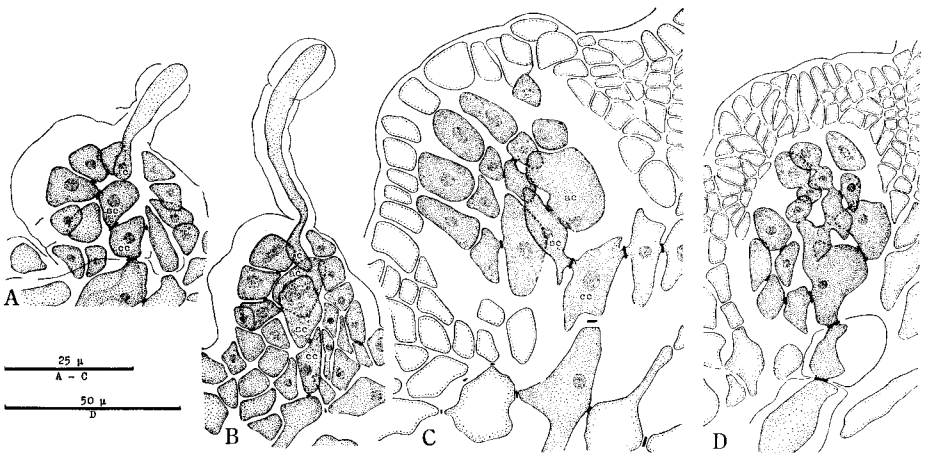

Fig. 33. *Laurencia intermedia* Yamada
A, Longitudinal section through a procarp ready for fertilization (cf. Pl. XIII, Fig. 5). **B**, Longitudinal section through a procarp after fertilization, showing the auxiliary cell formed on the supporting cell (cf. Pl. XIII, Fig. 6). **C**, Longitudinal section through a young cystocarp, showing the initial stage of fusion-cell formation (cf. Pl. XIII, Fig. 7). **D**, Longitudinal section through a more developed young cystocarp, showing the initial stage of gonimoblast development. ac: auxiliary cell. c: carpogonium. cc: central cell. sc: supporting cell.

fuse with each other. The fusion-cell continues to fuse with other sterile cells and the surrounding cells including the central cell and the older gonimoblast cells, and becomes large and irregular in shape (Text-fig. 33, C & D, Text-fig. 34). The pericarp originates from the pericentral cell of the procarp. These sterile cells were formed together with the supporting cell of the carpogonial branch. Before or after fertilization, the procarp is covered by a young pericarp, but the carpogonial branch is still naked on the inside (Text-fig. 33, A & B). With the growth of the branchlet, the developing procarp is gradually displaced toward the periphery of the apical depression, and some cortical cells of the branchlet contribute to the growth of the outer portion of the pericarp (Pl. XIII, Fig. 8). Thus the developed pericarp consists of two different origins. The ripe cystocarp, ovoid in shape and up to 850μ in diameter, is situated on the upper lateral side of the branchlet (Pl. XII, Fig. 5) and is provided with a carpostome. The cystocarpic cavity is filled with a mucilaginous substance which stains well with iron-alum haematoxylin. The innermost cells of the pericarp, which originated from the pericentral cells of the fertile central cell of the procarp, become markedly thin and filamentous in shape, and dense in content, indicating that they probably supplied nutrition to the gonimoblast through the fusion-cell. The terminal cells of the gonimoblast enlarge in size and become carpospores (Pl. XIII, Figs. 8 & 9, Text-fig. 34).

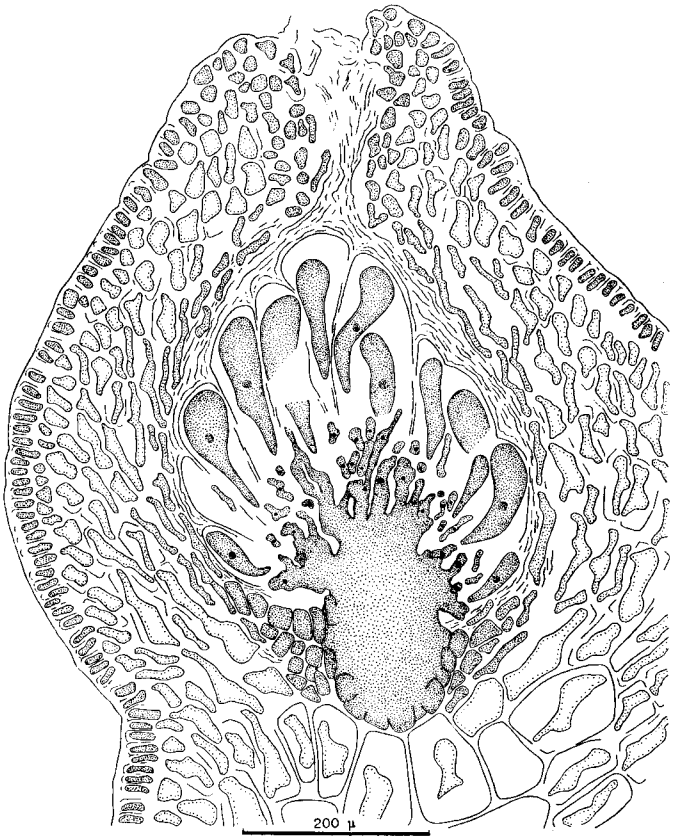

Fig. 34. *Laurencia intermedia* Yamada
Median longitudinal section through a ripe cystocarp.

In a female plant, a fertile branchlet with procarpic depression was once observed to bear an antheridial depression on the lateral surface as shown in Pl. XIII, Fig. 13. I believe this is the first discovery of a partially hermaphroditic individual in *Laurencia*.

The ultimate branchlets in the tetrasporphyte are converted into stichidia. The stichidia are cylindrical while sterile but become clavate with maturity, and some of them, especially those from the lower portion of a branch, bear wart-like stichidial branchlets. The stichidia are 690–920μ in diameter and beset with many dark purplish spots or tetrasporangia scattered over their apical surfaces. After the shedding of the spores, these spots become colourless and the stichidia look undulate on the surface (Pl. XII, Fig. 6, Pl. XIII, Fig. 10). The tetrasporangium originates from a pericentral cell near the growing apex in the apical depression of a branchlet. The fertile central cell cuts off a sporangium and a cover-cell, and becomes elongated and filamentous below with the growth of the branchelt tissues (Pl. XIII, Fig. 11, Text-fig. 35, A). The fertile pericentral cell is also linked by means of secondary

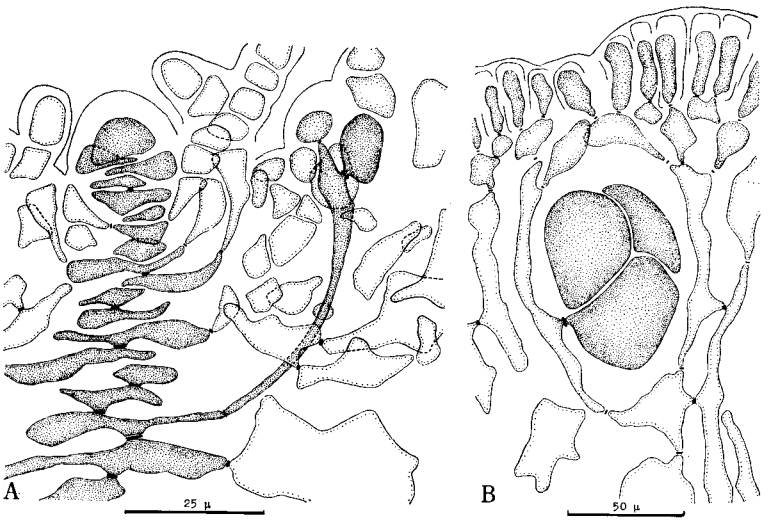

Fig. 35. *Laurencia intermedia* Yamada
A, Part of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on an elongated pericentral cell which is connected to an axial cell (cf. Pl. XIII, Fig. 11). **B,** Ditto, showing a divided tetrasporangium at the periphery of the apical surface of a stichidium.

pit-connections to some of the subcortical cells which have been derived from the divisions of the other pericentral cells lying beneath it. The cover-cell cut from the fertile pericentral cell covers the spornagium from the inside, and the other cover-cells which originated from the subcortical cells cover it from the outside and on the lateral side (Text-fig. 35, B). The elongated pericentral cell is later divided into several segments. Although potentiality for producing more sporangia has not been lost, the longitudinal growth of a stichidial branchlet is suppressed while the lateral growth is continued. The sporangia are displaced radially toward the periphery of the depression with the lateral growth of the stichidial branchlet, while the nuclear divisions are going on in them. The sporangium is divided tetrahedrally. The spores are shed before, or soon after the sporangium reaches the lateral surface of the stichidium. Thus, the sporangia are scattered, in surface view, on the apical surface of the stichidium, and are consequently arranged at right angles to the central axis as seen in a longitudinal section (Pl. XIII, Fig. 10).

8. ***Laurencia capituliformis*** Yamada
Plates XIV-XVI, Text-figs. 36–42

Yamada, 1931, p. 217, pl. 14; Yamada in Okamura, 1936, p. 858; Takamatsu, 1938, p. 64; 1939, p. 75; Kanamori, 1965, p. 64; Noda, 1967, p. 41.

Japanese name. Maru-sozo (Yamada).

Specimens examined. Growing on rocks in the littoral zone. *Hokkaido*:

Oshoro, Shiribeshi Province, 19 July 1962 (sterile); Esashi, Hiyama Province, 31 July 1963 (sterile); Matsumae, Oshima Province, 3 August 1962 (♂♀⊕), 23 July 1963 (♂ & sterile), 29 July 1964 (♂♀⊕); Moheji, near Hakodate, Oshima Province, 16 August 1962 (♀⊕); 13 August (♂⊕), 27 August (♂♀⊕) 1963; 10 August 1964 (⊕); Anama, Hakodate, 11 August 1962 (⊕ & sterile). *Japan Sea coast of Honshu*: Vicinity of Nou, Echigo Province, 19 August 1960 (♂♀⊕). All of these specimens were collected by Y. Saito.

Distribution. *JAPAN.* Mutsu Province (Yamada, 1931; Yamada in Okamura, 1936; Takamatsu, 1938); Ugo Province (Takamatsu, 1939); Uzen Province (Kanamori, 1965); Sado Island (Noda, 1967).

The present species was established by Yamada (1931) on the basis of the tetrasporiferous specimens from Ohshima, Mutsu Province, and there has been no information on the sexual plants to date. I collected the sexual as well as the asexual plants on the Japan Sea coast of both Hokkaido and Honshu as listed above. The following description is based upon the specimens from Matsumae, Hokkaido.

The fronds are erect, nearly 15 cm. high with several erect axes tufted below and attached to the substratum with a discoid base which is not strongly developed. They are generally purplish pink and sometimes brownish yellow in colour, somewhat cartilaginous when fresh but becoming soft when preserved in formalin seawater, and adhere to paper when dried. Stoloniferous coalesced basal branches are present but not abundant. The erect axes are cylindrical, 1210–2490μ in diameter by 5.0–14.5 cm. high (10.1 cm. high on the average among 54 individuals), and paniculately branched (Pl. XIV, Pl. XV, Fig. 4). The branching is alternate, opposite or subverticillate; the branches are 910–1250μ in diameter with the ultimate sterile branchelts 320–480μ in diameter. In a surface view, the cortical cells in the main axis are longitudinally elongated, 68–114μ long by 28–62μ broad

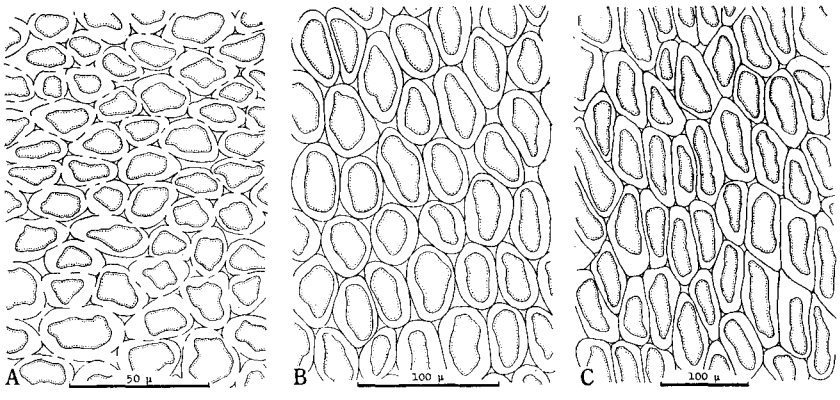

Fig. 36. *Laurencia capituliformis* Yamada
Surface view of frond showing the cortical cell arrangement in the apical portion of an ultimate branchlet (**A**), in the middle portion of a branch (**B**) and in the main axis (**C**).

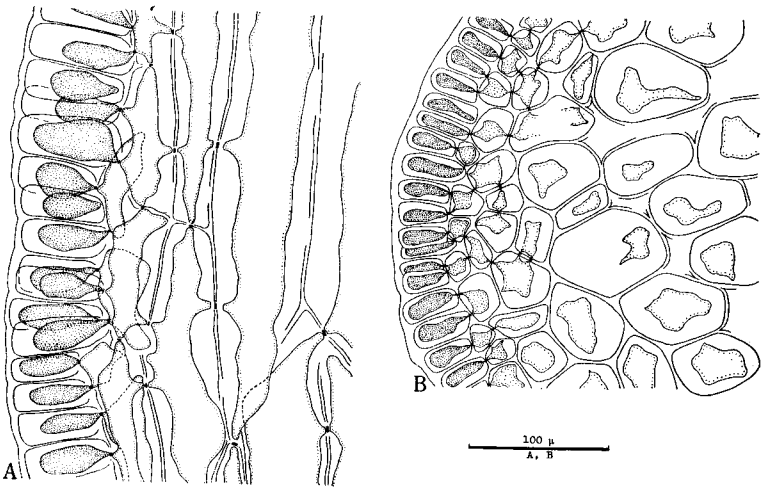

Fig. 37. *Laurencia capituliformis* Yamada
Longitudinal (A) and transverse (B) section through a branch.

(Text-fig. 36, C), while those in the middle portion of a branch are slightly elongated longitudinally, 43–66μ long by 23–36μ broad (Text-fig. 36, B). The cortical cells are nearly round, about 23–40μ in diameter in the upper part of a branch, while they are small, roundish and slightly elongated laterally, 13–31μ long by 15–34μ broad (Text-fig. 36, A) in the apical portion of an ultimate branchlet. In a transverse section of the frond, the cortical cells are elongated radially, 32–45μ long and 11–18μ wide, and are arranged like palisade cells (Text-fig. 37, B). They are not projected above the frond surface as seen in a longitudinal section (Text-fig. 37, A, Text-fig. 38, A). Lenticular thickenings of the medullary cell walls are absent. The apical cell of the ultimate branchlet is situated at the bottom of the apical depression, and it cuts off, by oblique walls, wedge-shaped segments which form the axial cell-row. All of the cells in the branchlet, including those of the trichoblasts and of the young reproductive organs, are linked directly to the axial cells or indirectly through the pericentral cells (Pl. XVI, Figs. 1–6 & 11, Text-fig. 38, A, Text-fig. 39, D, Text-fig. 40, A, Text-fig. 42, A). The cortical cells are never connected with each other by secondary pit-connections either longitudinally or laterally (Text-fig. 37, A & B, Text-fig. 38, A). The trichoblast arises from a young pericentral cell near the growing apex, and is gradually displaced toward the periphery of the apical depression with the advance of growth, branching dichotomo-alternately (Text-fig. 38, A & B).

The terminal portion of the ultimate branchlet in the male plant is characteristically thick, attaining 490–1270μ in diameter (Pl. XV, Fig. 1), and bears one to three or more antheridial depressions, 190–280μ deep and 2.7–2.9 times as broad as it is deep, which are furnished with many fertile and sterile trichoblasts (Pl. XVI, Figs. 4 & 5). The fertile trichoblast, or antheridium, also arises from a young

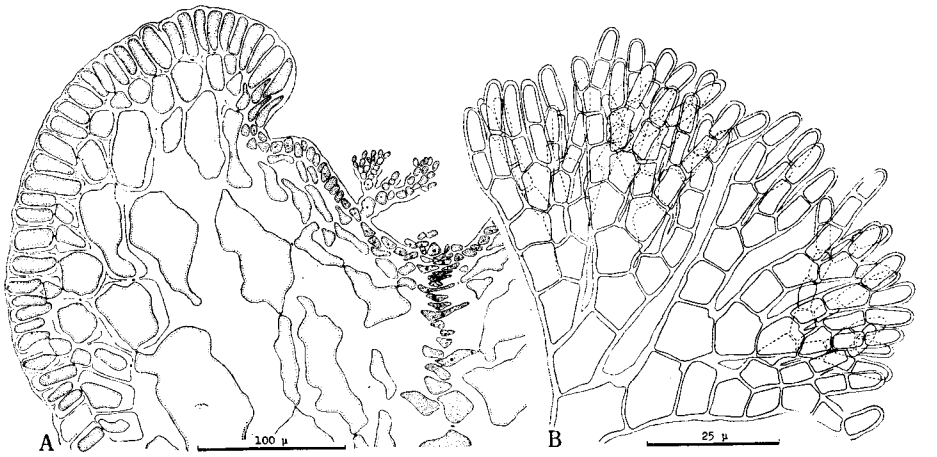

Fig. 38. *Laurencia capituliformis* Yamada
A, Part of a median longitudinal section through a sterile branchlet. **B**, A young trichoblast.

pericentral cell near the apical cell (Pl. XVI, Fig. 6, Text-fig. 39, D) and consists of a dichotomo-alternately branched central axis and four pericentral cells, or spermatangial mother-cells, on each axial cell (Text-fig. 39, A & C). Each mother-cell gives rise to 1–3 (or more) ovoid spermatangia, 8.5–11.2μ long by 4.2–5.7μ in diameter, which contain a large nucleus at their apices (Pl. XVI, Fig. 8, Text-fig. 39, A & C). Some of the axial cells are occasionally found to give rise directly to a spermatangium as a pericentral cell. Sometimes the axial cells cut off one more set of spermatangial mother-cells (Text-fig. 39, C). A pericentral cell from a lower segment of the axis usually produces a corymbose branch and a tuft of spermatangia. The terminal cell of the axis of a fertile trichoblast is vesicular in appearance, ovoid in shape, and often very large, up to 46μ long by 37μ in diameter (Pl. XVI, Fig. 8, Text-fig. 39, C).

The utlimtate branchlets in the female plant are cylindrical while sterile, but they become clavate with the development of the procarps and cystocarps (Pl. XV, Fig. 2). The initial cell of the procarp arises from a pericentral cell of the fertile branchlet and acts as the fertile central cell of the procarp. This fertile cell is linked to the axial cell of the branchlet through the pericentral cell which gradually becomes elongated and filamentous below, with the growth of the branchlet tissues (Text-fig. 40, A). The fertile central cell cuts off the supporting cell of the carpogonial branch on the inside, i.e. toward the growing point of the branchlet, as one of several pericentral cells, the number of which could not be counted exactly. The four-celled carpogonial branch is formed on the supporting cell. It is somewhat curved so as to embrace the supporting cell (Text-fig. 40, A). The pericentral cells other than the supporting cell also cut off several small cells which later form a part of the pericarp. Though the sterile cells were easily

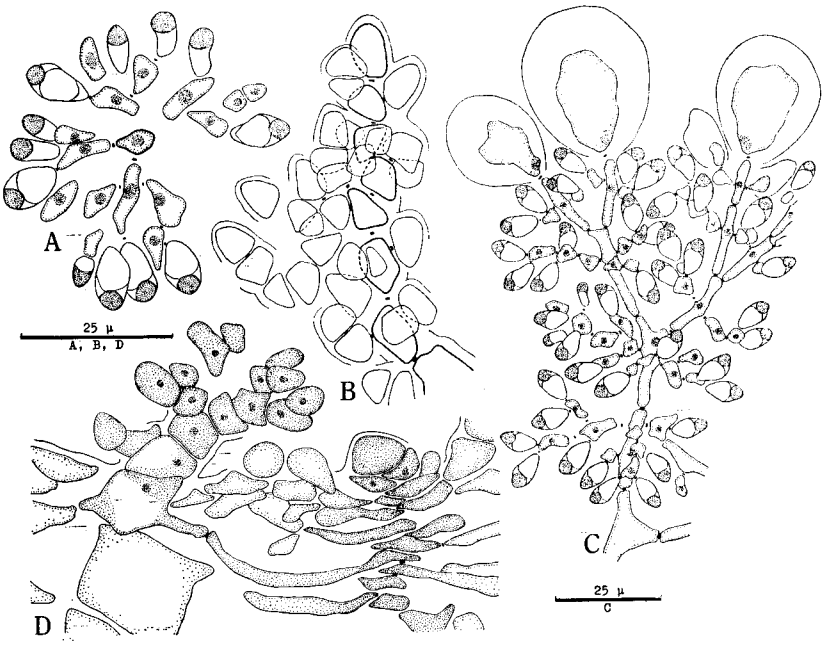

Fig. 39. *Laurencia capituliformis* Yamada
A, Transverse section through a mature antheridium. **B & C**, A young (**B**) and a mature (**C**) antheridium from a smeared preparation. **D**, Part of median longitudinal section through an antheridial receptacle, showing a young antheridium on an elongated pericentral cell which is connected to an elongated axial cell (cf. Pl. XVI, Fig. 6).

observed, their origin could not be clearly traced to a cell cut from the supporting cell. After fertilization a large auxiliary cell is cut from the supporting cell on the upper side and it fuses with the carpogonium which has already lost its protoplasmic continuity with the trichogyne (Pl. XVI, Figs. 9 & 10, Text-fig. 40, B & C). Their fusion is direct, and not through a special connecting cell (Text-fig. 40, B & C). After the fertilized nucleus has passed from the carpogonium into the auxiliary cell, the latter two cells are detached from each other (Text-fig. 40, B & C) and the supporting cell fuses with the auxiliary cell to form a fusion-cell (Pl. XVI, Figs. 11 & 12, Text-fig. 40, E). The fusion-cell gives rise to a process, the first gonimoblast cell, toward one of the sterile cells, and a little later these two cells fuse with each other (Pl. XVI, Figs. 11 & 12, Text-fig. 40, E). The sterile cells are derived from the original sterile cell group. The fusion-cell continues to fuse with other sterile cells and the surrounding cells, including the central cell and the older gonimbolast cells, and becomes large and irregular in shape (Text-fig. 40, F, Text-fig. 41). The pericarp originates from the pericentral cells of the fertile central cell of the procarp, as mentioned above. Before or after fertilization, the procarp is covered by a young pericarp but the carpogonial branch is still naked on its inner side (Pl. XVI, Figs. 9 & 10, Text-fig. 40, A-D). With the growth of the branchlet, the developed

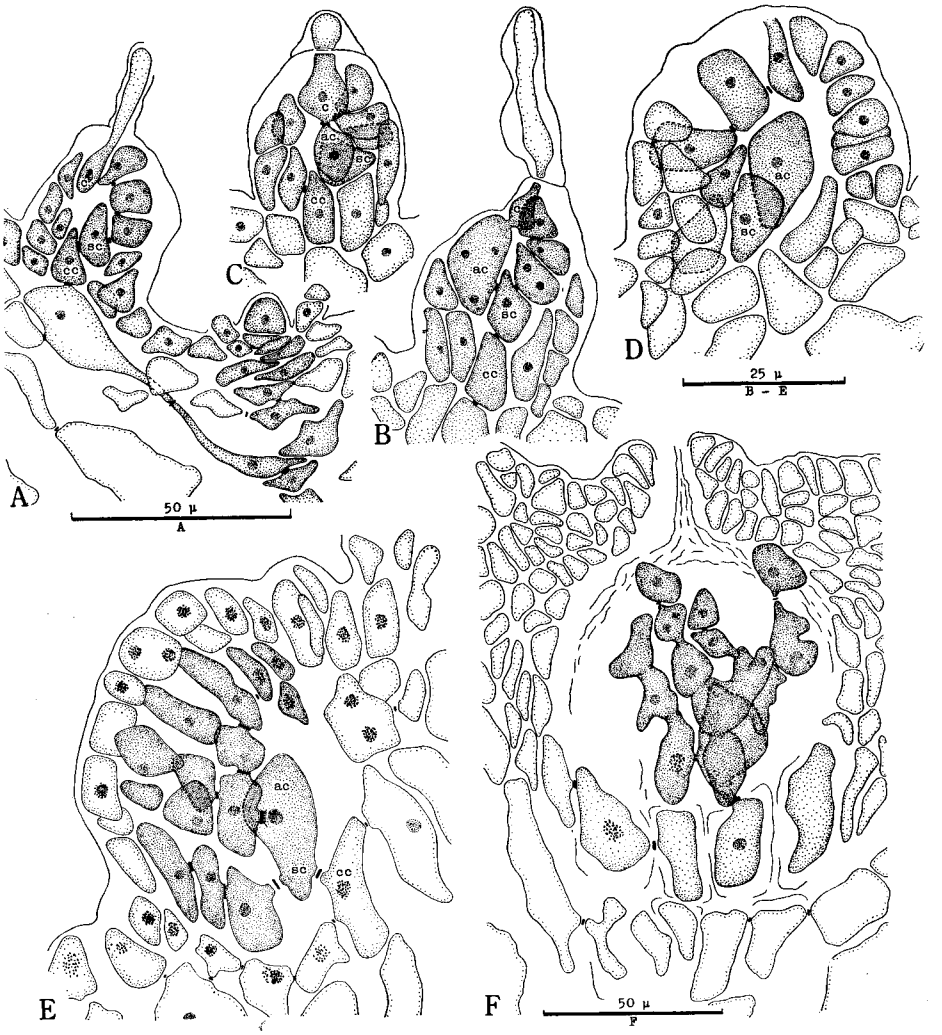

Fig. 40. *Laurencia capituliformis* Yamada

A, Part of median longitudinal section through a fertile branchlet of a female plant, showing a procarp ready for fertilization on an elongated pericentral cell. **B**, Longitudinal section through a procarp after fertilization, showing the auxiliary cell on the supporting cell and fused with the fertilized carpogonium (cf. Pl. XVI, Fig. 9). **C**, Ditto; the plane of section is at right angles to that of **B** (cf. Pl. XVI, Fig. 10). **D**, Longitudinal section through a more developed procarp after fertilization. **E** & **F**, Longitudinal section through a young cystocarp, showing various developmental stages of the fusion-cell and the gonimbolast. ac: auxiliary cell. c: carpogonium. cc: central cell. sc: supporting cell.

procarp is gradually displaced toward the periphery of the apical depression, and some cortical cells of the branchlet contribute to the growth of the outer portion of the pericarp. Thus the fully developed pericarp consists of cells of two different origins. The ripe cystocarp, conical in shape and up to 1400μ in diameter, is

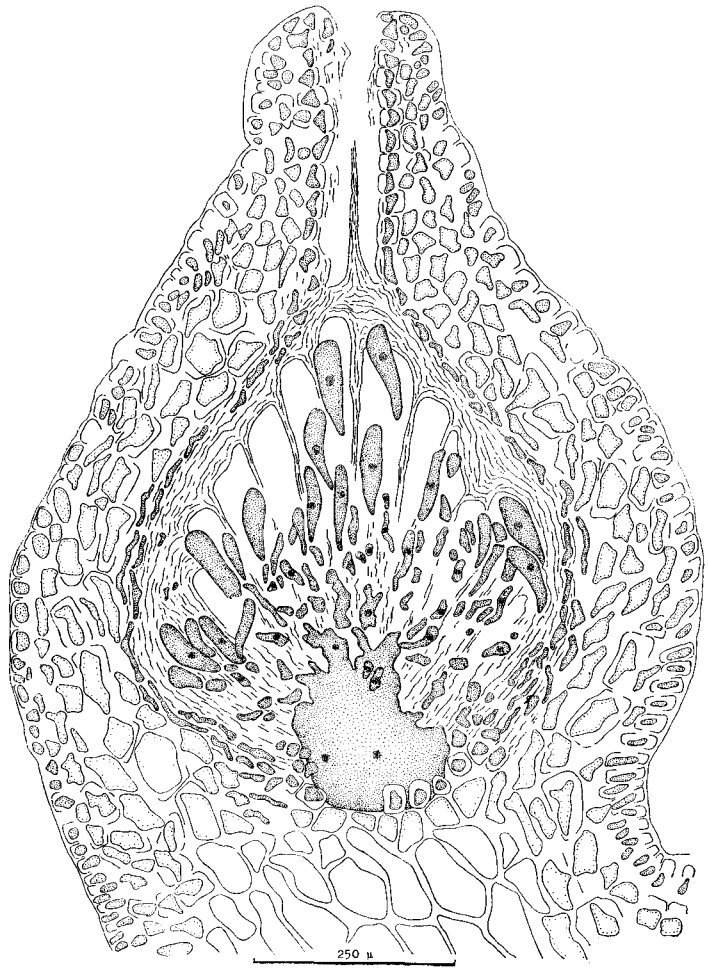

Fig. 41. *Laurencia capituliformis* Yamada
Median longitudinal section through a ripe cystocarp.

situated on the upper lateral surface of the branchlet (Pl. XV, Fig. 2) and provided with a rostrate carpostome. The cystocarpic cavity is filled with a mucilaginous substance which stains well with iron-alum haematoxylin. The innermost cells of the pericarp which originated from the pericentral cells of the fertile central cell of the procarp, become markedly thin and filamentous in shape, and dense in content, indicating that they probably supplied nutrition to the gonimbolast through the fusion-cell. The terminal cells of the gonimoblast grow larger and become carpospores (Pl. XVI, Fig. 13, Text-fig. 41).

The ultimate branchlets in the tetrasporophyte are converted into stichidia. The stichidia are cylindrical while young but become clavate with the advancing maturity, and some of them, especially from the lower portion of the branch,

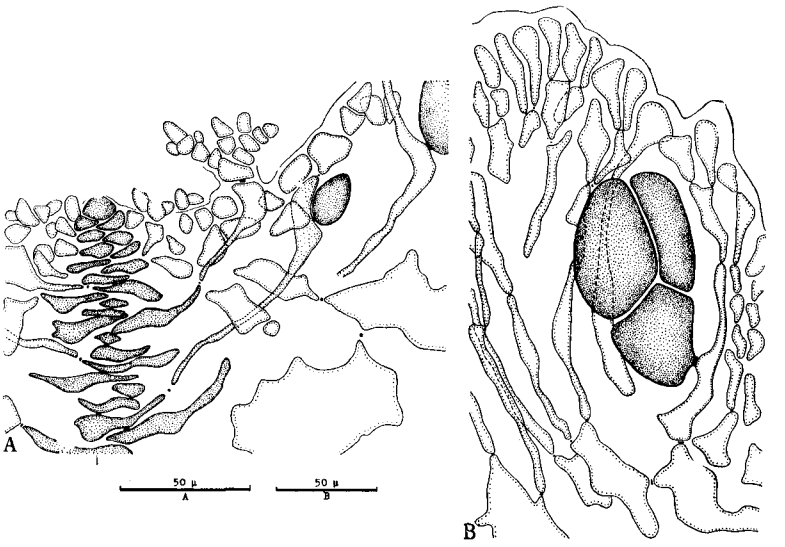

Fig. 42. *Laurencia capituliformis* Yamada
A, Part of median longitudinal section through a sthichdial branchlet, showing a tetrasporangium-initial on an elongated pericentral cell which is connected to an axial cell (cf. Pl. XVI, Fig. 3). **B**, Ditto, showing a divided tetrasporangium at the periphery of the apical surface of a stichidium.

bear wart-like stichidial branchlets. The stichidia, 540–810μ in diameter, are beset with many dark purplish spots or tetrasporangia scattered over their apical surfaces. After the shedding of the spores, these spots become colourless and the stichidia look undulate on the surface (Pl. XV, Fig. 3, Pl. XVI, Figs. 1 & 2). The tetrasporangium originates from a pericentral cell near the growing apex in the apical depression of a branchlet. The fertile pericentral cell cuts off a sporangium and a cover-cell, and then becomes elongated and filamentous below with the growth of the branchlet tissues (Pl. XVI, Fig. 3, Text-fig. 42, A). The fertile pericentral cell is also linked by means of secondary pit-connections to some of the subcortical cells which have been derived from the other pericentral cells lying beneath it. The cover-cell cut from the fertile pericentral cell covers the sporangium from the inside, and other cover-cells which have originated from the subcortical cells cover it from the outside and on the lateral side (Text-fig. 42, B). The elongated pericentral cell is later divided into several segments. The longitudinal growth of a stichidial branchlet is suppressed by the formation of sporangia in it, and the stichidium gradually increases in diameter. The sporangia are displaced toward the periphery of the apical depression, while the nuclear and cell divisions are carried on within them. Thus the sporangia are scattered on the apical surface of the stichidium (Pl. XV, Fig. 3), and are arranged at right-angles to the central axis of the stichidium as seen in a longitudinal

section (Pl. XVI, Fig. 1 & 2), as a result of their shedding of spores before or just after their arraival at the lateral surface of the stichidium. The sporangium is divided tetrahedrally (Pl. XVI, Fig. 2, Text-fig. 42, B).

9. *Laurencia cartilaginea* Yamada
Plates XVII & XVIII, Text-figs. 43–47

Yamada, 1931, p. 230, pl. 19, fig. a, text-fig. O; Yamada in Okamura, 1936, p. 857; Higashi, 1936, p. 298; Ohshima, 1950, p. 148; Imahori & Searashi, 1955, p. 73; Hirose, 1957, p. 103; 1958, p. 268; Kanamori, 1965, p. 22.

Japanese name. Kata-sozo (Yamada).

Specimens examined. Growing on rocks in the lower littoral zone. *Pacific const of Honshu*: Cape Nojima-zaki, Awa Province, 25 May 1963 (sterile); Hassei, near Aburatsubo, Sagami Province, 26 May 1963 (sterile); Shirahama, Kii Province, 22 May 1963 (♂ ♀ ⊕). All of these specimens were collected by Y. Saito.

Distribution. *JAPAN. Japan Sea coast of Honshu*: Uzen Province (Kanamori, 1965); Etchu Province (Higashi, 1936; Ohshima, 1950); Noto Province (Imahori & Searashi, 1955); Echizen Province (Higashi, 1936); Tajima Province (Hirose, 1958). *Kyushu*: Chikuzen Province (Yamada, 1931; Yamada in Okamura, 1936). *Shikoku*: Iyo Province (Yamada, 1931; Yamada in Okamura, 1936); Shiaku Islands (Hirose, 1957). *KOREA* (J. Agardh in Yamada, 1931).

The present species was established by Yamada (1931) on the basis of the tetrasporiferous specimens from southern Japan and upon specimens from Korea in the herbarium of J. G. Agradh. I collected many fertile male and female plants as well as the tetrasporophytes at Shirahama. The following description is based on the specimens from Shirahama.

The fronds, caespitose and erect, stand on a discoid base, without basal stoloniferous branches. They are generally dark purple or purplish brown in colour, cartilaginous and very rigid in texture and never adhere to paper when dried. The erect main branches are cylindrical near the base, 1230–1350μ in diameter, becoming angular or slightly compressed upward, up to 5200μ broad and 3.5–8.4 cm. high (5.5 cm. high on the average among 30 individuals). They are pinnately or subdichotomously branched (Pl. XVII, Figs. 1–3 & 7). These secondary branches are alternate, opposite or sometimes subverticillate, and 1540–2900μ in diameter. The ultimate branchlets are cylindrical, truncate or wart-like and 390–580μ in diameter while sterile. The cortical cells in a surface view are, as a rule, hexagonal in shape, longitudinally elongated in the main branches, 54–83μ long by 23–43μ broad (Text-fig. 43, A), while those in the secondary branch are nearly round and 22–45μ in diameter (Text-fig. 43, B). They are elongated laterally in the ultimate branchlets, 9–14μ long by 16–28μ broad (Text-fig. 43, C). The cortical cells in a transverse section of a branch are neither elongated laterally nor arranged like a palsiade, being 28–35μ long by 22–40μ broad (Text-fig. 43, D), while in a

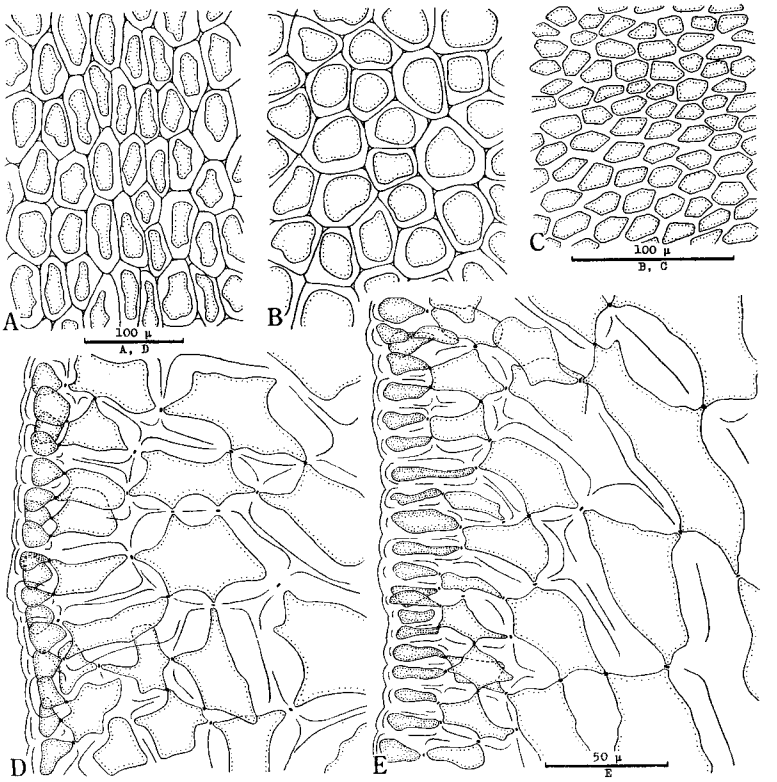

Fig. 43. *Laurencia cartilaginea* Yamada
A–C, Surface view of frond showing the cortical cell arrangement in the main branch (**A**), in the secondary branch (**B**) and in the ultimate branchlet (**C**). **D**, Transverse section through a branch. **E**, Longitudinal section through a branchlet.

longitudinal section of a branchlet, they are slightly elongated and arranged somewhat like a palisade, 15–25(–38)μ long by 8–14μ broad (Text-fig. 43, E). There are no secondary pit-connections among cortical cells either longitudinally or laterally (Text-fig. 43, D & E). Lenticular thickening of the medullary cell wall is absent (Text-fig. 43, D & E). The apical cell of the ultimate branchlet is situated at the bottom of the apical depression, and it cuts off, by oblique walls, wedge-shaped segments which form the axial cell-row. All of the cells in the branchlet, including those of the trichoblast and of the young reproductive organs, are linked directly to the axial cells or indirectly through the pericentral cells (Pl. XVIII, Figs. 1, 2, 5, 7, 11 & 13–15, Text-fig. 44, A, Text-fig. 45, A-C, Text-fig. 47, A). The trichoblast arises from a young pericentral cell near the growing apex, and is gradually displaced toward the periphery of the apical depression with the advance of growth, branching dichotomo-alternately.

The terminal portion of the ultimate branchlet in the male plant is characteristically thick, attaining 920–1460μ in diameter (Pl. XVII, Fig. 6), and bears one to

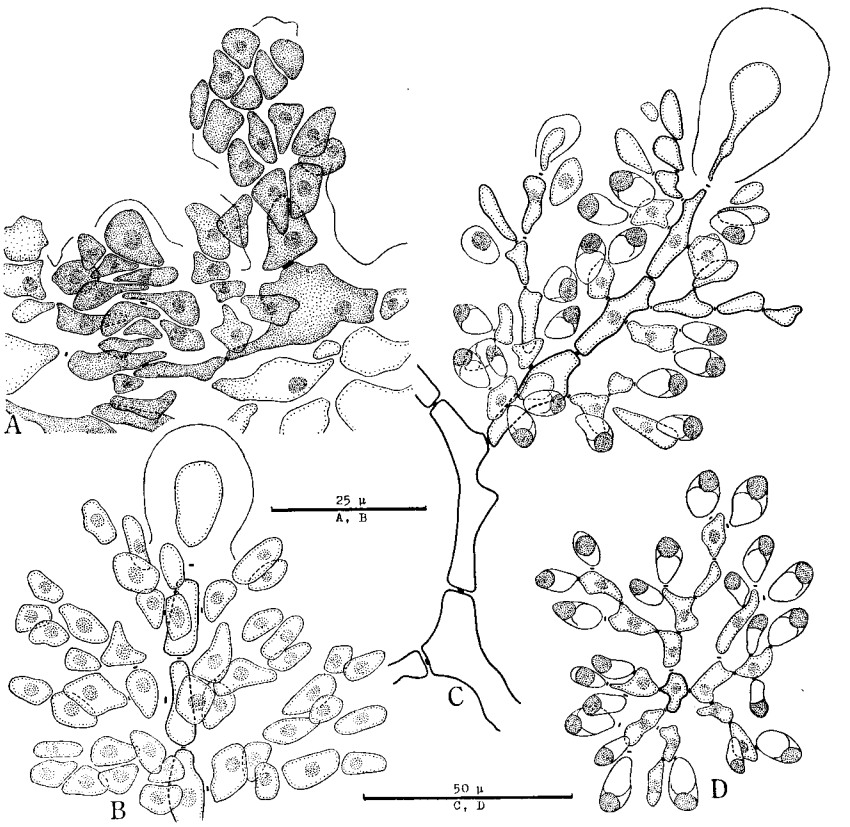

Fig. 44. *Laurencia cartilaginea* Yamada

A, Part of median longitudinal section through an antheridial receptacle, showing an antheridium-initial on an elongated pericentral cell which is connected to an axial cell (cf. Pl. XVIII, Fig. 2). **B** & **C**, Apical porition of a young (**B**) and a mature (**C**) antheridium in a smeared preparation. **D**, Transverse section through a mature antheridium.

three or more antheridial depressions, 280–810μ deep, and 0.9–1.3 times as broad as it is deep, which are furnished with many fertile and sterile trichoblasts (Pl. XVIII, Fig. 1). The fertile trichoblast, or antheridium, also arises from a young pericentral cell near the growing apex (Pl. XVIII, Fig. 2, Text-fig. 44, A) and consists of a dichtomo-alternately branched axial cell and four pericentral cells, or spermatangial mother-cells, on each axial cell (Text-fig. 44, C & D). Each mother-cell gives rise to 1–3 (or more) ovoid spermatangia, 9.8–13.2μ long by 5.4–7.2μ in diameter, which contain a large nucleus at their apices (Pl. XVIII, Fig. 4, Text-fig. 44, C & D). A pericentral cell from a lower segment of the axis usually produces a corymbose branch and a tuft of spermatangia. The terminal cell of the axis of a fertile trichoblast is vesicular in appearance, ovoid in shape, and often very large up to 47μ long by 39μ in diameter (Pl. XVIII, Figs. 3 & 4, Text-fig. 44, B & C).

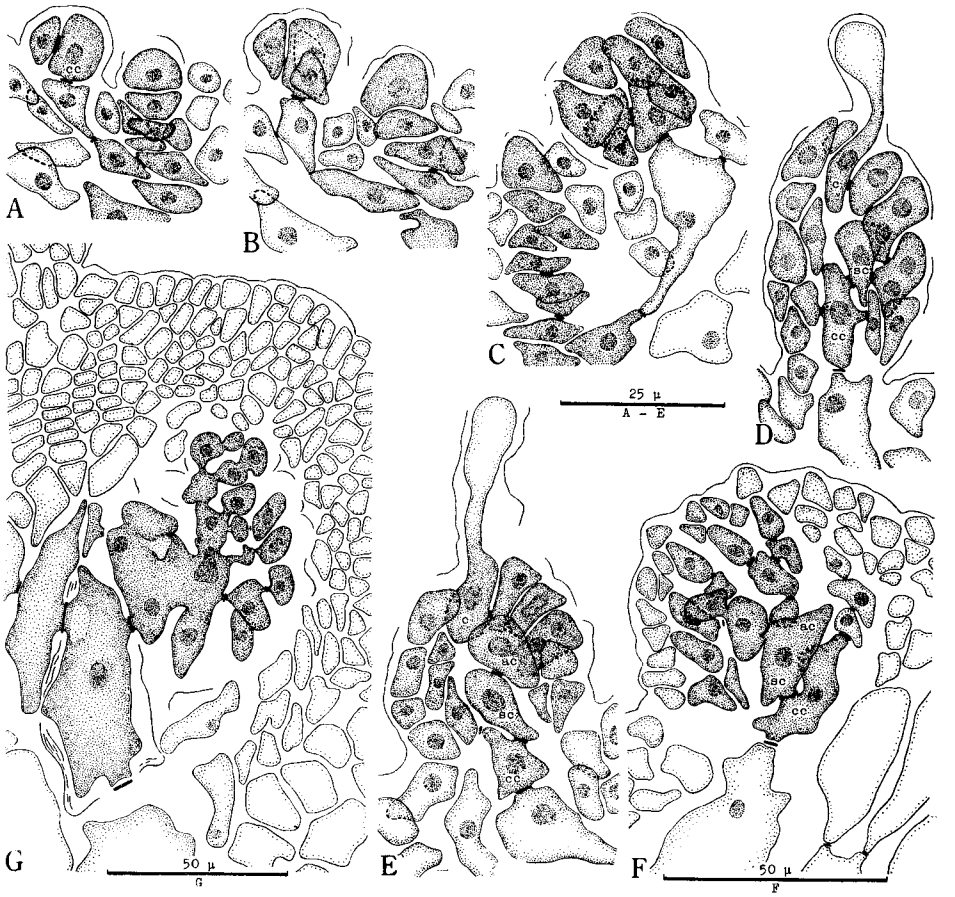

Fig. 45. *Laurencia cartilaginea* Yamada

A-C, Part of median longitudinal section through three fertile branchlets of a female plant, showing the various developmental stages of procarp-initials; the fertile central cell cuts off the first pericentral cell toward the outside (**A**, cf. Pl. XVIII, Fig. 5), the next two pericentral cells toward both lateral sides (**B**) and the last pericentral cell toward the inner side (**C**) which becomes the supporting cell of the carpogonial branch. **D**, Longitudinal section through a procarp ready for fertilization (cf. Pl. XVIII, Fig. 6). **E**, Longitudinal section through a procarp after fertilization, showing the auxiliary cell formed on the supporting cell. **F**, Longitudinal section through a young cystocarp, showing the initial stage of fusion-cell and gonimoblast (cf. Pl. XVIII, Fig. 8). **G**, Longitudinal section through a more developed young cystocarp, showing the gonimbolast development (cf. Pl. XVIII, Fig. 9). ac: auxiliary cell. c: carpogonium. cc: central cell. sc: supporting cell.

The ultimate branchlets in the female plant are cylindrical while sterile, but become clavate or irregularly thickened with the development of the procarps and cystocarps (Pl. XVII, Fig. 5). The initial cell of the procarp arises from a pericentral cell of the fertile branchlet and acts as the fertile central cell of the procarp (Pl. XVIII, Fig. 5, Text-fig. 45, A-C). This fertile cell is linked to the

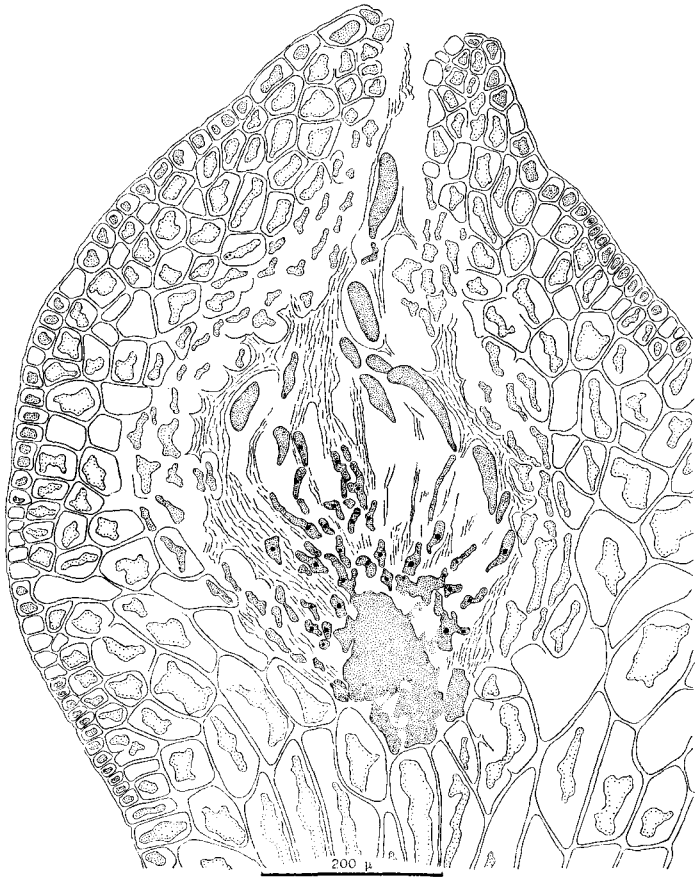

Fig. 46. *Laurencia cartilaginea* Yamada
Median longitudinal section through a ripe cystocarp.

axial cell of the branchlet through the pericentral cell which gradually becomes elongated filamentously below, with the growth of the branchlet tissues (Pl, XVIII, Fig. 7, Text-fig. 45, C). The fertile central cell progressively cuts off four pericentral cells, the first one on the outside, the next two on the lateral side and the last one on the inside, of which the last one functions as the supporting cell of the carpogonial branch (Pl. XVIII, Fig. 5, Text-fig. 45, A-C). The supporting cell cuts off several sterile cells in two groups on the inside and beneath the supporting cell. Then the four-celled carpogonial branch is formed on the supporting cell. It is curved so as to embrace the supporting cell (Pl. XVIII, Fig. 6, Text-fig. 45, D & E). The trichogyne is rather short and generally clavate (Pl. XVIII, Figs. 6 & 7, Text-fig. 45, D & E). The pericentral cells other than the supporting cell cut off several cells which form the inner part of the pericarp (Text-fig. 45, F & G). The sterile cells derived from the supporting cell are later divided into many sterile cells and

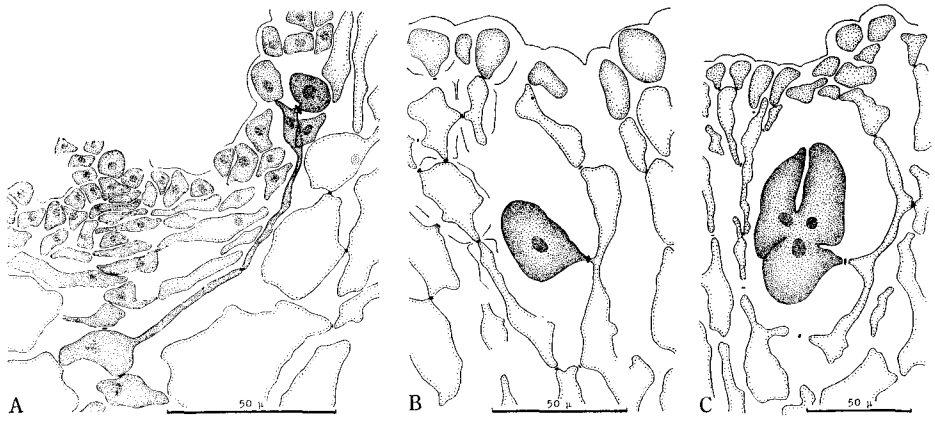

Fig. 47. *Laurencia cartilaginea* Yamada
A, Part of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on an elongated pericentral cell which is connected to the elongated axial cell (cf. Pl. XVIII, Fig. 14). **B**, Ditto, showing a more developed tetrasporangium beneath the apical surface of the stichidial branchlet. **C**, Ditto, showing a divided tetrasporangium at the periphery of the apical surface of the stichidial branchlet.

the latter provide nourishment for the growth of the gonimoblast. After fertilization a large auxiliary cell cuts off from the supporting cell on the upper side (Text-fig. 45, E) and fuses directly, not through a connecting cell, with the carpogonium. The supporting cell then fuses with the fertilized auxiliary cell to form a fusion-cell (Pl. XVIII, Figs. 8 & 9, Text-fig. 45, F & G). The fusion-cell gives rise to a process, or the first gonimoblast cell, toward the above mentioned sterile cell situated nearby, and they fuse with each other (Pl. XVIII, Figs. 8 & 9, Text-fig. 45, F & G). The fusion-cell continues to fuse with other sterile cells and the surrounding cells, including the central cell and the older gonimoblast cells, and becomes large and irregular in shape (Pl. XVIII, Figs. 9 & 10, Text-fig. 45, G). The pericarp originates from the pericentral cells of the fertile central cell of the procarp, as mentioned above. Before or after fertilization, the procarp is covered by a young pericarp, but the carpogonial branch is still naked on its inner side (Pl. XVIII, Fig. 6, Text-fig. 45, D & E). With the growth of the branchlet, the developing procarp is gradually displaced toward the periphery of the apical depression, and some cortical cells of the branchlet contribute to the growth of the outer portion of the pericarp (Pl. XVIII, Fig. 11). Thus the developed pericarp consists of cells of two different origins. The ripe cystocarp, ovoid in shape and up to 970μ in diameter, is situated on the upper lateral surface of the branchlet (Pl. XVII, Fig. 5), and provided with a carpostome. The cystocarpic cavity is filled with a mucilaginous substance which stains well with iron-alum haematoxylin and also with carm-alum. The innermost cells of the pericarp which originated from the pericentral cells of the fertile central cell of the procarp become markedly

thin and filamentous in shape, and protoplasmic in content, indicating that they probably supplied nutrition to the gonimoblast through the fusion-cell. The terminal cells of the gonimoblast grow larger and become carpospores (Pl. XVIII, Fig. 12, Text-fig. 46).

The ultimate branchlets in the tetrasporophyte are converted into stichidia. The stichidia are clavate or truncate, and some of them, especially from the lower portion of the branch, bear many small and wart-like stichidial branchlets (Pl. XVII, Fig. 4). The tetrasporangium originates from a pericentral cell near the growing apex in the apical depression of a stichidial branchlet. The fertile pericentral cell cuts off a sproangium and a cover-cell, and becomes elongated and filamentous below with the growth of the branchlet tissues (Pl. XVIII, Fig. 14, Text-fig. 47, A). The fertile pericentral cell is also linked by means of secondary pit-connections to some of the subcortical cells which have been derived from the other pericentral cells lying beneath it. The cover-cell cut from the fertile pericentral cell covers sporangium from the inside, and other cover-cells which originate from the subcortical cells cover it from the outside and on the lateral side (Text-fig. 47, B & C). The elongated pericentral cell is later divided into several segments. The longitudinal growth of a stichidial branchlet is suppressed soon after the formation of sporangia. The sporangia are displaced to the periphery of the apical depression, while the nuclear and cell divisions are carried on within them. The sporangia are also observed dividing after they have arrived at the periphery of the apical depression. The ripe sporagia usually shed spores before or just after their arrival at the lateral surface of the stichidium. Thus the tetrasporangia are scattered on the apical surface of the truncate or wart-like stichidium which is 690–970μ in diameter (Pl. XVII, Fig. 4). After the shedding of the spores, the sporangia which had been visible to the naked eye as dark reddish spots become colourless and the stichidia look undulate on the surface. In a longitudinal section of a stichidium, the sporangia are arranged at right angles to the central axis (Pl. XVIII, Fig. 13). The sporangia are divided tetrahedrally (Text-fig. 47, C).

10. *Laurencia undulata* Yamada

Plate III, Figs. 4–6, Plate IV, Figs. 5–7, Text-figs. 48 & 49

Yamada, 1931, p. 243, pl. 29, fig. a, text-fig. T; Yamada in Okamura, 1936, p. 859; Yamada & Tanaka, 1938, p. 85; Higashi, 1935, p. 157; Segawa, 1935, p. 89; Segawa & Ichiki, 1959, p. 112; Segawa & Kamura, 1960, p. 61; Segawa & Yoshida, 1961, p. 19; Noda, 1964, p. 74; Kang, 1966, p. 107.

Laurencia pinnata (non Yamada) Saito, 1956, p. 106 (in part).

Japanese name. Kobu-sozo (Okamura).

Specimens examined. Growing on rocks in the lower littoral zone. *Japan Sea coast of Honshu*: Nou and vicinity, Echigo Province, 10 June 1954 (sterile); 1 July 1955 (sterile); 26 June (sterile), 23 July (sterile), 20 August (⊕) 1960; Shi-

chirui, Idzumo Province, 21 June 1964 (⊕). *Pacific coast of Honshu*: Cape Nojimazaki & Cape Sunozaki, Awa Province, 25 May 1963 (⊕ & sterile); Shirahama, Kii Province, 22 May 1963 (⊕). All of these specimens were collected by Y. Saito.

Distribution. *JAPAN. Pacific coast of Honshu*: Iwaki Province (Noda, 1964); Awa Province (Higashi, 1935); Sagami Province (Yamada, 1931; Yamada in Okamura, 1936; Higashi, 1935); Idzu Province (Segawa, 1935). *Kyushu*: Higo Province (Segawa & Ichiki, 1959; Segawa & Yoshida, 1961). *RYUKYU* (Yamada & Tanaka, 1938; Segawa & Kamura, 1960).

The present species was established by Yamada (1931) on the basis of the cystocarpic specimens from Enoshima, Japan. Since then, there has been no information on the male and tetrasporiferous plants. I have collected many tetrasporiferous specimens from the localities listed above. The following description is based on the specimens from Shirahama.

The fronds are caespitose, erect, cartilaginous and rigid in texture and generally dark purple or purplish brown in colour. They stand on a discoid base and never adhere to paper when dried. Stoloniferous basal branches are present but not abundant. The erect main branches are cylindrical, measuring 1100–1800μ in diameter near the base but becoming complanate upward, 3700–5500μ broad by 3–6.5 cm. high (3.9 cm. high on the average among 56 individuals). They are pinnately, sometimes subdichotomously, branched (Pl. III, Figs. 4 & 5). The secondary branches generally issue many short and knobby ultimate branchlets. The ultimate stichidial branchlets are not compressed but truncate or wart-like, measuring 410–730μ in diameter (Pl. III, Fig. 6). Cortical cells in a surface view are elongated longitudinally, 39–67μ long by 21–33μ broad in the main branch (Text-fig. 48, B), and slightly elongated laterally, 6–13μ long by 11–24μ broad in the ultimate branchlet (Text-fig. 48, A). In a transverse section of a branchlet, the cortical cells are neither elongated radially nor arranged like palisade cells, measuring 17–24μ long radially by 12–24μ broad (Text-fig. 48, C), while in a longitudinal section of a branch, they are slightly elongated and arranged somewhat like palisade cells, measuring (16–)29–47μ long by 14–23μ braod (Text-fig. 48, D). There is no longitudinal secondary pit-connection among the cortical cells (Text-fig. 48, D). Lenticular thickenings in the walls of the medullary cells are absent (Text-fig. 48, C & D). The apical cell of the ultimate branchlet is situated at the bottom of the apical depression, and it cuts off, by oblique walls, wedge-shaped segments which form the axial cell-row. All of the cells in the branchlet, including those of the trichoblast and of the young tetrasporangium, are linked directly to the axial cells or indirectly through the pericentral cells (Pl. IV, Figs. 5–7, Text-fig. 49, A). The trichoblast arises from a young pericentral cell near the growing apex, branching dichotomo-alternately, and is gradually displaced toward the periphery of the apical depression with the advance of growth.

The initial cell of a tetrasporangium originates from a pericentral cell near the

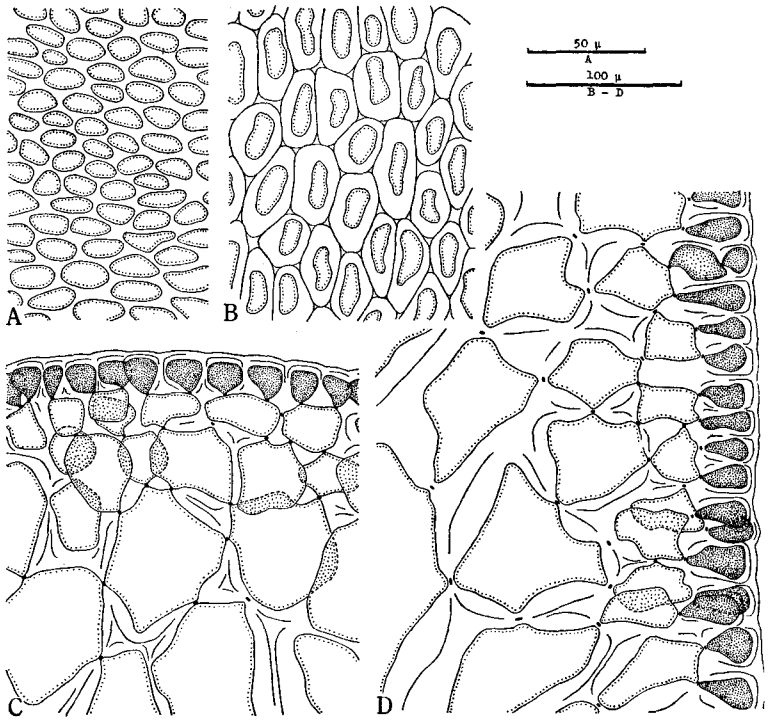

Fig. 48. *Laurencia undulata* Yamada
A & B, Surface view showing the cortical cell arrangement in the ultimate branchlet (**A**) and in the main branch (**B**). **C**, Transverse section of a branchlet. **D**, Longitudinal section of a branch.

growing apex in the apical depression of a stichidial branchlet. The fertile pericentral cell cuts off a sporangium-initial cell and a cover-cell, and becomes elongated and filamentous below with the growth of the branchlet tissues (Pl. IV, Fig. 7, Text-fig. 48, A). The fertile pericentral cell is also linked by means of secondary pit-connections to some of the subcortical cells which have derived from the divisions of the other pericentral cells lying beneath it. The cover-cell cut from the fertile pericentral cell covers the sporangium from the inside, while other cover-cells which originated from the subcortical cells cover it laterally from the outside. The elongated pericentral cell is later divided into several segments. Although the potentiality to produce more sproangia is not lost, the longitudinal growth of a stichidial branchlet is weakened soon after a sporangium has been formed. The sporangia are displaced to the periphery of the apical depression with the vigorous growth of a stichidial branchlets, and their nuclear and cellular divisions are observed while they are in the periphery of the apical depression. The ripe tetraspores are usually shed before or just after the arrival of the sporangium to the lateral surface of the stichidium. Thus, in a surface view of the stichidium, the

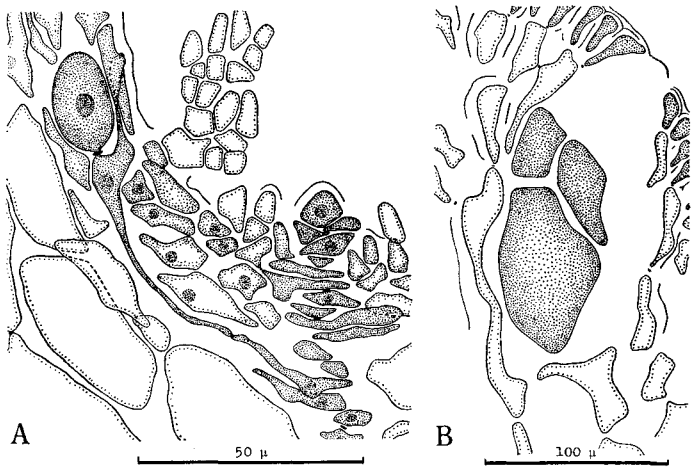

Fig. 49. *Laurencia undulata* Yamada
A, Part of apical portion of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on the elongated pericentral cell which is connected to the elongated axial cell (cf. Pl. IV, Fig. 7). B, Ditto, showing a divided tetrasporangium at the periphery of the apical portion of the stichidium.

tetrasporangia are scattered on the apical surface of the truncate or wart-like stichidium (Pl. III, Fig. 6). Consequently, the mature sporangia are arranged on the top of the stichidium at right angles to its central axis as seen in a longitudinal section (Pl. IV, Figs. 5 & 6). The division of a sporangium is tetrahedral (Pl. IV, Figs. 5 & 6, Text-fig. 49, B).

The above description generally agrees with that given by Yamada (1931). In some of my specimens from Cape Nojimazaki, the main branches are very broad, up to 7500μ, and poorly ramified. These specimens differ in appearance from those collected at Shirahama. Some thin and bushy ones of the latter are similar to *Laurencia cartilaginea* Yamada. In external appearance, at least, the present species seems to the writer to relate most closely to *Laurencia cartilaginea* Yamada, but not to other species with a compressed frond, such as *Laurencia pinnata* Yamada.

IV. Discussion

Of the ten Japanese species of *Laurencia* treated in this paper, *Laurencia intricata* Lamouroux and *Laurencia undulata* Yamada are represented in my collection by tetrasporiferous specimens and *Laurencia pinnata* Yamada is represented by sterile ones. The remaining seven species are represented by male, female as well as tetrasporiferous individuals. Although the structure of the reproductive organs in these species was nearly uniform and their vegetative structures resembled one

another, there were found some characteristics which may be useful in identifying a species. A comparative morphology of the species in consideration will be discussed here under the following topics.

1. Vegetative Structure

The vegeatative structure of the *Laurencia* species was described in detail by Falkenberg (1901). In the key to the sections and species of *Laurencia* prepared by Yamada (1931), the four sections are distinguished from each other chiefly on the basis of the vegetative, especially anatomical, structures. Cribb (1958) lays stress on the external structures, paying special attention to the stoloniferous portions, in his treatment of *Laurencia*.

a. External Structure

The fronds of the *Laurencia* species generally form clumps with several erect axes tufted below with stoloniferous basal branches or a discoid holdfast. The main axis is percurrent in some species but not in others. The discoid bases are remarkably developed in *Laurencia obtusa* (Hudson) Lamouroux, *Laurencia cartilaginea* Yamada and *Laurencia undulata* Yamada, while the stoloniferous basal branches are well developed in *Laurencia intricata* Lamouroux and *Laurencia venusta* Yamada.

The basic colour of the fronds is purple, but various kinds of colour, such as purplish pink, red, orange, brown or dark purple are also observable. *Laurencia okamurai* Yamada is attractive in its generally greenish or sometimes bluish colour. In *Laurencia intermedia* Yamada, *Laurencia cartilaginea* Yamada and *Laurencia undulata* Yamada, the colour of frond changes from dark purple to black when dried. *Laurencia capituliformis* Yamada also has a tendency for such change but to a lesser degree.

From the viewpoint of the texture of the frond, the studied species can be divided into four groups. The first group, comprising *Laurencia obtusa* (Hudson) Lamouroux, *Laurencia intricata* Lamouroux and *Laurencia pinnata* Yamada, is generally characterized by the soft and fleshy texture of the frond. The second group, comprising *Laurencia venusta* Yamada, *Laurencia okamurai* Yamada and *Laurencia nipponica* Yamada, is characterized by the cartilaginous but not so rigid, somewhat membranaceous and flexible texture of the frond. The third group, comprising *Laurencia intermedia* Yamada, *Laurencia cartilaginea* Yamada and *Laurencia undulata* Yamada, is characterized by the cartilaginous and rigid texture of the frond. The fourth group, comprising *Laurencia capituliformis* Yamada, is characterized by the cartilaginous texture of frond which becomes softened when preserved in formalin seawater.

The section Pinnatifidae is characterized by the possession of a compressed frond. Among the species examined, *Laurencia pinnata* Yamada and *Laurencia*

Table 2. Habitat and main external characters of the ten species of *Laurencia* examined

Species	Habitat	Stoloniferous basal branches	Main axis
L. obtusa	Growing on rocks	None	Percurrent
L. intricata	Epiphytic, or rarely growing on rocks	Present; intricated and coalesced, generally cushion-like	Not percurrent
L. venusta	Growing on rocks, or rarely epiphytic	Present; intricated and coalesced, somewaht cushion-like	Percurrent
L. okamurai	Growing on rocks	Present; intricated and coalesced	Percurrent
L. nipponica	Growing on rocks, or rarely epiphytic	Present; intricated and somewhat coalesced	Percurrent
L. pinnata	Growing on rocks	Rarely present	Rarely percurrent
L. intermedia	Growing on rocks	Present; loosely intricated	Percurrent
L. capituliformis	Growing on rocks, or rarely epiphytic	Rarely present	Percurrent
L. cartilaginea	Growing on rocks	None	Not percurrent
L. undulata	Growing on rocks	Rarely present	Not percurrent

undulata Yamada have compressed fronds, but they differ from one another in the nature of their ultimate branchlets which are also compressed in *Laurencia pinnata* but are terete or clavate in *Laurencia undulata*. The frond in the remaining eight species is generally cylindrical, but sometimes it is partly compressed, especially in the case of *Laurencia nipponica* Yamada. The main branches of *Laurencia cartilaginea* Yamada are generally angular.

b. Cortical Layer

The section Palisadae is characterized by having palisade-like cortical cells. Among the species examined, *Laurencia intermedia* Yamada clearly belongs to this section. *Laurencia capituliformis* Yamada also has palisade-like cortical cells, but it was placed in section Cartilagineae (=section Chondrophycus) by Yamada (1931 & in Okamura, 1936) since the palisade character of its cortical cells is not as remarkable as in the other members of the section Palisadae. However, Yamada recently confided to me his opinion that *Laurencia capituliformis* is qualified to be a member of section Palisadae. I am also of the same opinion. In these two species, the cortical cells are elongated radially and arranged like palisade cells in a transverse section of a branch, while in the remaining eight species, the cortical cells are neither elongated radially nor arranged like palisade cells.

In the apical portion of the ultimate branchlet, the cortical cells in most of the species are characteristically compressed longitudinally or elongated laterally,

so that their arrangement is somewhat palisade-like in a longitudinal section. Thus, Flakenberg's illustration of *Laurencia obtusa* (Hudson) Lamouroux showing the palisade-like cortical layer of cells in longitudinal section of the ultimate branchlet (1901, pl. 23, fig. 16) does not seem strange to me, although Yamada (1931) doubted whether Flakenberg's plant was a true *Laurencia obtusa*.

The cortical cells in the apical portion of the ultimate branchlet are slightly projected above the frond surface in *Laurencia obtusa* (Hudson) Lamouroux and *Laurencia pinnata* Yamada, but not very remarkably, especially in the former.

The cortical cells in some species are observed to have longitudinal secondary pit-connections among themselves. In other species they are observed to have none or very few such connections. The ten species examined can be divided into two groups according to the presence or absence of pit-connections among the cortical cells.

Cortical cells having pit-connections

Laurencia obtusa (Hudson) Lamouroux
Laurencia intricata Lamouroux
Laurencia venusta Yamada
Laurencia okamurai Yamada
Laurencia nipponica Yamada
Laurencia pinnata Yamada

Cortical cells generally lacking pit-connections

Laurencia intermedia Yamada
Laurencia capituliformis Yamada
Laurencia cartilaginea Yamada
Laurencia undulata Yamada

The above mentioned pit-connections, when present, can be easily observed in the branches, sometimes even from the surface, but it is often difficult to observe them in the main axis or in the main branches. I believe the presence or absence of pit-connections among the cortical cells is a characteristic of systematic importance. The group of the species which lack pit-connections seems to be of a more primitive nature as compared to the group having pit-connections.

c. Medullary Layer

The medullary layer is composed of large pseudoparenchymatous cells which are longitudinally elongated and not rich in protoplasmic content.

In the medullary layer, most attractive are the lenticular thickenings of the cell walls in some species. The section Forsterianae was characterized by Yamada (1931) as having the lenticular thickenings in those species with cylindrical fronds. The thickenings are, however, observable in *Laurencia pinnatifida* (Gmelin) Lamouroux from Europe which is a member of the section Pinnatifidae. Among the ten species examined, *Laurencia venusta* Yamada, *Laurencia okamurai*

Yamada and *Laurencia nipponica* Yamada possess the thickenings while the remaining seven species either lack them or possess very few of them. The thickenings in *Laurencia venusta* are abundant in the younger tissues in the apical portion of the ultimate branchlet, while they are rarely observed in the younger tissues of the two other species mentioned above. In *Laurencia nipponica*, the thickenings are not always present while young, but generally present when old. Thus we must exmaine fully grown specimens for an identification of certain species such as *Laurencia nipponica*. The thickenings are usually very abundant in the forked portions of the frond and at the base of the cystocarp.

d. Apical Depression

There is an apical depression at the top of the ultimate branchlet in all of the species studied. It is generally conical in shape. At the central bottom of the depression is situated the growing apical cell. Around the apical cell stand the trichoblasts which are arranged radially from nearly the center to the periphery of the depression.

e. Growing Point and Central Axis

The growing apical cell is situated at the central bottom of the apical depression of the ultimate branchlet as mentioned above. It cuts off, by oblique walls, wedge-shaped segments which form the axial cell-row. This axial cell-row is clearly observable in the apical portions of the ultimate branchlet but becomes quite obscure in the lateral branches and in lower portions. This is one of the generic characteristics of the present genus distinguishes it from *Chondria*.

All of the cells in the upper portion of the branchlet, including those of the trichoblasts and of the young reproductive organs, are linked directly to the axial cells or indirectly through the pericentral cells.

f. Trichoblast

The trichoblast arises from a young pericentral cell near the growing apex, and is gradually displaced toward the periphery of the apical depression with the advance of growth, branching dichotomo-alternately. They are homologous in origin with the reproductive organs, of which the male reproductive organ or antheridium is quite similar in appearance to the trichoblast, showing no essential difference.

2. Structure of Male Reproductive Organs

The male plant was observed in the following seven species: *Laurencia obtusa* (Hudson) Lamouroux, *Laurencia venusta* Yamada, *Laurencia okamurai* Yamada, *Laurencia nipponica* Yamada, *Laurencia intermedia* Yamada, *Laurencia capituliformis* Yamada and *Laurencia cartilaginea* Yamada.

The ultimate fertile branchlet in the male plant are characteristically broad

and called the antheridial receptacle. They are as broad as 1 mm. but may be up to 1.66 mm. in diameter in *Laurencia intermedia*. The shape of the branchlet is somewhat peculiar to each species. Old branchlets of *Laurencia nipponica* are most attractive in shape being longitudinally elongated and later becoming cylindrical.

The branchlet has one to three or four broad apical depressions which are furnished with numerous sterile and fertile trichoblasts or antheridia and are called antheridial depressions. *Laurencia nipponica* has only one depression in its ultimate branchlet. The ratio of width to depth of the depression (Text-fig. 50) is nearly constant for a species, and among the species exmained it ranges from 0.9–1.3 for *Laurencia cartilaginea* to 2.7–2.9 for *Laurencia venusta* and *Laurencia capituliformis*.

The fertile trichoblast or antheridium originates from a young pericentral

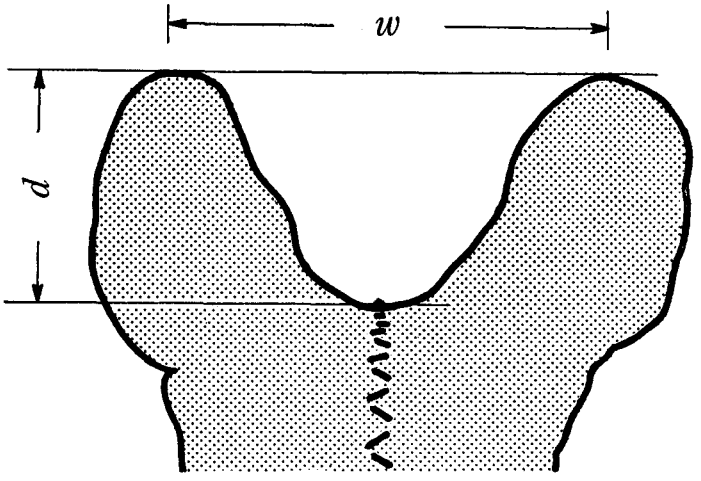

Fig. 50. A diagram showing the ratio of width (w) to depth (d), in a longitudinal section of an antheridial depression.

Table 3. Dimensions of male reproductive organs observed in seven species

Species	Diameter of antheridial receptacle in μ	w/d*	Size of spermatangium in μ	
			length	diameter
L. obtusa	390-1100	2.2 - 2.7	6.6 - 8.4	3.5 - 5.1
L. venusta	340 - 910	2.7 - 2.9	7.8 - 7.9	4.7 - 5.6
L. okamurai	400 - 910	1.2 - 1.4	6.9 - 9.7	4.2 - 5.6
L. nipponica	410-1120	2.1 - 2.3	7.7 - 9.8	4.8 - 6.9
L. intermedia	770-1660	2.1 - 2.7	8.8 - 12.2	4.6 - 6.3
L. capituliformis	490-1270	2.7 - 2.9	8.5 - 11.2	4.5 - 5.7
L. cartilaginea	920-1460	0.9 - 1.3	9.8 - 13.2	5.4 - 7.2

* w/d: Ratio of width to depth of the depression as measured in its median longitudinal section, as shown in Text-fig. 50.

cell near the growing apex and consists of a dichotomo-alternately branched central axis and four pericentral cells on each axial cell. Each mother-cell gives rise to one to three or more spermatangia, which are ovoid in shape, up to 10μ or more in length in *Laurencia intermedia*, *Laurencia capituliformis* and *Laurencia cartilaginea*, and 10μ or less in the other four species. Each spermatangium contains a large nucleus which usually occupies the upper part of the cell cavity, and sometimes the central part as can be seen in *Laurencia nipponica*. A pericentral cell from a lower segment of the axis usually produces a corymbose branch and a tuft of spermatangia. The terminal cell of the fertile trichoblast is vesicular in appearance, ovoid in shape and often attains the very large size of up to 50μ long by 42μ in diameter as observed in *Laurencia intermedia*.

3. Structure of Female Reproductive Organs

The female plant was observed in the following seven species: *Laurencia obtusa* (Hudson) Lamouroux, *Laurencia venusta* Yamada, *Laurencia okamurai* Yamada, *Laurencia nipponica* Yamada, *Laurencia intermedia* Yamada, *Laurencia capituliformis* Yamada and *Laurencia cartilaginea* Yamada. The ultimate fertile branchlets in the female plant are cylindrical while young, but usually becoming clavate with the development of the procarp and cystocarp.

a. Development of the Procarp

The initial cell of the female reproductive organ arises from a pericentral cell of the fertile branchlet and acts as the fertile central cell of the procarp. This fertile cell is thus linked to the axial cell of the branchlet through a pericentral cell which gradually becomes elongated and filamentous below with the growth of the branchlet tissues.

In *Laurencia cartilaginea*, the fertile central cell cuts off four pericentral cells; the first is formed on the outside, the second two on the lateral side, and the last one on the inside. Of these four cells, the last mentioned functions as the supporting cell of the carpogonial branch. The number of pericentral cells could not be counted exactly in *Laurencia obtusa*, *Laurenica venusta* and *Laurencia capituliformis*. In the remaining three species, i.e. *Laurencia okamurai*, *Laurencia nipponica* and *Laurencia intermedia*, the pericentral cells were established to be four in number, but their sequence was not clear.

In all of the species examined, the four-celled carpogonial branch is formed on the supporting cell which is the pericentral cell on the inside of the fertile central cell of the procarp. The carpogonial branch is curved so as to embrace the supporting cell. The apical carpogonium is usually provided with a long slender trichogyne, but the carpogonium in *Laurencia cartilaginea* has a short clavate trichogyne. Other pericentral cells on the fertile central cell cut off many small cells which function as pericarp initials.

The sterile cells derived from the supporting cell are gathered into a number of groups. The number of these groups is of systematic importance, but were hardly countable in a paraffin preparation. These cells increase in number by division, and provide nutrition for the developing gonimoblast.

The procarp ready for fertilization is generally 24–32μ broad in a longitudinal section in all of the species examined except *Laurencia obtusa* which has a larger procarp, up to 43μ broad.

b. Development of the Cystocarp

After fertilization a large auxiliary cell cuts off from the supporting cell on the upper side and fuses with the carpogonium. In all of the species examined except *Laurencia capituliformis*, it was clearly observed that they fuse with each other directly and not through a connecting cell. The supporting cell then fuses with the fertilized auxiliary cell to form a fusion-cell, which gives rise to a process, the first gonimoblast cell, toward the nearby sterile cell. A little later these cells fuse with each other. As the fusion-cell continues to fuse with other sterile cells, and with the surrounding cells including the central cell and the gonimoblast cells formed in earlier stages of gonimoblast development, it becomes large and irregular in shape. Coalescence between the fusion-cell and the pericarp initials can be observed in some species such as *Laurencia venusta*.

The pericarp, especially its inner part, consists of cells derived from the pericentral cells on the fertile central cell of the procarp and from the surrounding cells of the carpongonial branch, as mentioned above. Either before or just after fertilization, the procarp is partly covered by the young pericarp and the carpogonial branch is still naked on its inner side as illustrated by Kylin (1923, p. 126, fig. 79, a & b). Kylin also illustrates a procarp in which the auxiliary cell already formed being wholly covered by the pericarp (l. c., fig. 79, e). In all of the specimens examined, however, the procarp in a similar stage of development are in part still naked.

With the growth of the fertile branchlet, the developing procarp is gradually displaced toward the periphery of the apical depression, and some cortical cells of the branchlet contribute to the growth of the outer portion of the pericarp. Thus the developed pericarp consists of cells of two different origins.

The ripe cystocarp, ovoid in shape, up to 820–970μ in diameter, is situated on the lateral surface of the branchlet, and provided with a carpostome. *Laurencia capituliformis* has an attractively shaped cystocarp, which is usually conical with a rostrate carpsotome, and often very large, up to 1400μ in diameter. The cystocarpic cavity is filled with a mucilaginous substance which sometimes shows the stratified appearance and stains well with iron-alum haematoxylin or carm-alum. The innermost cells of the pericarp which originated from the pericentral cells of the fertile central cell of the procarp become markedly thin and filamentous in shape and protoplasmic in content, indicating that they probably supplied nutrition to

the gonimoblast through the fusion-cell. The terminal cells of the gonimoblast enlarge and become carpospores.

4. Tetrasporangia

The tetrasporangia are formed in the stichidia converted from the ultimate branchlets. The stichidia are similar to the branchlets in shape, but usually thicker in diameter. They have a knobby appearance except when very young. Although Yamada (1931) attached specific significance to the nature of stichidial branchlet as to its simplicity or complexity, I think its nature is too variable to be used as a distinctive characteristic of a species as it has already been pointed out by Cribb (1958).

a. Origin of the Tetrasporangium

The genus *Laurencia* has long been noticed as unique in the origin of its tetrasporangium, since Kylin (1923) reported in *Laurencia pinnatifida* (Gmelin) Lamouroux that the tetrasporangium is converted from a cortical cells in the apical depression. Such an origin seems unusual and doubtful in view of the pericentral origin of the homologous organ in the other genera of Rhodomelaceae.

As far as I could observe in my specimens, the tetrasporangium originates from a young pericentral cell in the apical depression of the stichidial branchlet. The fertile pericentral cell first cuts off a sporangium-initial and a cover-cell, then becomes elongated and filamentous below with the growth of the branchlet tissues. The elongated pericentral cell is later divided into several segments, which become linked by means of secondary pit-connections to some of the subcortical cells derived from other pericentral cells lying beneath the fertile one. As a result, the sporangium tends to be erroneously interpreted as having been produced from a cortical cell. The triangular cell beneath the sporangium in Kylin's figure (1923, p. 130, fig. 82, b) must be the terminal segment of these which were cut from the fertile pericentral cell.

The cover-cell cut from the fertile pericentral cell covers the sporangium from the inside or adaxial side while the other cover-cells produced from the subcortical cells cover the sporangium from the outside or abaxial side and both lateral sides.

The sporangium is always divided tetrahedrally.

b. Tetrasporangium Arrangement

In the arrangement of the tetrasporangia on a stichidium, I could distinguish two types among the species examined, namely, "parallel type" and "right angle type" (Saito, 1963). The following five species belong to the parallel type.

Laurencia obtusa (Hudson) Lamouroux
Laurencia intricata Lamouroux
Laurencia venusta Yamada

Laurencia okamurai Yamada
Laurencia nipponica Yamada

In these species, the longitudinal growth of the stichidium is continued even after production of the sporangia. Consequently, the mature tetrasporangia become scattered on the lateral surface of the stichidium, and they are arranged parallel to the central axis in a longitudinal section of the stichidium. *Laurencia pinnata* Yamada also belongs to this type, according to the illsutration by Okamura (1922, pl. 192, fig. 6).

On the other hand, the following four species belong to the right angle type.

Laurencia intermedia Yamada
Laurencia capituliformis Yamada
Laurencia cartilaginea Yamada
Laurencia undulata Yamada

The longitudinal growth of the stichidium in these species is more or less suppressed after production of the sporangia, and the stichidium increases in diameter by lateral growth. The sporangia are gradually displaced from the center toward the periphery of the apical depression, and are shed before or just after their arrival at the lateral surface. Consequently the mature sporangia are found scattered only over the apical surface of the stichidium, and are arranged at right angles to the central axis in a longitudinal section of the stichidium.

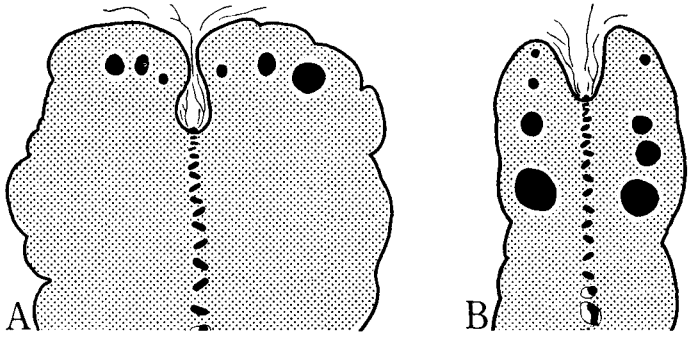

Fig. 51. **A**, *Laurencia intermedia* Yamada (Subgen. *Chondrophycus* Tokida et Saito); a diagram showing the right angle type of tetrasporangial arrangement in a median longitudinal section through a stichidial branchlet. **B**, *Laurencia nipponica* Yamada (Subgen. *Laurencia*); a diagram showing the parallel type of tetrasporangial arrangement in a median longitudinal section through a stichidial branchlet.

V. Proposal of a New Classification for *Laurencia* species

As a result of my investigation, it has become necessary to offer some suggestions for modification of the current classification of the *Laurencia* species as follows:

1. *Laurencia cartilaginea* Yamada and *Laurencia undulata* Yamada are related to each other since both are cartilaginous in texture, similar in appearance, have cortical cells with no secondary pit-connections, and exhibit the right angle type of tetrasporangium arrangement. Thus both species should be classified in the same section, Section Cartilagineae Yamada or Section Chondrophycus according to the thesis. However, *Laurencia undulata* has been classified in Section Pinnatifidae J. Agardh, despite the fact that it differs in major characteristics from *Laurencia pinnata* Yamada, one of the typical members of that section.

2. *Laurencia cartilaginea*, a type of the Section Cartilagineae, differs in major characteristics from the other members of the section, i.e. *Laurencia obtusa* (Hudson) Lamouroux and *Laurencia intricata* Lamouroux. Thus these latter two species should be separated from *Laurencia cartilaginea* and be placed in Section Laurencia since *Laurencia obtusa* is the type of this genus.

3. *Laurencia pinnatifida* (Gmelin) Lamouroux has lenticular thickenings, as do the members of Section Forsterianae. However, they are divided into two sections which are independent of each other. I am sure that these species are related, and should be classified together.

I propose that the genus *Laurencia* be divided into two subgenera. The first subgenus would include *Laurencia obtusa* (Hudson) Lamouroux, type species of the genus, and should be named Subgenus *Laurencia*. It would comprise six of the species examined, which are characterized as having cortical cells with secondary pit-connections and parallel type of the tetrasporangium arrangement. The second subgenus including *Laurencia cartilaginea* Yamada, as the type, would be named *Chondrophycus**. It would include the remaining four species which are characterized as having cortical cells with no secondary pit-connections and right angle type of the tetrasporangium arrangement. Thus the ten species examined would be arranged in the subgenera and sections as follows:

Subgenus I. ***Laurencia***
Section 1. **Laurencia**
Laurencia obtusa (Hudson) Lamouroux
Laurencia intricata Lamouroux
Section 2. **Forsterianae** Yamada
Laurencia venusta Yamada

* *Chondrophycus* Tokida et Saito, subgenus nov. Thallus nullas foveo-colligationes inter cellulae corticales contiguas praebens. Tetrasporangia in superficie apicali ramuli stichidialis, ad angulm 90° axis centralis. Incrassationes lenticulares membranarum cellularum medullarium nullae. (Species typica: *Laurencia cartilaginea* Yamada).

Chondrophycus Tokida et Saito, subgenus nov. Thallus with cortical cells having no secondary pit-connections between adjacent cortical cells. Tetrasporangia arranged on the apical surface of a stichidial branchlet at an angle of 90° (right-angles) to the central axis. Lenticular thickenings of medullary cell walls absent. (Type species: *Laurencia cartilaginea* Yamada).

Laurencia okamurai Yamada
Laurencia nipponica Yamada
Section 3. **Pinnatifidae** J. Agardh
Laurencia pinnata Yamada
Subgenus II. ***Chondrophycus*** Tokida et Saito
Section 4. **Chondrophycus**
Laurencia cartilaginea Yamada
Laurencia undulata Yamada
Section 5. **Palisadae** Yamada
Laurencia intermedia Yamada
Laurencia capituliformis Yamada

VI. Key to the Subgenera, Sections and Species of *Laurencia* thus far Examined

A. Secondary pit-connections among cortical cells present; tetrasporangial arrangement of the parallel type ..... Subgen. I. ***Laurencia***
Frond cylindrical
Lenticular thickenings absent in the walls of the medulla ..... Sect. 1. **Laurencia**
Stoloniferous basal branches lacking ..... *L. obtusa*
Stoloniferous basal branches abundant; generally cushion-like ..... *L. intricata*
Lenticular thickenings present in the walls of the medulla ..... Sect. 2. **Forsterianae**
Plant reddish in colour
Plant large and slender ..... *L. nipponica*
Plant dwarf ..... *L. venusta*
Plant generally greenish or bluish in colour ..... *L. okamurai*
Plant distinctly compressed ..... Sect. 3. **Pinnatifidae** ..... *L. pinnata*

B. Secondary pit-connections among cortical cells absent; tetrasporangial arrangement of the parallel type..... Subgen. II. ***Chondrophycus***
Cortical cells never elongated radially nor arranged like palisade cells in a transverse section..... Sect. 4. **Chondrophycus**
Frond never compressed ..... *L. cartilaginea*
Frond generally compressed except in ultimate branchlets .... *L. undulata*
Cortical cells elongated radially and arranged like palisade cells in a transverse section ..... Sect. 5. **Palisadae**
Frond thick and rigid; cystocarp ovoid ..... *L. intermedia*
Frond somewhat thin and soft; cystocarp conical .... *L. capituliformis*

VII. Practical Problems of *Laurencia*

Generally speaking, the *Laurencia* species of algae are of little practical value. However, there is some information about *Laurencia* which may attract one's interest from a practical point of view.

Yendo (1911) once reported that some species of *Laurencia* were harvested by fishermen to be used as food after drying in the Kaifu District of Echigo Province or Niigata Prefecture. When I lived in that prefecture, I tried a soup of *Laurencia nipponica* which was not palatable, but *Chondria crassicaulis* boiled down with soy tasted very delicious. Contrary to the comment made by Scagel (1961, p. 24), *Laurencia* is not at all common in the Japanese diet. In Japan, some peopole believe that *Laurencia* has an abortive effect when eaten.

Laurenica pinnatifida is also called "pepper dulse" and used as a condiment in Scotland, and as a kind of chewing tobacco in Iceland (Chapman, 1950). *Laurencia spectabilis* from Pacific North America which resembles *Laurencia pinnatifida* in external appearance, also has a peppery flavour when fresh (tried by myself after the private communication from Dr. Doty). Native Hawaiians eat many kinds of *limu* or algae including *Laurencias* which are called *Lipeepee, Lipuupuu, Hoonunu, Lipalu* or *Oolu* (Setchell, 1905).

The chemical components of *Laurencia* have lately been investigated in two species. The mucilage of *Laurencia pinnatifida* was extracted and analyzed by O'Colla et al. (cf. O'Colla in Lewin, 1962, p. 346). A compound containing bromine was isolated from *Laurencia nipponica* (under the name of *Laurencia glandulifera*) and named "Laurencin" by Irie et al. (1965) who studied its chemical structure in detail.

The superficial cells of *Laurencia* are often found in a surface view to contain a single large globular drop which is highly refractive. Although it appears to possess a cell content of a terpene nature, its actual component and physiological function are as yet unknown.

VIII. Summary

1. The Japanese species of *Laurencia* treated in this thesis are ten in number, most of which were studied on the basis of the materials which I had collected. Seven of them, *L. capituliformis* Yamada, *L. cartilaginea* Yamada, *L. intermedia* Yamada, *L. nipponica* Yamada, *L. obtusa* (Hudson) Lamouroux, *L. okamurai* Yamada and *L. venusta* Yamada, were studied with the male, female and tetrasporic specimens, while *L. intricata* Lamouroux and *L. undulata* Yamada were studied with the tetrasporic specimens and *L. pinnata* Yamada with only the sterile specimens.

2. *L. intricata* Lamouroux is reported herein as new to Japan.

3. During the coruse of my research, one or two phases of the life-history were newly recorded in seven species as follows: (1) antheridial phase in *L. capituliformis* Yamada, *L. cartilaginea* Yamada, *L. intermedia* Yamada, *L. nipponica* Yamada, *L. okamurai* Yamada and *L. venusta* Yamada; (2) cystocarpic phase in *L. capituliformis* Yamada, *L. cartilaginea* Yamada, *L. intermedia* Yamada, *L. okamurai* Yamada and *L. venusta* Yamada; and (3) tetrasporic phase in *L. undulata* Yamada.

4. The fronds generally form clumps with several erect axes or main branches standing either on a small disc and tufted below with stoloniferous basal branches, or on a well developed discoid holfast without stoloniferous branches. The main axes are percurrent in some species but not in others; their length are usually less than 20 cm. but may vary up to 37 cm. in the specimens of *L. nipponica* Yamada from Oshoro or even larger in those from Akkeshi and Nou.

5. The presence or absence of longitudinal secondary pit-connections among the superficial cells of the branches is believed to be a characteristic of taxonomic significance. The pit-connections are present in six of the species examined but absent or occurring very rarely in the others.

6. The superficial cortical cells in a cross section of the branchlets are elongated radially and arranged like palisade cells in *L. capituliformis* Yamada and *L. intermedia* Yamada, though former was classified by Yamada (1931) in the group characterized by cortical cells not arranged like palisade cells.

7. *L. nipponica* Yamada is unique in having only one antheridial depression at the apex of the fertile branchlet, while the other species have one to three or more depressions in the branchlet. The ratio of width to depth of the depression is nearly constant for each species. As observed by Kylin (1923) in *L. pinnatifida* (Gmelin) Lamouroux, the fertile trichoblast or antheridium originates from a pericentral cell near the growing apex and consists of a dichotomo-alternately branched central axis and four pericentral cells which bear spermatangia.

8. The central cell of the procarp arises from a pericentral cell of the fertile branchlet. Developmental stages of the procarp and cystocarp are traced in detail and found to be nearly identical with those described by Kylin (1923) in *L. pinnatifida* (Gmelin) Lamouroux. *L. obtusa* (Hudson) Lamouroux and *L. capituliformis* Yamada are noteworthy, the former in having large procarps and the latter in having large conical cystocarps with a rostrate carpostome.

9. The tetrasporangium-initial is revealed for the first time to arise from the pericentral cell of the stichidial branchlet, contrary to the view of Kylin (1923) who attributed the origin of the sporangia to the cortical cells. The arrangement of the sporangia as seen in a median longitudinal section through the stichidium is either parallel or at right angles to the central axis and called the "parallel type" and "right angle type" respectively (Text-fig. 51).

10. As a result of the morphological studies alluded to above, I propose to distinguish in *Laurencia* the following two subgenera, Subgen. *Laurencia* and

Subgen. *Chondrophycus* Tokida et Saito, subgen. nov. These subgenera differ from each other in the presence or absence of pit-connections among the superficial cells and in the type of tetrasporangium arrangement. I also propose a new systematic arrangement of the species examined as shown on p. 72–73 and in the key on p. 73.

11. Practical problems of the *Laurencia* species, including occasional records of their utilization as food, the Hawaiian names and the latest studies of their chemical components, are briefly reviewed.

Appendix

The following types and reliable specimens were examined during the present study in order to make the identification of the enumerated species as correct as possible.

Laurencia obtusa: A reliable specimen collected at Galway, Ireland, on 27 July 1966, and determined by Dr. M. de Valera (deposited in my herbarium); a reliable specimen collected at St. Servan, France, and determined by Dr. Y. Yamada (Herbarium of the Botanical Institute, Faculty of Science, Hokkaido University, Sapporo, 7971).

Laurencia intricata: A reliable specimen collected in Florida on 22 June 1926, and determined by Dr. W. R. Taylor (Herbarium of the Tokyo University of Fisheries, Tokyo, 1435).

Laurencia venusta: The type specimen (Herbarium of the Botanical Institute, Faculty of Science, Hokkaido University, Sapporo, 13873).

Laurencia okamurai: The type specimen (Herbarium of the Botanical Institute, Faculty of Science, Hokkaido University, Sapporo, 13875).

Laurencia nipponica: The type specimen (Herbarium of the Botanical Institute, Faculty of Science, Hokkaido University, Sapporo, 13877).

Luarencia pinnata: The type specimen (Herbarium of the Botanical Institute, Faculty of Science, Hokkaido University, Sapporo, 13872).

Laurencia intermedia: The type specimen (Herbarium of the Botanical Institute, Faculty of Science, Hokkaido University, Sapporo; this specimen, bearing no number, is shown on Plate 2 of Yamada, 1931).

Laurencia capitulfiormis: The type specimen (Herbarium of the Botanical Institute, Faculty of Science, Hokkaido University, Sapporo, 13880).

Laurencia cartilaginea: Reliable specimens collected at several localities in Japan and determined by Dr. Y. Yamada (Herbarium of the Botanical Institute, Faculty of Science, Hokkaido University, Sapporo, 13070, 26379, 27685, 28659 & 28712).

Laurencia undulata: The type specimen (Herbarium of the Botanical Institute, Faculty of Science, Hokkaido University, Sapporo, 13869).

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Explanation of Plates

Plate I

Laurencia obtusa (Hudson) Lamouroux

Fig. 1. Habit of an herbarium male specimen (All of the specimens shown in this plate were collected at Moheji, Hokkaido, on August 10, 1964)

Fig. 2. Habit of an herbarium female specimen

Fig. 3. Habit of an herbarium tetrasporangial specimen

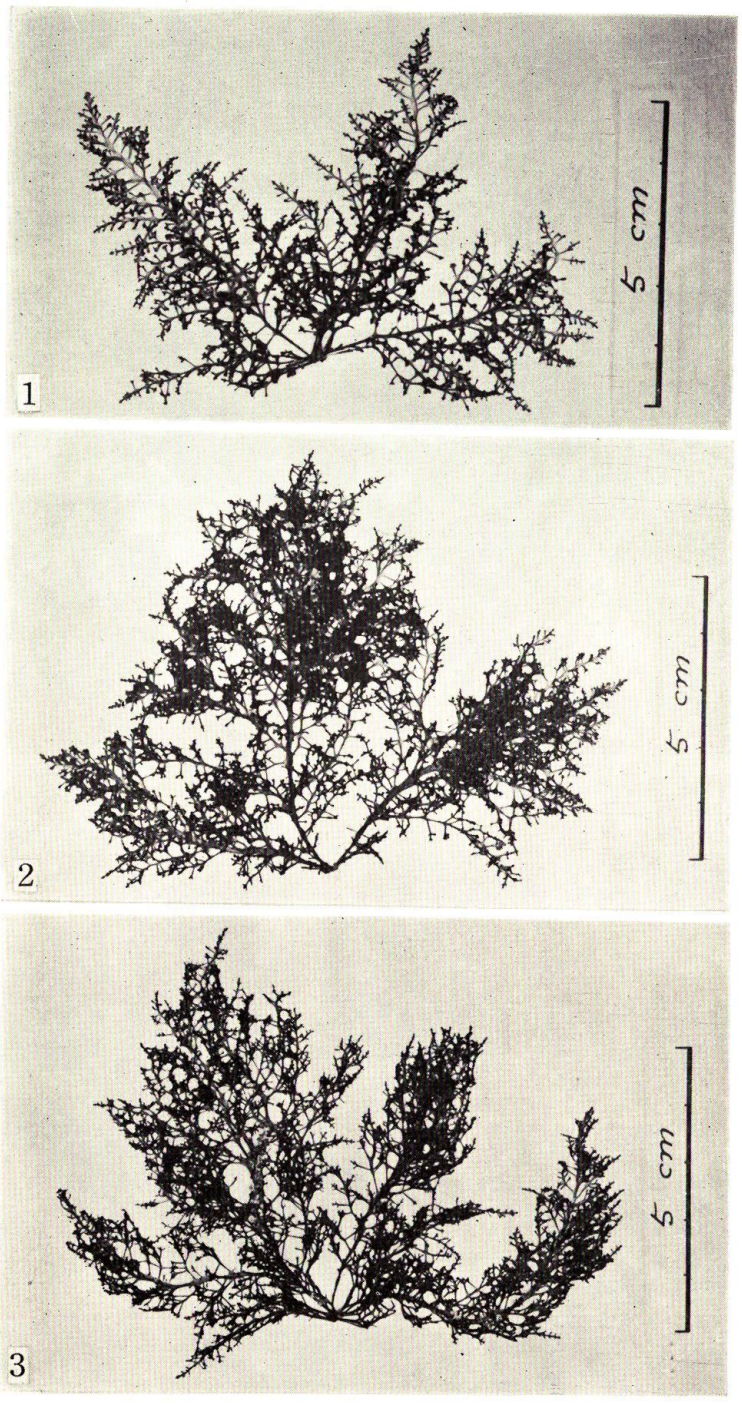

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Plate II

Laurencia obtusa (Hudson) Lamouroux

Fig. 1. Habit of a tetrasporangial plant preserved in formalin-seawater ×1

Fig. 2. Part of a male plant ×5

Fig. 3. Part of a tetrasporangial plant in its early stage of maturity ×5

Fig. 4. Part of an old tetrasponragial plant ×5

Fig. 5. Part of a female plant ×5

Fig. 6. Median longitudinal section through a stichidial branchlet ×56

Fig. 7. Part of apical portion of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on an elongated pericentral cell which is connected to an axial cell ×224

Fig. 8. Median longitudinal section through an antheridial receptacle ×56

Figs. 9 & 10. A young (Fig. 9) and a mature (Fig. 10) antheridia in a smeared preparation ×256

Fig. 11. Part of the apical portion of a median longitudinal section through the antheridial receptacle, showing the growing point and an antheridium-initial ×560

Fig. 12. Part of apical portion of median longitudinal section through a fertile branchlet of female plant, showing a procarp attached to the top of the elongated pericentral cell which is connected to the axial cell ×320

Fig. 13. Longitudinal section through a procarp ready for fertilization (cf. Text-fig. 4, A) ×480

Fig. 14. Longitudinal section through a young cystocarp (cf. Text-fig. 4, D) ×320

Fig. 15. Median longitudinal section through a ripe cystocarp ×44

Plate III

Laurencia intricata Lamouroux

Fig. 1. Habit of a tetrasporangial plant; an herbarium specimen colleted at Moheji, Hokkaido, on September 5, 1963

Fig. 2. Habit of a tetrasporangial plant preserved and slightly bleached in formalin-seawater, from the same collection as above ×1

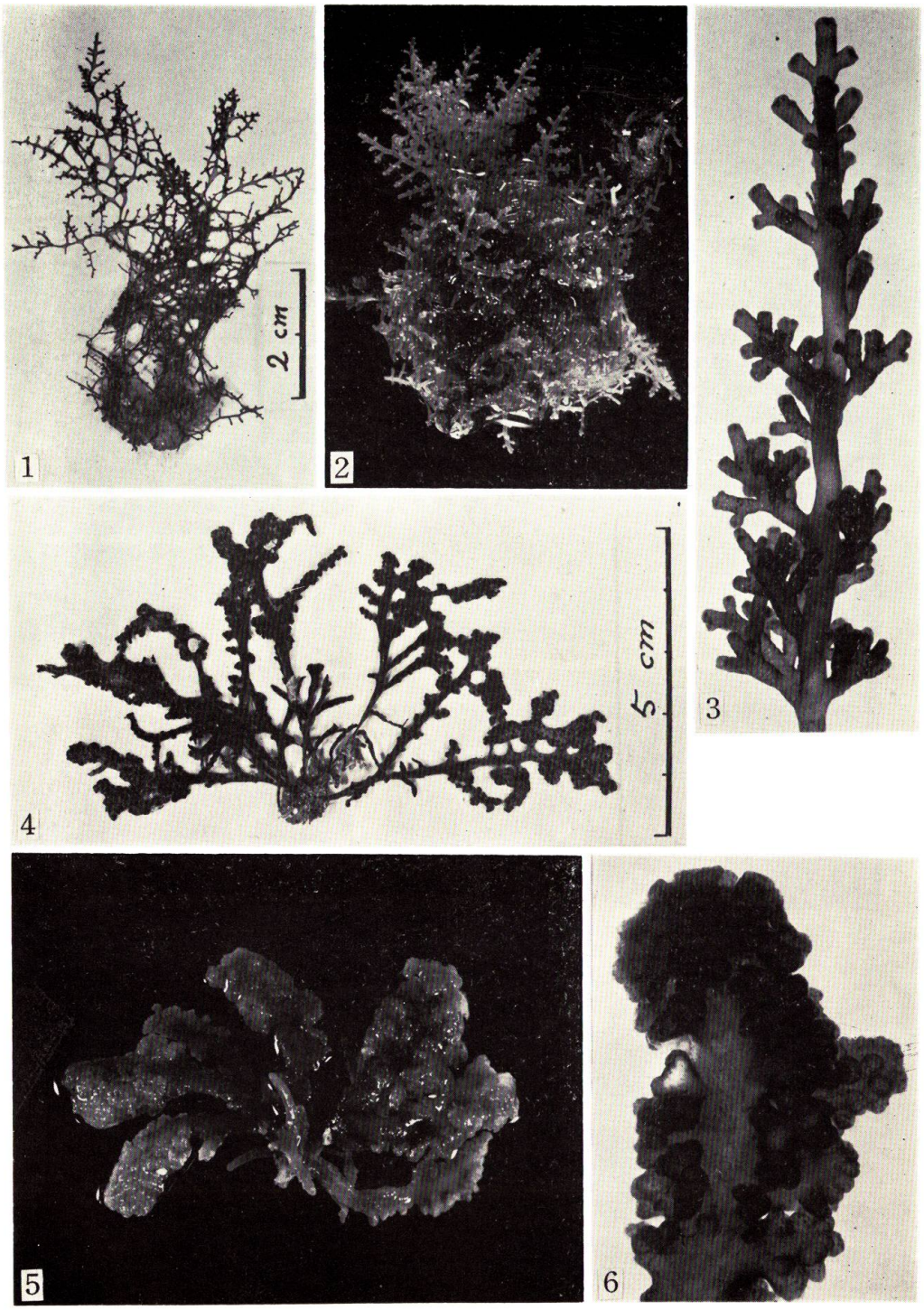
Fig. 3. Part of the same plant as shown in Fig. 2 ×5

Laurencia undulata Yamada

Fig. 4. Habit of a tetrasporangial plant; an herbarium specimen collected at Shirahama, on May 22, 1963

Fig. 5. Habit of a tetrasporangial plant preserved and slightly bleached in formalin-seawater, from the same collection as above ×1

Fig. 6. Part of the same plant as shown in Fig. 5 ×4



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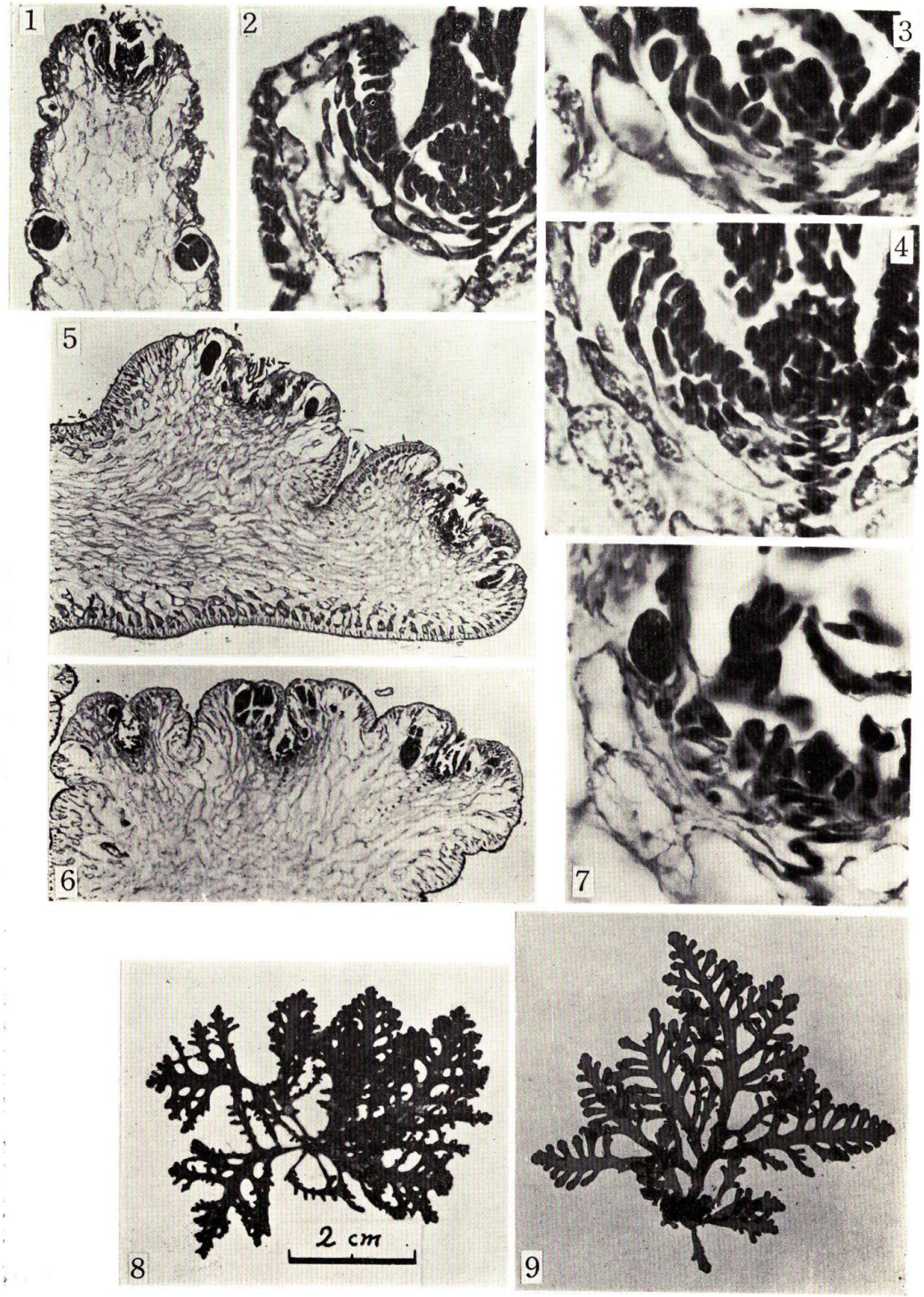

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Plate IV

Laurencia intricata Lamouroux

Fig. 1. Median longitudinal section through a stichidial branchlet ×80

Fig. 2. Part of median longitudinal section through a branchlet ×360

Fig. 3. Part of apical portion of median longitudinal section through a stichidial brachlet, showing a tetrasporangium-initial on an elongated pericentral cell which is connected to an axial cell (cf. Text-fig. 7, A) ×600

Fig. 4. Ditto, showing a filamentous, elongated, fertile pericentral cell ×480

Laurencia undulata Yamada

Fig. 5. Marginal portion of transverse section of a tetrasporangial plant ×48

Fig. 6. Median longitudinal section through a tuft of stichidial branchlets ×48

Fig. 7. Part of apical portion of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on an elongated pericentral cell which is connected to an elongated axial cell (cf. Text-fig. 49, A) ×480

Laurencia pinnata Yamada

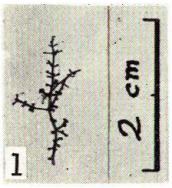
Fig. 8. Habit of a sterile plant; an herbarium specimen collected at Matsumae, Hokkaido, on April 23, 1963

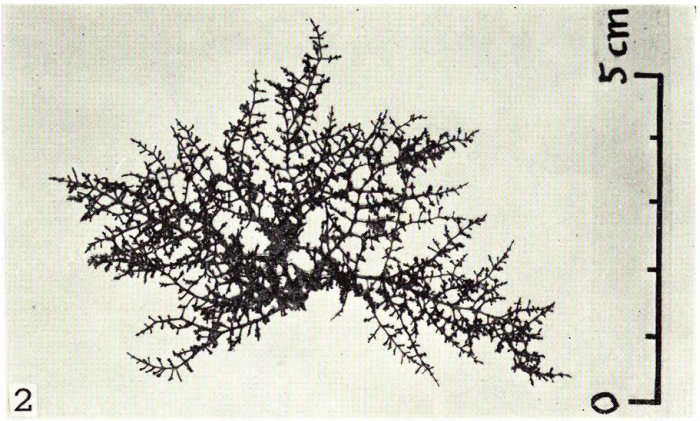
Fig. 9. Habit of a sterile plant preserved in formalin-seawater, from the same collection as above ×1

Plate V

Laurencia venusta Yamada

Fig. 1. Fragment of a male specimen
Fig. 2. Habit of a female plant in an herbarium specimen
Fig. 3. Habit of a tetrasporangial plant in an herbarium specimen
Fig. 4. Habit of a tetrasporangial plant preserved in formalin-seawater $\times 1$
All of the specimens shown in this plate were collected at Moheji, Hokkaido, on September 13, 1963





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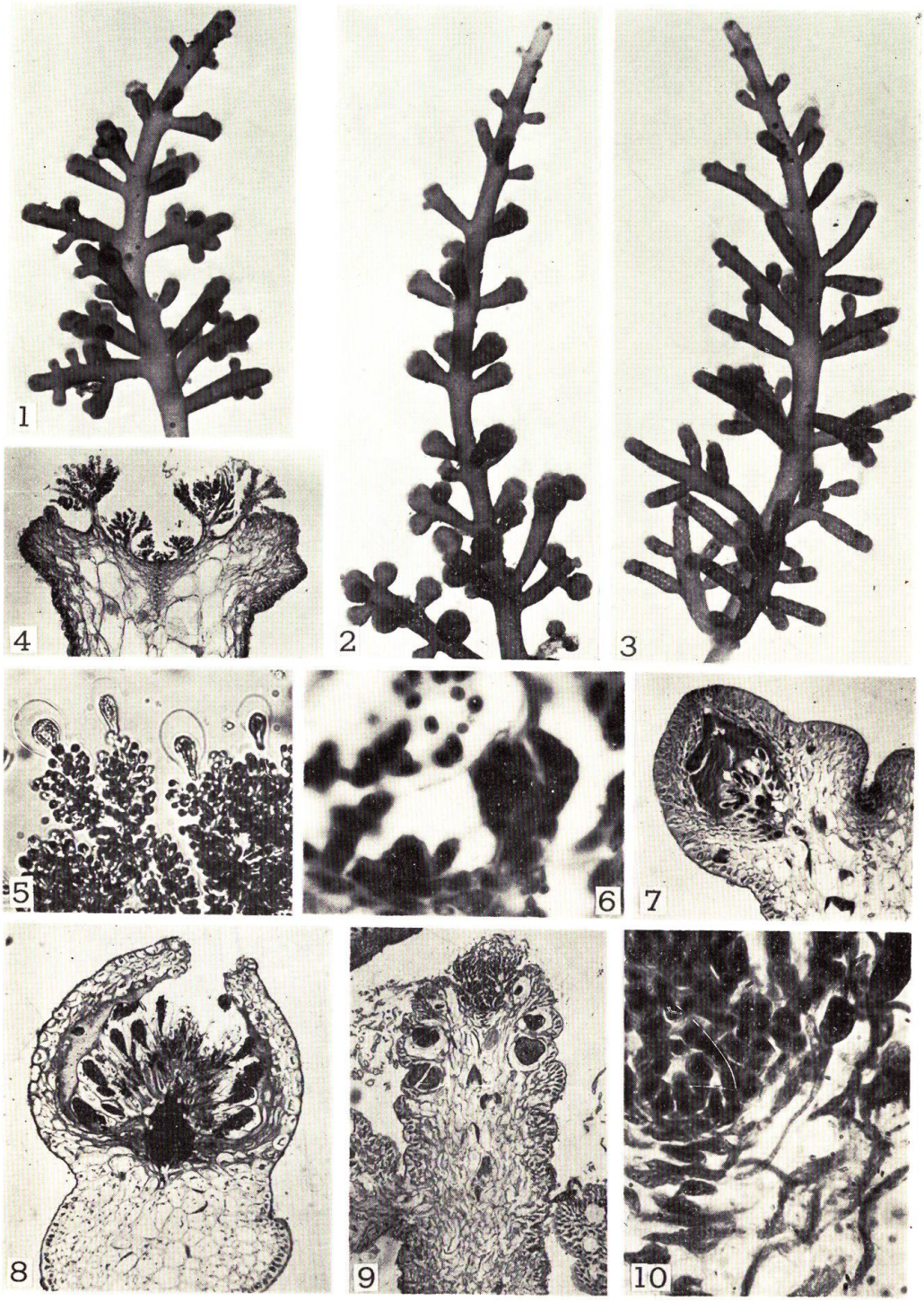

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Plate VI

Laurencia venusta Yamada

Fig. 1. Part of a female plant ×6

Fig. 2. Part of a male plant ×6

Fig. 3. Part of a tetrasporangial plant ×6

Fig. 4. Median longitudinal section through an antheridial receptacle (cf. Text-fig. 10) ×60

Fig. 5. A group of antheridia from a smeared preparation ×320

Fig. 6. Part of apical portion of median longitudinal section through a fertile branchlet of a female plant, showing the growing point and a procarp which is ready for fertilization (cf. Text-fig. 12, B) ×600

Fig. 7. Median longitudinal section through a fertile branchlet with a young cystocarp ×60

Fig. 8. Median longitudinal section through a ripe cystocarp ×54

Fig. 9. Median longitudinal section through a stichidial branchlet ×72

Fig. 10. Part of apical portion of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on an elongated pericentral cell which is connected to an axial cell ×600

Plate VII

Laurenica okamurai Yamada

Fig. 1. Habit of a female plant in an herbarium specimen collected at Moheji, Hokkaido, on September 13, 1963

Fig. 2. Habit of a male plant in an herbarium specimen from the same collection as above

Fig. 3. Habit of a tetrasporangial plant in an herbarium specimen collected at Moheji, on August 27, 1963

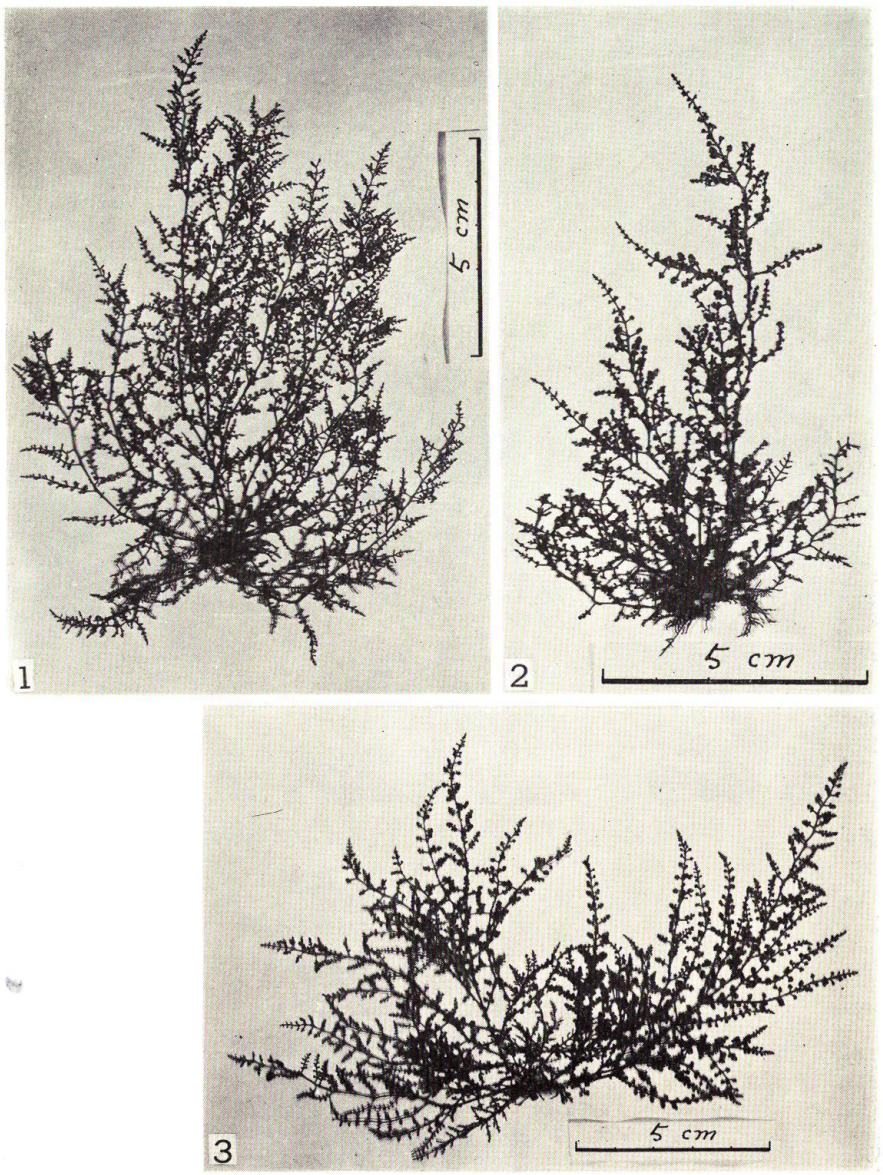

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Plate VIII

Laurencia okamurai Yamada

Fig. 1. Part of a tetrasporangial plant ×7.5
Fig. 2. Part of a female plant ×7.5
Fig. 3. Part of a male plant ×7.5
Fig. 4. Habit of a tetrasporangial plant preserved in formalin-seawater ×1

Plate IX

Laurencia okamurai Yamada

Fig. 1. Median longitudinal section through an antheridial receptacle ×80

Fig. 2. Part of median longitudinal section through the antheridial receptacle, showing the growing point and an antheridium-initial ×360

Figs. 3 & 4. A group of young (Fig. 3) and mature (Fig. 4) antheridia from a smeared preparation ×320

Fig. 5. Part of median longitudinal section through a fertile branchlet of a female plant, showing a procarp which is ready for fertilization attached to the top of the elongated pericentral cell (cf. Text-fig. 19, A) ×640

Fig. 6. Longitudinal section through a procarp after fertilization, showing the auxiliary cell formed on the supporting cell (cf. Text-fig. 19, B) ×640

Fig. 7. Longitudinal section through a more developed procarp, showing the initial stage of fusion-cell (cf. Text-fig. 19, D) ×320

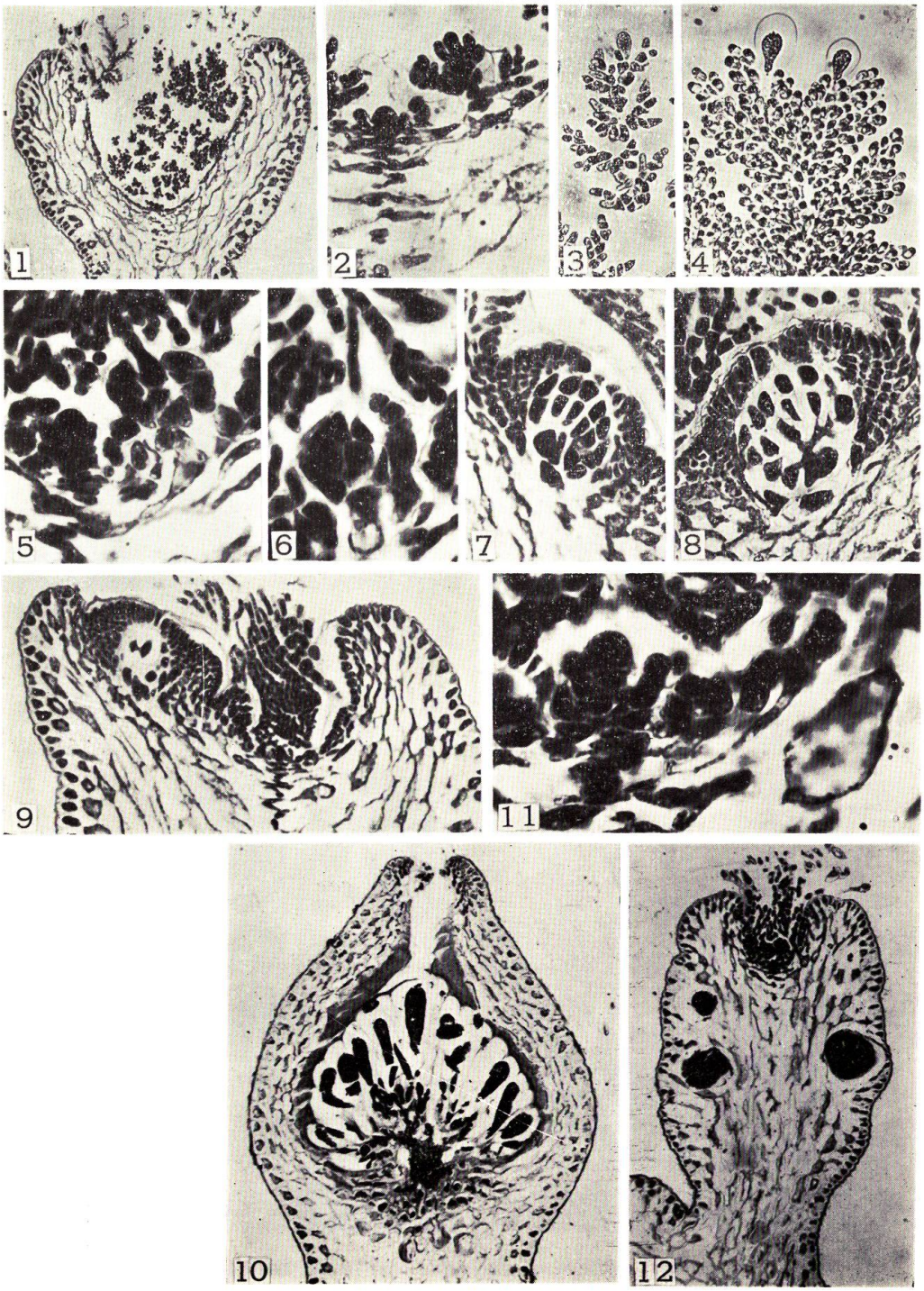
Fig. 8. Longitudinal section through a young cystocarp, showing the initial stage of gonimoblast development ×320

Fig. 9. Median longitudinal section through the apical portion of a fertile branchlet of female plant, showing two stages of cystocarp development ×160

Fig. 10. Median longitudinal section through a ripe cystocarp (cf. Text-fig. 20) ×80

Fig. 11. Part of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on an elongated pericentral cell (cf. Text-fig. 21, A) ×800

Fig. 12. Median longitudinal section through a stichidial branchlet ×80



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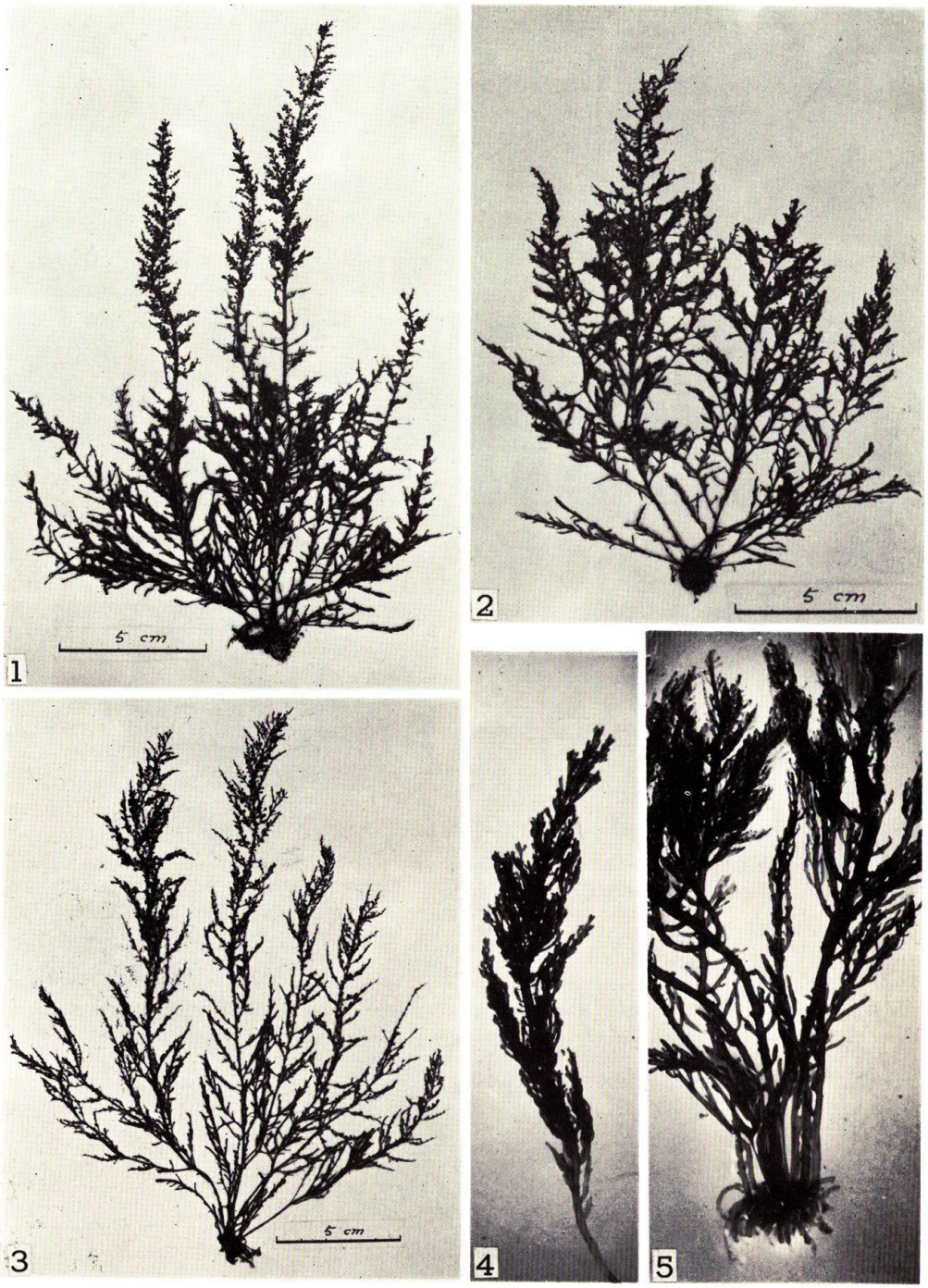

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Plate X

Laurencia nipponica Yamada

Fig. 1. Habit of a female plant in an herbarium specimen collected at Oshoro, on July 19, 1962

Fig. 2. Habit of a male plant in an herbarium specimen collected at Oshoro, on July 20, 1964

Fig. 3. Habit of a tetrasporangial plant in an herbarium specimen collected at Oshoro, on July 19, 1962

Figs. 4 & 5. Habit of the upper (Fig. 4) and the basal (Fig. 5) portion of a tetrasporangial plant preserved in formalin-seawater $\times 1$

Plate XI

Laurencia nipponica Yamada

Figs. 1 & 2. A young (Fig. 1) and an old (Fig. 2) part of a male plant ×5

Fig. 3. Part of a female plant ×5

Fig. 4. Part of a tetrasporangial plant ×5

Fig. 5. Median longitudinal section through an antheridial receptacle ×60

Fig. 6. Part of median longitudinal section through the antheridial receptacle, showing the growing point and an antheridium-initial (cf. Text-fig. 25, A) ×600

Figs. 7 & 8. A group of young (Fig. 7) and mature (Fig. 8) antheridia from a smeared preparation ×240

Fig. 9. Part of median longitudinal section through a fertile branchlet of a female plant, showing a procarp attached to the top of the elongated pericentral cell which is connected to the axial cell (cf. Text-fig. 26, A) ×600

Fig. 10. Longitudinal section through a procarp ready for fertilization (cf. Text-fig. 26, B) ×600

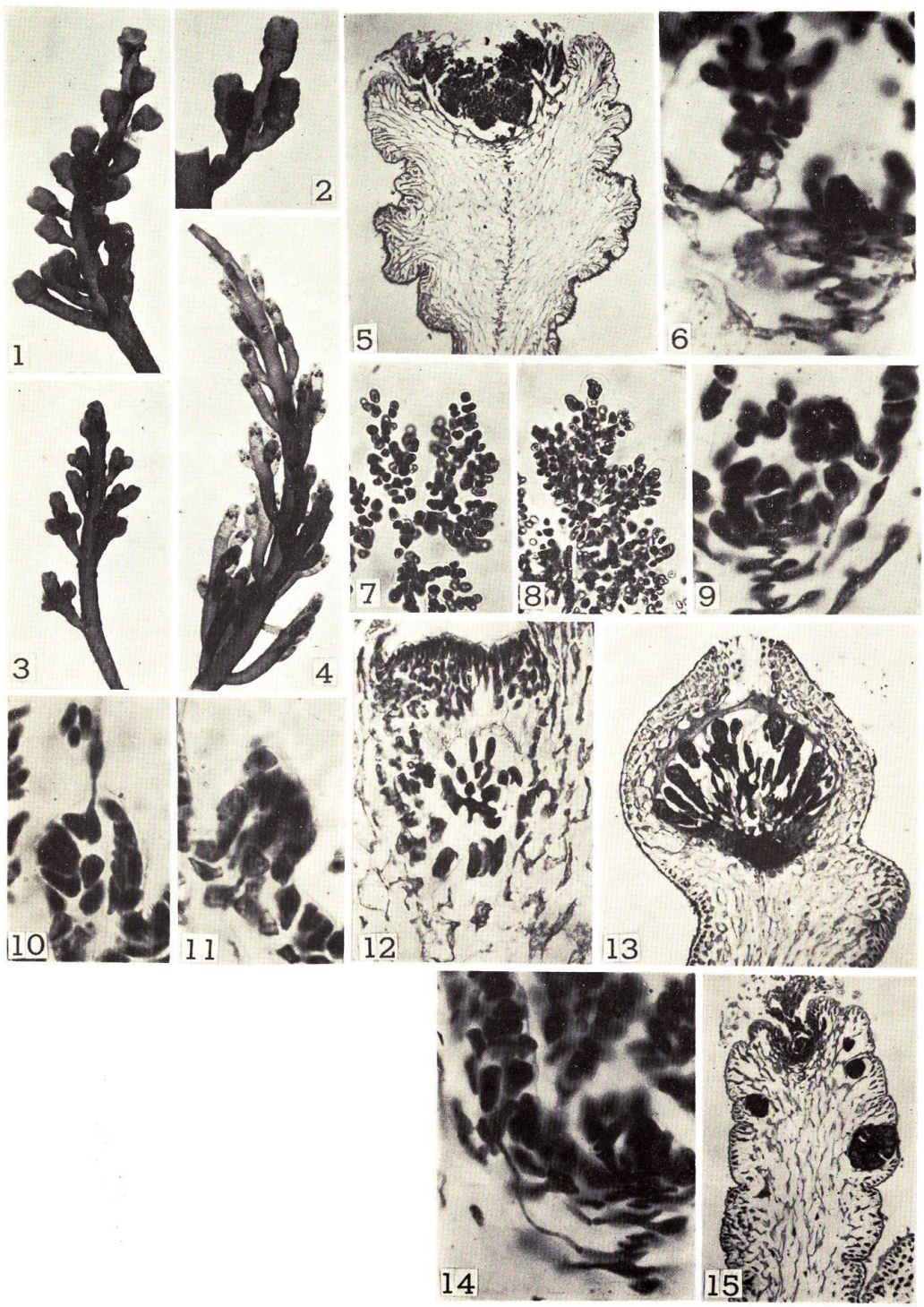
Fig. 11. Longitudinal section through a procarp after fertilization (cf. Text-fig. 26, C) ×600

Fig. 12. Longitudinal section through a young cystocarp, showing the initial stage of gonimoblast formation (cf. Text-fig. 27, B) ×240

Fig. 13. Median longitudinal section through a ripe cystocarp ×60

Fig. 14. Part of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on the elongated pericentral cell which is connected to the elongated axial cell (cf. Text-fig. 29, A) ×600

Fig. 15. Median longitudinal section through a stichidial branchlet ×60



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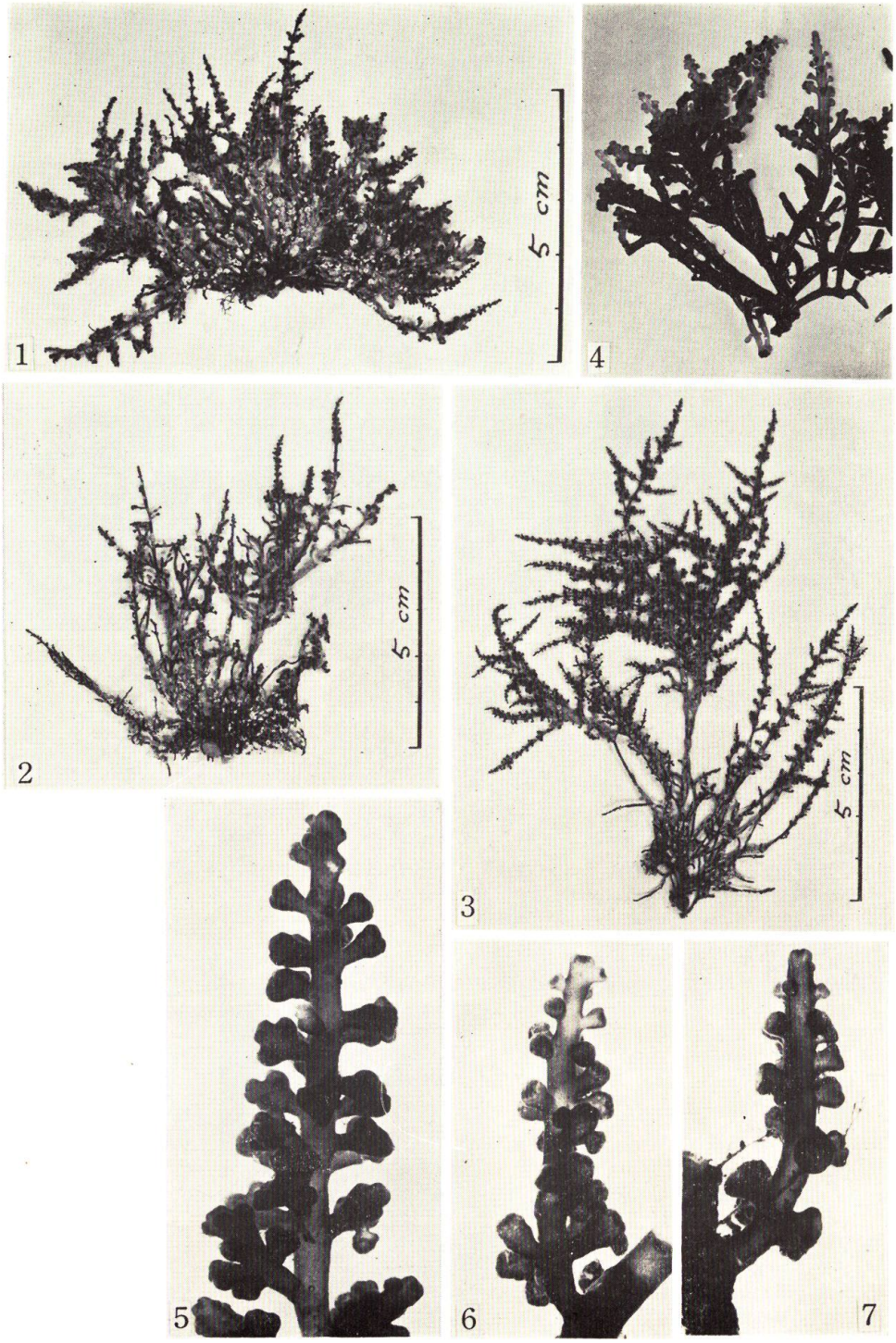

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Plate XII

Laurencia intermedia Yamada

Fig. 1. Habit of a male plant, in an herbarium specimen
Fig. 2. Habit of a female plant, in an herbarium specimen
Fig. 3. Habit of a tetrasporangial plant, in an herbarium specimen
Fig. 4. Habit of a male plant, in a specimen preserved in formalin-seawater ×1
Fig. 5. Part of a female plant ×5
Fig. 6. Part of a tetrasporangial plant ×5
Fig. 7. Part of a male plant ×5
All of the specimens shown in this plate were collected at Moheji, on August 16, 1962

Plate XIII

Laurencia intermedia Yamada

Fig. 1. Median longitudinal section through an antheridial receptacle ×64

Fig. 2. Part of median longitudinal section through an antheridial receptacle, showing a young antheridium attached to the top of the elongated pericentral cell ×480

Figs. 3 & 4. A group of young (Fig. 3) and mature (Fig. 4) antheridia from a smeared preparation ×320

Fig. 5. Longitudinal section through a procarp ready for fertilization (cf. Text-fig. 33, A) ×640

Fig. 6. Longitudinal section through a procarp after fertilization, showing the auxiliary cell formed on the supporting cell (cf. Text-fig. 33, B) ×640

Fig. 7. Longitudinal section through a young cystocarp, showing the initial stage of fusion-cell formation (cf. Text-fig. 33, C) ×360

Fig. 8. Part of median longitudinal section through a cystocarp-bearing branchlet of a female plant ×64

Fig. 9. Median longitudinal section through a ripe cystocarp ×48

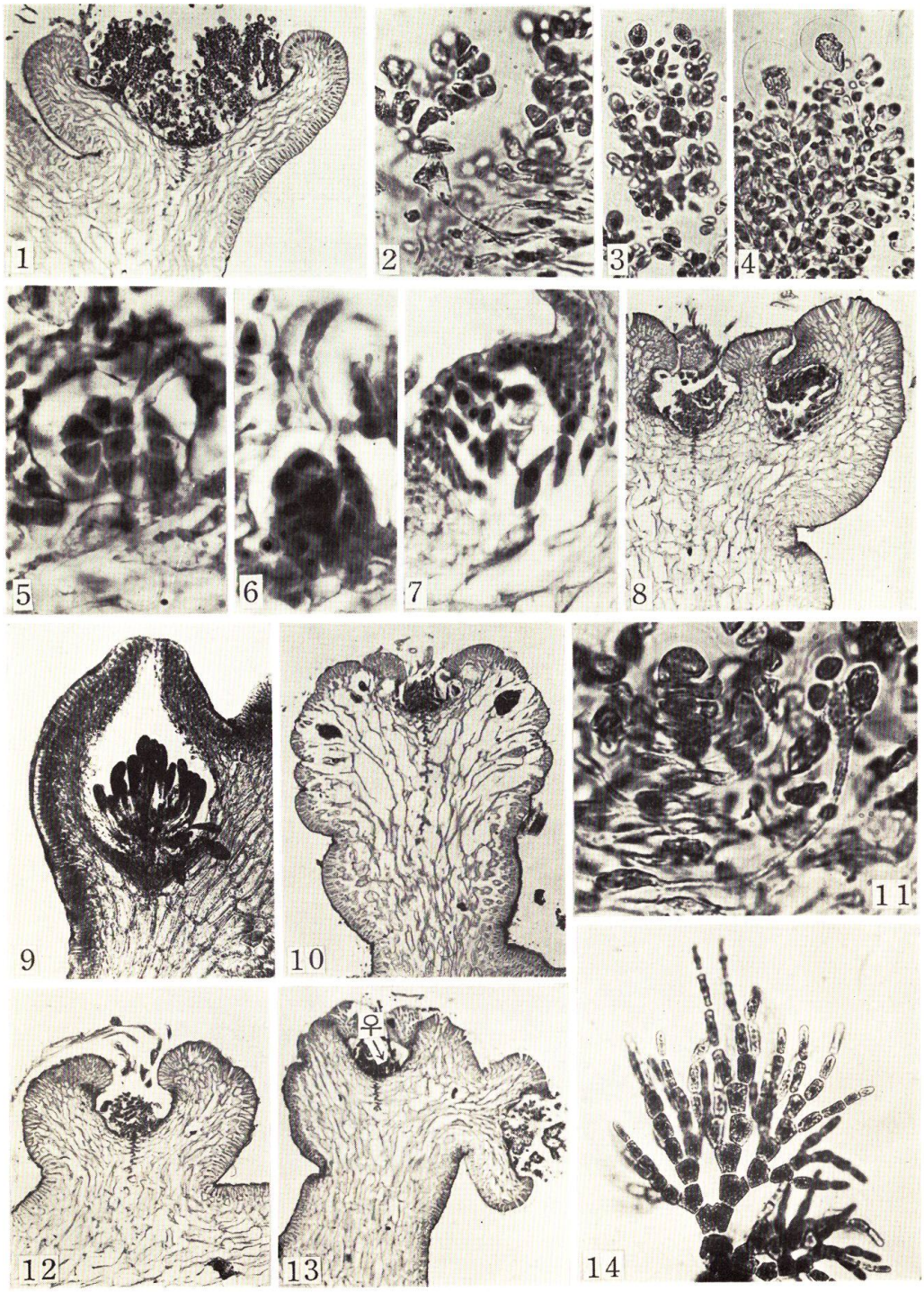
Fig. 10. Median longitudinal section through a stichidial branchlet ×40

Fig. 11. Part of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on an elongated pericentral cell which is connected to an axial cell (cf. Text-fig. 35, A) ×640

Fig. 12. Median longitudinal section through a sterile branchlet ×64

Fig. 13. Median longitudinal section through a fertile branchlet of a female plant, showing a procarpic depression at the top and an antheridial one on the right-hand side ×40

Fig. 14. A young trichoblast from a smeared preparation ×320



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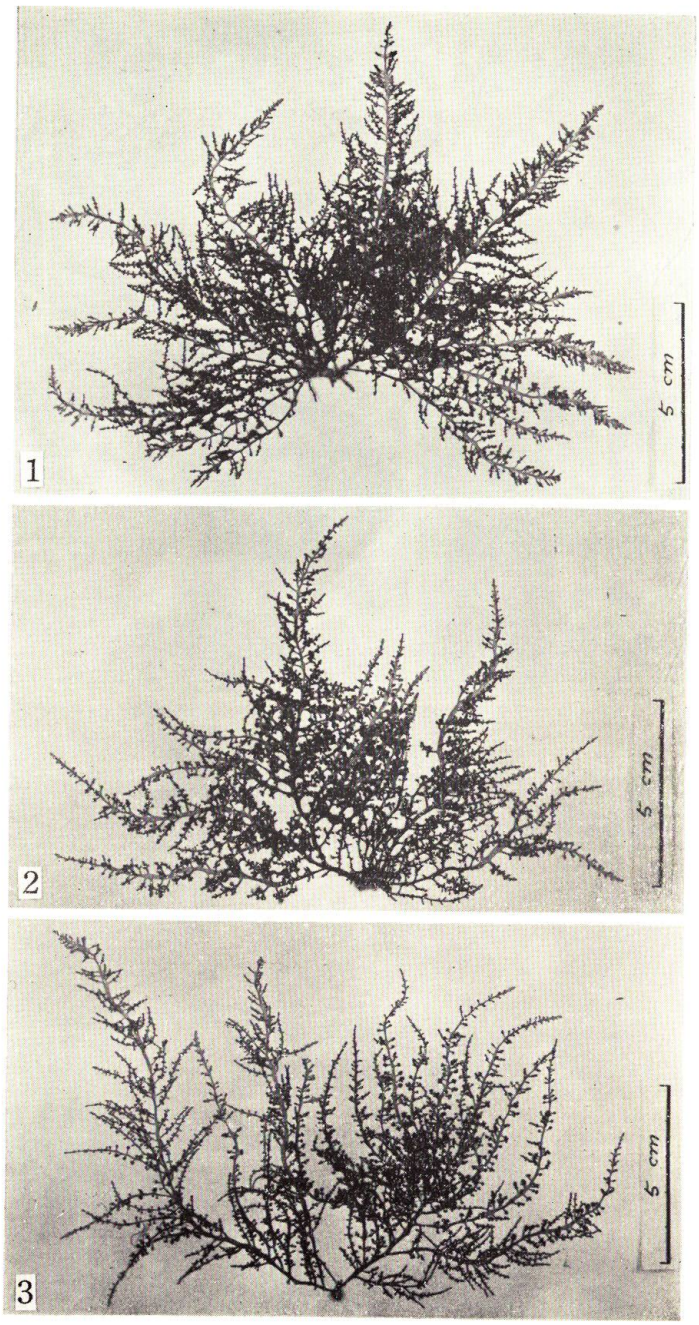

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Plate XIV

Laurencia capituliformis Yamada

Fig. 1. Habit of a male plant in an herbarium specimen collected at Matsumae, on July 29, 1964

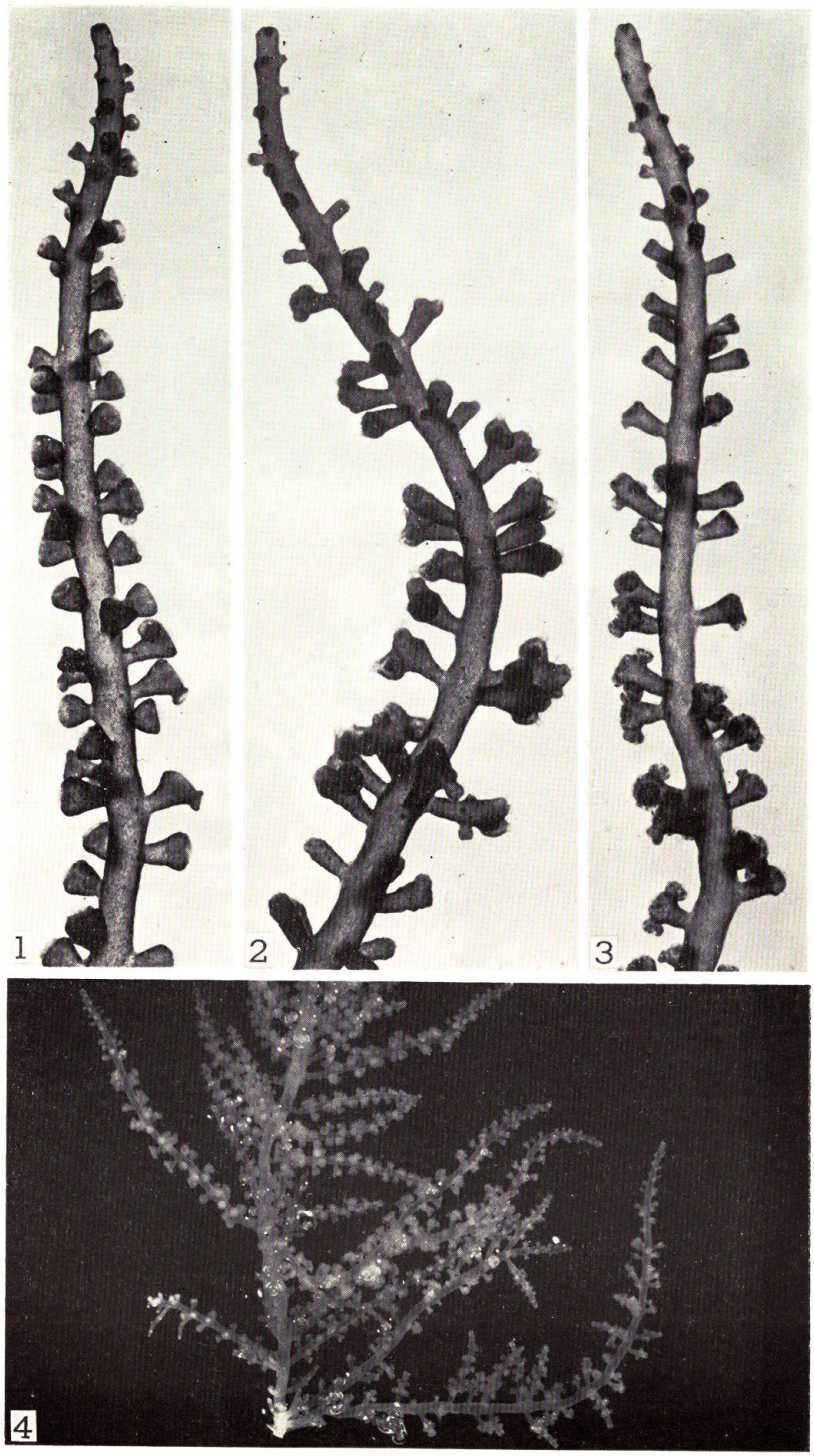
Fig. 2. Habit of a female plant in an herbarium specimen from the same collection as above

Fig. 3. Habit of a tetrasporangial plant in an herbarium specimen from the same collection as above

Plate XV

Laurencia capituliformis Yamada

Fig. 1. Part of a male plant ×5
Fig. 2. Part of a female plant ×5
Fig. 3. Part of a tetrasporangial plant ×5
Fig. 4. Habit of a tetrasporangial plant preserved and bleached in formalin-seawater ×1



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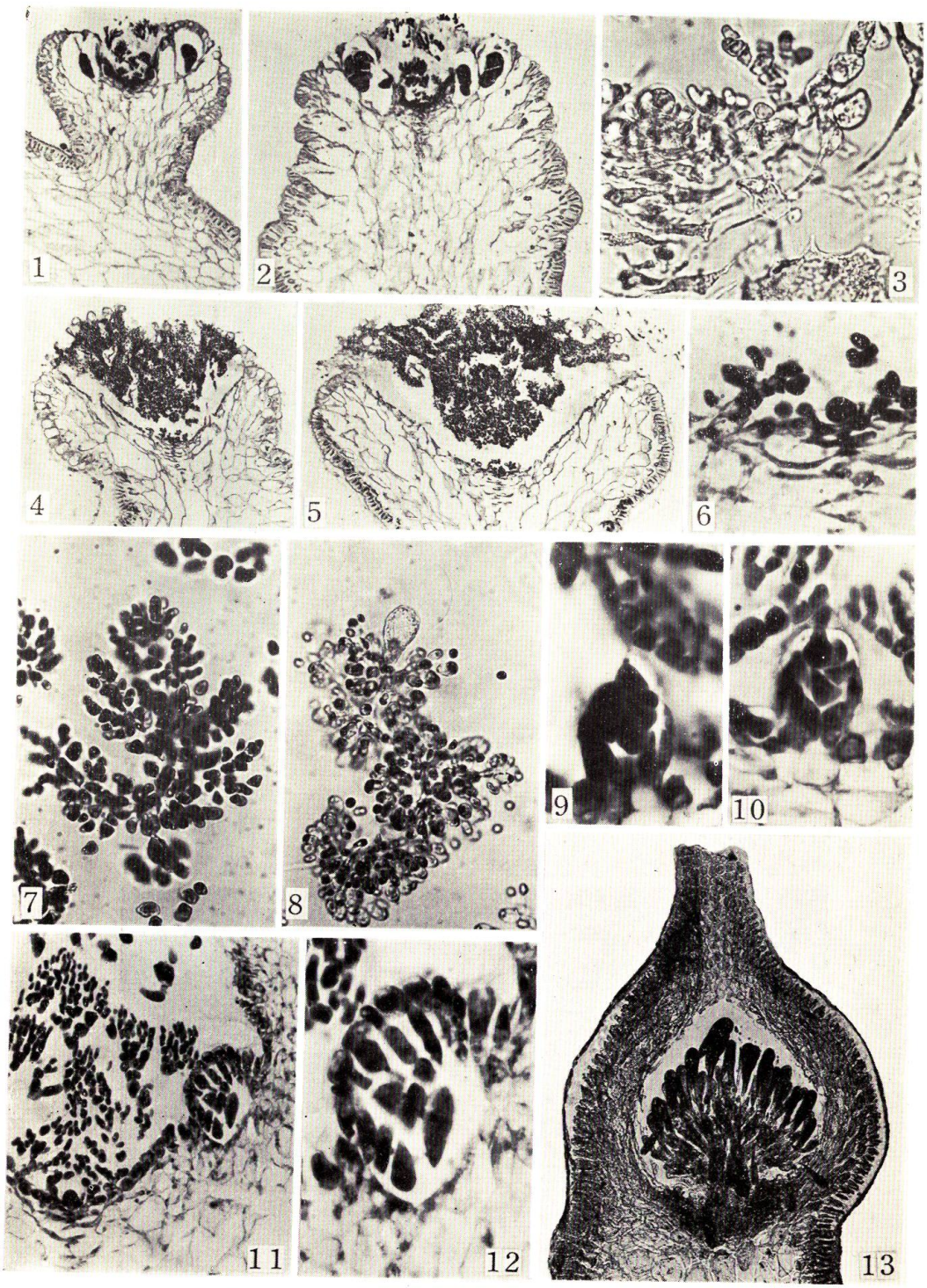

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Plate XVI

Laurencia capituliformis Yamada

Figs. 1 & 2. Median longitudinal section through a young (Fig. 1) and old (Fig. 2) stichidial branchlet ×60

Fig. 3. Part of median longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on an elongated pericentral cell which is connected to an elongated axial cell (cf. Text-fig. 42, A) ×320

Figs. 4 & 5. Median longitudinal section through two antheridial receptacles showing their development ×54

Fig. 6. Part of median longitudinal section through an antheridial receptacle, showing an antheridium-initial on an elongated pericentral cell which is connected to an elongated axial cell (cf. Text-fig. 39, D) ×320

Figs. 7 & 8. A young (Fig. 7) and a mature (Fig. 8) antheridium from a smeared preparation ×320

Fig. 9. Longitudinal section through a procarp after fertilization, showing the auxiliary cell formed on the supporting cell (cf. Text-fig. 40, B) ×600

Fig. 10. Ditto; the plane of section is at right angles to that of Fig. 9 (cf. Text-fig. 40, C) ×600

Fig. 11. Part of median longitudinal section through a fertile branchlet of a female plant, showing the growing point and a young cystocarp ×240

Fig. 12. Part of Fig. 11, a close-up of the young cystocarp, showing the initial stage of gonimoblast development (cf. Text-fig. 40, E) ×600

Fig. 13. Median longitudinal section through a ripe cystocarp ×54

Plate XVII

Laurencia cartilaginea Yamada

Fig. 1. Habit of a tetrasporangial plant in an herbarium specimen collected at Shirahama on May 22, 1963

Fig. 2. Habit of a female plant in an herbarium specimen from the same collection as above

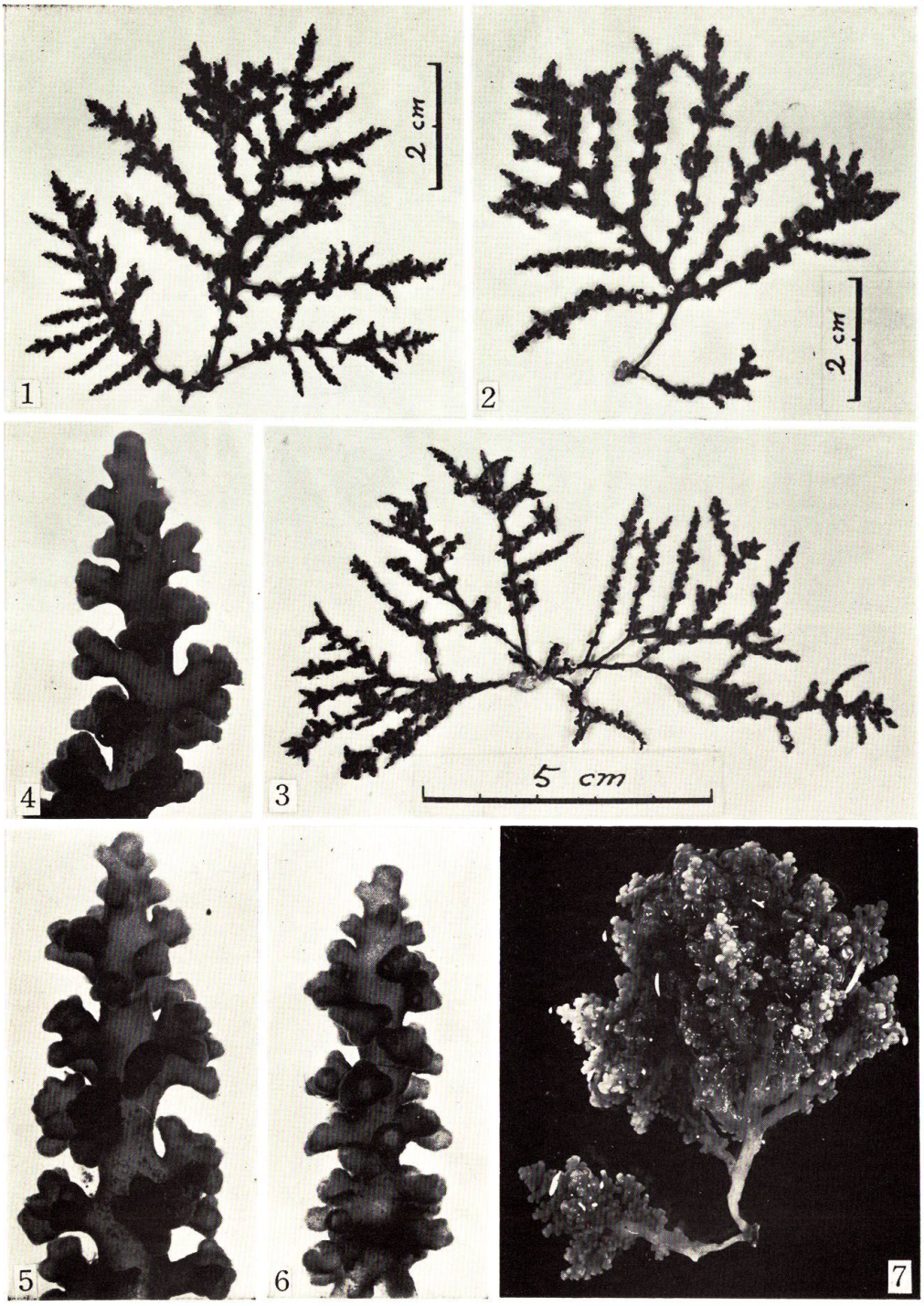
Fig. 3. Habit of a male plant in an herbarium specimen from the same collection as above

Fig. 4. Part of a tetrasporangial plant ×5

Fig. 5. Part of a female plant ×5

Fig. 6. Part of a male plant ×5

Fig. 7. Habit of a tetrasporangial plant preserved and somewhat bleached in formalin-seawater from the same collection as Figs. 1–3 ×1



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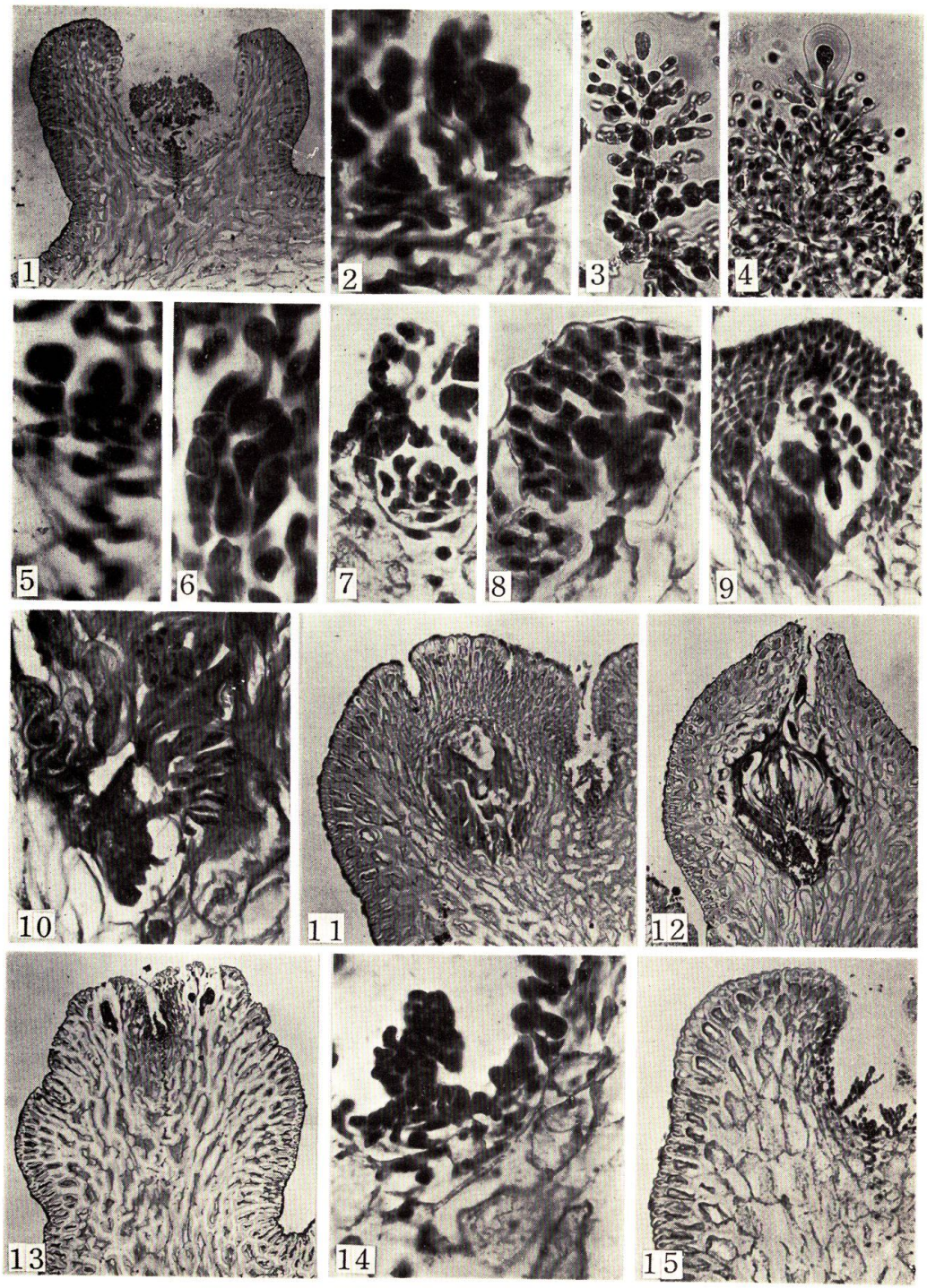

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Plate XVIII

Laurencia cartilaginea Yamada

Fig. 1. Median longitudinal section through an antheridial receptacle ×36

Fig. 2. Part of median longitudinal section through an antheridial receptacle, showing an antheridium-initial on an elongated pericentral cell which is connected to an axial cell (cf. Text-fig. 44, A) ×640

Fig. 3. Apical portion of a young antheridium in a smeared preparation (cf. Text-fig. 44, B) ×320

Fig. 4. Apical portion of a mature antheridium in a smeared preparation ×240

Fig. 5. Part of median longitudinal section through a fertile branchlet of a female plant, showing an axial cell-row with apical growing point and a procarp-initial (cf. Text-fig. 45, A) ×640

Fig. 6. Longitudinal section through a procarp ready for fertilization (cf. Text-fig. 45, D) ×640

Fig. 7. Part of median longitudinal section through a fertile branchlet of a female plant, showing a procarp on an elongated fertile pericentral cell ×360

Fig. 8. Longitudinal section through a young cystocarp, showing the initial stages of fusion-cell and gonimoblast (cf. Text-fig. 45, F) ×480

Fig. 9. Longitudinal section through a more developed young cystocarp, showing the gonimoblast development (cf. Text-fig. 45, G) ×256

Fig. 10. Part of longitudinal section through a nearly mature cystocarp, showing a well developed fusion-cell and the network of gonimoblast ×256

Fig. 11. Part of median longitudinal section through a cystocarpic branchlet ×80

Fig. 12. Median longitudinal section through a ripe cystocarp (cf. Text-fig. 46) ×48

Fig. 13. Median longitudinal section through a stichidial branchlet ×48

Fig. 14. Part of longitudinal section through a stichidial branchlet, showing a tetrasporangium-initial on an elongated pericentral cell which is connected to the elongated axial cell (cf. Text-fig. 47, A) ×360

Fig. 15. Part of apical portion of median longitudinal section through a sterile branchlet ×120