SYSTEMATIC AND ANATOMICAL STUDY OF THE GENUS *GRACILARIA* IN JAPAN*

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Contents

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Abbreviations used in the present paper

a:	apical cell.	p:	procarp.
aux:	auxiliary cell.	psm:	primordium of spermatangial mother cell.
ca:	carposporangium.		
cb:	carpogonial branch.	sc:	spermatangial conceptacle.
cbi:	carpogonial branch initial.	sm:	spermatium.
cbp:	carpogonial branch primordium.	sp:	spermatangium.
cp:	carpogonium.	spmc:	spermatangial mother cell.
fu:	fusion cell.	su:	supporting cell.
g:	gonimoblast.	ts:	tetrasporangium.
hb:	basal cell of hair.	tsm:	tetrasporangial mother cell.
hy:	hypogynous cell.	v:	vegetative cell.
nf:	nutritive filament.	ve:	ventral side.

A. Introduction

The genus *Gracilaria* was established by Greville in 1830. He assigned 14 species to this genus, of which the following four are currently retained there: *G. compressa* (C. Ag.) Grev. (now *G. bursa-pastris* (Gmel.) Silva), *G. confervoides* (L.) Grev. (now *G. verrucosa* (Huds.) Papenf.), *G. lemanaeformis* (Bory) Grev., and *G. lichenoides* (Turn.) Grev. (now *G. edulis* (Gmel.) Silva). The genus was lectotypified with *G. confervoides* by Schmitz (1889).

J. Agardh revised the genus *Gracilaria* in 1852 and distinguished three subgenera on the basis of differences in external form and internal structure.

Early concepts of the species of *Gracilaria* were mainly based on external form. However, the nature of the reproductive organs has been considered in the classification of species since 1926, when Sjöstedt revealed the developmental process of the female reproductive system of three species: *G. confervoides*, *G. compressa*, and *G. robusta* Setch. According to him, there was no true auxiliary cell, the carpogonium being the starting point of the fusion cell in all three species. Nutritive filaments were present in the first two species but absent in the last. Kylin (1930) considered the lack of nutritive filaments to be of diagnostic value and described the specimen assigned to *G. robusta* by Sjöstedt as a new species, *G. sjoestedtii*. Dawson (1949) regarded nutritive filaments as a diagnostic character at the generic level and distinguished the genus *Gracilariopsis* from *Gracilaria* on the basis of the absence of nutritive filaments and the small size of the gonimoblast cells.

In a cytological study of *Gracilaria multipartita* (Clem.) Harv. (now *G. foliifera* (Forssk.) Børg.), Greig-Smith (1954) reported that an auxiliary cell was produced by the supporting cell of the carpogonial branch and that the connection between the auxiliary cell and the fertilized carpogonium was made by a short sporogenous filament. Her observations on the carpogonium and its post-fertilization development were very different from those made by Sjöstedt.

In 1966, Papenfuss reported that the presence of nutritive filaments could not always be confirmed in British material of *Gracilaria verrucosa*. Consequently he concluded that the presence of nutritive filaments could not be used as a basis for separating *Gracilaria* and *Gracilariopsis* and thus merged the two genera.

Okamura was the first to study *Gracilaria* in Japan, recognizing 12 species between 1916 and 1936, one of which was new. Afterward, Yamada (1938, 1941) added two more species to the Japanese flora.

Ohmi (1955, 1956, 1958) made an extensive study of Japanese species, introducing the recent classification proposed by Dawson. In 1958 he gave descriptive accounts of 15 species and one forma of *Gracilaria* and of three species of *Gracilariopsis*, including one new species described in his previous paper (1956). Of these species, one each of *Gracilaria* and *Gracilariopsis* was new to Japan.

After a period of about ten years, during which very little new information on the anatomy, systematics, and ecology of Japanese gracilariaceous plants was made known, the writer (1969, 1973, 1973a, 1973b, 1974) published a series of papers on the male reproductive organ and on the distribution of the various species in Hokkaido. Especially the developmental and anatomical studies of the male reproductive organs of Japanese species have brought to light some features which seem worthy of consideration for the establishment of the relationship between *Gracilariopsis* and *Gracilaria*. As a result, the writer (1975) concluded that the genus *Gracilariopsis* should be merged with the genus *Gracilaria*, thus agreeing with Papenfuss (1966), and proposed the recognition of three subgenera on the basis of the three types of spermatangial patterns.

The present paper presents the results of earlier studies in greater detail than in previous publications. In addition, an attempt is made to determine whether the following anatomical and vegetative characters, which have been used to distinguish the species by many authors in the past, still appear to be of diagnostic value at the specific level: 1, the shape of the circumference of the main axis; 2, the degree of the constriction at the base of the branch; 3, the gradation in size of cells from the periphery to the center as observed in cross section; and 4, the feature of the nutritive filaments in a cystocarp.

This study is based on collections of 16 species made by the writer and preserved in sea water-formalin.

Before going further, the writer wishes to express his gratitude to Prof. T. Masaki, Faculty of Fisheries, Hokkaido University, for his kind advice during the course of the present study and for reading the manuscript. Cordial thanks are due to Prof. H. Ohmi, Faculty of Fisheries, Hokkaido University, for the loan of his valuable specimens of *Gracilaria* and reading the manuscript, and to Dr. T. Igarashi and Dr. H. Yabu, Faculty of Fisheries, Hokkaido University, for reading manuscript. Grateful appreciation is extended to Dr. Y. Saito, Faculty of Fisheries, Hokkaido University, for his encouragement during the present work. The writer also expresses his thanks to Dr. P. C. Silva, University of California, for correcting the English and making valuable comments. The writer acknowledges his great obligation to the following gentlemen for their offer of materials of *Gracilaria* and for their kind help during the writer's field trip: Dr. E. Fukuhara, Hokkaido Regional Fisheries Research Laboratory, Mr. S. Torii, Hokkaido Hakodate Fisheries Experimental Station, Mr. T. Kaneko, Hokkaido Central Fisheries Experimental Station, Dr. H. Kito, Tohoku Regional Fisheries Research Laboratory, Dr. N. Yamada, Shizuoka Prefectural Experiment Station, Mr. S. Sasaki, Hokkaido Kushiro Fisheries Experimental Station, Dr. M. Ohno, Usa Marine Biological

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B. Materials and methods

1. *Collecting places*

The writer collected specimens for examination at the following places (Fig. 1): several localities along the coast between Matsumae and Hakodate (including Cape Shirakami, Izumisawa, Moheji, and Shinori), Usu, Yūdō-numa, Akkeshi Lagoon, Onne Lagoon, Fūren Lagoon, Odaitō, Saroma Lagoon, Notoro Lagoon, Tokoro, Shiribetsu and Oshoro, Hokkaido; Mangoku-ura and Matsukawa-ura, Miyagi

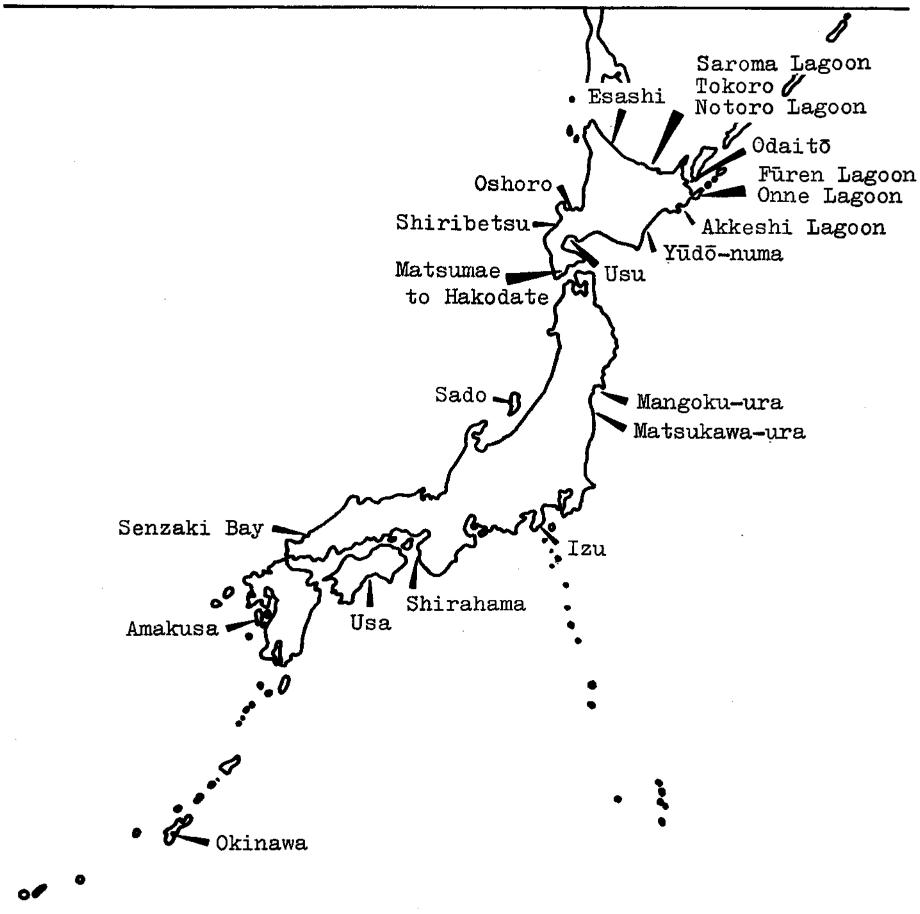


Fig. 1. Map showing collection sites.

Pref.; Shirahama, Toi and Irōzaki, Izu Pen., Shizuoka Pref.; Shirahama, Wakayama Pref.; Usa, Kōchi Pref.; Amakusa, Kumamoto Pref.; and Nashiro, Komesu and Yagachi, Okinawa Pref. Additional specimens, which were also used for the present study, were sent on the author's request from Esashi, Kitami Prov., Hokkaido, Matsushima, Miyagi Pref., Akadama, Sado Prov., Niigata Pref., and Senzaki Bay, Yamaguchi Pref.

General features of the sea bottom at each locality were noted, serving as a basis for habitat descriptions for each species.

2. *Methods for microscopic observation*

Most of the materials was fixed and preserved in 5–8% sea water-formalin for anatomical study, but Carnoy's solution was also used for fixation for the purpose of cytological observations. Sections were made by the freezing microtome and sometimes squashed preparations were used. Anilin blue and Wittmann's solution were employed for staining.

The procedure for the measurement of reproductive organs and vegetative cells

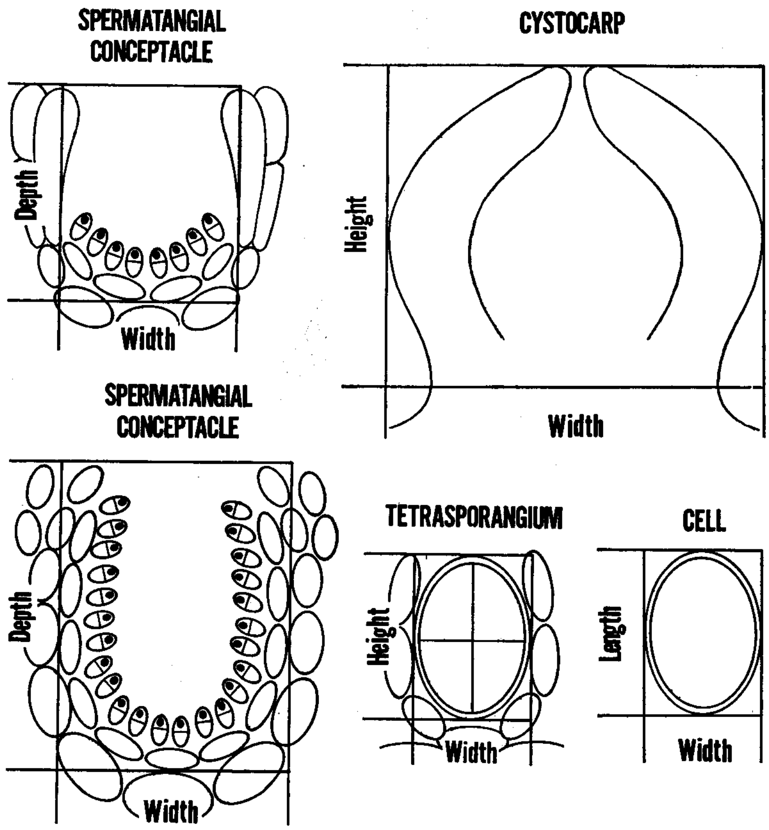


Fig. 2. Schemes showing the procedure for measuring reproductive organs and vegetative cells.

was as follows (Fig. 2): 1, cystocarpic conceptacles: widths were measured at the point of maximum external diameter, heights between the conceptacle tip and the point of greatest basal constriction. 2, spermatangial conceptacles: widths were measured at the point of maximum internal diameter, depths between the conceptacle tip and the conceptacle floor. 3; tetrasporangia: widths and heights were measured at the outside of the cell wall at the point of maximum diameter and length. 4, cells: lengths and widths were measured in the same manner as in the tetrasporangia and dimensions are always indicated in the form of length × width in μm. For medullary cells, which lack a definite length/width orientation, the larger measurement is given first.

C. General considerations

1. *External form of the frond and basal constriction of the branch*

As was mentioned in the Introduction, species of *Gracilaria* were at first classified solely on the character of the stem — whether cylindrical, partially compressed, or flattened. Anatomical structure was introduced into the classification of this genus by J. Agardh (1852–1901).

In 1948, May found that frond shape, which until then had been considered a stable, genetically fixed character, was rather changeable in some Australian species. For example, *G. lichenoides* had been characterized by its cylindrical form, but May also described a flattened form. Consequently she concluded that external form was not always a reliable diagnostic character.

Japanese species have been classified generally into two groups depending upon whether the frond is flattened or cylindrical. The cylindrical species were further divided into two groups depending upon the degree of constriction at the base of the branch (Okamura, 1936). The frond form of each of the eight cylindrical and four flat species described by Okamura has been confirmed by the present study. As to the basal constriction of the branch, Ohmi (1958) considered the degree of this constriction to be an important character in distinguishing among three species: *G. verrucosa*, *G. chorda* Holmes, and *G. blodgettii* Harv. From personal observation, however, it would seem that this character varies with age and habitat. Especially in *G. verrucosa*, branches both with and without a constriction are often observed in the same frond. Basal constriction of branches is not pronounced in *G. chorda*, but in *G. blodgettii* the base of a branch is always markedly constricted. In Japanese species, at least, this character thus seems to be of limited diagnostic value.

2. *The hair and its basal cell*

Rosenvinge (1911) was the first to report the existence of hairs in the genus *Gracilaria*. Sjöstedt (1926) described their development and structure in *G. bursa-pastoris* (as *G. compressa*).

Hairs have been observed in all Japanese species of *Gracilaria*, although the frequency of their occurrence varies between individuals. A hair-cell primordium is a transformed superficial cell, not differing in size from surrounding vegetative cells in the beginning. A protuberance is produced from the apex of the primordium after enlargement of the cell volume. The protuberance grows to be a hair which attains a certain length. A constriction takes place at the base of the hair, so that in the mature condition the hair and its basal cell are connected by a pit.

A hair contains about 10–15 nuclei in its middle portion or above. Hairs may be found throughout the frond, but usually occur only in younger portions. Owing to the ephemeral nature of the hairs, only the basal cells remain in older portions of the frond, easily recognized by their large size and densely protoplasmic content.

The mode of hair formation observed by the writer agrees fundamentally with that described by Sjöstedt. Hairs are sparse, but more or less uniformly distributed over the frond surface in most Japanese species. In *G. punctata* (Okam.) Yamada and *G. arcuata* Zanard., however, they are grouped in extraordinary sorus-like assemblages, a discovery made in the present study. In *G. punctata* the clusters of basal cells of hairs appear as dark spots to the naked eye (Pl. 17, figs. 1, 4).

3. *Gradation in size of cells from cortex to medulla*

J. Agardh (1901) differentiated series within the subgenera of *Gracilaria* on the

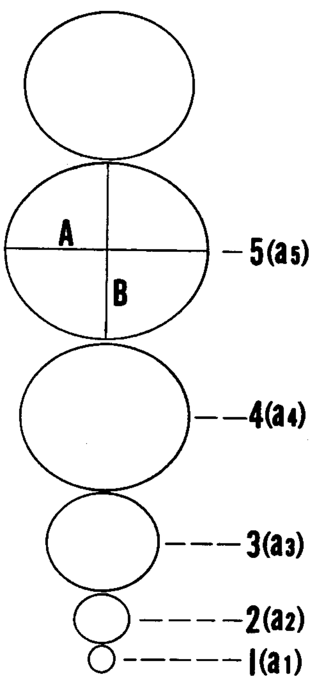


Fig. 3. Diagram showing the vegetative cells in transverse section of frond. A and B indicate long and short diameters respectively. The numbers show the order of cells from outermost cell to medulla.

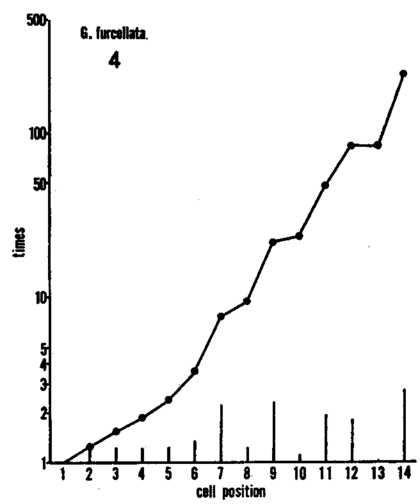


Fig. 4. Semi-logarithmic graph showing the gradation of cell size from outermost cell to medulla. ●—●: the increased ratio of cell size to outermost cell; —: the increased ratio of cell size to the preceding cell.

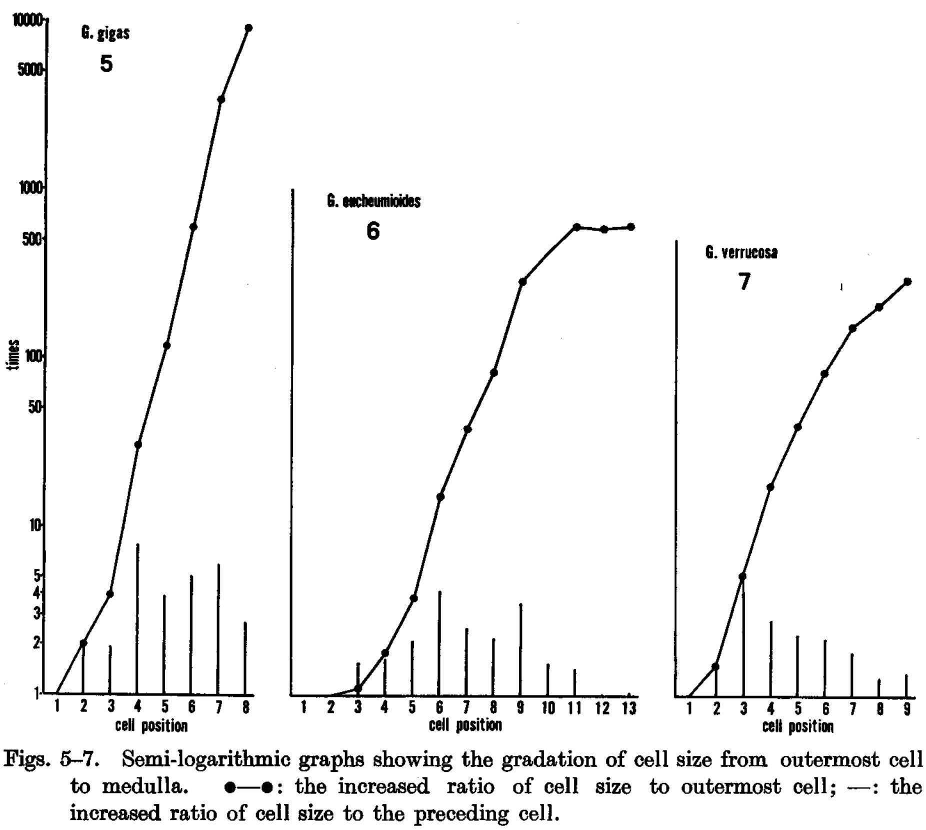
basis of several structural differences as seen in transverse section of the frond. Gradation in size of cells from cortex to medulla was used by J. Agardh to differentiate between two series of species, the Macrocystideae, with an abrupt change of size, and the Microcystideae, with a gradual change of size. This character has been used in distinguishing species by several authors (May, 1948; Dawson, 1949; Ohmi, 1958).

Previously, the rate of change in size of cells has been judged simply from rough observations under the microscope. The writer has attempted to establish a statistical treatment of cell size in Japanese species. Cell size is expressed as an area calculated by using the following formulae (Fig. 3):

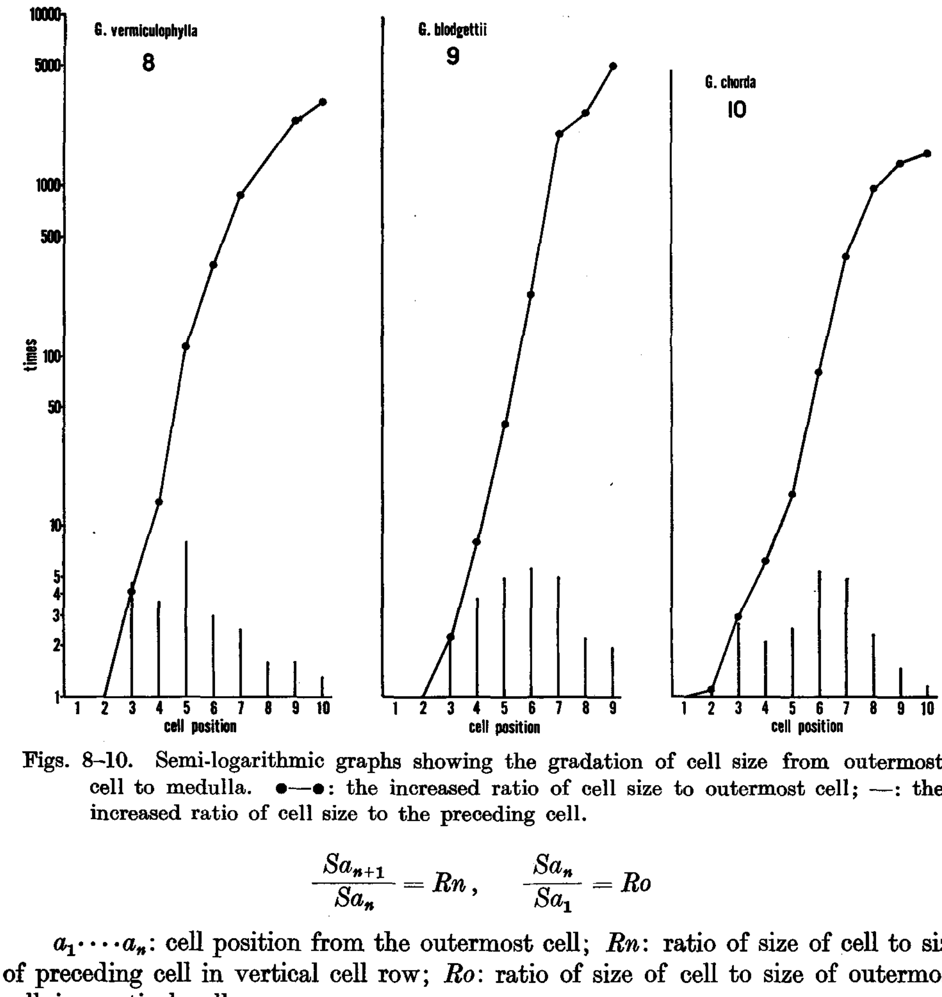
$$\frac{A+B}{2}=M, \qquad \frac{M}{2}=r, \qquad \pi r^2=S$$

A: cell length; B: cell width; M: mean cell width; r: radius; S: cell size.

The size of each cell in a vertical cell row was compared with that of the next inner cell and with the outermost cell, respectively, by using the following formulae (Fig. 3):



Figs. 5–7. Semi-logarithmic graphs showing the gradation of cell size from outermost cell to medulla. ●—●: the increased ratio of cell size to outermost cell; —: the increased ratio of cell size to the preceding cell.



Figs. 8–10. Semi-logarithmic graphs showing the gradation of cell size from outermost cell to medulla. ●—●: the increased ratio of cell size to outermost cell; —: the increased ratio of cell size to the preceding cell.

$$\frac{Sa_{n+1}}{Sa_n} = Rn, \quad \frac{Sa_n}{Sa_1} = Ro$$

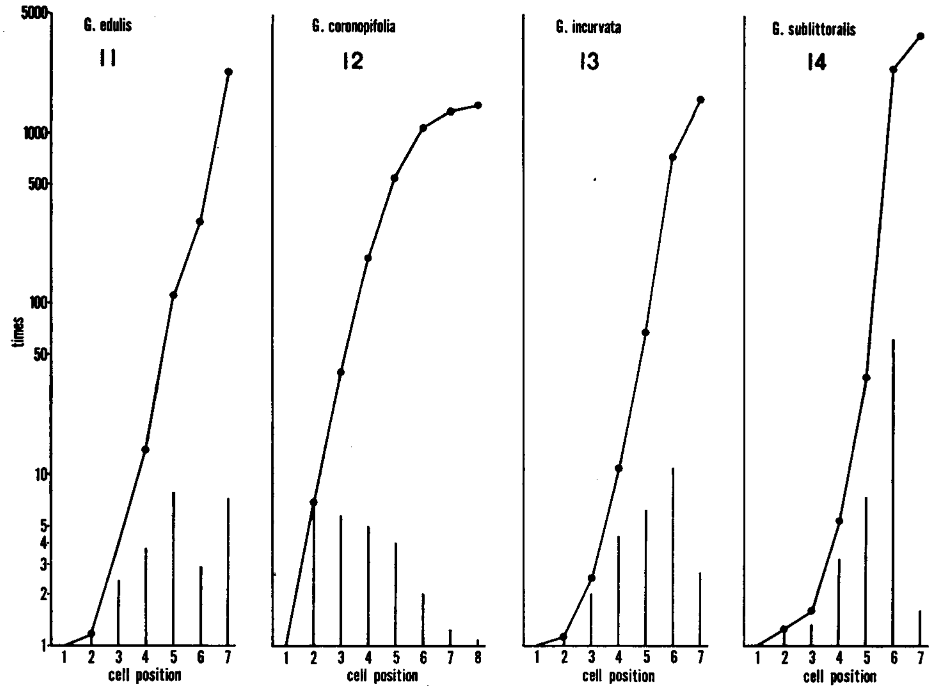
$a_1 \cdots a_n$: cell position from the outermost cell; Rn: ratio of size of cell to size of preceding cell in vertical cell row; Ro: ratio of size of cell to size of outermost cell in vertical cell row.

When Rn is 4 or less, the transition in cell size is gradual. For example, in *G. furcellata* (Mont.) Zanard., an Australian species which May (1948) considered as having a linear gradation in cell size, measurements taken from May's fig. 9 yield a value for Rn less than 3. In the Japanese species *G. eucheumioides* Harv., which also shows a linear gradation in cell size, the Rn values is somewhat greater than 4 (Fig. 6). Sudden change in cell size is correlated with Rn values of 5 and above.

Statistical examination of 15 Japanese species shows that all except *G. eucheumioides* have a sharp demarcation between cortex and medulla, although there is some variation in the transition rate (Figs. 5–19).

4. *Tetrasporangium*

Tetrasporangia are scattered over the surface of the frond except in the basal and apical portions. The primordium is a transformed superficial cell and is not



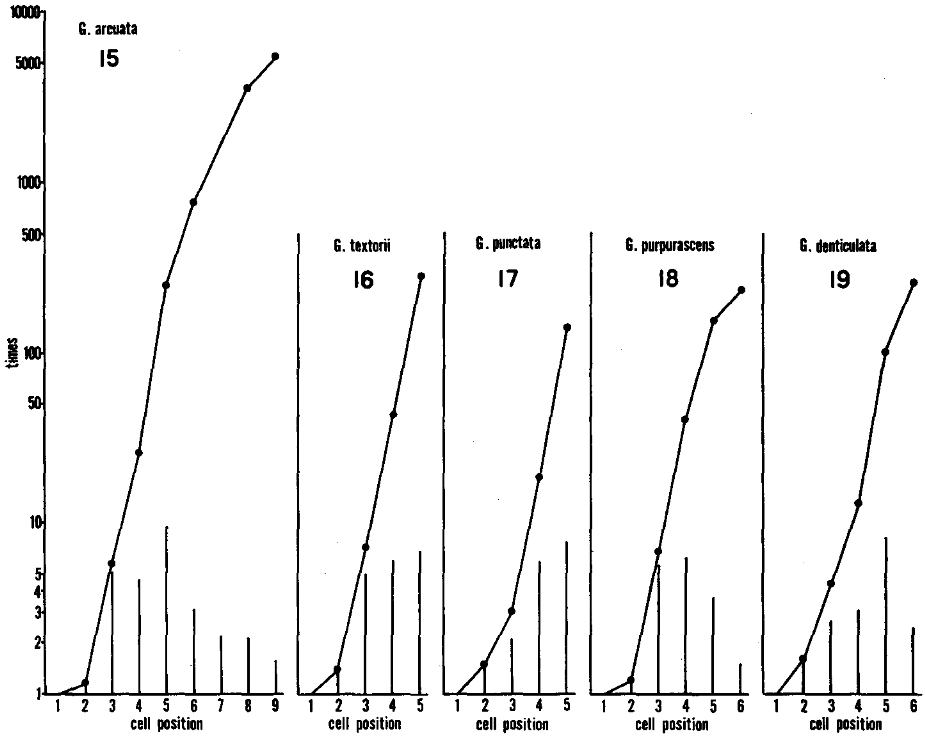
Figs. 11–14. Semi-logarithmic graphs showing the gradation of cell size from outermost to medulla. ●—●: the increased ratio of cell size to outermost cell; —: the increased ratio of cell size to the preceding cell.

different in its size and position from surrounding vegetative cells in early stages. However, a primordium may be distinguished by its karyological state in that it always contains a single resting nucleus even when the nucleus of a neighboring cortical cell is in prophase. A primordium enlarges into a tetrasporangial mother cell. Cell divisions take place cruciately in the fully grown mother cell, and the resulting tetrasporangium is surrounded by narrowly elongated and inwardly curved vegetative cells (Fig. 25). Division of the tetrasporangial mother cell is irregular in some species and often tetrahedral in *G. vermiculophylla* (Ohmi) Papenfuss (Pl. 29, fig. 6). Tetrasporangia are easily distinguished from surrounding vegetative cells under low magnification by their bright red color.

The formation of tetrasporangia in Japanese species of *Gracilaria* is as described in other species by Sjöstedt (1926) and Kylin (1930). Tetrasporophytes have been reported previously for 17 species in Japan. The writer has confirmed nine of these and described tetrasporophytes for two additional species (Table 1).

5. *Carpogonium and its development*

The carpogonium in *Gracilaria* has been observed by Bornet and Thuret (1878), Johnson (1887), Phillips (1925), and Sjöstedt (1926). The investigtions of the first three authors, however, were fragmentary and inaccurate in part (cf. Sjöstedt,

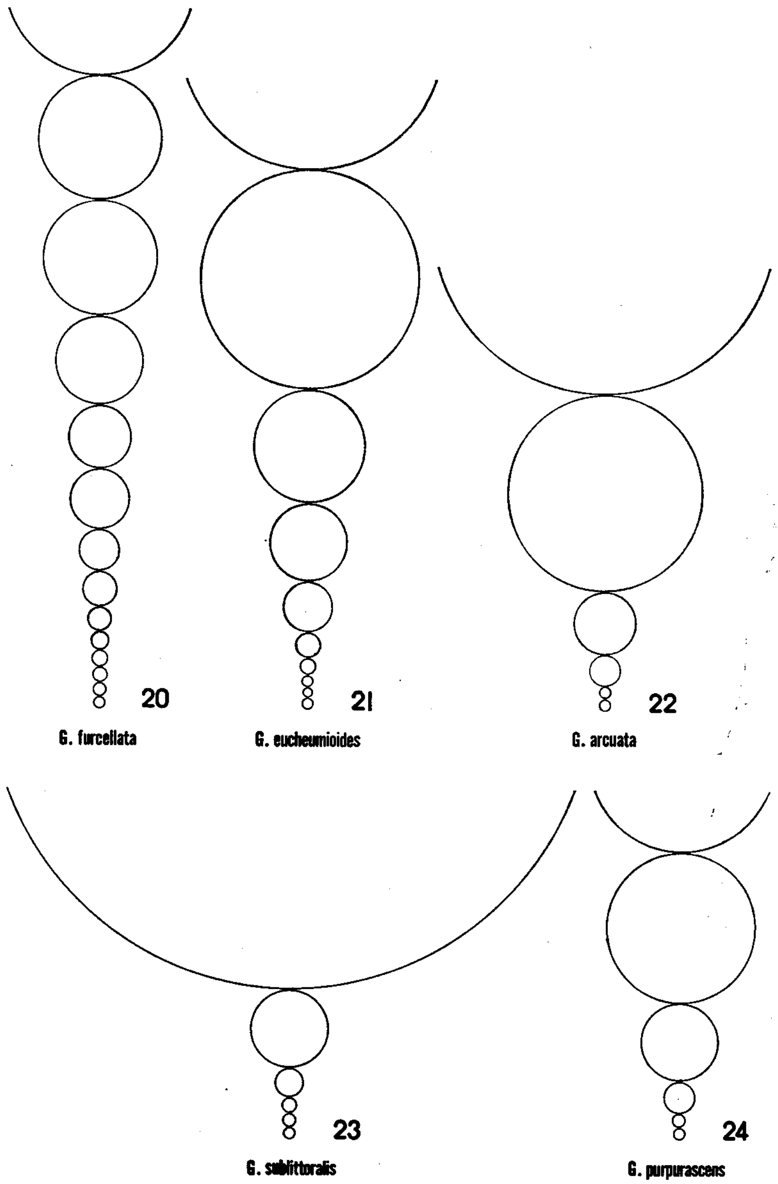


Figs. 15–19. Semi-logarithmic graphs showing the gradation of cell size from outermost to medulla. ●—●: the increased ratio of cell size to outermost cell; —: the increased ratio of cell size to the preceding cell.

1926). The last-mentioned author was the first to make detailed observations on the carpogonium and its development in *G. verrucosa* (as *G. confervoides*), *G. bursa-pastoris* (as *G. compressa*), and *G. sjoestedtii* (as *G. robusta*). He reported that the fertilized female nucleus remained in the carpogonium, which fused with the bottom cell of a vegetative filament arising from the supporting cell. This bottom cell thus functions as a nutritive auxiliary cell. Later, Greig-Smith (1954) reported in *G. foliifera* (as *G. multipartita*) the existence of a generative auxiliary cell which is cut off by the supporting cell, becomes connected to the fertilized carpogonium by a short filament, and originates the fusion cell. According to these observations, this species should be transferred into the Rhodymeniales or Ceramiales. The writer has never encountered this situation in Japanese species.

Dawson (1949) described the carpogonial branch in 8 species from the northeast Pacific region of America. The carpogonial branch has not been known hitherto in Japanese species, but is described here in 11 species for the first time (Table 1).

The primordium of the carpogonium is a transformed cortical cell lying close to the frond surface. It cuts off a cell terminally by an approximately transverse wall. The lower cell becomes the supporting cell while the upper cell elongates and



Figs. 20–24. Diagrams showing the patterns of gradation of cell size. Fig. 20 shows typical gradual transition. Figs. 21 and 22 are representative of the most gradual and the most abrupt transition in cylindrical species. Figs. 23 and 24 the same in flattened species.

Table 1. Japanese species of *Gracilaria* and the author who first described the reproductive organs. An asterisk indicates the kind of reproductive organ that the writer has been able to confirm.

Species name	Cystocarp	Carpogonial branch	Spermatangium			Tetra-sporangium
			Chorda type	Textorii type	Verrucosa type	
Gracilaria chorda	Okamura* (1916)	Yamamoto (present)	Yamamoto (1969)			Okamura* (1916)
G. bursa-pastris	Okamura (1927)			Ohmi (1958)		Okamura (1927)
G. gigas	Okamura* (1927)	Yamamoto (1973)		Yamamoto (1969)		Okamura* (1927)
G. blodgettii	Okamura* (1936)	Yamamoto (present)		Yamamoto (present)		Okamura* (1936)
G. textorii	Okamura* (1936)	Yamamoto (present)		Ohmi* (1955)		Okamura* (1936)
G. incurvata	Okamura* (1931)	Yamamoto (present)		Yamamoto (1973)		Ohmi* (1958)
G. punctata	Yamada* (1941)	Yamamoto (present)		Okamura* (1929)		Okamura (1929)
G. denticulata	Yamada* (1938)			Yamamoto (present)		Yamamoto (present)
G. purpurascens	Okamura* (1936)	Yamamoto (present)		Yamamoto (present)		Ohmi (1958)
G. purpurascens f. *spinulosa*	Yamada (1941)			Okamura (1934)		Okamura (1934)
G. verrucosa	Okamura* (1916)	Yamamoto (present)			Okamura* (1916)	Okamura* (1916)
G. vermiculophylla	Ohmi* (1956)	Yamamoto (present)			Ohmi* (1956)	Ohmi* (1956)
G. arcuata	Okamura* (1931)	Yamamoto (present)			Ohmi* (1958)	Ohmi* (1958)
G. edulis	Yamamoto (present)				Yamamoto (present)	Ohmi (1958)
G. sublittoralis	Ohmi* (1958)	Yamamoto (present)			Yamamoto (present)	Ohmi* (1958)
G. coronopifolia						Ohmi (1958)
G. crassa						Ohmi (1958)
G. salicornia						Ohmi (1958)
G. eucheumioides						Yamamoto (present)

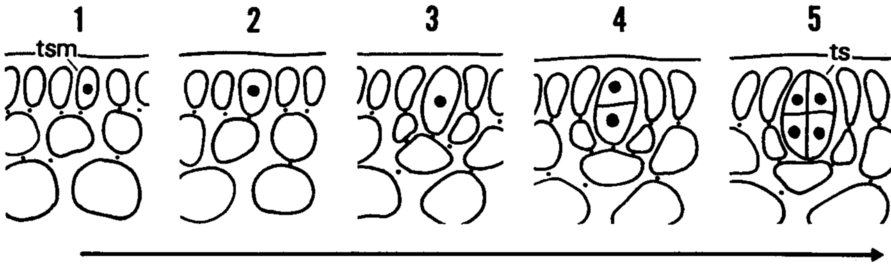


Fig. 25. Scheme showing the development of a tetrasporangium.

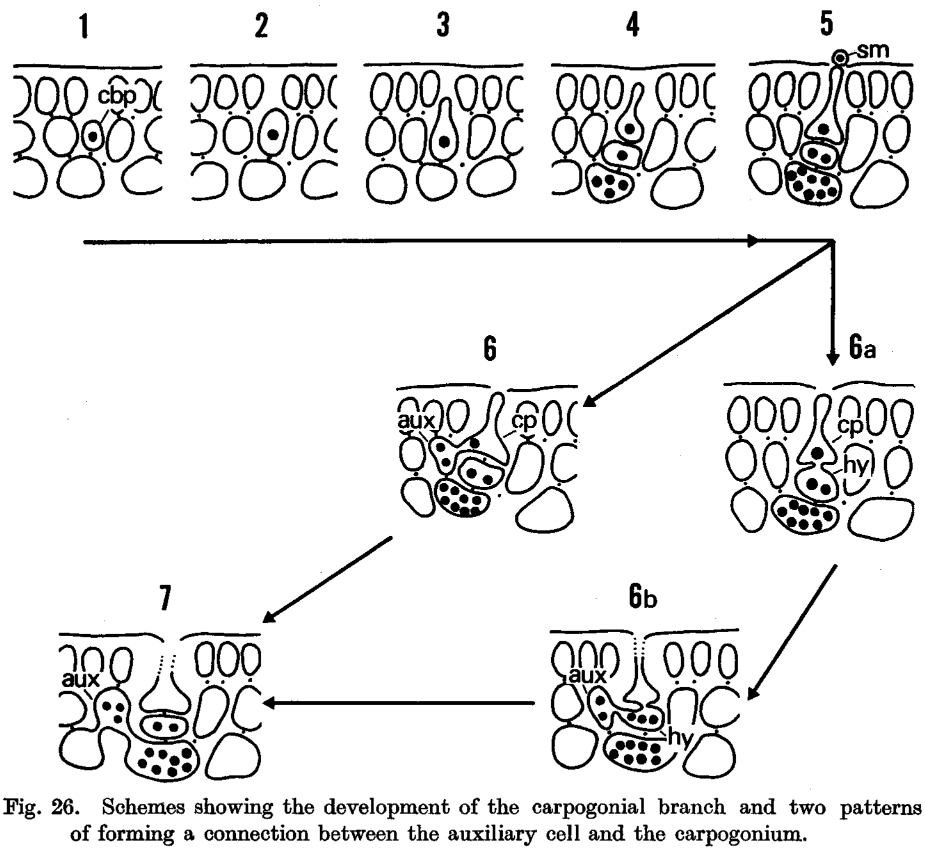


Fig. 26. Schemes showing the development of the carpogonial branch and two patterns of forming a connection between the auxiliary cell and the carpogonium.

divides transversely. The apical cell of the resulting two-celled branch elongates into a trichogyne and functions as the carpogonium, while the lower cell becomes the hypogynous cell (Pl. 25, figs. 1–4). Carpogonial branches may be found throughout the frond except in basal and terminal portions.

The trichogyne is rather short and protrudes a little from the frond surface. One nucleus is seen in the carpogonium and two in the hypogynous cell. While the supporting cell contains only one or two nuclei initially, at maturity it may contain four to eight (Pl. 6, figs. 4–7; Pl. 14, figs. 1–5).

The vegetative cells surrounding the carpogonial branch are very rich in chloroplasts and contain several nuclei which are clearly visible with stain and larger than those in other parts of the vegetative tissue.

After fertilization, a connecting tube emerges from the inflated basal portion of the carpogonium and effects union with the basal cell of a lateral branch filament produced by the supporting cell. The fertilized carpogonial nucleus (diploid) probably enters the basal cell, which could thus be considered an auxiliary cell. In exceptional cases, occurring rarely in only a few species and always in association with the usual pattern described above, the pit connection between the carpogonium and the hypogynous cell gradually widens, allowing the diploid nucleus to move into the hypogynous cell which then forms a connection with the auxiliary cell (Fig. 26). The connecting tube is difficult to observe because of its relatively ephemeral nature. Immediately after the completion of this connection, the carpogonium becomes poor in content and finally degenerates (Pl. 14, fig. 5; Pl. 18, fig. 5).

After fusing with the connecting tube, the auxiliary cell unites with a neighboring vegetative cell and communicates with the supporting cell through the widened pit (Fig. 26: 7). These associated cells seem to have the function of providing nutriment to the carposporophyte. As the process advances, the auxiliary cell serves as the starting-point of a large fusion cell (Pl. 6, fig. 1). This coalescent cell involves the hypogynous cell and the supporting cell and eventually produces gonimoblasts on its periphery (Pl. 3, fig. 3).

In Japanese species of *Gracilaria* the carpogonial branch is always two-celled, as described in European and American species by Sjöstedt (1926), Kylin (1930), and Dawson (1949). Its post-fertilization development, however, differs from that previously reported. As already mentioned, Sjöstedt concluded that there was no generative auxiliary cell in this genus, the fusion cell originating from the fertilized carpogonium. In Japanese species, by contrast, the carpogonium degenerates and the auxiliary cell serves as the starting-point of the fusion cell.

In members of Gigartinales with procarps, there are two kinds of auxiliary cells with respect to their location. In certain genera (e.g. *Hypnea*) the auxiliary cell is the basal cell of a lateral branch filament produced by the supporting cell. In most other genera, however, the supporting cell functions as the auxiliary cell (cf. Fritsch, 1945, pp. 663–669). On the basis of the results of the present study, the genus *Gracilaria* would be referred to the former group of procarpic members.

In a recent publication, Oza (1976) reported that in *G. corticata* (J. Ag) J. Ag. from India he found some evidence that the fertilized carpogonium fused with the hypogynous cell, the supporting cell, and sterile cells. Although he interpreted the situation as lacking an auxiliary cell, his figures are sufficiently similar to the writer's as to suggest the need for re-examining the Indian species.

6. *Cystocarp and nutritive filaments*

The cystocarp is known for most species of *Gracilaria*. In Japan it is known for 14 species, 12 of which have been examined with respect to nutritive filaments by the writer. In addition, the cystocarp in one species is first described in the present paper (Table 1).

While the shape and the size of mature cystocarps are variable between species, a relationship seems to exist between the form of the frond and the external appearance of the young cystocarp. Specifically, a young cystocarp produced on a cylindrical frond is ovoid with a height greater than its outer diameter, while a young cystocarp on a flat frond is compressed. At maturity, however, the cystocarps in both cases become mostly similar not only in shape, but also in the degree of constriction at their bases. The cells which constitute the pericarp vary in shape in the course of the development of the cystocarp. In early stages these cells elongate and show an anticlinal arrangement while in advanced stages they become flattened parallel to the surface of the cystocarp.

In conclusion, it is apparent that the external appearance of the cystocarp and the shape of the cells in the pericarp are not reliable as diagnostic characters.

The term "nutritive filament" has been used for the filaments formed by the gonimoblast cells and growing toward the pericarp. Regarding their function, Sjöstedt (1926) speculated that nourishment was supplied from the pericarp through the tubular cells to the gonimoblast. The term "nutritive filament" is retained here, even though its function has not been confirmed.

In the course of carposporophyte development, nutritive filaments are produced from the margin of the gonimoblast tissue, with which they are connected through a pit (Pl. 7, figs. 1–2). Some of them reach the pericarp and penetrate that tissue, their irregularly shaped tips connecting with cells of the pericarp through several pits (Pl. 7, fig. 1). Others, even in a mature cystocarp, do not reach the pericarp, lying free in the cystocarp cavity. The filaments are usually unbranched, but sometimes they branch dichotomously. Most filaments possess dense cytoplasmic contents and stain well with such stains as haematoxylin and anilin blue.

The number of nutritive filaments varies between species. For example, in *G. punctata*, *G. purpurascens* (Harv.) J. Ag., *G. denticulata* (Kütz.) Weber van Bosse, and *G. vermiculophylla*, they are sometimes too few to find even in the fully developed cystocarp or are too short to reach the pericarp (Pl. 21, fig. 3; Pl. 24, fig. 1; Pl. 29, fig. 1). On the other hand, they are abundant and easily discernible in early stages of gonimoblast formation in *G. verrucosa* and *G. sublittoralis* Yamada et Segawa (Pl. 34, fig. 3).

Because of the irregularity of the number of nutritive filaments in species assigned to *Gracilaria* and their unexpected occurrence in species of *Gracilariopsis* (e.g. *G. vermiculophylla*), the writer concludes that it is not a character of diagnostic value at the generic level. The relationship between the incidence of nutritive filaments and the types of spermatangial patterns is discussed below.

7. *Spermatangium and its pattern*

The spermatangia in the genus *Gracilaria* were described by Thuret (*in* Le Jolis, 1863) in *G. verrucosa* and by Thuret (*in* Bornet, 1878) in *G. armata* (C. Ag.) J. Ag. and *G. bursa-pastoris* (cf. Hoyle, 1975). In his treatment of Gracilariaceae on the Pacific coast of Mexico and the United States, Dawson (1949) revealed that three diverse types of spermatangial patterns exist and that these are of diagnostic value in separating certain species. A fourth type was reported by Børgesen (1953) in *G. multifurcata* Børg. from Mauritius and by Ohmi (1958a) in *G. henriquesiana* Hariot from the Gold Coast (now Ghana). In this pattern, the spermatangial conceptacles are buried in the thallus near the surface, without openings. Before the work of the writer, male plants were known for only 7 species in Japan (Table 1). Through careful examination of 13 Japanese species, including eight in which the spermatangium was discovered for the first time, the

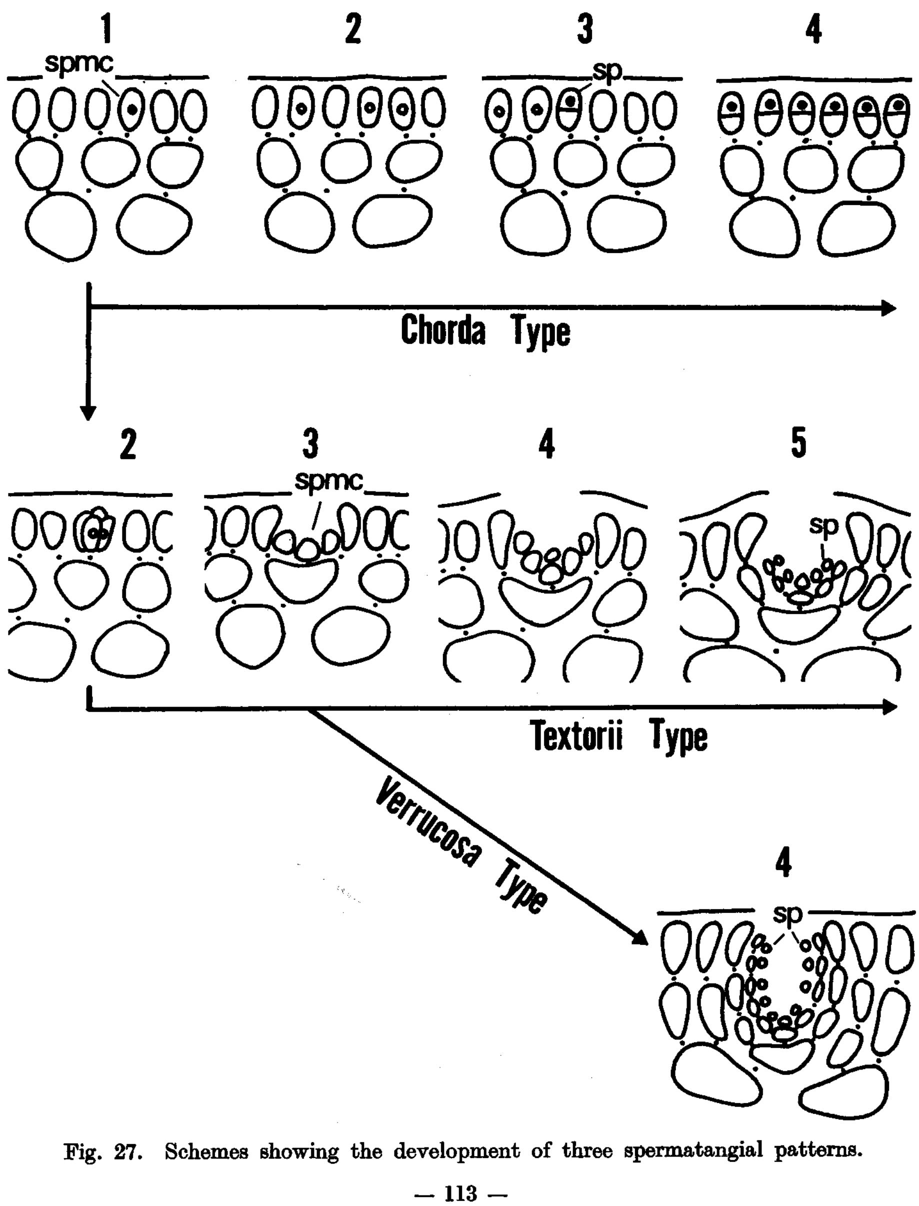


Fig. 27. Schemes showing the development of three spermatangial patterns.

writer has determined that each of the first three of these types is represented in Japan. These three types are named the Chorda type, the Textorii type, and the Verrucosa type. The development of the spermatangium in each type is described as follows:

1. *Chorda type*: This type is represented by *Gracilaria chorda*. A spermatangial mother cell is converted from an outermost cell of the cortical layer. No branch system of mother cells is formed. Spermatangia are produced by the transverse division of mother cells and are continuously superficial (Pl. 4, figs. 3–7).

2. *Textorii type*: This type is represented by *Gracilaria textorii* (Sur.) De Toni. A spermatangial mother cell primordium is converted from an outermost cell of the cortical layer. Each mother cell primordium forms a branch system by dividing repeatedly. The growth of a branch system results in the formation of a shallow cup-shaped conceptacle. The surrounding cortical cells become elongated owing to the compression caused by the developing branch system, which finally covers the floor of the conceptacle. The elongated cortical cells form a slightly raised nemathecium in which the conceptacles are embedded (Pl. 11, figs. 3–5; Pl. 15, fig. 5).

3. *Verrucosa type*: This type is represented by *Gracilaria verrucosa*. A spermatangial mother cell primordium is converted from an outermost cell of the cortical layer. Each mother cell primordium forms a branch system by dividing repeatedly. The vigorous growth of a branch system results in the formation of a deep, pot-shaped conceptacle and compresses the surrounding vegetative cells, causing them to become narrow and elongated. Spermatangia are produced by one or two divisions of each mother cell of the branch system, which finally covers the entire inner surface of the conceptacle. The conceptacles are not raised above the frond surface (Pl. 27, figs. 4–10).

The phylogenetic relationships among these types are discussed below.

8. *The relationship between Gracilariopsis and Gracilaria*

It has been considered that the most definite character for the distinction between species of the genus *Gracilaria* is the shape of the frond including the contour of the cross section and branching. Though these characters are important and used widely in separating species at present, the distinction of species is often confused because of the frequent occurrences of diverse environmental growth forms. Therefore, several proposals including the comparison of certain reproductive features have been made by previous workers to give a more detailed treatment of the classification of the genus *Gracilaria* and of the family Gracilariaceae. In the foregoing pages an attempt has been made to determine whether these characters are of diagnostic value and to obtain a better understanding of the relationships among Japanese species. At the same time, a problem has existed in differentiating among groups of species, especially between those assignable to *Gracilariopsis* and those remaining in *Gracilaria*.

As mentioned in the Introduction, *Cracilariopsis* was distinguished from *Gracilaria* by Dawson mainly on the basis of the absence of nutritive filaments. A second character concerns the size of the gonimoblast cells, which supposedly are small in *Gracilariopsis*, large in *Gracilaria*. Dawson's segregation was accepted by many authors, but Papenfuss proposed that these two genera should be merged, the reasons being that the presence of nutritive filaments can not always be confirmed in British material of *Gracilaria verrucosa* (the type species of its genus) and that there is no fundamental difference in the size of the gonimoblast cells in that species as compared with *Gracilariopsis sjoestedtii* (the type species of its genus).

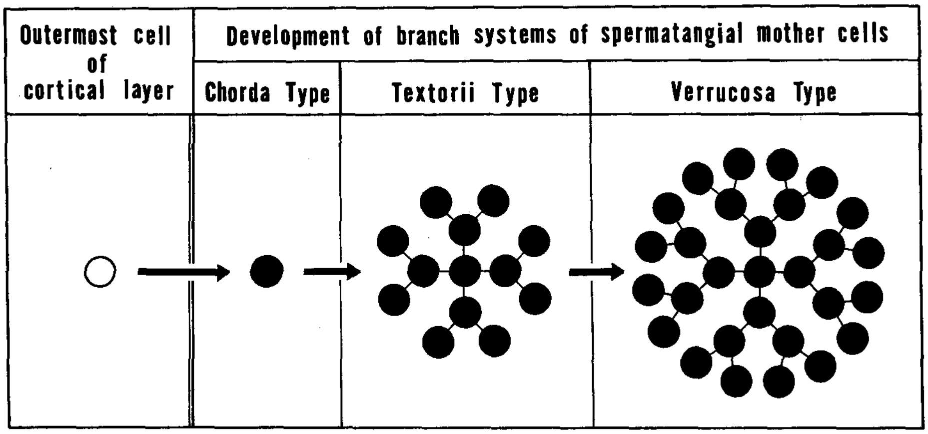


Fig. 28. Scheme showing possible phylogenetic line of advance among the three spermatangial patterns.

In a careful examination of Japanese materials, the writer found that the nutritive filaments varied considerably in number not only between species, but also in different cystocarps in the same species. Taking Papenfuss's results and the writer's observations into consideration, it seemed very difficult to draw a definite line between these two genera on the basis of the presence or absence of nutritive filaments. As a result, the writer tried to establish a possible relationship between the two genera on the basis of the three spermatangial patterns in Japanese plants which he had reported previously in detail (Yamamoto, 1975). As stated in the section on the Spermatangium and its pattern, these three types vary with respect to the degree of the conversion of the outermost cortical cells into spermatangial mother cells or mother cell primordia. In the Chorda type, all of the outermost cells may be converted into mother cells. In the other two types, on the other hand, there are some outermost cells that always remain sterile. The number of mother cell primordia per unit area is greater in the Textorii type than in the Verrucosa type, and consequently the difference in the density of the conceptacles between these two types is apparent even in surface view. The fully mature conceptacles in the former are so crowded as to come in contact with one another and fuse in some cases. The conceptacles in the latter are distinctly separated by the outermost vegetative cells even at maturity (Figs. 28–29).

In view of the formation of a branch system of mother cells that covers the entire inner surface of a deep conceptacle, the Verrucosa type is considered to be the most efficient type with respect to spermatangial production. It seems

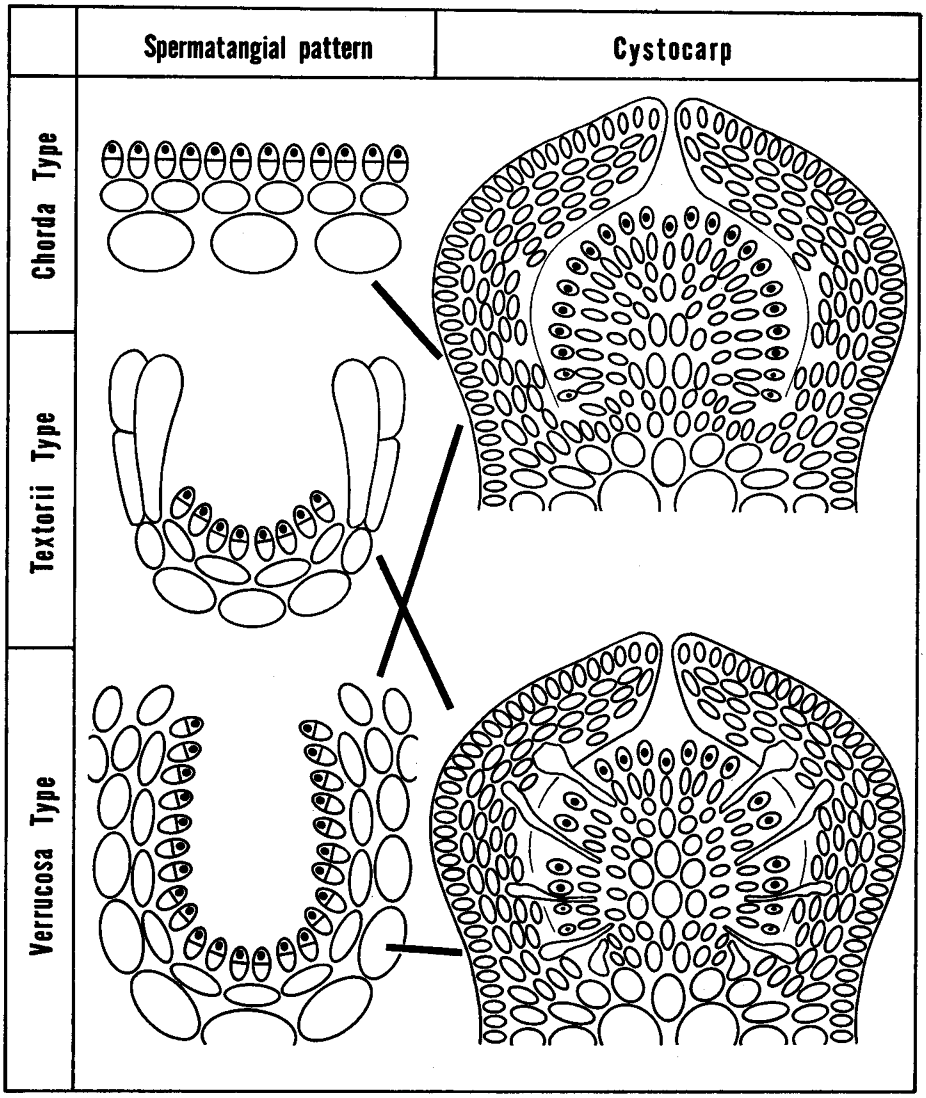


Fig. 29. Scheme showing the relationship between the three spermatangial patterns and the structure of the cystocarps.

likely that the Chorda type is the most primitive from the view point of phylogeny and the Verrucosa type the most advanced. The writer has looked in vain among Japanese materials for a bridge between the Chorda type (continuous superficial layer) and the other two types (conceptacles). It would appear, however, that *Gracilaria symmetrica* Dawson and *Gracilariopsis costaricensis* Dawson, which Dawson (1949) described from Costa Rica as new species, are intermediate forms. In these species there is an anastomosis of small, circular, superficial sori separated by sterile cortical cells, but further detailed study of the developmental process would be necessary to clarify the situation.

After reviewing the literature (Okamura, 1916, 1929, 1936; Dawson, 1949, 1961; Ohmi, 1958; Papenfuss, 1966) and examining the Japanese species of *Gracilaria*, the writer suggests that a relationship may exist between the type of spermatangial pattern and the presence or absence of nutritive filaments (Fig. 29). Species belonging to the Chorda type always have cystocarps destitute of nutritive filaments, whereas the Textorii type appears exclusively in species having cystocarps provided with nutritive filaments. Though the Verrucosa type is almost the same as the Textorii type, Dawson and Papenfuss reported some species destitute of nutritive filaments in this type (Fig. 29). Nutritive filaments are variable in number even in the same species depending on age and habitat, and are also found frequently in species usually assigned to the genus *Gracilariopsis*. The use of the nutritive filaments as a taxonomic character is thus seen to be unreasonable. Each type of spermatangial patterns, on the other hand, can be distinctly separated from each other in anatomy and arranged in a phylogenetic line. It thus seems more reasonable to consider the type of spermatangial pattern as a fundamental character and the nutritive filaments as a subsidiary element in the systematics of this group of species. Papenfuss's proposal that the genus *Gracilariopsis* should be merged with the genus *Gracilaria* is therefore supported.

In conclusion, the developmental process of spermatangial formation, especially the presence and nature of the conceptacle and the branch system of mother cells, is considered to be of high diagnostic value. It thus seems reasonable that the genus *Gracilaria* be divided into the following three subgenera on the basis of the three types of spermatangial patterns: *Gracilariella, Textoriella* and *Gracilaria.*

D. Key to the species of *Gracilaria*

The specific identification of *Gracilaria* is often difficult when sexual organs are not available. Therefore, a key using vegetative characters solely is given in addition to one based on both reproductive and vegetative characters.

Reproductive key to species

I. Spermatangia superficial, scattered continuously over frond surface; cystocarps destitute of nutritive filaments .... **Subgenus *Gracilariella***
   A. Fronds cylindrical, large, 60–150(–200) cm long, 2–5 mm diam., generally sparingly branched, sometimes provided with abundant short branchlets .... *Gracilaria chorda*

II. Spermatangial conceptacles depressed, spermatangia covering floor of conceptacle; cystocarps provided with nutritive filaments ...... **Subgenus *Textoriella***
   A. Fronds cylindrical
      1. Branch bases markedly constricted .... *Gracilaria blodgettii*
      2. Branch bases generally slightly constricted .... *Gracilaria gigas*
   B. Fronds flattened
      1. Frond margins entire
         a. Fronds less than 5 cm long.................. *Gracilaria punctata*
         b. Fronds more than 5 cm long
            +. Fronds curved and twisted; fleshy .... *Gracilaria incurvata*

++. Fronds not above; leathery............*Gracilaria textorii*
2. Frond margins dentate
a. Fronds usually more than 3 mm wide......*Gracilaria denticulata*
b. Fronds usually less than 3 mm wide ....*Gracilaria purpurascens*

III. Spermatangial conceptacles deeply pot-shaped, spermatangia covering entire inner surface of conceptacle; cystocarps provided with many or few nutritive filaments ....**Subgenus *Gracilaria***
A. Fronds cylindrical
1. Fronds more than 3 mm wide, cartilaginous ......*Gracilaria arcuata*
2. Fronds less than 3 mm wide, abundantly branched
a. Fronds vermiform, cartilaginous, dark purplish; nutritive filaments seldom.............................*Gracilaria vermiculophylla*
b. Fronds slender, cartilaginous, pale to dark brown; nutritive filaments abundant........................*Gracilaria verrucosa*
c. Fronds rigid, pale or yellowish brown..........*Gracilaria edulis*
B. Fronds flattened ....*Gracilaria sublittoralis*

Vegetative key to species

I. Fronds cylindrical or slightly compressed
A. Fronds articulated ....*Gracilaria salicornia*
B. Fronds not as above
1. Fronds erect
a. Branch bases markedly constricted
+. Fronds more than 50 cm long; cortical layer consisting of 2–3 cells...............................*Gracilaria chorda*
++. Fronds less than 50 cm long; cortical layer consisting of 1–2 cells..............................*Gracilaria blodgettii*
b. Branch bases slightly constricted
+. Fronds more than 3 mm diam. ....*Gracilaria gigas*
++. Fronds less than 3 mm diam.
*. Fronds vermiform, dark purplish
...........................*Gracilaria vermiculophylla*
**. Fronds slender, pale to dark brown..*Gracilaria verrucosa*
c. Branch bases not as above
+. Fronds cartilaginous, more than 3 mm wide
......................................*Gracilaria arcuata*
++. Fronds rigid, less than 3 mm wide ......*Gracilaria edulis*
2. Fronds partially prostrate in basal portion or completely so
a. Fronds sometimes slightly compressed, partially prostrate in basal portion...............................*Gracilaria coronopifolia*
b. Fronds completely compressed, prostrate throughout
..................................*Gracilaria eucheumioides*

II. Fronds flattened
A. Margins entire
1. Fronds more than 5 cm long
a. Fronds curved and twisted, fleshy.........*Gracilaria incurvata*

b. Fronds not as above, leathery
+. Medullary cells less than 600 μm maximum diam. ....*Gracilaria textorii*
++. Medullary cells more than 600 μm maximum diam. ....*Gracilaria sublittoralis*
2. Fronds less than 5 cm long ....*Gracilaria punctata*
B. Margins dentate
1. Fronds usually more than 3 mm wide ....*Gracilaria denticulata*
2. Fronds usually less than 3 mm wide ....*Gracilaria purpurascens*

E. Descriptions of species

1. Subgenus ***Gracilariella***

Spermatangia superficialia, dispersa continuo super paginam frondis.
Spermatangia superficial, scattered continuously over frond surface.
Type species. *Gracilaria chorda* Holmes.

Gracilaria chorda Holmes
(Pls. 1–4, 38–40)

Holmes, 1895, p. 253; 1897, p. 23; De Toni, 1900, p. 454; 1924, p. 257; Okamura, 1902, p. 39; 1916, p. 41, pl. 161, figs. 1–6; 1936, p. 629; Yendo, 1911, p. 647, fig. 184; Takamatsu, 1936, p. 33; 1938, p. 128 (as *G. chorda* Holmes ?); 1939, p. 60 (as *G. chorda* Holmes ?); Yamamoto, 1969, p. 22, fig. I.

Syn. Gracilariopsis chorda (Holmes) Ohmi; Ohmi, 1958, p. 50, text-fig. 24, pl. 10; Yamamoto, 1973a, p. 86, figs. 1–5; 1974, p. 19, fig. 4.

Japanese name. Tsuru-shiramo.

Habitat. This species grows on pebbles, shells, rocks, and ropes of cultivation rafts, from the lower tide mark down to the upper sublittoral zone in comparatively calm waters. The present plant frequently grows in association with *G. gigas* in the estuaries along the open coast and in bays.

Distribution. This species has comparatively wide distribution along the Pacific coast from Kyushu to Hokkaido.

Specimens collected. Hokkaido: Kamiiso, near Hakodate (⊕♀, Sept. 9, 1972; ⊕♂♀, Sept. 14, 1972; ⊕, Mar. 15, 1973, Yamamoto); Akkeshi Lagoon (⊕, Sept. 18, 1971; ⊕, Aug. 2, 1972, Yamamoto); Miyagi Pref.: Matsushima Bay (sterile, May 1974, Yamamoto); Shizuoka Pref.: Irō-zaki (♂, Mar. 30, 1971, Yamamoto); Toi (♂, Mar. 29, 1971, Yamamoto); Wakayama Pref.: Shirahama (⊕♂♀, May 15, 1968, Yamamoto); Kōchi Pref.: Usa (⊕♂♀, Feb. 5, 1973, Yamamoto); Kumamoto Pref.: Ushibuka in Amakusa (⊕♂♀, April 7, 1970, Yamamoto).

Fronds solitary or cespitose, cylindrical throughout, up to 150(–200) cm long, up to 5 mm diam.; main axis more or less traceable, or distinctive, attenuated toward base, tapering into a filiform apical portion; axis not abundantly branched, generally provided with long or short filiform branchlets arising alternately or on all sides at irregular intervals, generally slightly or markedly constricted at base, but sometimes compressed as they become broader; reddish purple to brownish purple; fleshy when young, but becoming cartilaginous with age.

Cortical layer consisting of 1–2(–3) series of anticlinally arranged cells, cells 8–14 μm long, 4.5–5 μm wide, containing abundant chloroplasts and 1–3 nuclei; intermediate layer consisting of 3–4 series of cells, cells slightly elongated parallel to frond surface in longitudinal section, containing a moderate number of chloroplasts and one to several nuclei; medulla consisting of large polygonal and nearly empty cells, cells 590–830 μm diam., secondary pit-connections present between surrounding cell; hairs provided with basal cells which are conspicuous in cortical layer, containing ca. 10–15 nuclei in the middle portion and above; frond tissue collapsing and becoming hollow in the central portion of aged frond.

Tetrasporangia borne among cortical cells, scattered over entire frond surface except basal and apical portions, 46–56 μm high, 26–35 μm wide, surrounded with elongated cortical cells, regularly divided, strictly cruciate.

Spermatangia formed on the entire frond surface except basal and apical portions of frond, continuously superficial, spermatangia subtriangular in young stages, spherical at maturity, 3–4(–5) μm diam.

Carpogonial branches two-celled; cystocarps formed on entire frond surface except basal and apical portions of frond, up to ca. 2 mm wide, 1.7 mm high, slightly beaked, constricted at bases in fully grown stages; pericarp consisting of 6–8 rows of cells which are flattened parallel to pericarp surface; gonimoblast cells rather small, 33–50 μm × 6–30 μm, more or less filled with chloroplasts; nutritive filaments absent.

Remarks. Measurement of medullary cells was taken in the young solid frond, because the fronds become hollow with age.

The frond is very variable in shape depending on age and habitat. Hokkaido specimens generally are irregular in branching and are provided with short filiform branchlets, and seem to be very luxuriant at a glance. On the other hand, plants in the middle and southern parts of Japan have sparse branches which alternate rather regularly, and as they grow older, branches and branchlets almost decay. As a result, only the naked main axis and long branches remain. Such an old frond is different in appearance from a young one and is sometimes mistaken for *G. gigas* in the field.

The life history of the present species is peculiar in Hokkaido. In Akkeshi Lagoon, the northern limit of distribution, cystocarpic and male plants have never been found. It thus seems that species reproduces there by means of unreduced tetraspores and vegetative proliferation. Although a cytological study of this local form would prove interesting, it is left for the future. In Hakodate Bay, where the sea water is warmer than in Akkeshi Lagoon, cystocarpic and male plants can be found, but only occasionally. On the other hand, in southern districts such as Honshu, Shikoku, and Kyushu, all three reproductive phases are commom. The suggestion is that the lower temperatures of Hokkaido inhibit the carrying out of the normal, full life history.

The distinctive spermatangial pattern of this species is first described here. The present plant has often been misidentified as *G. verrucosa* in Hokkaido because of the absence of male plants. The writer assigns plants from Akkeshi Lagoon to this species, despite the absence of male plants, because of their resemblance in external form and vegetative cell size.

In Akkeshi Lagoon, the present plant had been harvested along with *G. vermiculophylla* as the source of agar, but this industry has ceased at present because of the low market price.

2. Subgenus ***Textoriella***

Conceptacula spermatangiorum vadose depressa, utrumque primordium cellularum matricalium spermatangialium systema ramorum demum fundum conceptaculi obtectante formans, utraque cellula matricalis spermatangia procreans.

Spermatangial conceptacles shallowly depressed, each spermatangial mother cell primordium forming a branch system which covers floor of conceptacle at maturity, each mother cell producing spermatangia.

Type species. Gracilaria textorii (Sur.) De Toni.

Gracilaria gigas Harvey
(Pls. 5–8, 41)

Harvey, 1859, p. 331; De Toni, 1895, p. 28; 1900, p. 454; Yendo, 1911, p. 648; Okamura, 1927, p. 156, pl. 241, figs. 1–3; pl. 242, figs. 1–4; 1936, p. 631; Ohmi, 1958, p. 10, pl. I; pl. II, A, text-fig. 3.

Japanese name. Ō-ogonori.

Habitat. This species grows on various objects such as shells, pebbles, and rocks covered with sand from low tide mark down to the upper sublittoral zone, and on ropes of cultivation rafts.

Distribution. From Kyushu to middle Honshu.

Specimens collected. Shizuoka Pref.: Nakagi (♂, Mar. 30, 1971, Yamamoto); Wakayama Pref.: Shirahama (⊕♂♀, May 15, 1968; ⊕♀, April 3, 1972, Yamamoto); Kōchi Pref.: Usa (⊕♂♀, Feb. 5, 1973, Yamamoto); Kumamoto Pref.: Tsūji in Amakusa (⊕♂, April 8, 1970, Yamamoto); Ushibuka in Amakusa (♂, April 9, 1970, Yamamoto).

Fronds solitary, cylindrical, sometimes slightly complanate in middle portion, about 30 cm long, 4–7 mm diam.; main axis traceable, attenuated toward base, tapering into filiform apical portion, branching somewhat regularly alternate or secund; branches short, oblong, sometimes slightly constricted at base, tapering toward apical portion, provided with short branchlets which are similar in shape to the branches; pale green to pale purplish brown; cartilaginous.

Cortical layer consisting of 1–2(–3) series of anticlinally arranged cells, cells 5.5–13.5(–18) μm long, 5.5–9.5 μm wide, containing 1–3 nuclei and a number of chloroplasts; medulla consisting of ca. 10 layers of cells, 560–1138 μm $\times$ 437–910 μm in maximum dimensions, cells in center large, polygonal, somewhat radiately arranged, becoming smaller towards the exterior; transition of cells from cortex to medulla abrupt; hairs present, containing about 10–15 nuclei in the middle portion or above.

Tetrasporangia borne over entire frond surface except basal and apical portions of frond, 49–53 μm high, 23–30 μm wide, regularly divided, strictly cruciate, surrounded by elongated cortical cells.

Spermatangia borne over entire surface of frond except basal and apical portions; conceptacles shallow and cup-shaped, separated by anticlinally elongated cells, becoming frequently confluent to form indefinite patches in surface view, 21–35(–40) μm deep, 26–40 μm wide.

Carpogonial branches two-celled; cystocarps generally rather compressed when young, increasing in height gradually and beaked slightly in age, slightly or markedly constricted at base, 1.9–2.2 mm high, 2.3–2.5 mm wide; pericarp composed of somewhat compressed cells; rather empty, 80–140 μm×170–260 μm; nutritive filaments commonly present.

Remarks. The present species has a rather wide distribution and grows luxuriantly in calm places. As the frond becomes old, branches and branchlets are lost and sometimes the constrictions at branch bases become conspicuous. As a result, the aged plant of the present species is similar in shape to the old frond of *G. chorda* which is also naked. Accordingly, old plants of the two species are apt to be confused.

Gracilaria blodgettii Harvey
(Pls. 9–11, Pl. 42, figs. 1–4)

Harvey, 1853, p. 111; J. Agardh, p. 416; De Toni, 1900, p. 437; 1924, p. 258; Taylor, 1928, p. 151, pl. 23, fig. 9; pl. 33, fig. 6; Weber van Bosse, 1928, p. 430, fig. 174; Okamura, 1936, p. 629; Ohmi, 1958, p. 13, pls. II-III, text-figs. 4–5.

Japanese name. Kubire-ogonori.

Habitat. This species grows on pebbles, shells, and rocks in the lower littoral and sublittoral zones in the open sea.

Distribution. From Okinawa Pref. to middle Honshu.

Specimens collected. Okinawa Pref.: Nashiro (⊕♀, Feb. 5, 1974, Yamamoto); Yagachi (⊕♂♀, Feb. 6, 1974, Yamamoto).

Fronds solitary or cespitose, cylindrical throughout; main axis slightly traceable, attenuated toward base and tapering gradually toward apex, 30 cm long, 2.7(–3) mm diam., provided with short filiform branchlets, markedly constricted at base; generally dark to pale reddish brown; fleshy to somewhat cartilaginous.

Cortex consisting of 1–2(–3) series of cells filled with chloroplasts, cells in surface layer 6.7–11(–13) μm long, 6–8 μm wide, containing 1–2(–3) nuclei; medulla consisting of polygonal cells, becoming larger toward center, 490–660 μm × 360–600 μm; transition of cells from cortex to medulla sudden; hairs abundant, deciduous, basal cells 29–43 μm×(13–)20–29 μm.

Tetrasporangia borne among cortical cells continuously over entire frond surface except basal and apical portions, regularly cruciate, 40–60 μm high, 23–40 μm wide, surrounded by elongated cortical cells.

Spermatangia borne over entire frond surface except basal and apical portions; conceptacles rather deeply embedded in the tissue, cup-shaped, 33–56 μm deep, 33–43 μm wide, confluent at maturity and forming irregular shapes in surface view; spermatangia about 5 μm×4 μm.

Carpogonial branches consisting of two cells; cystocarps borne over entire frond surface except basal and apical portions, 1.7 mm high, 1.7(–2) mm wide, generally slightly constricted at base, slightly beaked in fully grown stage; pericarp generally consisting of compressed cells; gonimoblast cells large, rather empty, and elongated, 230–340 μm×80–135 μm; nutritive filaments abundant, sometimes penetrating so deeply into pericarp as to reach nearly the outer surface of cystocarp.

Remarks. The present species is similar to *G. chorda* in external appearance. It is distinguishable, however, by the marked basal constriction of the branches and by the cup-shaped spermatangial conceptacle. In *G. chorda* the branches are constricted only slightly at the base and the spermatangia are borne continuously over the surface of the frond.

In having a well developed branch system of spermatangial mother cells, this species closely resembles the Verrucosa type, but it apparently belongs to the Textorii type because of the surrounding elongated cells and the confluent conceptacles.

This species is confined to southern districts of Japan, and luxurient growths occur especially in Okinawa Pref., where fronds are cast ashore in abundance after storms.

Gracilaria textorii (Sur.) De Toni
(Pls. 12–14, Pl. 42, figs. 5–7, Pl. 43, figs. 1–4)

J. Agardh, 1876, p. 426; De Toni, 1895, p. 27; 1900, p. 449; Okamura, 1901, p. 65, pl. 23; 1936, p. 632; Yendo, 1911, p. 650, fig. 185; Inagaki, 1933, p. 37, fig. 12 Takamatsu, 1936, p. 34; 1938, p. 56; 1939, p. 60, pl. 11, fig. 1; Dawson, 1949, p. 34, pl. 2, figs. 4–6; pl. 14, figs. 1–6; pl. 15, figs. 1–6; Ohmi, 1955, p. 320, pls. 1–6; 1958, p. 40, text-figs. 20–21.

Syn. Sphaerococcus (Rhodymemia) textorii Suringar, Suringar, 1867, p. 259; 1870, p. 135.

Gracilaria vivesii Howe, Howe, 1911, p. 503, pls. 30, 33; Dawson, 1949, p. 34, pl. 2, figs. 4–6; pl. 14, figs. 1–6.

Gracilaria vivipara Setchell et Gardner, Setchell and Gardner, 1924, p. 750, pl. 24, figs. 28–29, pl. 63.

Gracilaria sinicola Setchell et Gardner, Setchell and Gardner, 1924, p. 752, pl. 62.

Gracilaria johnstonii Setchell et Gardner, Setchell and Gardner, 1924, p. 752, pl. 22, figs. 11–14; pl. 60; Dawson, 1944, p. 293.

Japanese name. Kabanori.

Habitat. This species grows on rocks and is especially abundant in tide pools in the lower tidal and upper sublittoral zones.

Distribution. From Okinawa Pref. to the western coast of Hokkaido.

Specimens collected. Hokkaido: Hakodate Bay (⊕, Aug. 1960; ♀, Nov. 28, 1960; sterile, April 1, 1962; ⊕, Aug. 1973; ⊕, Sept. 1974, Yamamoto); Shinori, near Hakodate (sterile, May 27, 1968; sterile, Jan. 14, 1970; sterile, Mar. 13, 1970; sterile, April 12, 1970; sterile, Oct. 15, 1970, Yamamoto); Oshoro (sterile, April 27, 1969; sterile, July 27, 1969; ⊕, Oct. 5, 1969; ⊕, Nov. 9, 1970, Yamamoto); Shizuoka Pref.: Susaki (⊕♀, Mar. 30, 1971, Yamamoto); Shirahama (⊕♀, April 28, 1971, Yamamoto); Wakayama Pref.: Shirahama (⊕♂♀, May 15, 1968, Yamamoto); Kōchi Pref.: Usa (♂, Feb. 5, 1973, Yamamoto); Kumamoto Pref.: Tsūji in Amakusa (⊕♂, April 5, 1970, Yamamoto); Gesu-jima (⊕♂♀, April 8, 1970, Yamamoto); Tomioka (⊕♂♀, April 6, 1970, Yamamoto).

Fronds generally cespitose; stipe cylindrical, 5–20 cm long; fronds irregularly dichotomous or flabellate-cuneate below with round axillae; segments 1–2 cm wide, 500–800(–1000) μm thick, sometimes undulate, becoming slender in upper portions, margins entire or proliferous, apices blunt, bifurcate, sometimes rather ligulate; dull or brownish red to somewhat yellowish red; coriaceous or membranous.

Cortical layer consisting of 1–2(–3) rows of cells; outermost cells 9.5–13.5(–16) μm long, 6.5–11 μm wide, containing 1–3 nuclei, densely protoplasmic; medulla consisting of 7–9 layers of cells, cells increasing in diameter toward the center, reaching 200–310 μm×150–270 μm; transition of cells from cortex to medulla abrupt; hairs present, basal cells 26–37(–46) μm×13.5–16.5 μm, sometimes divided transversely into two or rarely three cells.

Tetrasporangia borne on both surfaces of entire frond except basal and apical portions, 40–50 μm high, 23–30 μm wide, cruciately divided, surrounded by elongated cortical cells.

Spermatangia borne on both surfaces of entire frond except basal and apical portions; conceptacles shallow, cup-like, becoming confluent with each other with age, 20–30 μm deep, slightly raised above the frond surface; spermatangia 3.5–4 μm diam.

Carpogonial branches two-celled; cystocarps borne on both surfaces of entire frond except basal and apical portions, 1.8 mm high, 2 mm wide at maturity, constricted at base, slightly beaked; nutritive filaments abundant; gonimoblast cells polygonal, 140–230 μm×130–165 μm.

Remarks. This warm-current species is very variable in its external appearance depending upon habitat. Generally speaking, those which grow in the northern part of Japan are smaller than those from the southern part. Fronds from Oshoro, the northern limit of its range, are less than 7 cm in length and 8 mm in width and the branching is comparatively regular, while those from Shirahama and Amakusa are considerably larger with irregularly divided branches.

The larger fronds in the southern part of Japan are very similar to *G. sublittoralis* in external form and the two species are often confused. A detailed comparison between them is given in the account of *G. sublittoralis*.

Inagaki (1933) and Ohmi (1955) reported gland-like cells in the cortex of plants from Oshoro, but the writer has not been able to observe them.

The writer often found old plants with new branches regenerated from the thick stipe. It would seem, therefore, that some fronds of this species are biennial. A similar phenomenon has occasionally been observed in Hokkaido specimens of *G. verrucosa* and *G. chorda*, which can propagate vegetatively.

This species has a comparatively wide distribution.

Gracilaria incurvata Okamura
(Pls. 15–16, Pl. 43, figs. 5–6, Pl. 44, figs. 1–2)

Okamura, 1931, p. 41, pl. 273, figs. 1–6; 1936, p. 633; Ohmi, 1958, p. 38, pls. VIII-IX, text-fig. 19; Yamamoto, 1973, p. 57, figs. 1–2.

Japanese name. Mizo-ogonori.

Habitat. This species grows on pebbles and rocks, which are often covered with sandy mud, in the lower tidal zone in protected waters.

Distribution. From Kyushu to the middle part of Honshu.

Specimens collected. Shizuoka Pref.: Susaki (sterile, April 3, 1971, Yamamoto); Wakayama Pref.: Shirahama (⊕♂♀, May 15, 1968, Yamamoto); Kōchi Pref.: Usa (⊕♂♀, Feb. 5, 8, 1973, Yamamoto); Kumamoto Pref.: Gesu-jima in Amakusa (♂, April 8, 1970, Yamamoto).

Fronds cespitose or solitary, 6–11 cm long, 8–14 mm wide, 1–1.8 mm thick, flattened completely with cylindrical stipe expanding into segment; segments wedge-shaped in lower portion, 4–6 times dichotomously or sometimes flabellately, rarely trichotomously branched in upper portion, entire or sometimes proliferous at margin, more or less curved and twisted, tips round or somewhat bifurcate; pinkish red to brownish red; soft, fleshy.

Cortical layer consisting of 2(–3) rows of cells; outermost cells 9–16.5 μm long, 7.5–11.5 μm wide; medullary layer consisting of 8–10 layers of polygonal cells, increasing in size toward center, 430–760 μm×230–560 μm in maximum dimensions; transition of cells from cortex to medulla abrupt; hairs abundant, basal cells 29.5–36.5 μm×19–23.5 μm, sometimes divided transversely into two cells.

Tetrasporangia borne on both surfaces of entire frond except basal and apical portions, 40–60 μm high, 25–35 μm wide, cruciately divided, surrounded by modified cortical cells.

Spermatangia borne on both surfaces of entire frond except basal and apical portions; conceptacles shallow, cup-like, ca. 40–50 μm deep, 40–45 μm wide, surrounded by elongated cortical cells up to 30 μm long, very often confluent at maturity, forming irregular shape in surface view, embedded in a slightly raised nemathecium; spermatangia 3–4 μm diam.

Carpogonial branches two-celled; cystocarps borne on both surfaces of entire frond except basal and apical portions, 1–1.4 mm high, 1.4–1.5 mm wide, sometimes slightly beaked, constricted at base; gonimoblast cells densely protoplasmic, 80–100 μm×30–50 μm; nutritive filaments abundant, penetrating deeply into pericarp.

Remarks: In his original description, Okamura (1931) stated that this species seems quite similar to *G. textorii*. The two species are easily distinguished in the field, however, by texture. The habitat of the two species also differs, *G. incurvata* growing in rather protected and calm waters, *G. textorii* in places more or less exposed to waves.

Ohmi (1958) described and illustrated long terminal branches and put stress on them as a character distinguishing this species from *G. textorii*. Unfortunately, such branches have not been seen by the writer.

Gracilaria punctata (Okamura) Yamada
(Pls. 17–19, P. 44, figs. 3–6)

Yamada, 1941, p. 203; Ohmi, 1958, p. 35, pls. VII-VIII, text-figs. 17–18.

Syn. Rhodymenia punctata Okamura, Okamura, 1929, p. 13, pl. 258, figs. 1–6; 1936, p. 676, fig. 323.

Japanese name. Itsutsu-ginu.

Habitat. This species grows on rocks and stones covered slightly with sand in tide pools and crevices in the lower tidal zone of open sea, in association with *G. denticulata* and *G. purpurascens*.

Distribution. Okinawa Pref.; Tosa, Kōchi Pref.

Specimens collected. Okinawa Pref.: Komesu (⊕♂♀, Feb. 11, 1974, Yamamoto).

Fronds completely flattened, up to 5 cm high, 1.5 cm wide, 300–400 μm or less in thickness, divided 1–3 times somewhat dichotomously into lobes; lobes generally obovate, sometimes provided with small, obovate proliferations at margin; frond margin slightly undulate or often entire; stipes short, cylindrical, expanding abruptly into broad frond; dark brown spots scattered over the entire frond surface except lower portion, nearly circular, often becoming confluent into irregular outline, ca. 160–660 μm diam.; brilliant red or dark red; rigidly membranous.

Cortical layer composed of 1–2 rows of cells, cells of surface layer 6.8–13.5 μm long, sometimes having secondary pit connections; medulla consisting of 3–4 layers of large vacant cells in transverse section, cells increasing in diameter toward the center, 66–116 μm×62–89 μm in maximum dimensions; transition of cells from cortex to medulla abrupt; hair basal cells 16–21 μm×9–13 μm, forming a group.

Tetrasporangia embedded in a slightly raised nemathecium, surrounded by elongated cortical cells.

Carpogonial branches two-celled, supporting cells containing always four nuclei or less before fertilization; cystocarps borne on both surfaces of entire frond, up to 1.2 mm high and 1.8 mm wide, constricted at base; gonimoblast cells large, 155–250 μm×65–115 μm, rather densely protoplasmic; nutritive filaments present, but few.

Remarks. Dark brown spots have previously been reported as occurring on the surface of this plant. Close examination has revealed that they consist of clusters of basal cells of hairs. Such prominent clustering of hair basal cells is not known in other species of *Gracilaria* except in *G. arcuata*, where it is not as conspicuous as in the present species.

There are some differences in the dimensions of the outermost cells when the two surfaces of the frond are compared. The cells of the ventral surface are rather longer and narrower than those of the upper surface.

The writer has not observed mature tetrasporangia, so the description is based on undivided tetrasporangia.

Gracilaria denticulata (Kütz.) Weber van Bosse
(Pls. 20–22, Pl. 45, figs. 1–5)

Weber van Bosse, 1928, p. 432; Yamada, 1938, p. 125, pl. 25, fig. 2; Børgesen, 1943, p. 76; Papenfuss, 1951, p. 177; Ohmi, 1958, p. 29, pl. VI, text-fig. 13.

Syn. Sphaerococcus denticulatus Kützing, Kützing, 1869, p. 19, pl. 51, figs. e–g.

Japanese name. Toge-kabanori.

Habitat. This species grows on rocks in tide pools in the lower tidal and upper sublittoral zones in association with *G. purpurascens* and *G. punctata.*

Distribution. Okinawa Pref.

Specimens collected. Okinawa Pref.: Komesu (⊕♂♀, Feb. 11, 1974, Yamamoto).

Fronds cespitose, flattened, 5–8 cm high, 3–7 mm wide, dichotomously or irregularly branched, branches somewhat twisted, truncate at tips; margins dentate, provided with spines which are 1.5 mm in maximum length; stipes cylindrical, 3 cm in maximum length, 1.5–3 mm wide, expanding gradually or abruptly into blade; pinkish or purplish red; membranous.

Outermost cells 8.3–15 μm$\times$6.6–11 μm, densely protoplasmic; cortical layer consisting of 1(–2) rows of cells; medulla composed of 5–7 cells in transverse section, 100–167 μm$\times$100–159 μm; transition of cells from cortical layer to medulla abrupt; hairs present, basal cells 16–33 μm$\times$16–23 μm, often divided transversely.

Tetrasporangia borne on both surfaces of entire frond except basal and apical portions, 18–30 μm high, 11–20 μm wide, surrounded by unmodified cortical cells.

Spermatangia borne on both surfaces of entire frond except basal and apical portions; conceptacles shallow, cup-like, 23–33 μm deep, 16–35 μm wide, becoming confluent at maturity; spermatangia spherical, ca. 4 μm diam.

Cystocarps borne on both surfaces of entire frond except basal and apical portions, up to 1.7 mm high, 2 mm wide, slightly beaked, constricted at base; gonimoblast cells densely protoplasmic, 56–90 μm$\times$19–33 μm; nutritive filaments present but very rare.

Remarks. The present species was first reported from Japan by Yamada in 1938 together with *G. purpurascens.* The two species have a close resemblance in external appearance, but may be distinguished by differences in the width of the frond and the shape of the spinuous marginal processes. With respect to the spines, Ohmi (1958) described denticulate processes in the present species and short spinulate ones in *G. purpurascens.* However, a single specimen of the present species showing both kinds of spines has been collected by the writer, suggesting a need for further study of the differences between the two species.

An apical cell is easily observable at the tip of each small marginal spine in the present species as well as in *G. purpurascens.* In all other Japanese species of *Gracilaria* recognition of such an apical cell is difficult.

The tetrasporangia are not mature in the writer's materials, so that the description and measurements are based on undivided sporangia.

This species has a limited distribution in Japan.

Gracilaria purpurascens (Harvey) J. Agardh
(Pl. 23, Pl. 24, figs. 1–3, Pl. 45, fig. 6)

J. Agardh, 1885, p. 63; De Toni, 1900, p. 454; 1924, p. 271; Yamada, 1938, p. 125, pl. 25, fig. 1 (as *G. purpurascens* J. Ag.); Ohmi, 1958, p. 30, pl. VI, text-fig. 14.

Syn. Rhodymenia purpurascens Harvey, Harvey, Ceylon Alg., no. 96 (nomen nudum).

Japanese name. Murasaki-kabanori.

Habitat. This species grows on walls of tide pools and crevices in the lower tidal zone washed by waves in association with *G. denticulata.*

Distribution. Okinawa Pref.

Specimens collected. Okinawa Pref.: Komesu (♂ ♀, Feb. 11, 1974, Yamamoto).

Fronds flattened, cespitose, up to ca. 6 cm high, more or less flabelliform, cuneate below to short, subcylindrical stipe, with subdichotomously or irregularly branched fronds, fronds twisted very often, 2–4 mm wide, ca. 400 μm thick, margins abundantly furnished with spinous processes which reach 1 mm in length; dark purplish red; rather coriaceous.

Cortical layer consisting of 1(–2) rows of cells, outermost cells 6.5–15 μm long, 6–13.5 μm wide; medulla consisting of 6–8 layers of cells, cells increasing in size toward center, reaching 120–180 μm $\times$ 100–160 μm in transverse section; transition of cells from cortex to medulla abrupt; hairs present but not abundant, basal cells 16.5–23.5 μm long, 12–16.5 μm wide.

Tetrasporangia densely scattered over both surfaces of entire frond, roundish, ca. 15 μm diam. in surface view, ovoid, 12 μm $\times$ 15 μm in section, surrounded by unmodified cortical cells.

Spermatangia borne on both surfaces of entire frond except basal and apical portions; conceptacles shallow, cup-like, up to 34 μm deep, very frequently becoming confluent with each other with age; spermatangia ca. 4 μm diam.

Carpogonial branches two-celled; cystocarps borne on both surfaces of entire frond except basal and apical portions, ca. 1.2 mm high, ca. 1.4 mm wide, constricted at base, slightly beaked; gonimoblast cells rather small, 60–130 μm $\times$ 23–40(–60) μm; densely protoplasmic; nutritive filaments extending to pericarp but very few.

Remarks. As no tetrasporic plant has been collected by the writer, the description of tetrasporangia given above is a modification of that given by Ohmi (1958). Judging from Ohmi's illustration, his description is probably based on young sporangia. Further studies would be needed to clarify the nature of the mature tetrasporophyte.

Nutritive filaments are rare in the writer's materials, while they seem to be more abundant in Ohmi's illustration. Similar variability in the number of nutritive filaments between specimens has been observed in *G. denticulata*.

3. Subgenus *Gracilaria*

Conceptacula spermatangiorum profunde olliformia, utrumque primordium cellularum matricalium spermatangialium systema ramorum demum superficiem interioram totam conceptaculi obtectante formans, utraque cellula matricalis spermatangia procreans.

Spermatangial conceptacles deeply pot-shaped, each spermatangial mother cell primordium forming a branch system which covers entire inner surface of conceptacle at maturity, each mother cell producing spermatangia.

Type species. *Gracilaria verrucosa* (Huds.) Papenfuss.

Gracilaria verrucosa (Huds.) Papenfuss
(Pl. 24, figs. 4–7, Pls. 25–27, 46, Pl. 47, fig. 1)

Papenfuss, 1950, p. 195; Ohmi, 1958, p. 6, pl. I, text-figs. 1–2.

Syn. Fucus verrucosus Hudson, Hudson, 1762, p. 470.

Fucus confervoides Linnaeus, Linnaeus, 1763, p. 1629 (not *Fucus confervoides* Hudson 1762).

Gracilaria confervoides (L.) Greville, Greville, 1830, p. 123; J. Agardh, 1852, p. 587; 1876, p. 413; De Toni, 1900, p. 431; Yendo, 1911, p. 637, fig. 182; Okamura, 1916, p. 1, pl. 151, figs. 1–9; 1936, p. 628, fig. 298, 1–5; Sjöstedt, 1926, p. 51; Kylin, 1930, p. 55; Takamatsu, 1936, p. 33; 1938, p. 56; 1938a, p. 128; 1939, p. 60; Dawson, 1949, p. 13, pl. 15, fig. 9.

Gracilariopsis rhodotricha sensu Ohmi (non Dawson), Ohmi, 1958, p. 47, pl. X, text-fig. 23.

Japanese name. Ogonori.

Habitat. This species grows on pebbles and rocks, which are often covered with sand and mud, in the intertidal and upper sublittoral zones.

Distribution. From Okinawa Pref. to the northern part of Hokkaido.

Specimens collected. Hokkaido: Matsumae (♀, Aug. 3, 1962, Yamamoto); Cape Shirakami (sterile, June 13, 1971, Yamamoto); Shinori, near Hakodate (⊕♀, June 24, 1970, Yamamoto); Nanae-hama, near Hakodate (♀, April 1, 1968, Yamamoto); Usu (sterile, July 31, 1972, Yamamoto); Yūdo-numa (sterile, Aug. 2, 1972, Yamamoto); Odaitō, near Nozuke (sterile, Aug. 3, 1972, Yamamoto); Notoro Lagoon (⊕♀, Aug. 4, 1972, Yamamoto); Notoro (⊕♂♀, Aug. 4, 1972, Yamamoto); Tokoro (⊕♀, Aug. 4, 1972, Yamamoto); Esashi, Kitami Prov. (⊕♀, Aug. 1973, Kaneko); Cape Notto (⊕♂♀, Aug. 7, 1972, Yamamoto); Miyagi Pref.: Matsukawa-ura (⊕♂♀, May 8, 1972, Yamamoto); Shizuoka Pref.: Tsumeki-zaki, near Shimoda (⊕♂♀, April 3, 1971, Yamamoto); Wakayama Pref.: Shirahama (♀, May 15, 1968, Yamamoto); Kōchi Pref.: Usa (⊕♂♀, Feb. 5, 1973, Yamamoto); Yamaguchi Pref.: Yoshimi (⊕♂♀, May 5, 1974, Matsui); Okinawa Pref.: Yagachi (⊕♂♀, Feb. 7, 1974, Yamamoto).

Fronds cespitose or solitary, 8–50 cm tall, ca. 2 mm wide; main axis traceable, provided with branches on all sides; branching irregularly alternate, sometimes secund or dichotomous, branches variable in length, tapering toward apices and bases, provided with many or sometimes few branchlets; branchlets long or short, sometimes spine-like; branch bases slightly constricted or rarely non-constricted; pale brown to dark brown; somewhat cartilaginous.

Cortical layer composed of 2–3 rows of anticlinally elongated cells, cells of surface layer 8.4–17 μm long, 4–6(–7.5) μm wide, highly protoplasmic; medulla consisting of 8–10 layers of cells, 400–540 μm × 270–400 μm, slightly elongated in a direction parallel to axis of frond in the outer region, sometimes collapsing with age, resulting in hollow frond; transition of cells from cortex to medulla sudden; hairs especially abundant in younger part of fronds, basal cells large and prominent.

Tetrasporangia borne over entire surface of frond except basal and apical portions, 52–66 μm high × 26–43 μm wide, regularly cruciate, surrounded by elongated and curved cortical cells.

Spermatangia borne over entire surface of frond except basal and apical portions; conceptacles deeply pot-like, 100–120 μm deep, 56–83 μm wide, very often elongated parallel to axis of frond in surface view, completely separated by vegetative cortical cells; spermatangia spherical, 4–4.8 μm diam.

Carpogonial branches two-celled; cystocarps borne over entire surface of frond except basal and apical portions, generally 0.9–1.3 mm high, 1.3–1.6 mm wide, slightly or markedly beaked, constricted at bases; nutritive filaments abundant or rarely scarce, penetrating into pericarp; gonimoblast cells elongated, 80–170 μm×30–60 μm.

Remarks. The hitherto unknown procarp of the present species is described for the first time, and the carpogonium and its development are not different from those of the other Japanese species.

The present species is of the widest distribution not only in Japan, but also in the world.

The morphology of the species, especially the length of fronds and the branching mode, is very changeable depending on habitat, and there are problems in identification of plants destitute of reproductive organs.

The writer had the opportunity to examine the cystocarpic specimens assigned to *Gracilariopsis rhodotricha* Dawson by Dr. Ohmi by his courtesy, and confirmed unexpectedly the presence of nutritive filaments in a cystocarp. These nutritive filaments, however, were few and not as fully developed as in *G. verrucosa.* Ohmi (1958) mentioned that the small size of the spermatangial conceptacle was one of characters which differentiated the plant in question from *G. verrucosa.* In fact, this discrepancy is covered by the range of the size variation in the spermatangial conceptacle of the latter species. Accordingly, it seems reasonable that the plant assigned to *Gracilariopsis rhodotricha* Dawson by Ohmi should be merged with *G. verrucosa.*

Gracilaria vermiculophylla (Ohmi) Papenfuss
(Pls. 28–29, Pl. 47. figs. 2–3)

Papenfuss, 1966, p. 101.

Syn. Gracilariopsis vermiculophylla Ohmi, Ohmi, 1956, p. 271, pls. 1–2, text-figs. 1–4; 1958, p. 46.

Japanese name. Ogo-modoki.

Habitat. This species grows on pebbles covered with sandy mud, in the intertidal and upper sublittoral zones.

Distribution. Akkeshi Lagoon, Hokkaido.

Specimens collected. Hokkaido: Akkeshi Lagoon (⊕♂♀, July 4, 1968; ⊕♂♀, Aug. 2, 1972, Yamamoto).

Fronds solitary or cespitose, cylindrical, somewhat vermiform, arising from a small disc, 20–60 cm long, 2.5–3 mm wide, provided with branches similar to main axis; branches of 2–3 orders, attenuating toward bases and generally slightly constricted at the base, tapering toward apex; purplish brown or dark brown; rather soft cartilaginous.

Cortical layer consisting of 1–2(–3) rows of cells, cells of surface layer rather long, 9–16 μm×4.5–6 μm, containing 1–3(–5) nuclei, seconary pits sometimes present between outermost cells; medulla composed of ca. 6–7 cell layers, cells increasing in diameter toward the center, 400–490 μm×270–365 μm, containing ca. 20–50 nuclei; transition of cells from cortex to medulla sudden; hairs present, basal cells 20–30 μm×12–17 μm, sometimes divided transversely into two cells.

Tetrasporangia scattered uniformly over surface of frond except basal and apical portions, 49–66 μm high, 29–40 μm wide, mostly cruciate but frequently tetrahedral, sometimes irregularly divided, surrounded by elongated cortical cells.

Spermatangia borne on surface of entire frond except basal and apical portions; conceptacles deep, pot-like, 100–150 μm deep, 60–100 μm wide, separated by the outermost vegetative cells; spermatangia ca. 4 μm diam.

Carpogonial branches two-celled; cystocarps borne on surface of entire frond except basal and apical portions, triangular in appearance when young, becoming broader with age, 1.5 mm high, 1.8 mm wide in greatest dimensions, slightly beaked, constricted at base; gonimoblast cells rather small, 80–100 μm×23–35 μm; nutritive filaments present, but rare, sometimes difficult to find, mostly not reaching the pericarp.

Remarks. Ohmi (1956) established the present species and stressed the lack of nutritive filaments in the cystocarp. However, as a result of a close examination, their presence has been confirmed. They are generally rare, but are sometimes conspicuous around the lower portion of the gonimoblast. The division of sporangia is often tetrahedral as well as cruciate in the same plant, a feature apparently characteristic of this species.

Three species of *Gracilaria* occur in Akkeshi Lagoon: *G. chorda, G. verrucosa*, and *G. vermiculophylla*. In recent years *G. vermiculophylla* has increased in abundance to the point of approaching dominance.

It is interesting to note that this species occurs only in Akkeshi Lagoon and that it is similar to *G. verrucosa* with regard to the spermatangial pattern and to *G. chorda* in having only a few nutritive filaments in the cystocarp. Thus, a hybrid origin is suggested.

Gracilaria arcuata Zanardini
(Pl. 30, figs. 1–3, Pl. 47, figs. 4–5).

Zanardini, 1858, p. 265, n. 82, t. 5, fig. 2; De Toni, 1900, p. 439; 1924, p. 252; Okamura, 1936, p. 632; Børgesen, 1943, p. 69, fig. 35; Ohmi, 1958, p. 23, pl. V, text-fig. 10.

Japanese name. Yumigata-ogonori.

Habitat. This species grows on pebbles and rocks in the lower intertidal and upper sublittoral zones more or less exposed to the open sea, and is very often cast ashore together with *G. blodgettii*.

Distribution. Okinawa Pref. and Kōchi Pref.

Specimens collected. Okinawa Pref.: Yagachi (⊕♂♀, Feb. 7, 1974, Yamamoto).

Fronds usually solitary, cylindrical or slightly compressed, 6–10 cm long, 3–4 mm wide; main axis attenuated toward base, frequently curved, with attenuated apices; branching irregularly alternate or dichotomous and sometimes secund, corymbose; branches slightly curved, similar in shape to main axis, tapering toward apex, unconstricted at base, provided with similarly shaped branchlets on opposite sides at irregular intervals; yellowish or purplish green to pale pinkish purple or greenish purple; cartilaginous.

Cortical layer composed of 1–2 rows of cells, outermost cells elongated or slightly compressed, 6.7–13.5 μm×5.5–8.8 μm, densely protoplasmic; outer layer of medulla composed of 1–3 rows of small cells which are moderately protoplasmic; inner medullary cells polygonal, empty, 660–760 μm×490–660 μm; transition of cells from cortex to medulla sudden; hairs present, basal cells 20–35 μm×13–20 μm, grouped in irregularly shaped patches which at times coalesce.

Tetrasporangia scattered over surface of entire frond except basal and apical portions, 45 μm×24 μm in maximum dimensions, cruciate, surrounded by curved and anticlinally elongated cortical cells.

Spermatangia borne on surface of entire frond except basal and apical portions; conceptacles deep, pot-like, 80–100 μm deep, 55–80 μm wide, separated completely from one another, ostiole round in surface veiw.

Carpogonial branches two-celled; cystocarps globoid, prominently protruding, non-rostrate, 1 mm high, up to 1.2 mm diam., constricted at base; gonimoblast cells elongated and extremely vacuolate; nutritive filaments present.

Remarks. Mature cystocarps and tetrasporangia were not available to the writer, and their descriptions are taken from Ohmi (1958).

Gracilaria arcuata is one of the more easily recognizable Japanese species, being distinguished by its shrubby appearance.

The present species is restricted to the southern districts of Japan.

Gracilaria edulis (Gmelin) Silva
(Pl. 30, figs, 4–6, Pl. 31, Pl. 49, fig. 1)

Silva, 1952, p. 293; Ohmi, 1958, p. 16, pl. III, text-fig. 6.

Syn. Fucus edulis Gmelin, Gmelin, 1768, p. 113.

Gracilaria lichenoides (L.) Harvey, J. Agardh, 1852, p. 558; 1876, p. 412; De Toni, 1900, p. 430; Okamura, 1931, p. 39, pl. 271, figs. 1–5; 1936, p. 631; Takamatsu, 1938, p. 56; 1939, p. 60.

Japanese name. Kata-ogonori.

Habitat. This species grows on rocks covered with sand and on small coral fragments in the middle and upper intertidal zones.

Distribution. Okinawa Pref. and Kyushu.

Specimens collected. Okinawa Pref.: Nashiro (♂ ♀, Feb. 5, 1974, Yamamoto).

Fronds cespitose or solitary, cylindrical to somewhat compressed, arising from a small discoid holdfast, up to 10 cm high, increasing gradually in thickness from both ends toward the middle, attaining as much as ca. 1 mm diam., apices pointed; branches dichotomously divided, sometimes irregularly, bases slightly constricted or unconstricted; pale brown; rigidly cartilaginous.

Cortical layer consisting of 1–2 rows of cells; outermost cells 6.5–15 μm long, 8–15 μm wide; medulla 240–410 μm×215–300 μm in transverse section, consisting of 7–8 layers of polygonal cells; cells in outer layer slightly elongated parallel to the axis of the frond; transition of cells from cortex to medulla abrupt; hairs deciduous, basal cells 24–31 μm long, 20–22 μm wide, often divided transversely into two cells, containing ca. 20–50 nuclei.

Tetrasporangia densely scattered over entire surface of frond except basal and apical portions, ovoid, 45–50 μm×18–36 μm diam., cruciate, surrounded by more or less modified cortical cells.

Spermatangia borne over entire surface of frond except basal and apical portions; conceptacles deep, pot-like, 50–70 μm deep, 35–50 μm wide; spermatangia spherical, ca. 4 μm diam.

Cystocarps borne over entire surface of frond except basal and apical portions, up to 1.9 mm high, 2 mm wide, constricted at base; nutritive filaments extending into the pericarp.

Remarks. The specimens collected by the writer in Okinawa Pref. are smaller than those reported from southern Asia. Tetrasporangia were not available to the writer and are described here after Ohmi (1958). In addition, the spermatangia were not fully mature in the writer's material so that the size of the conceptacle may be greater than reported here.

Gracilaria coronopifolia J. Agardh
(Pl. 32, Pl. 49, figs. 2–3)

J. Agardh, 1852, p. 692; 1876, p. 414; De Toni, 1900, p. 434; Yamada, 1941, p. 202, pl. 45, text-fig. 8; Dawson, 1949, p. 22, pl. 24, figs. 2–5; Ohmi, 1958, p. 20, pl. IV, text-figs. 8–9; Segawa and Kamura, 1960. p. 52.

Japanese name. Mosa-ogonori.

Habitat. This species grows in a group, on rocks of crevices in the lower intertidal zone exposed to full surf.

Distribution. Okinawa Pref.

Specimens collected. Okinawa Pref.: Komesu (sterile, Feb. 11, 1974, Yamamoto).

Fronds cylindrical throughout or often somewhat compressed in middle portion and upwards, somewhat cespitose, forming loosely entangled mass, branching dichotomous or sometimes secund; branches with wide axillae, at times provided with numerous branchlets in part, apices gradually pointed; reddish purple; cartilaginous.

Cortical layer consisting of 1(–2) rows of cells, outermost cells subquadrate, 6.7–10.8(–13.5) μm × 6.8–8 μm; medulla consisting of ca. 15 layers of cells increasing in size toward the center, reaching 310–470 μm × 270–410 μm; transition of cell from cortex to medulla abrupt; hairs present, basal cells 13.5–18 μm × 10–13.5 μm.

Sexual and asexual reproductive organs unknown in Japanese material.

Remarks. Although the writer has not seen fertile Japanese material of this species, it can be easily assigned to the subgenus *Gracilaria* by the presence of nutritive filaments in the cystocarp and the deep pot-like shape of the spermatangial conceptacle described in specimens from Hawaii by Dawson (1949). The writer observed that the branches sometimes anastomose in young plants. Further study is needed to determine the incidence and significance of this phenomenon.

This species is very rare in Japan.

Gracilaria sublittoralis Yamada et Segawa
(Pls. 33–35, 48)

Takamine and Yamada, 1950, p. 268; Ohmi, 1958, p. 44, pl. IX, text-fig. 22; Tanaka, 1963, p. 86, pl. III; Yamamoto, 1969, p. 24, pl. I, figs. 5–7.

Japanese name. Shinkai-kabanori.

Habitat. This species grows on rocks in the sublittoral zone in the open sea.

Distribution. Sado, Niigata Pref.; Kōzu-shima, Izu Isl.; Shirahama, Wakayama Pref.; Uwajima, Ehime Pref.; Mage-shima, Kagoshima Pref.

Specimens collected. Niigata Pref.: Akadama in Sado (⊕♀, July 17, 1974, Taniguchi); Wakayama Pref.: Shirahama (⊕♂♀, May 15, 1968, Yamamoto; ⊕♀, April 25, 1972, Taniguchi).

Fronds flattened completely, generally solitary, with very short terete stipe 1–2 mm diam., reaching 5 mm in length, attached to substratum by small disc 5 mm maximum diam.; fronds 15–25 cm high, 3–5 cm wide, sometimes 6 cm in greatest width around axillae, up to 1 mm thick in the upper portion, up to 1.6 mm thick in the lower portion, divided dichotomously and trichotomously in 2–3 orders into lobes; lobes gradually increasing in width to the middle portion and tapering toward the tip, axillae round; apices attenuated or sometimes bifurcate, margins generally entire, but rarely proliferous; reddish brown or yellowish brown to pale brown; leathery, becoming increasingly so with age.

Cortical layer composed of 1–2 rows of cells, cells rather quadrate, 5.6–9.8 μm long, 5.6–9 μm wide, containing 1–2 nuclei; medulla composed of 3–5 layers of large cells up to 830 μm$\times$660 μm in the upper portion of frond, up to 1160 μm $\times$1020 μm in lower portion of frond, cell wall up to 10 μm thick in aged frond; transition of cells from cortex to medulla abrupt; hairs present, basal cells 13–20 μm$\times$15–17 μm.

Tetrasporangia scattered over both surfaces except basal and apical portions, 42–63 μm$\times$28–35(–53) μm, regularly cruciate, surrounded by slightly elongated cortical cells.

Spermatangia borne on both surfaces of frond except basal and apical portions; conceptacles pot-like, 32–50 μm deep, 28–62 μm wide, surrounded by elongated and curved cortical cells which form a slightly elevated nemathecial upheaval.

Carpogonial branches two-celled; cystocarps borne on both surfaces of frond except basal and apical portions, up to 1.4(–1.6) mm high, up to 1.8(–2) mm wide, constricted at base, slightly beaked or non-beaked; gonimoblast cells rather small and elongated, 55–165 μm$\times$23–35 μm, carposporophyte 435–480 μm diam. at base at maturity; nutritive filaments abundant, extending into the pericarp, but generally not penetrating deeply; pericarps consisting of flattened cells which are ca. 25 μm$\times$35 μm.

Remarks. This species was accredited to Yamada and Segawa and listed in a paper by Takamine and Yamada in 1950, but without any description. Later, Ohmi (1958) gave a detailed description and illustrations based on a few tetrasporangial and cystocarpic specimens provided by Segawa, but his account does not represent exact features of this species satisfactorily. The writer was fortunate enough to obtain numerous specimens collected by fishermen's dragnets or washed ashore. This species closely resembles *G. textorii* externally, with which it probably has sometimes been confused. The present species, however, is distinguishable by its larger frond, leathery texture, and large vegetative cells. Moreover, a clear distinction is presented by the spermatangial pattern, which in this species belongs to the Verrucosa type while in all other foliaceous species they belong to the Textorii type.

4. *Species of uncertain position*

Gracilaria salicornia (C. Agardh) Dawson
(Pl. 36, Pl. 49, fig. 4)

Dawson, 1954, p. 4, fig. 3; Ohmi, 1958, p. 27, pls. V-VI, text-fig. 12.

Syn. Sphaerococcus salicornia C. Agardh, C. Agardh, 1820, p. 302.

Corallopsis salicornia (C. Agardh) Greville, Greville, 1830; Kylin, 1932, p. 58.

Japanese name. Tokida-fushikurenori.

Habitat. This species grows on rocks and coral fragments covered with sand in the upper and middle intertidal zones. It grows often together with *G. edulis.*

Distribution. Okinawa Pref.

Specimens collected. Okinawa Pref.: Nashiro (sterile, Feb. 5, 1974, Yamamoto; sterile, April, 1974, Iida).

Fronds cylindrical throughout, arising from small disc, 2–3 cm high, up to 3.5 mm wide, forming an entangled mass when prostrate on substratum; branches divided dichotomously, sometimes alternately or irregularly, standing in an opposite manner, constricted at base when young, but less conspicuous in aged plants; internode somewhat club-lik, provided with fine basal portion when young; several connecting protuberances often developed between neighbouring branches or between branches and adjacent substratum; yellowish or brownish purple; rather rough, cartilaginous.

Cortical layer consisting of 1–2 rows of cells, thickest at constricted portion of frond, outermost cells 6.5–13.5 μm high, 6.5–15 μm wide; medulla consisting of about 15 layers of cells, increasing in diameter toward central portion of internode, 270–440 $\mu m \times 250$–340 μm, cells in peripheral zone somewhat elongated parallel to the axis of frond; transition of cells from cortex to medulla rather gradual; hairs present, basal cells prominent, scattered in the cortical layer, 23–35 $\mu m \times 19$–35 μm.

Tetrasporangia scattered over almost entire surface of frond, round in surface view, ovoid or oblong in transverse section, 45 $\mu m \times 15$–20 μm, cruciate, bounded by somewhat anticlinally elongated cortical cells.

Cystocarps globoid, prominently protruding, non-rostrate, up to 1.8 mm diam., constricted at base; gonimoblast more or less lobulate, narrow at its base, composed of conspicuously vacuolate cells; pericarp ca. 240 μm thick, connected with gonimoblast by numerous nutritive filaments.

Spermatangia unknown.

Remarks. No fertile material of this species was available to the writer, so that the descriptions given above are taken from Ohmi (1958). He states "The present species closely resembles *G. crassa* Harv. in the internal structure as well as in the external character. It is, however, easily distinguished from the latter in its extremely narrowed or sharply defined base of branches and branchlets". As far as the writer has observed, the degree of the constriction varies considerably from specimen to specimen. Further study is needed to assess the diagnostic value of this character in separating these two species

Gracilaria salicornia has a very limited distribution in Japan.

Gracilaria eucheumioides Harvey
(Pl. 37, Pl. 49, fig. 5)

Harvey, 1859, p. 331; Okamura, 1936, p. 634; Dawson, 1954a, p. 438, fig. 48; Segawa and Kamura, 1960, p. 53.

Japanese name. Ryukyu-ogonori.

Habitat. This species grows prostrate on rocks in the upper sublittoral zone.

Specimens collected. Okinawa Pref.: Sunayama in Miyako-jima (⊕: young, sterile, Oct. 7, 1973, Kamura).

Main axis compressed to rather flattened, ca. 2–3.5 mm thick, 7–10 mm wide, prostrate on substratum, branching irregular or somewhat pinnate in opposite manner; branches compressed or somewhat cylindrical, provided with short club-shaped, proliferous or spinous branchlets which are produced on opposite sides or sometimes on surface; dark purplish; cartilaginous.

Cortical layer consisting of 1–2 rows of cells, outermost cells (7–)8–13.5 μm long, 4.5–9 μm wide; medulla consisting of about 15 layers of cells, cells round, increasing in diameter toward the center, reaching 240–300 μm$\times$160–220 μm, cells in outer region of medulla rather elongated parallel to the axis of frond; transition of cells from cortex to medulla gradual; hairs present, basal cells 29–40 μm$\times$11.5–17 μm, sometimes divided transversely into 2(–3) cells, scattered over entire surface of frond in groups of 10–20 cells.

Tetrasporangia in undivided stage 39–50 μm high, 15–20 μm wide, oblong or club-like, surrounded by elongated cortical cells.

Male and cystocarpic plants unknown.

Remarks. The writer was fortunate to obtain tetrasporangial plants. They are, however, quite young and have undivided oblong sporangia which contain only one resting nucleus in the center. Although this is the first record of the asexual reproductive organ in this species, some doubts of the systematic position of the specimen from Okinawa ramain because of the lack of sexual plants. On the other hand, the internal structure of these specimens agrees with that of the genus *Gracilaria*.

The present species has the most gradual transition of cell size from cortex to medulla of all Japanese species.

F. Discussion

The nutritive filaments found in the cystocarp of *Gracilaria* were first elucidated by Sjöstedt (1926), who discussed their role in relation to the cell content in the gonimoblast tissue. The presence or absence of nutritive filaments was first assigned diagnostic value on the generic level by Dawson (1949), who segregated *Gracilariopsis* from *Gracilaria* to contain those species lacking such filaments. However, nutritive filaments are very unstable with respect to their occurrence in Japanese species and may at times be found in species that usually lack them (i.e., species which would thus be assigned to *Gracilariopsis*). On the other hand, Papenfuss (1966) reported that he was not always able to find nutritive filaments in British material of *Gracilaria verrucosa* and therefore merged the two genera.

During the course of the present study it became clear that some character other than the presence or absence of nutritive filaments could be used to arrange the species of *Gracilaria* into groups, namely, the nature of the spermatangial pattern. Three types, divergent in their morphology and development, are found in Japanese species. The same three types were described by Dawson (1949) in species of the Pacific coast of Mexico and the United States.

The present classification of Florideophycidae is to a large extent based on developmental details of the reproductive organs. A careful examination of female structures and their development in Japanese species has revealed no fundamental differences in this character between species assigned to *Gracilaria* and those assigned to *Gracilariopsis* on the basis of the presence or absence of nutritive filaments. Differences in the male reproductive system, although generally considered to be of lesser diagnostic value than differences in the female system, appear to constitute a reasonable basis for dividing *Gracilaria* sensu lato into three subgenera.

As mentioned in the General considerations, two additional types of spermatangial patterns have been described. One of them was reported in *G. symmetrica* and *G. costaricensis* by Dawson (1949) and another in *G. multifurcata* and *G. henriquesiana* by Børgesen (1953) and Ohmi (1958a) respectively. Further detailed study of the developmental processes involved in these two types is necessary to determine their systematic relationship to the three types described from Japanese species.

Greig-Smith (1954) studied the female organ and its development in a plant which she identified as *G. multipartita*. Her results are quite different from those obtained by the writer working with Japanese species of the genus. She showed the presence in her material of an auxiliary cell characteristic of Rhodymeniales. In view of the similarity of the tissues of *Gracilaria* and *Rhodymenia*, the question arises whether Greig-Smith might not have had a representative of the former genus in hand.

G. Summary

Gracilariaceous plants of Japan were studied anatomically and systematically, with the following results:

1. Descriptions and illustrations of sixteen species were prepared on the basis of materials collected mainly by the writer at various places in Hokkaido, Honshu, Shikoku, Kyushu and Okinawa.

2. The anatomical and vegetative features previously used to separate the species were examined. They proved to be relatively unimportant as diagnostic criteria except in the following two species. By the decided constriction at the branch base in *G. blodgettii*, and by the gradual transition from cortex to medulla seen in the transverse section of a frond in *G. eucheumioides*, these two species are distinguishable from other previously known species.

3. Tetrasporangial specimens were collected and described in *G. denticulata* and *G. eucheumioides* for the first time. In addition, hitherto known tetrasporo-

phytes of nine species were reexamined.

4. Carpogonial branches are first reported in Japan in the following eleven species: *G. chorda**, *G. gigas**, *G. blodgettii**, *G. textorii*, *G. incurvata*, *G. punctata*, *G. purpurascens*, *G. verrucosa**, *G. vermiculophylla**, *G. arcuata* and *G. sublittoralis**. In species marked with an asterisk, post-fertilization development was studied in detail. In all cases the basal cell of a lateral filament borne on the supporting cell is regarded as a generative auxiliary cell.

5. Cystocarpic specimens of *G. edulis* were collected and described for the first time.

6. Male specimens were collected and described for the first time in the following eight species: *G. chorda*, *G. gigas*, *G. blodgettii*, *G. incurvata*, *G. denticulata*, *G. purpurascens*, *G. edulis* and *G. sublittoralis*. The developmental process of spermatangial formation in thirteen species, including the eight species just named, has been observed, and three types of spermatangial patterns have been shown to exist in Japanese plants.

7. The relationship between the existence of nutritive filaments in a cystocarp and the three types of spermatangial patterns has been discussed. It is concluded that the genus *Gracilariopsis* should be merged with the genus *Gracilaria* in accordance with Papenfuss (1966), and three subgenera are proposed on the basis of the three types of spermatangial patterns.

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Explanation of Plates

PLATE 1

Gracilaria chorda Holmes

Fig. 1. Surface view of mature frond, showing a hair basal cell (hb) which is distinguishable in size from surrounding vegetative cells. × 890.
Fig. 2. Vertical section of male frond, showing five spermatangia (sp), a hair and its basal cell. × 890.
Fig. 3. Part of vertical section through cortex, showing cells with resting nuclei. × 890.
Fig. 4. Transverse section of mature frond, showing abrupt transition in cell size from cortex to medulla. × 45.
Fig. 5. Enlargement of part of fig. 4, showing rather well-developed cortex. × 360.
Fig. 6. Longitudinal section of mature frond. × 45.

PLATE 2

Gracilaria chorda Holmes

Figs. 1–5. Vertical section of female frond, showing stages in development of procarp. Figs. 1–2. Stage in formation of carpogonial branch primordium (cbp). Fig. 3. The results of the transverse division of the carpogonial branch primordium into a lower cell (which becomes the supporting cell) and an upper cell (the carpogonial branch initial (cbi). Figs. 4–5. Mature procarp before fertilization, showing two-celled carpogonial branch and its supporting cell. × 890.
Fig. 6. Enlargement of part of vertical section through basal region of cystocarp, showing two elongated vegetative cells extending into gonimoblast. These cells closely resemble nutritive filaments and sometimes are mistaken for them. × 890.
Fig. 7. Detail of periphery of young gonimoblasts (g). × 890.
Fig. 8. Part of periphery of gonimoblast with carpospores (ca) formed at terminal portion. × 360.

PLATE 3

Gracilaria chorda Holmes

Fig. 1. Longitudinal section through mature cystocarp, showing absence of nutritive filaments. × 84.
Fig. 2. Part of vertical section through pericarp of mature cystocarp. × 340.
Fig. 3. Vertical section through fusion cell of young cystocarp, showing gonimoblast (g) in early stage of formation. × 840.

PLATE 4

Gracilaria chorda Holmes

Fig. 1. Part of longitudinal section of mature frond, showing cortex and a part of medulla. × 360.
Fig. 2. Surface view of male frond, showing spermatangia (sp) and vegetative cells (v). × 890.
Figs. 3–6. Part of vertical section of male frond, showing stages in formation of spermatangia (sp). × 890.
Fig. 7. Part of vertical section of male frond, showing mature spermatangia which are formed continuously in surface layer of frond. This spermatangial pattern belongs to the Chorda type. × 890.
Figs. 8–11. Part of vertical section of asexual frond, showing stages in formation of tetrasporangia. × 890.

PLATE 5

Gracilaria gigas Harvey

Fig. 1. Transverse section of main axis, showing abrupt transition of cell size from cortex to medulla. × 25.
Fig. 2. Enlargement of part of fig. 1, showing cortex and a part of medulla. × 250.
Fig. 3. Part of longitudinal section of main axis, showing cortex and a part of medulla. × 250.
Fig. 4. Transverse section of young frond, showing cortical layer in less developed stage than that in old one. × 890.
Fig. 5. Part of vertical section of mature frond, showing hair basal cell (hb). × 890.

PLATE 6

Gracilaria gigas Harvey

Figs. 1–3. Various stages in early development of carposporophyte. Fig. 1. Stage just after fertilization, showing auxiliary cell (aux) and supporting cell (su) which are densely protoplasmic. Note the growth of cortical cells. Fig. 2. Stage in formation of gonimoblast initial. Note densely protoplasmic content of surrounding vegetative cells. 1: × 636, 2–3: × 360.
Figs. 4–5. Mature procarp before fertilization. × 890.
Fig. 6. Procarp just before fertilization, showing spermatium (sm) attached to tip of trichogyne. × 890.
Figs. 7–8. Two successive stages of procarp in postfertilization. Fig. 7. Stage in formation of wide opening between carpogonium and hypogynous cell. Fig. 8. Stage in completion of connection between hypogynous cell and auxiliary cell. × 890.

PLATE 7

Gracilaria gigas Harvey

Figs. 1–3. Detail of nutritive filaments, showing terminal portion which communicates with cells of pericarp through pit and cell fusion. 1–2: × 450, 3: × 89.
Figs. 4–5. Surface view of male frond, showing spermatangial mother cells (spmc) in early stage of development. × 890.

PLATE 8

Gracilaria gigas Harvey

Figs. 1–3. Surface view of male frond, showing spermatangia (sp) in various developmental stages of formation. 1–2: × 890, 3: × 530.
Fig. 4. Vertical section of mature male frond through spermatangial conceptacles embedded in slightly raised nemathecium. × 196.
Figs. 5–6. Vertical section through spermatangial conceptacles (spmc). Fig. 5. Undeveloped conceptacle. × 890. Fig. 6. Mature conceptacle. × 890.

PLATE 9

Gracilaria blodgettii Harvey

Figs. 1–2. Habit of branches with constriction. × ca. 1.6.
Fig. 3. Transverse section of mature frond, showing abrupt transition of cell size from cortex to medulla. × 25.
Fig. 4. Enlargement of part of fig. 3. × 890.
Fig. 5. Part of longitudinal section of mature frond, showing cortex and a part of medulla.

× 250.

Fig. 6. Part of vertical section of mature frond, showing two hair basal cells (hb). × 636.

PLATE 10

Gracilaria blodgettii Harvey

Figs. 1–2. Procarp just before fertilization. × 890.

Fig. 3. Vertical section through mature cystocarp, showing many nutritive filaments. × 64.

Figs. 4–5. Detail of nutritive filament. Fig. 4. Nutritive filament (nf) protruding from gonimoblast to cavity of cystocarp. × 360. Fig. 5. Nutritive filament penetrating into pericarp. × 360.

Figs. 6–9. Surface view of male frond, showing spermatangia (sp) in various developmental stages. × 890.

PLATE 11

Gracilaria blodgettii Harvey

Figs. 1–2. Surface view of mature male frond, showing spermatangial conceptacle. × 360.

Figs. 3–5. Vertical section through spermatangial conceptacle, showing stages in formation of spermatangial conceptacle. × 890.

Fig. 6. Tetrasporangium in two-celled stage. × 890.

PLATE 12

Gracilaria textorii (Sur.) De Toni

Fig. 1. Transverse section of mature frond, showing abrupt transition of cell size from cortex to medulla. × 89.

Figs. 2–3. Part of vertical section through cortex, showing hair and its basal cell. × 890.

Figs. 4–6. Nutritive filament extending from gonimoblast to pericarp. × 360.

PLATE 13

Gracilaria textorii (Sur.) De Toni

Figs. 1–3. Three kinds of nutritive filaments. Fig. 1. Fully developed filaments which penetrate into pericarp. × 360. Figs. 2–3. Simple (fig. 2) and irregularly shaped (fig. 3) filaments. × 360.

Figs. 4–7. Part of vertical section through cortex of female frond, showing various stages in development of procarp before fertilization. × 890.

Fig. 8. Vertical section through mature cystocarp. × 45.

PLATE 14

Gracilaria textorii (Sur.) De Toni

Figs. 1–4. Part of vertical section through cortex of female frond, showing stages in development of procarp before fertilization. × 890.

Fig. 5. Vertical section through procarp in postfertilization, showing union of hypogynous cell with auxiliary cell through connecting tube. × 890.

Fig. 6. Surface view of female frond, showing procarp (p) before fertilization and surrounding vegetative cells (v). × 890.

Figs. 7–8. Fusion cell and young gonimoblast. × 290.

Figs. 9–10. Vertical section through cortex showing undivided tetrasporangia (t) and modified cortical cells. × 890.

PLATE 15

Gracilaria incurvata Okamura

Fig. 1. Transverse section of fertile frond, showing abrupt transition of cell size from cortex to medulla. × 36.
Fig. 2. Part of transverse section of mature frond, showing two discernible hair basal cells (hb). × 360.
Fig. 3. Part of longitudinal section of mature frond. × 89.
Fig. 4. Transverse section through the marginal portion of a mature frond. × 36.
Fig. 5. Part of vertical section of male frond through spermatangial conceptacle embedded in slightly raised nemathecium. × 196.

PLATE 16

Gracilaria incurvata Okamura

Figs. 1–5. Surface view of male frond, showing spermatangial conceptacles in developmental stages and their union during development. × 890.
Figs. 6–7. Surface view of male frond, showing spermatangial conceptacles. Fig. 6. Stage in early development of conceptacle. × 360. Fig. 7. Fused mature conceptacle. × 360.
Figs. 8–10. Part of vertical section through fertile portion of male frond, showing stages of formation of spermatangial mother cells. × 890.
Fig. 11. Vertical section through mature spermatangial conceptacle. × 890.

PLATE 17

Gracilaria punctata (Okamura) Yamada

Fig. 1. Surface view of mature frond, showing densely dotted hair basal cells (hb). × 340.
Fig. 2. Vertical section of fertile frond, showing outermost cells of cortical layer of ventral surface (ve) which are longer than those of upper surface. × 340.
Fig. 3. Longitudinal section of mature frond. × 340.
Fig. 4. Part of vertical section through a group of hair basal cells. × 840.

PLATE 18

Gracilaria punctata (Okamura) Yamada

Fig. 1. Transverse section through marginal portion of mature frond. × 360.
Figs. 2–3. Part of vertical section through fully mature procarp before fertilization. × 890.
Figs. 4–5. Part of vertical section through cortex containing procarp in postfertilization, showing union of hypogynous cell with auxiliary cell through connecting filament. Number of nuclei in supporting cell is four at the most; such a small number of nuclei is characteristically observed only in the present species. × 890.
Fig. 6. Vertical section through mature cystocarp, showing nutritive filaments which are rather few. × 89.

PLATE 19

Gracilaria punctata (Okamura) Yamada

Fig. 1. Enlargement of part of gonimoblast, showing young carposporangia (ca) produced in chain from peripheral portion of gonimoblast (g). × 388.
Fig. 2. Part of vertical section through pericarp of mature cystocarp. × 388.
Figs. 3–4. Enlargement of part of gonimoblast, showing nutritive filaments. × 388.
Fig. 5. Surface view of mature male frond, showing spermatangial conceptacles. × 388.
Fig. 6. Part of vertical section of asexual frond, showing undivided tetrasporangia. × 958.

PLATE 20

Gracilaria denticulata (Kütz.) Weber van Bosse

Fig. 1. Longitudinal section of mature frond, showing abrupt transition of cell size from cortex to medulla. × 360.

Figs. 2–3. Enlargement of part of fig. 1. × 890.

Fig. 4. Optical view of apex of young processes, showing distinctive apical cells (a). × 890.

PLATE 21

Gracilaria denticulata (Kütz.) Weber van Bosse

Fig. 1. Transverse section through marginal portion of mature frond. × 360.

Fig. 2. Part of vertical section of mature frond, showing two hair basal cells. × 890.

Fig. 3. Vertical section through mature cystocarp, showing two nutritive filaments. The nutritive filaments are few in this species, and their existence is often overlooked. × 89.

Figs. 4–5. Detail of peripheral portion of gonimoblast. × 360.

PLATE 22

Gracilaria denticulata (Kütz.) Weber van Bosse

Fig. 1. Vertical section through pericarp of mature cystocarp. × 360.

Figs. 2–6. Surface view of male frond, showing stages in development of spermatangial conceptacle. Fig. 6. Mature spermatangial conceptacles. Note the fusion between conceptacles. 2–5: × 890, 6: × 360.

Fig. 7. Transverse section through mature spermatangial conceptacle which belongs to the Textorii type. × 890.

Fig. 8. Transverse section of asexual frond, showing young tetrasporangia (t). × 360.

PLATE 23

Gracilaria purpurascens (Harvey) J. Agardh

Fig. 1. Habit of part of frond margin bearing simple or branched processes. × 45.

Fig. 2. Optical view of apex of very young process, showing distinct apical cell (a). × 890.

Fig. 3. Transverse section through marginal portion of mature frond, showing abrupt transition of cell size from cortex to medulla. × 89.

Fig. 4. Enlargement of part of fig. 3, showing hair basal cell (hb). × 360.

Fig. 5. Surface view of mature male frond, showing fused spermatangial conceptacles. × 360.

Fig. 6. Vertical section through pericarp of mature cystocarp. × 360.

PLATE 24

Gracilaria purpurascens (Harvey) J. Agardh

Fig. 1. Vertical section through mature cystocarp, showing three nutritive filaments. × 64.

Fig. 2. Nutritive filament, showing irregularly shaped tip. × 360.

Fig. 3. Detail of peripheral portion of gonimoblast, showing carposporangia (ca) which are produced in chain. × 360.

Gracilaria verrucosa (Hudson) Papenfuss

Fig. 4. Part of vertical section through cortex, showing outermost cells containing 1-5 nuclei. × 890.

Figs. 5–7. Part of vertical section through cortex, showing hair cells in various stages of formation. Figs. 5–6. Early stage in which the constriction between hair and its basal cell is not complete. × 890. Fig. 7. Fully developed stage in which hair is cut off from its basal cell. × 890.

PLATE 25

Gracilaria verrucosa (Hudson) Papenfuss

Figs. 1–5. Part of vertical section through fertile portion of female frond. Figs. 1–4. Procarp in various stages of development. × 890. Fig. 5. Fertilized procarp. Note the fusion between carpogonium and auxiliary cell. × 890.

Fig. 6. Fusion cell (fu) and degenerating carpogonial branch (cb). × 890.

Fig. 7. Vertical section through young cystocarp, showing early stage in formation of gonimoblast initials (g) produced from fusion cell (fu). × 636.

Fig. 8. Part of vertical section through young cystocarp in more advanced stage than that in fig. 7. × 636.

PLATE 26

Gracilaria verrucosa (Hudson) Papenfuss

Fig. 1. Part of vertical section through young cystocarp, showing early stage in formation of nutritive filaments (nf). × 636.

Fig. 2. Semi-diagrammatic sketch of cystocarp of specimen identified as *G. rhodotricha* by Ohmi, showing the presence of the nutritive filaments (nf). × 89.

Figs. 3–5. Enlargement of part of fig. 2, showing detail of nutritive filaments extruding from periphery of gonimoblast. × 360.

PLATE 27

Gracilaria verrucosa (Hudson) Papenfuss

Figs. 1–3. Surface view of male frond, showing early stages in development of spermatangial mother cells. × 890.

Figs. 4–10. Part of transverse section of male frond, showing various stages in development of spermatangial conceptacle. × 890. Fig. 4. primordium of spermatangial mother cell (psm). Fig. 10. Fully developed spermatangial conceptacle, which belongs to the Verrucosa type.

PLATE 28

Gracilaria vermiculophylla (Ohmi) Papenfuss

Fig. 1. Transverse section of main axis, showing rather thick cortex consisting of small cells. × 45.

Fig. 2. Enlargement of part of fig. 1, showing abrupt transition of cell size from cortex to medulla. × 360.

Fig. 3. Longitudinal section of main axis. × 45.

Fig. 4. Part of vertical section of mature frond, showing outermost cells containing 1–5 nuclei. × 530.

Figs. 5–7. Various stages in development of procarp before fertilization. × 890.

PLATE 29

Gracilaria vermiculophylla (Ohmi) Papenfuss

Fig. 1. Vertical section through young cystocarp, showing nutritive filaments occurring in lower part of gonimoblast. × 360.

Fig. 2. Enlargement of part of fig. 1, showing one fully developed nutritive filament penetrating into pericarp and another less developed one free in the cavity of cystocarp. × 530.

Figs. 3–6. Various stages in development of tetrasporangium (t). × 530. Fig. 6. Mature tetrasporangium. The characteristic tetrahedral division is observed clearly in this species.

PLATE 30

Gracilaria arcuata Zanardini

Fig. 1. Part of transverse section of female frond. × 890.

Fig. 2. Surface view of male frond, showing spermatangial conceptacles separated completely by vegetative cells. × 360.

Fig. 3. Vertical section through mature spermatangial conceptacle, which belongs to the Verrucosa type. × 450.

Gracilaria edulis (Gmelin) Silva

Fig. 4. Transverse section of mature frond, showing abrupt transition of cell size from cortex to medulla. × 45.

Fig. 5. Longitudinal section of the same frond as fig. 4, showing outermost cells of medulla which are elongatedly parallel to frond surface. × 45.

Fig. 6. Enlargement of part of fig 5. × 890.

PLATE 31

Gracilaria edulis (Gmelin) Silva

Fig. 1. Part of vertical section of mature frond, showing two hair basal cells (hb) which are discernible from surrounding vegetative cells. × 890.

Fig. 2. Vertical section of pericarp of mature cystocarp. × 360.

Figs. 3–5. Nutritive filaments. In fig. 5 is shown the fusion with cells of pericarp. × 360.

Fig. 6. Surface view of mature male frond, showing spermatangial conceptacles separated completely by vegetative cells. × 890.

Figs. 7–8. Vertical section through spermatangial conceptacles. Fig. 7. Spermatangial mother cells (spmc). × 890. Fig. 8. Mature conceptacles, which belong to the Verrucosa type. × 360.

PLATE 32

Gracilaria coronopifolia J. Agardh

Fig. 1. Surface view of mature frond, showing hair basal cells (hb) scattered among vegetative cells. × 408.

Fig. 2. Part of vertical section of mature frond, showing a hair basal cell. × 408.

Fig. 3. Transverse section of mature frond. × 41.

Fig. 4. Enlargement of part of fig. 3. × 408.

Fig. 5. Part of longitudinal section of the same frond as in fig. 4. × 408.

PLATE 33

Gracilaria sublittoralis Yamada et Segawa

Fig. 1. Surface view of female frond. × 890.

Fig. 2. Transverse section of mature frond, showing abrupt transition of cell size from cortex to medulla. × 45.

Fig. 3. Enlargement of part of fig. 2. × 360.
Fig. 4. Part of vertical section of female frond, showing thin layered cortex. × 360.
Fig. 5. Transverse section through marginal portion of mature frond. × 360.

PLATE 34

Gracilaria sublittoralis Yamada et Segawa

Fig. 1. Part of vertical section of mature frond, showing a hair basal cell. × 890.
Fig. 2. Part of vertical section of female frond, showing two-celled carpogonial branch. × 890.
Fig. 3. Vertical section through mature cystocarp. × 32.
Fig. 4. Part of vertical section through young gonimoblast in stage of cell-fusion. × 890.
Fig. 5. Part of vertical section through pericarp of mature cystocarp. × 250.
Fig. 6. Enlargement of part of vertical section through gonimoblast tissue, showing arrangement of cells. × 250.

PLATE 35

Gracilaria sublittoralis Yamada et Segawa

Figs. 1–3. Nutritive filaments. Figs. 1 and 3. Filaments with irregularly shaped tip. × 360. Fig. 2. Filament with simple tip. × 360.
Fig. 4. Surface view of mature male frond, showing spermatangial conceptacles separated completely by vegetative cells. × 360.
Fig. 5. Part of vertical section of mature male frond, showing fully mature spermatangial conceptacles. × 89.
Fig. 6. Vertical section through fully mature spermatangial conceptacle, which belongs to the Verrucosa type. This type of conceptacle is observed only in the present species among foliaceous plants of *Gracilaria* studied in Japan. × 890.
Fig. 7. Part of vertical section of asexual frond, showing tetrasporangia formation in various stages. × 360.

PLATE 36

Gracilaria salicornia (C. Agardh) Dawson

Fig. 1. Surface view of sterile frond. × 340.
Fig. 2. Transverse section of sterile frond, showing moderately gradual transition of cell size from cortex to medulla. × 34.
Fig. 3. Enlargement of part of fig. 2. × 340.
Fig. 4. Part of longitudinal section of sterile frond, showing a hair basal cell (hb). × 340.
Fig. 5. Longitudinal section through constricted portion of sterile frond, showing medullary cells elongated vertically to frond surface and thickened cortex. × 42.

PLATE 37

Gracilaria eucheumioides Harvey

Fig. 1. Surface view of mature frond, showing hair basal cells (hb) scattered among vegetative cells. × 600.
Fig. 2. Transverse section of mature frond, showing gradual transition of cell size from cortex to medulla. The present species shows the most gradual degree of transition among species of *Gracilaria* in Japan. × 21.
Fig. 3. Longitudinal section of the same frond as fig. 2. × 21.
Fig. 4. Part of vertical section of mature frond, showing cells of cortical layer which are elongated vertically to frond surface. × 600.

Fig. 5. Part of transverse section of asexual frond, showing young undivided tetrasporangia. × 600.

PLATE 38

Gracilaria chorda Holmes

Figs. 1–2. Tetrasporic fronds from Akkeshi Lagoon, Hokkaido (dried specimens).
Figs. 3–4. Female fronds from Kamiiso, near Hakodate, Hokkaido (dried specimens).

PLATE 39

Gracilaria chorda Holmes

Fig. 1. Male frond from Kamiiso, near Hakodate, Hokkaido (dried specimen).
Fig. 2. Male frond from Izu, Shizuoka Pref. (dried specimen).
Fig. 3. Tetrasporic frond from Izu (dried specimen).
Fig. 4. Female frond from Shirahama, Wakayama Pref. (dried specimen).

PLATE 40

Gracilaria chorda Holmes

Fig. 1. Tetrasporic frond from Shirahama, Wakayama Pref. (specimen preserved in formalin-sea water).
Fig. 2. Male frond from Usa, Kōchi Pref. (dried specimen).
Figs. 3–4. Fronds from Shirahama, Wakayama Pref., in fig. 3 is shown conspicuous constriction at base of branch and in fig. 4 non-constricted base of branch (specimens preserved in formalin-sea water).
Fig. 5. Frond from Akkeshi Lagoon, showing filiform branchlets and fasciated base of branch (specimen preserved in formalin-sea water).

PLATE 41

Gracilaria gigas Harvey

Fig. 1. Sterile frond from Izu, Shizuoka Pref. (dried specimen).
Fig. 2. Female frond from Shirahama, Wakayama Pref. (specimen preserved in formalin-sea water).
Fig. 3. Tetrasporic frond from the same locality as in fig. 2 (dried specimen).
Fig. 4. Male frond from Amakusa, Kumamoto Pref. (dried specimen).
Fig. 5. Tetrasporic frond from Usa, Kōchi Pref. (dried specimen).

PLATE 42

Gracilaria blodgettii Harvey

Figs. 1–2. Female fronds from Yagachi, Okinawa Pref. (specimens preserved in formalin-sea water).
Figs. 3–4. Tetrasporic fronds from the same locality as in figs. 1–2 (specimens preserved in formalin-sea water).

Gracilaria textorii (Sur.) De Toni

Fig. 5. Female frond from Oshoro, Hokkaido (dried specimen).
Fig. 6. Sterile fronds from the same locality as in fig. 5 (dried specimens).
Fig. 7. Sterile fronds from Shinori, near Hakodate, Hokkaido (dried specimens).

PLATE 43

Gracilaria textorii (Sur.) De Toni

Fig. 1. Female frond from Usa, Kōchi Pref. (dried specimen).
Fig. 2. Male frond from the same locality (dried specimen).
Figs. 3–4. Sterile fronds from Amakusa, Kumamoto Pref. (dried specimens).

Gracilaria incurvata Okamura

Fig. 5. Female frond from Shirahama, Wakayama Pref. (specimen preserved in formalin-sea water).
Fig. 6. Male frond from Usa, Kōchi Pref. (dried specimen).

PLATE 44

Gracilaria incurvata Okamura

Figs. 1–2. Sterile fronds from Usa, Kōchi Pref. (specimens preserved in formalin-sea water).

Gracilaria punctata (Okamura) Yamada

Fig. 3. Female fronds from Komesu, Okinawa Pref. (specimens preserved in formalin-sea water).
Fig. 4. Sterile frond from the same locality as above, showing typical form and dark spots on the branches (specimen preserved in formalin-sea water).
Figs. 5–6. Sterile fronds from the same locality as above, showing overlapping branches (specimens preserved in formalin-sea water).

PLATE 45

Gracilaria denticulata (Kütz.) Weber van Bosse

Figs. 1–3. Sterile fronds from Komesu, Okinawa Pref. (1–2: specimens preserved in formalin-sea water, 3: dried specimen).
Fig. 4. Male frond from the same locality as above (dried specimen).
Fig. 5. Sterile frond from the same locality as above, showing the both features of *G. denticulata* and *G. purpurascens* on a single frond (dried specimen).

Gracilaria purpurascens (Harvey) J. Agardh

Fig. 6. Female frond from Komesu, Okinawa Pref. (dried specimen).

PLATE 46

Gracilaria verrucosa (Hudson) Papenfuss

Fig. 1. Sterile fronds from Onne Lagoon, near Kushiro, Hokkaido (dried specimens).
Fig. 2. Female fronds from Esashi, Sōya Prov., Hokkaido (specimen preserved in formalin-sea water).
Fig. 3. Tetrasporic fronds from Oshoro, Hokkaido (dried specimens).
Figs. 4–5. Tetrasporic fronds from Shinori, near Hakodate, Hokkaido (dried specimens).

PLATE 47

Gracilaria verrucosa (Hudson) Papenfuss

Fig. 1. Female frond from Amakusa, Kumamoto Pref. (dried specimen).

Gracilaria vermiculophylla (Ohmi) Papenfuss

Figs. 2–3. Tetrasporic fronds from Akkeshi Lagoon, Hokkaido (dried specimens).

Gracilaria arcuata Zanardini

Fig. 4. Sterile frond growing on stone from Yagachi, Okinawa Pref. (specimen preserved in formalin-sea water).

Fig. 5. Sterile frond from the same locality as above, showing typical arcuate feature of branching (dried specimen).

PLATE 48

Gracilaria sublittoralis Yamada et Segawa

Figs. 1–3. Female fronds from Shirahama, Wakayama Pref. (dried specimens).

Fig. 4. Male frond from the same locality as above (dried specimen).

Figs. 5–6. Tetrasporic fronds from the same locality as above (dried specimens).

PLATE 49

Gracilaria edulis (Gmelin) Silva

Fig. 1. Sterile fronds from Nashiro, Okinawa Pref. (specimens preserved in formalin-sea water).

Gracilaria coronopifolia J. Agardh

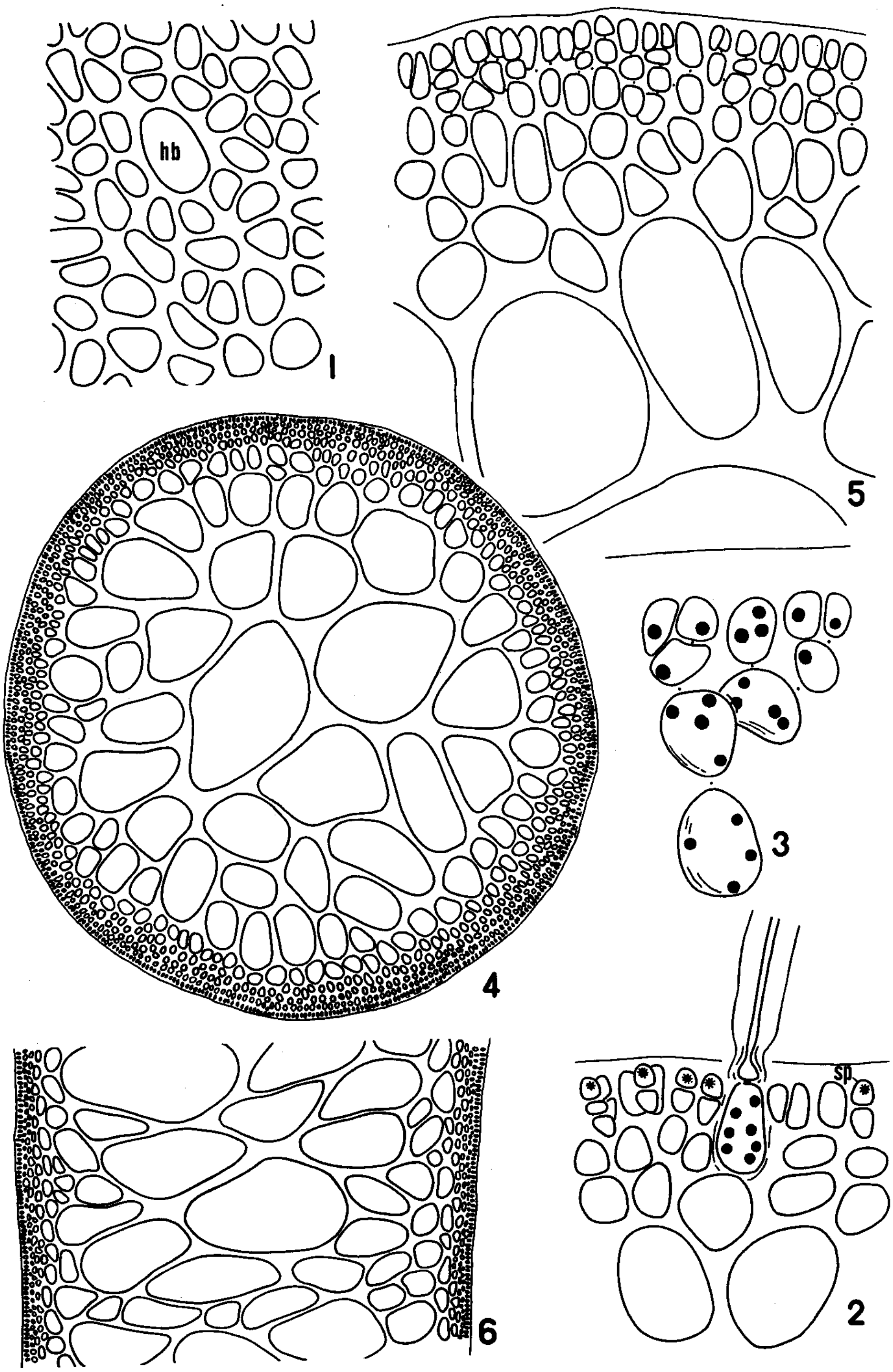
Figs. 2–3. Sterile fronds from Komesu, Okinawa Pref. (2: dried specimens, 3: specimens preserved in formalin-sea water).

Gracilaria salicornia (C. Agardh) Dawson

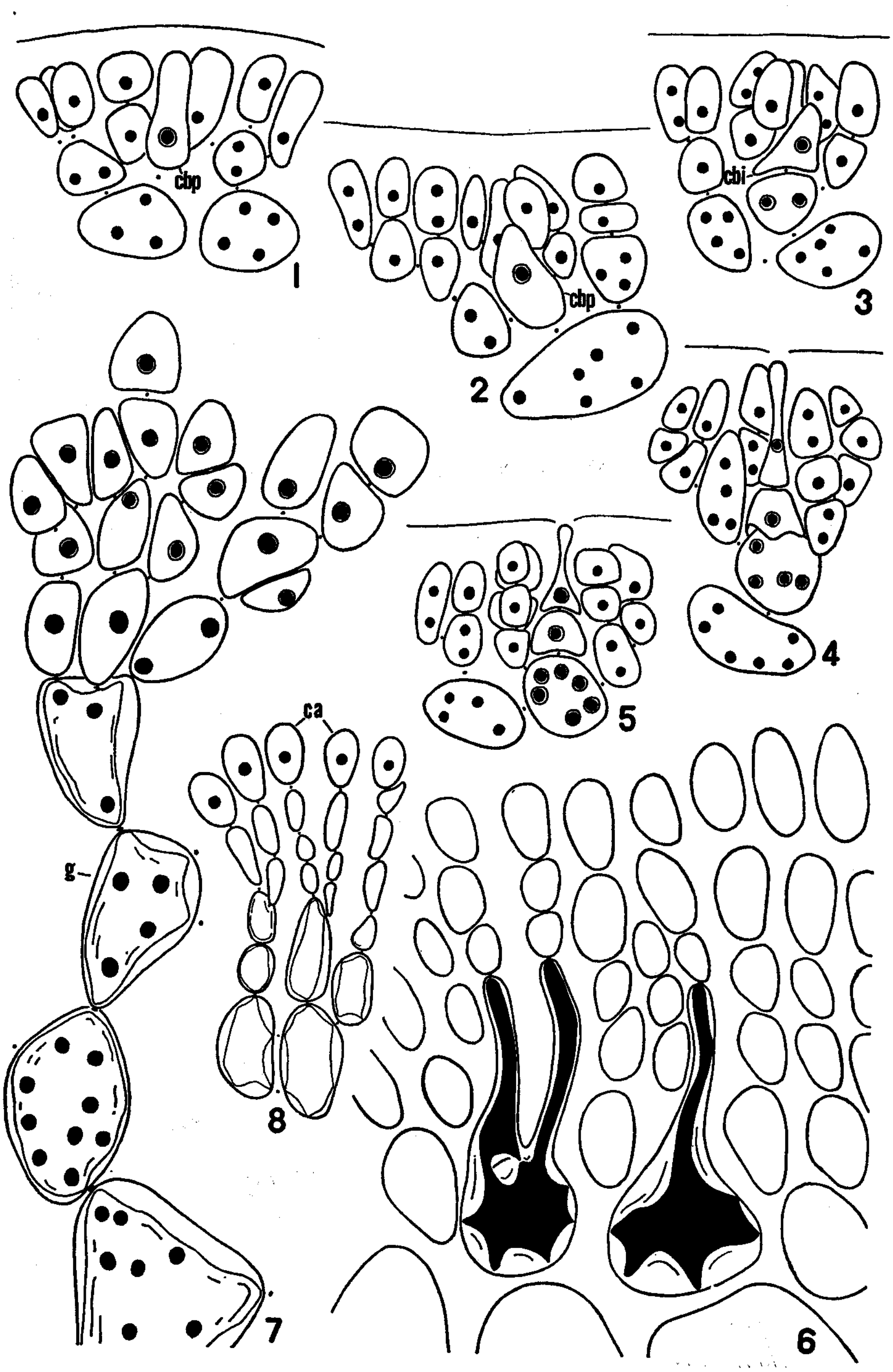
Fig. 4. Sterile fronds from Nashiro, Okinawa Pref. (specimens preserved in formalin-sea water).

Gracilaria eucheumioides Harvey

Fig. 5. Young tetrasporic fronds from Sunayama, Miyako-jima, Okinawa Pref. (specimens preserved in formalin-sea water).



YAMAMOTO: Study of *Gracilaria* in Japan



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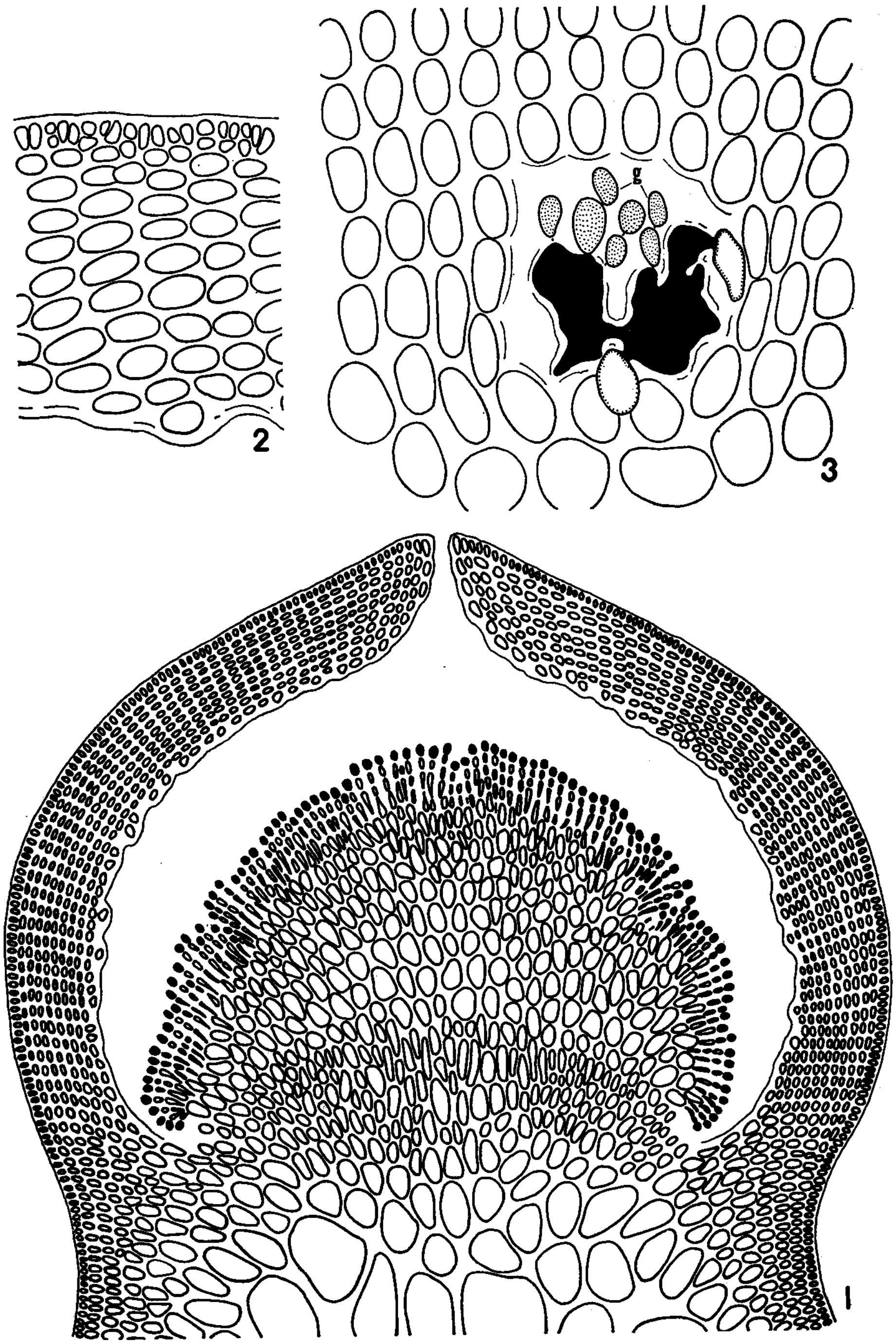

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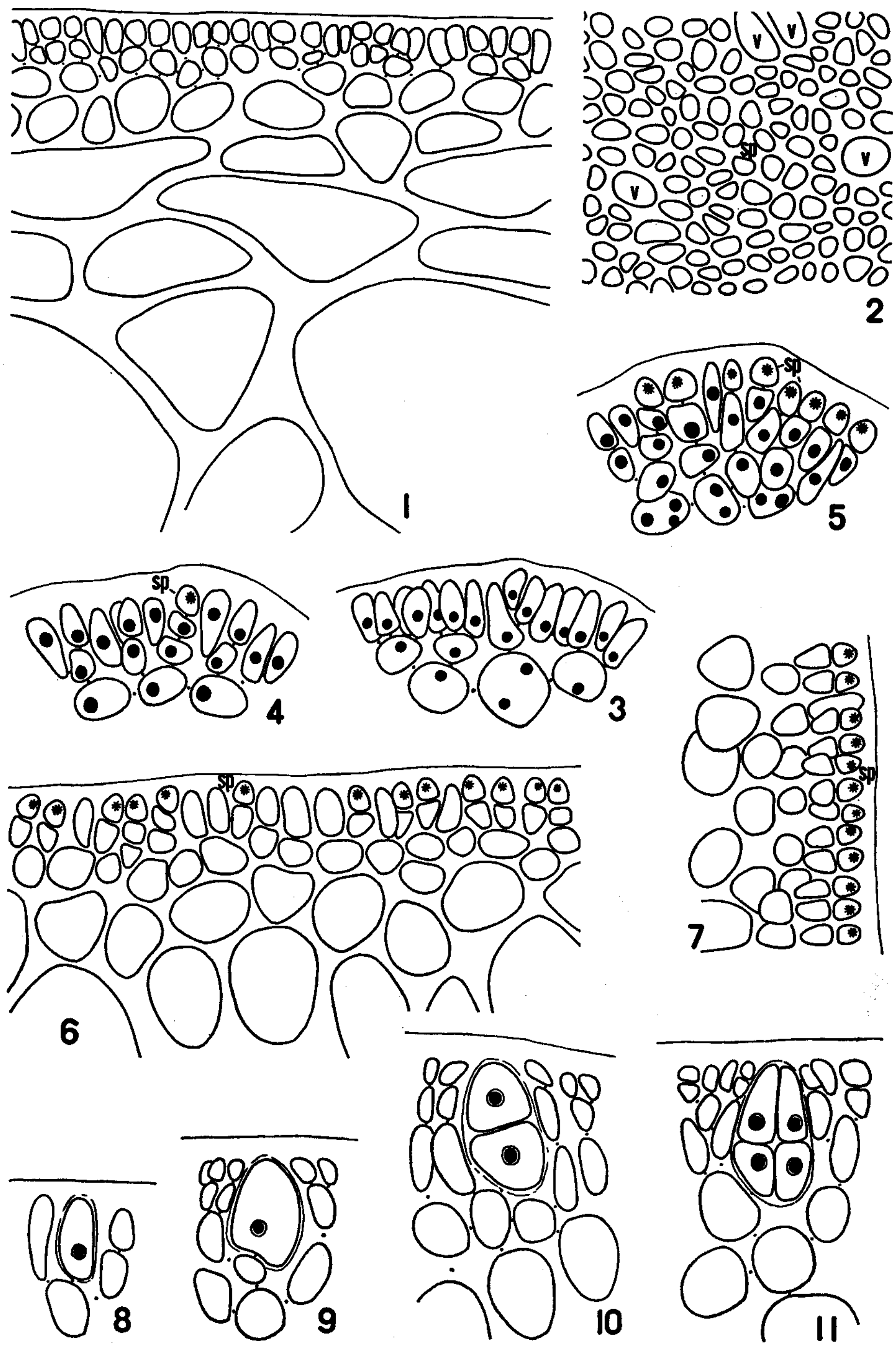

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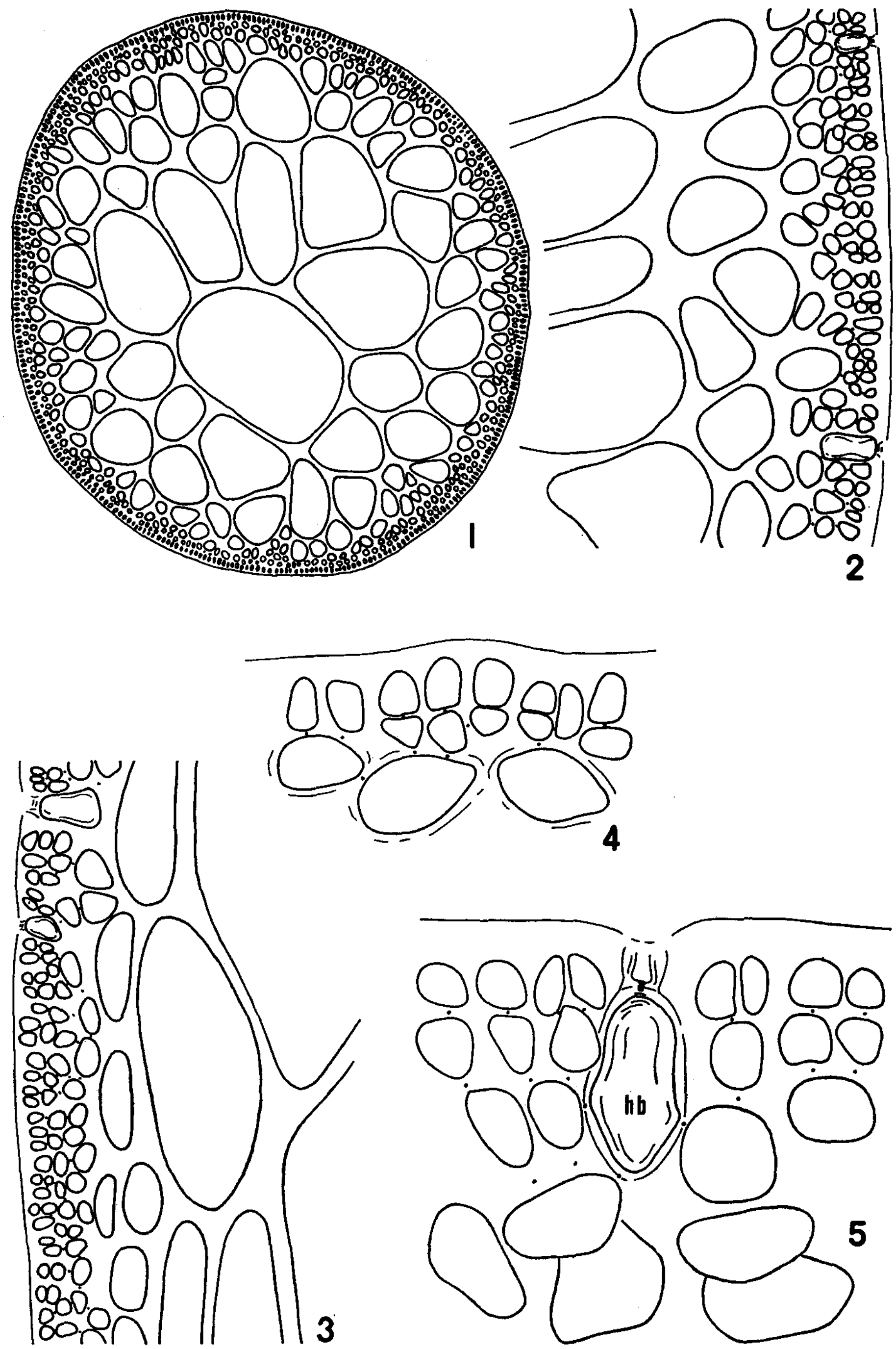

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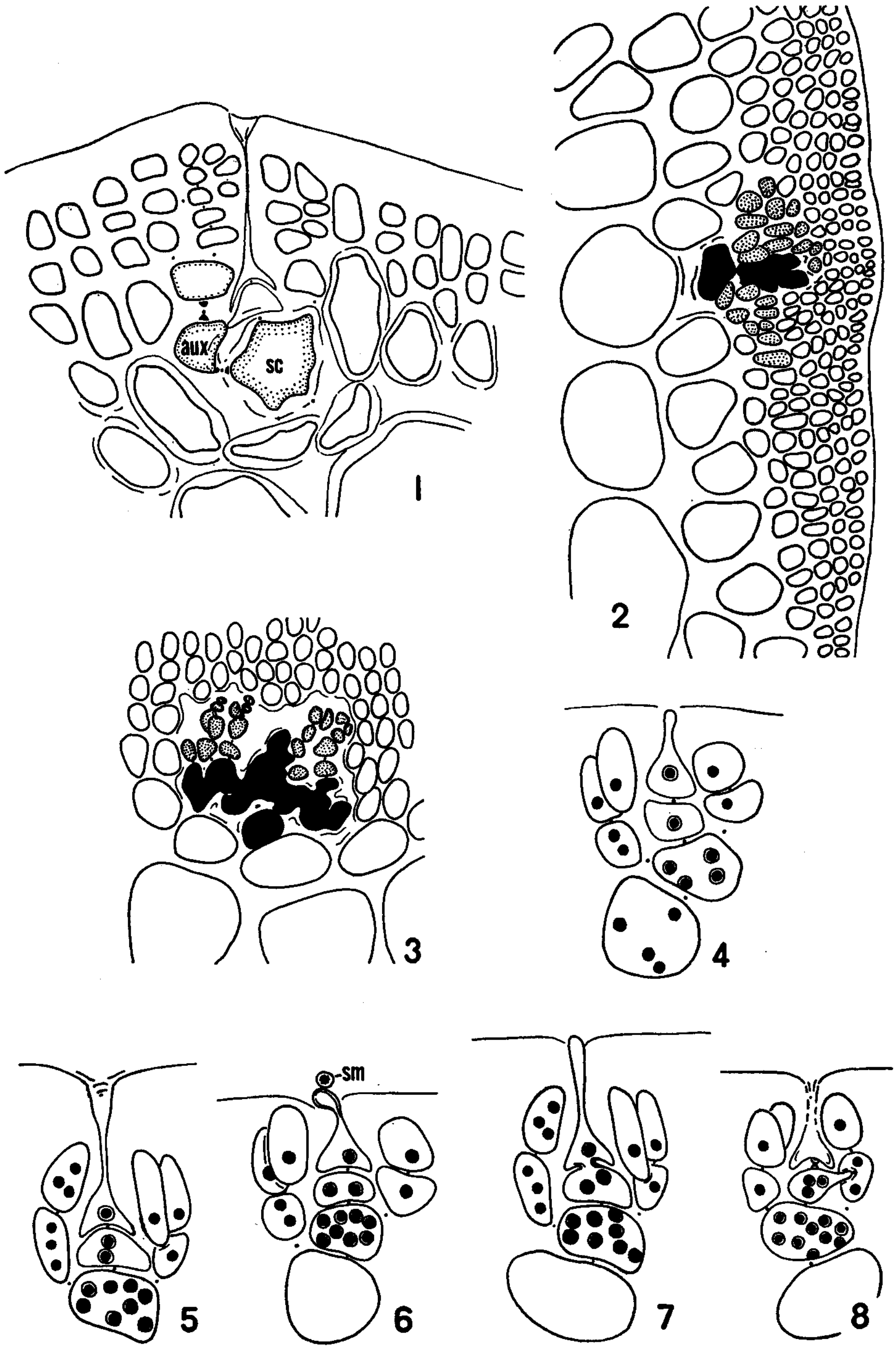

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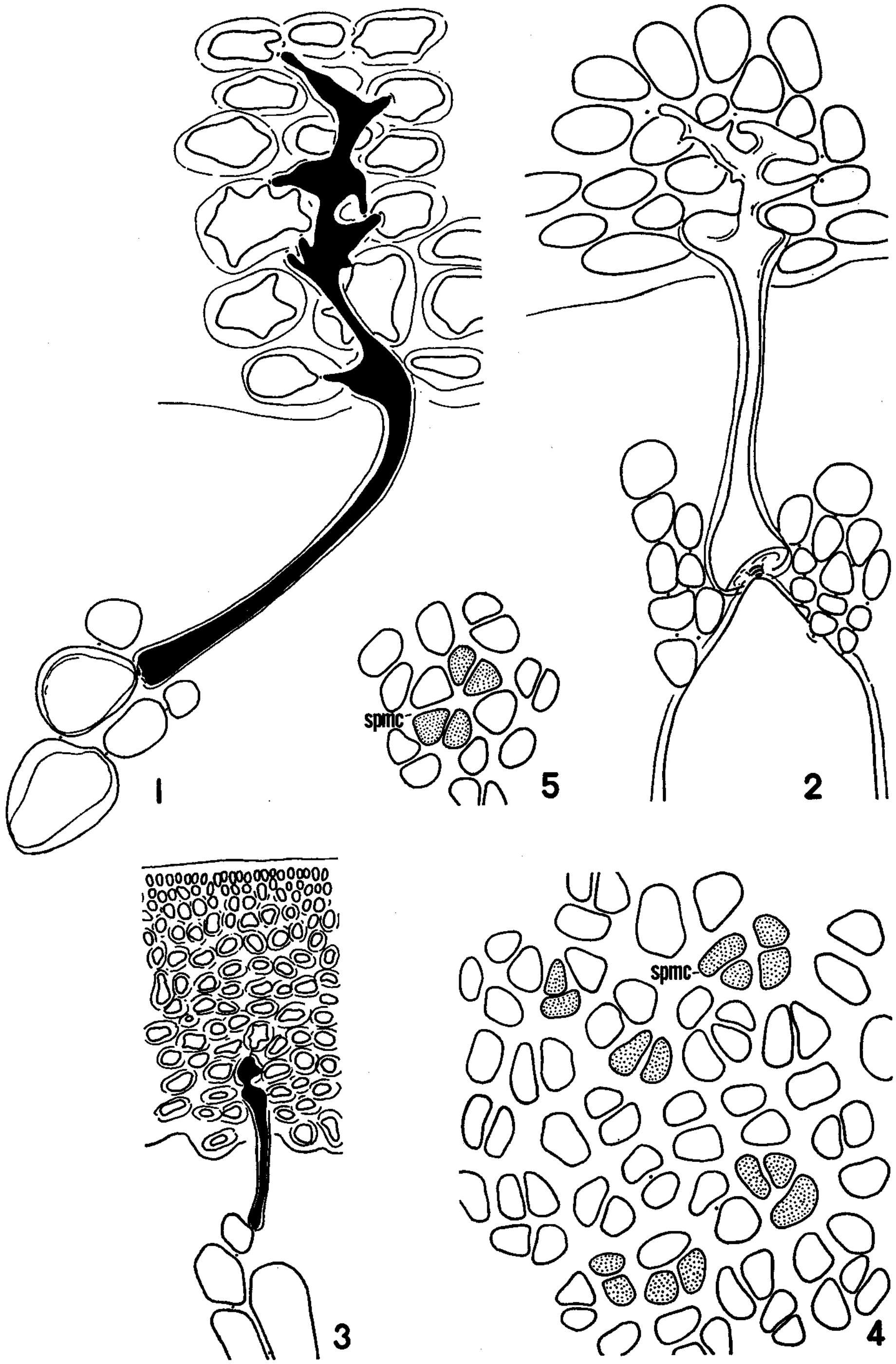

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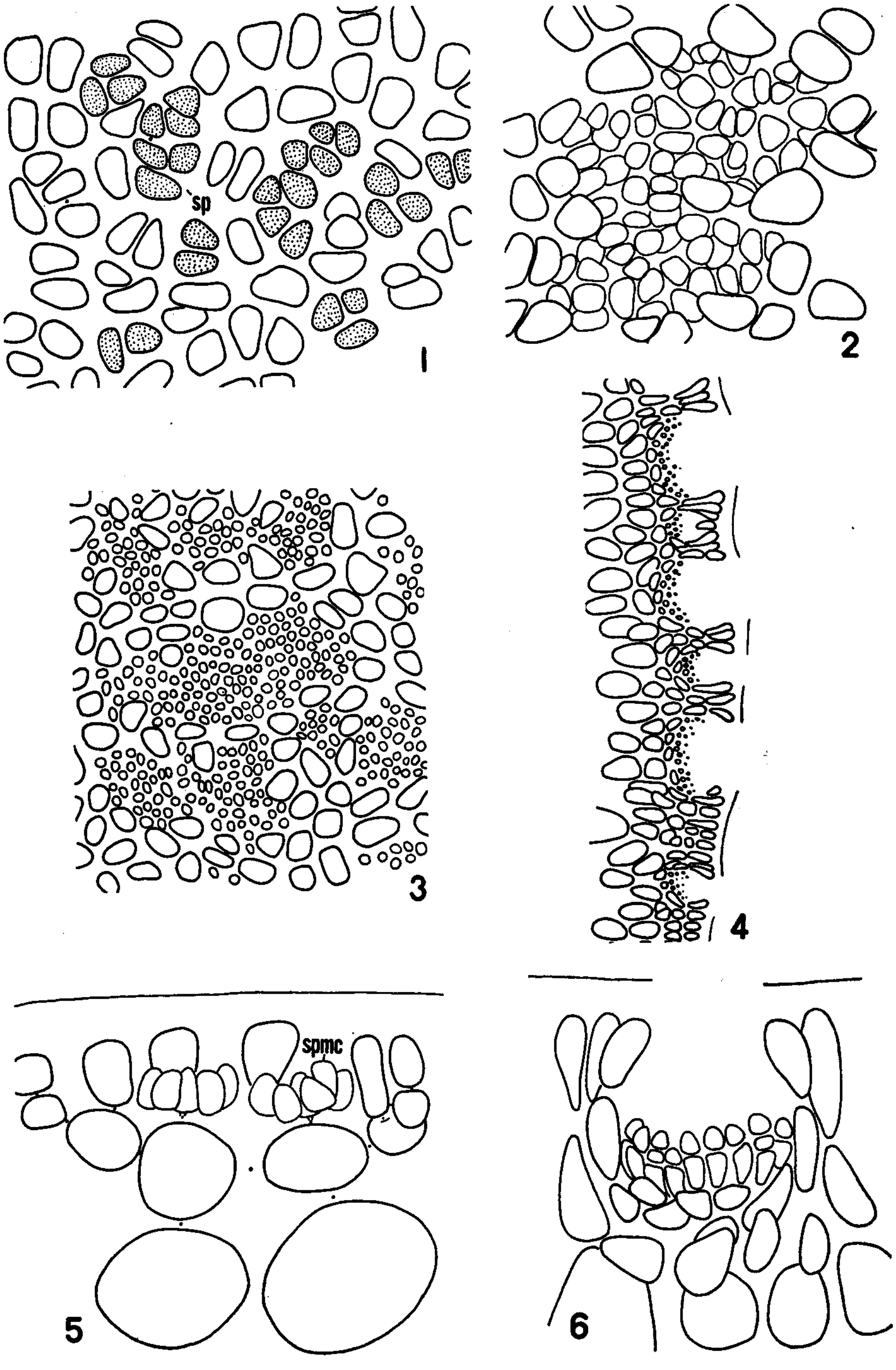

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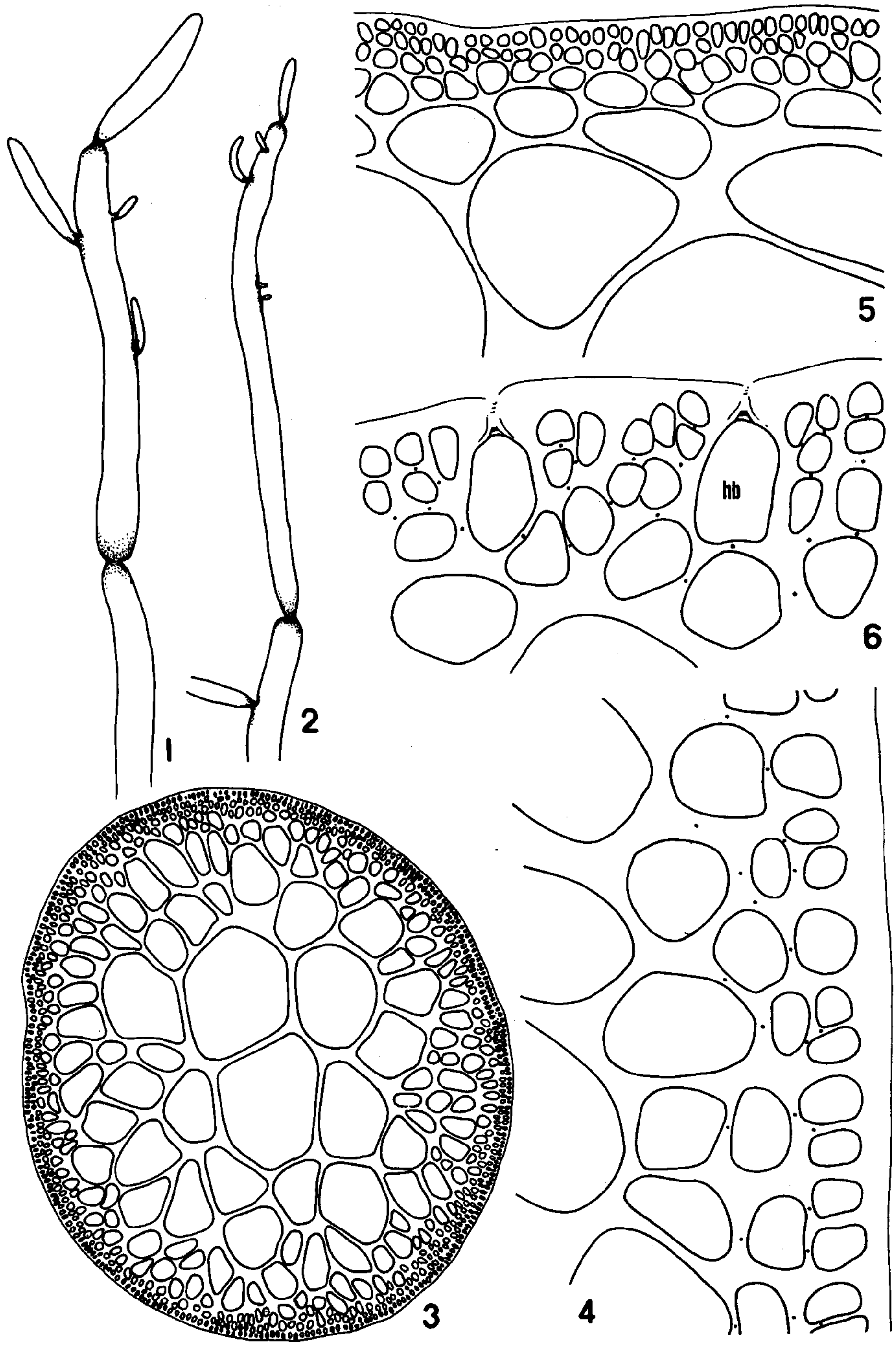

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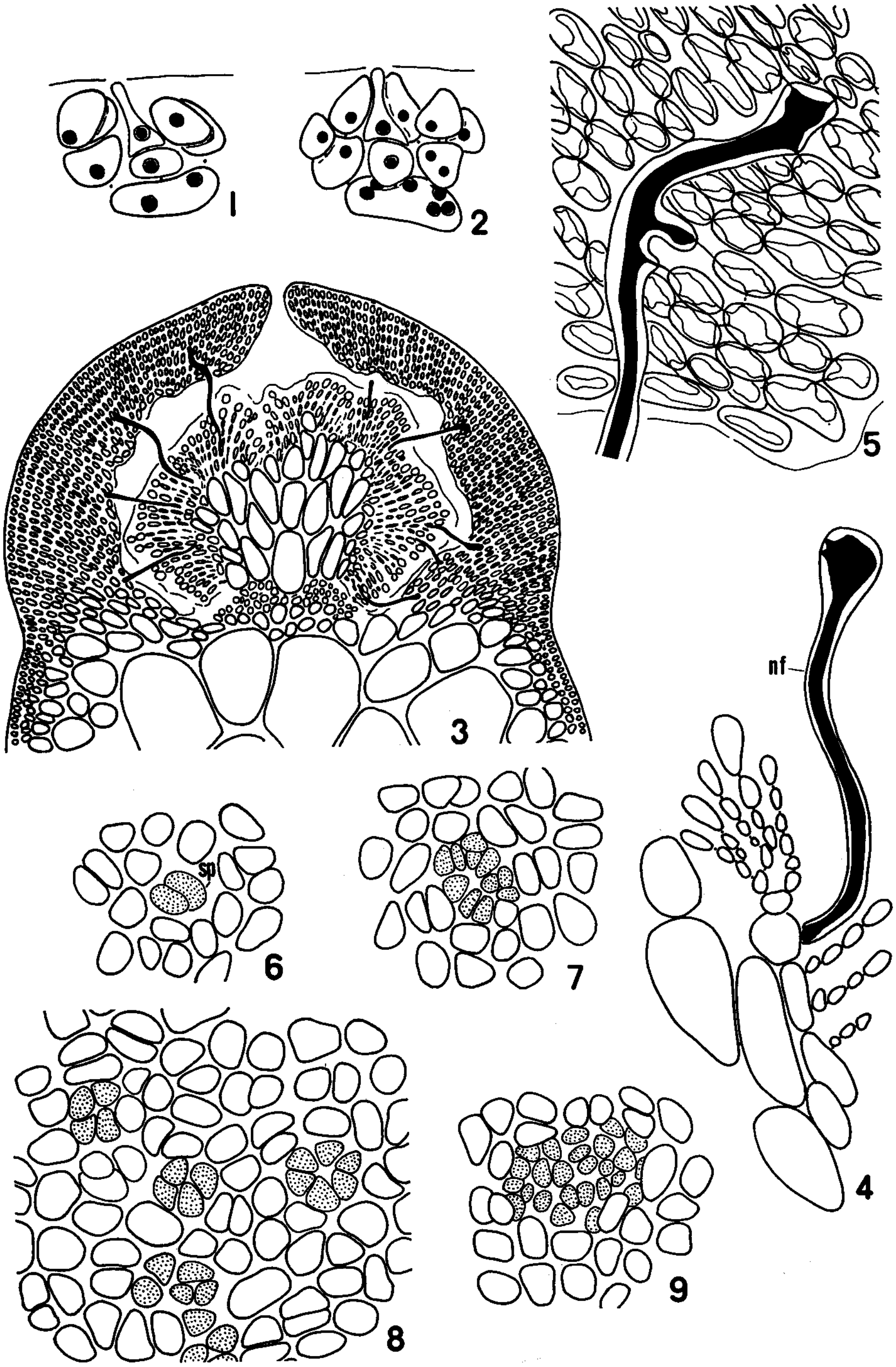

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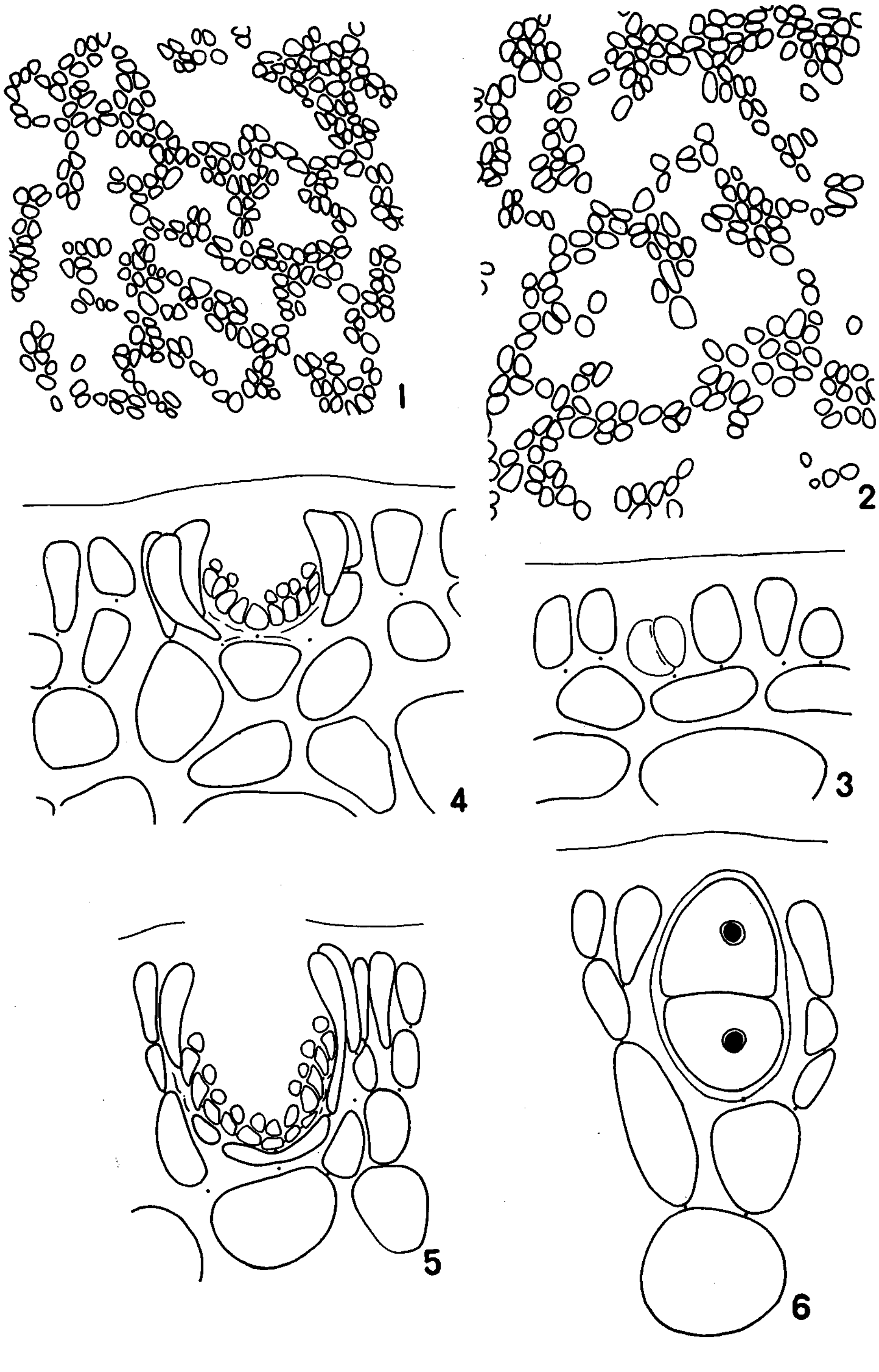

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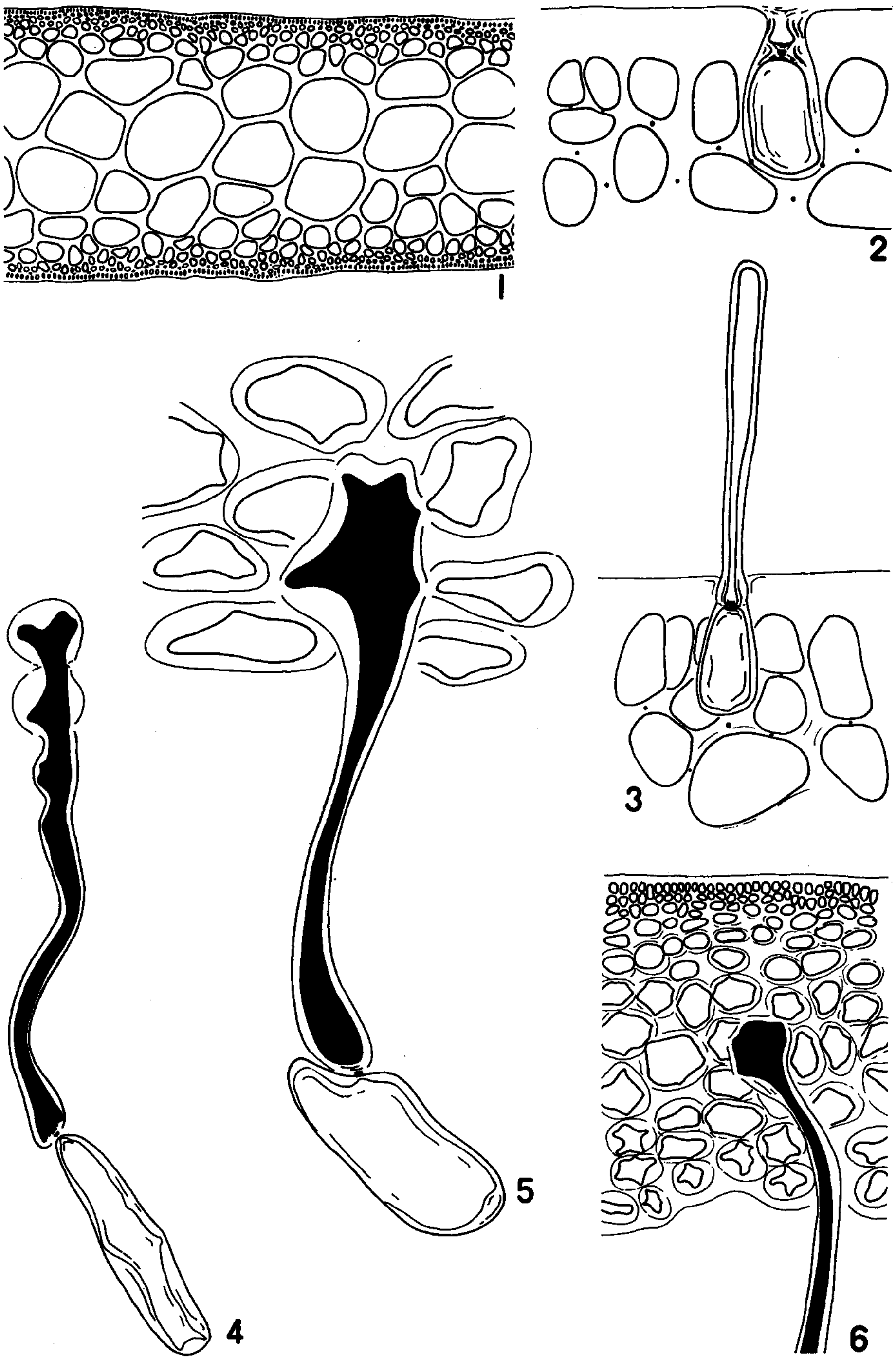

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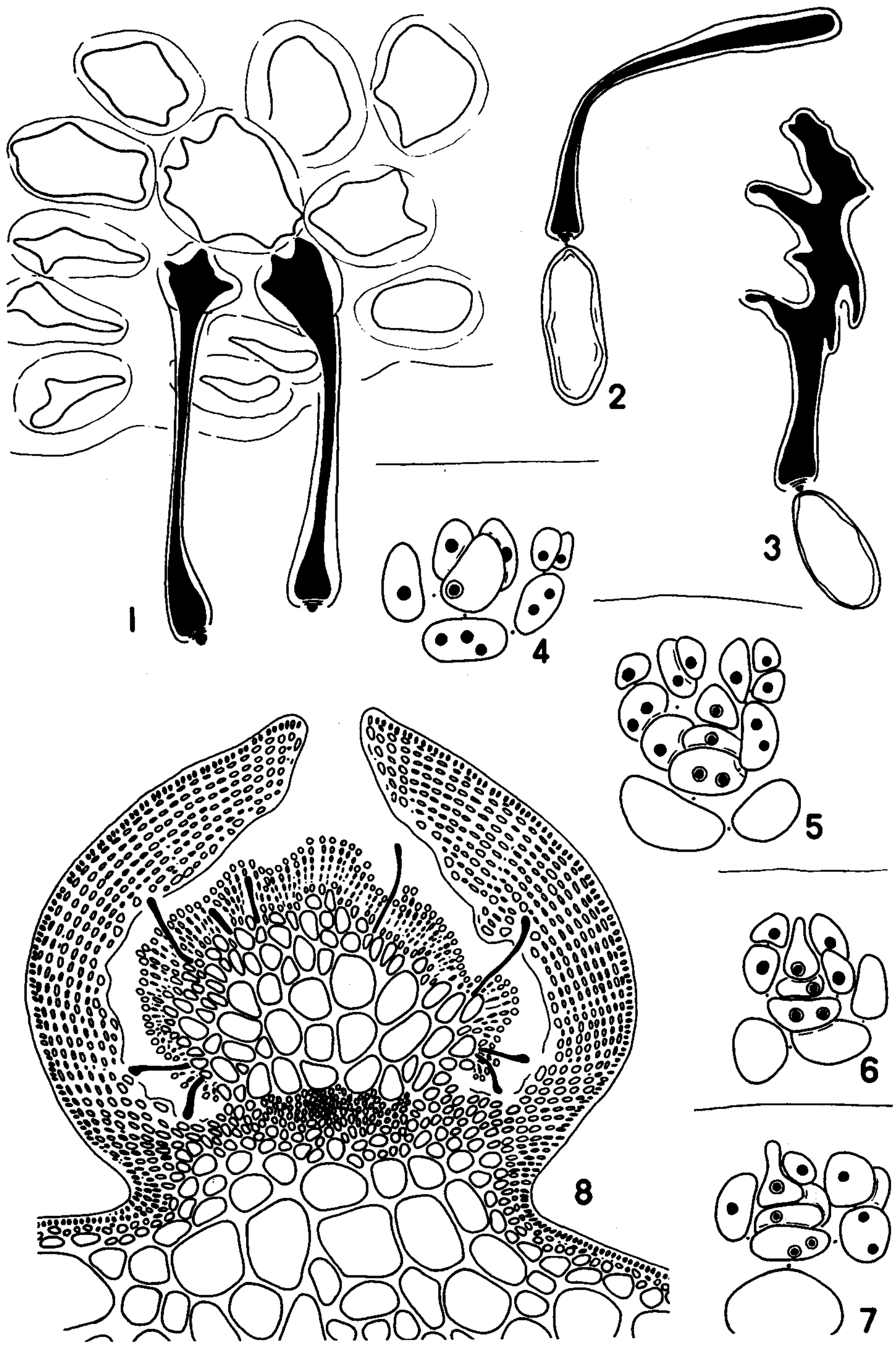

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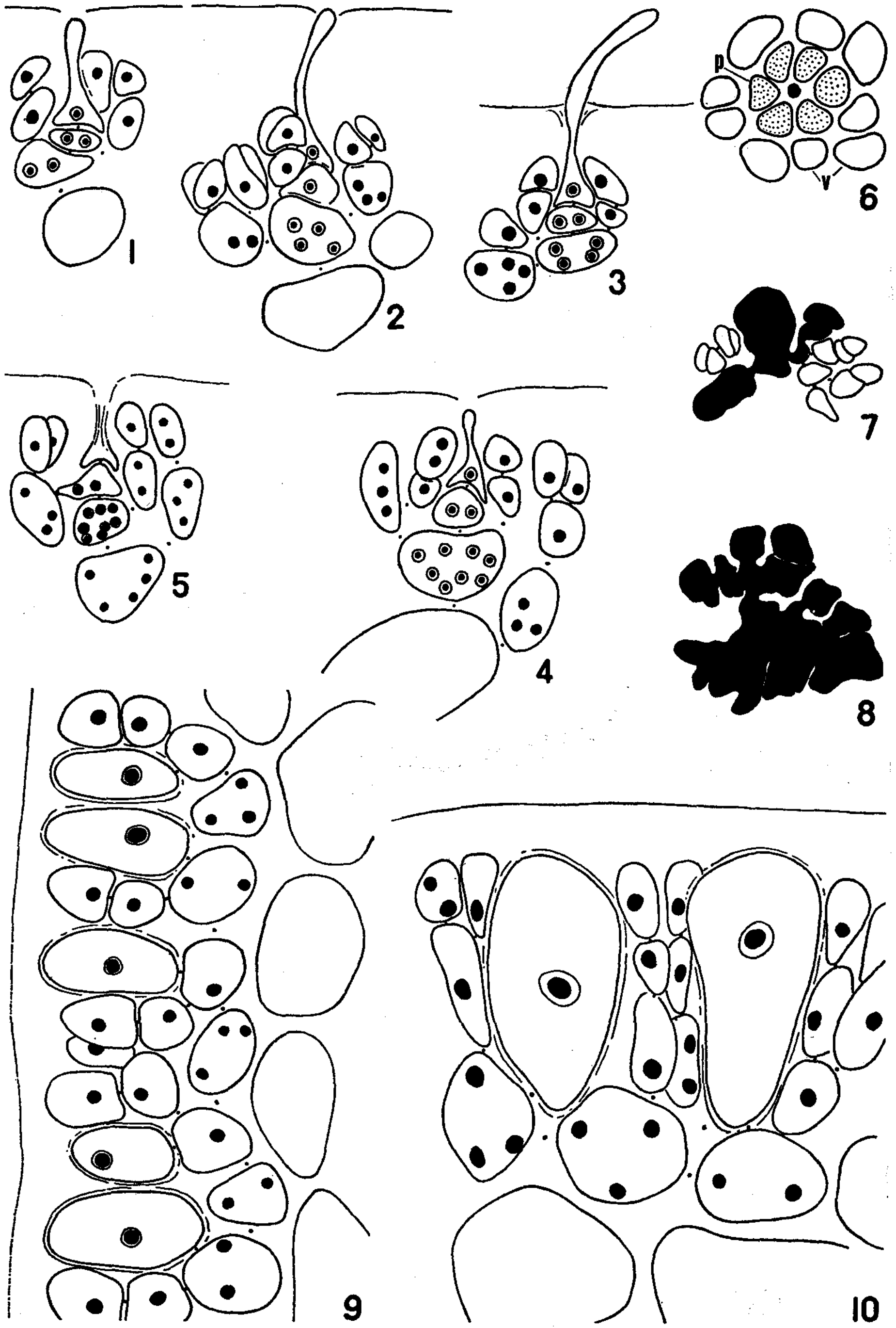

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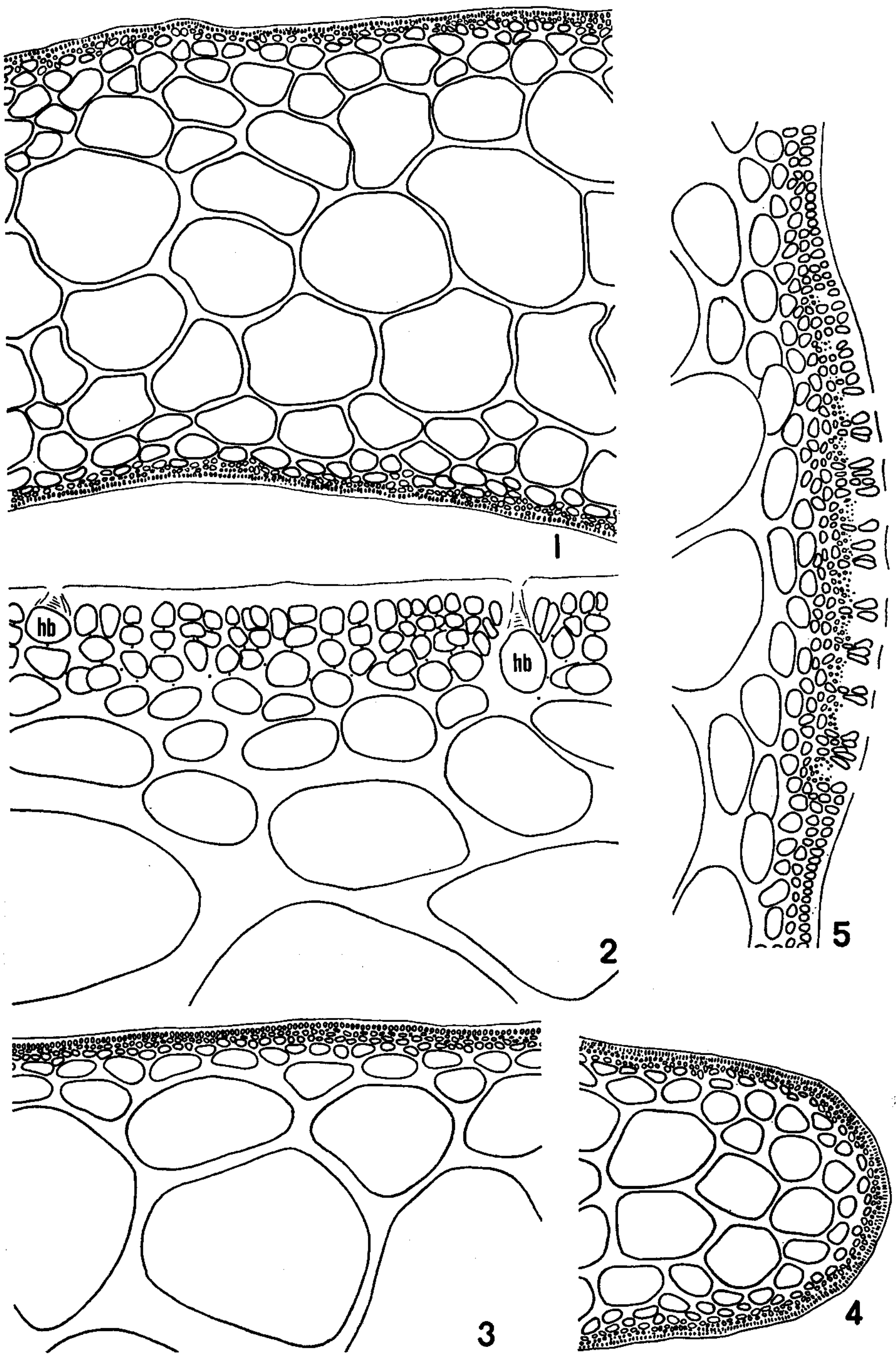

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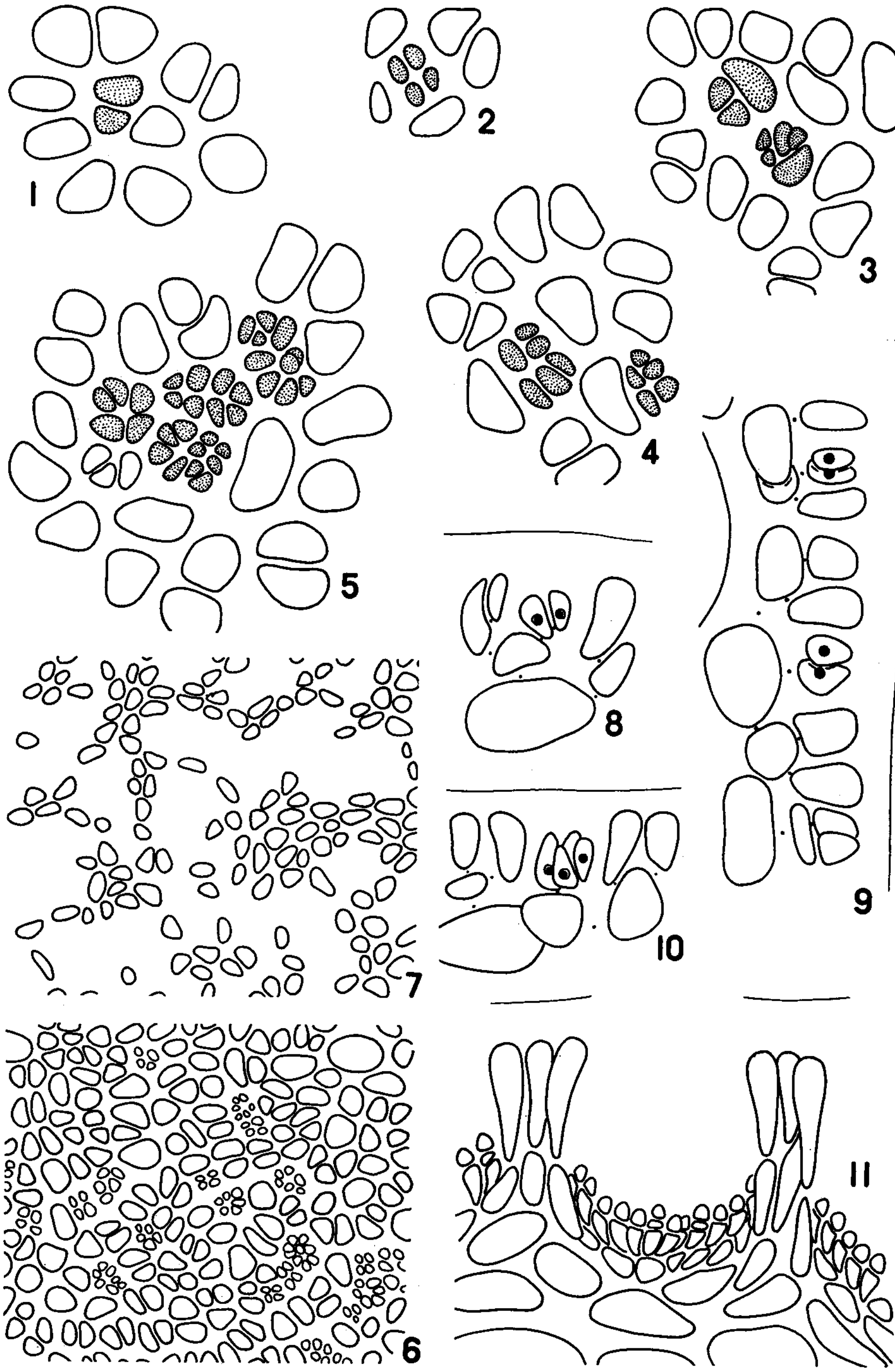
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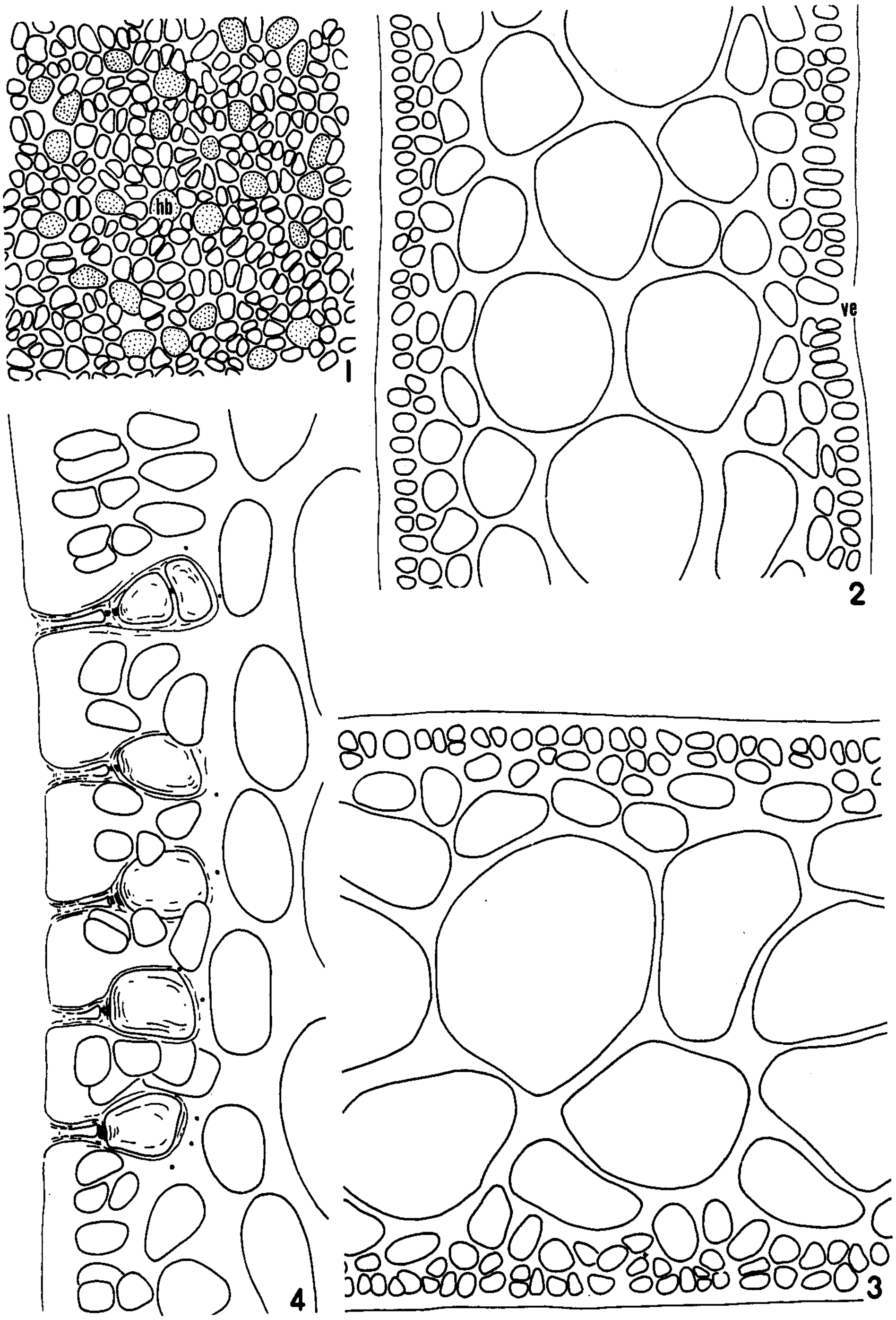

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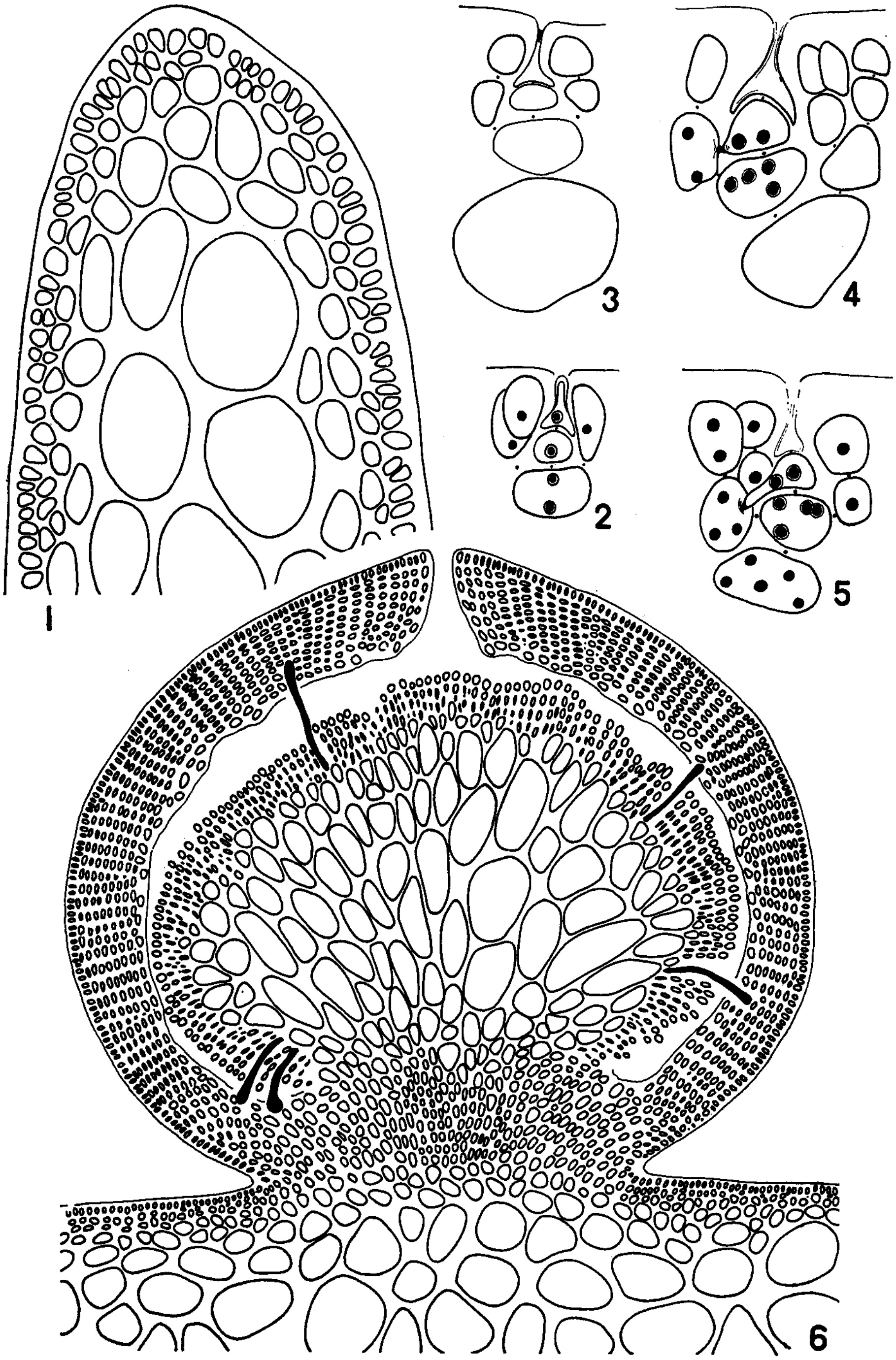

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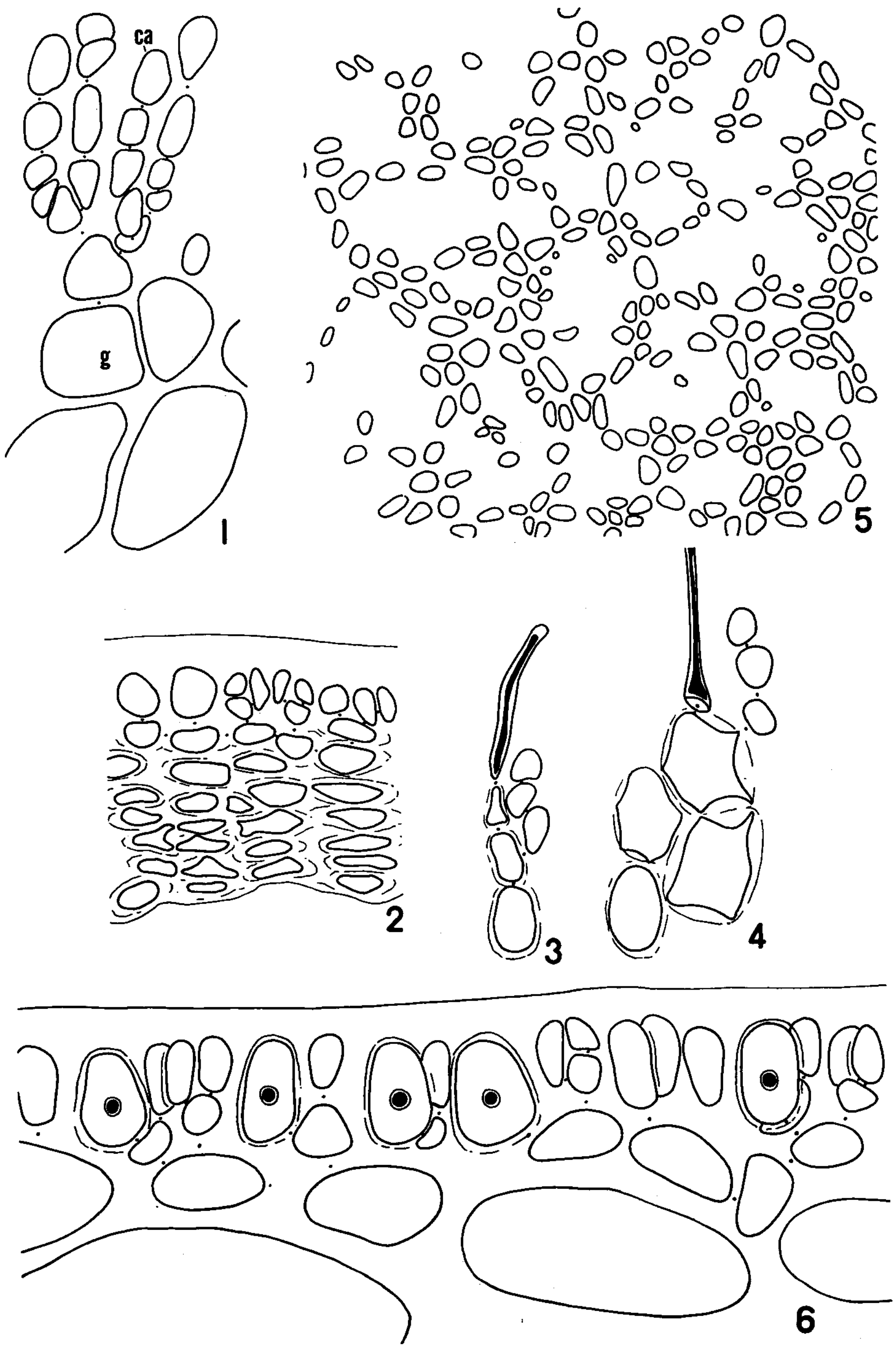

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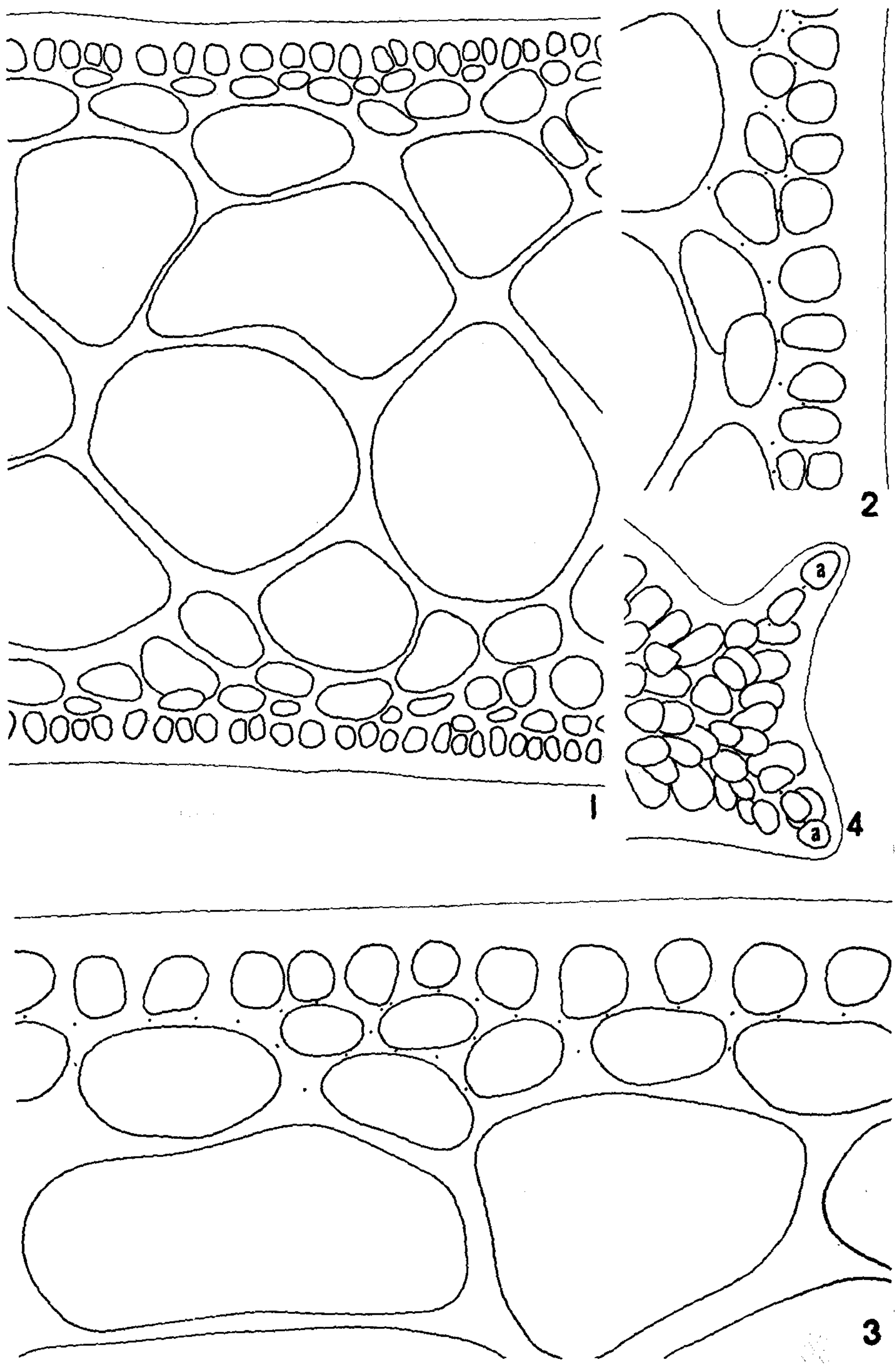

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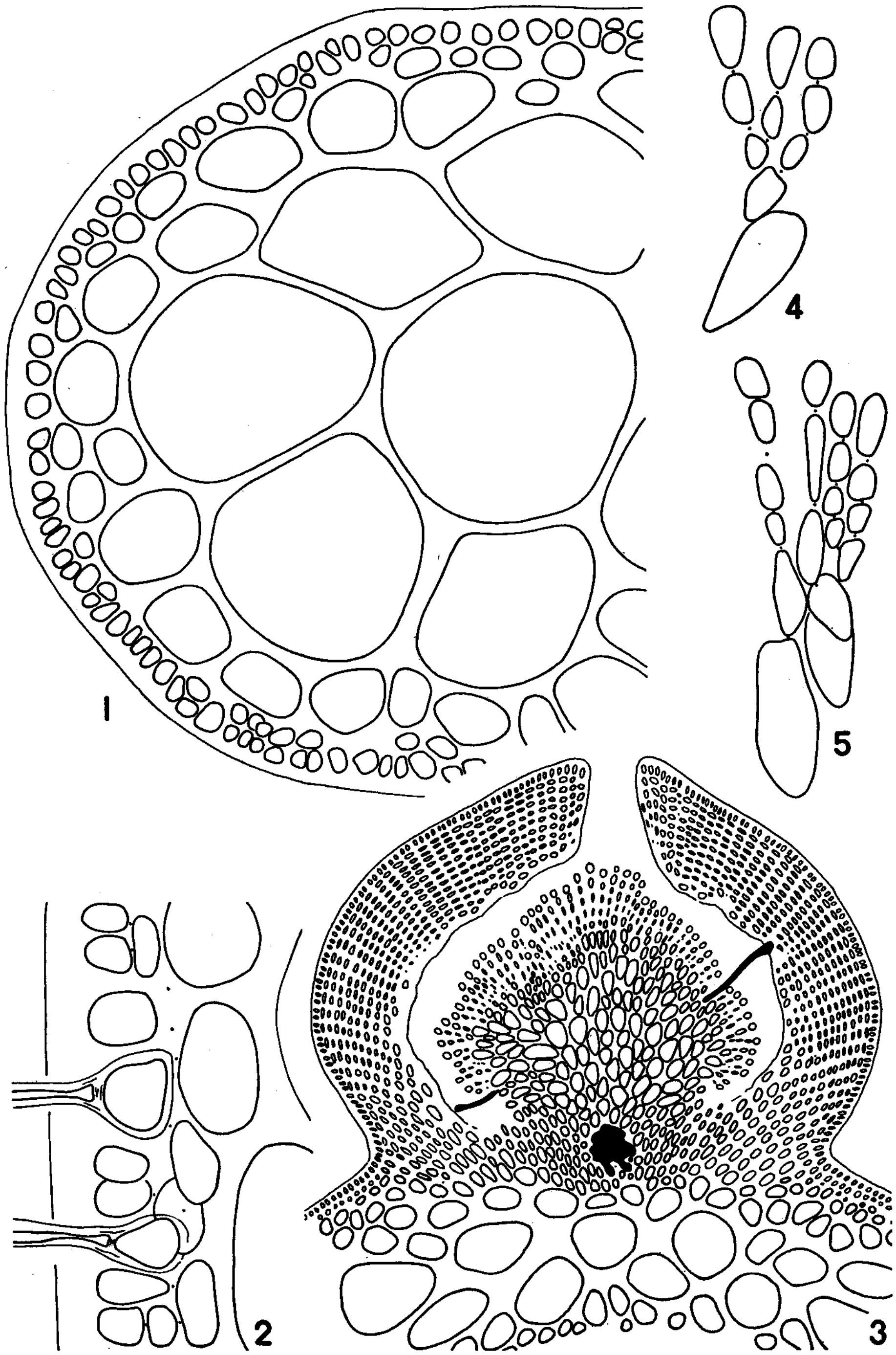
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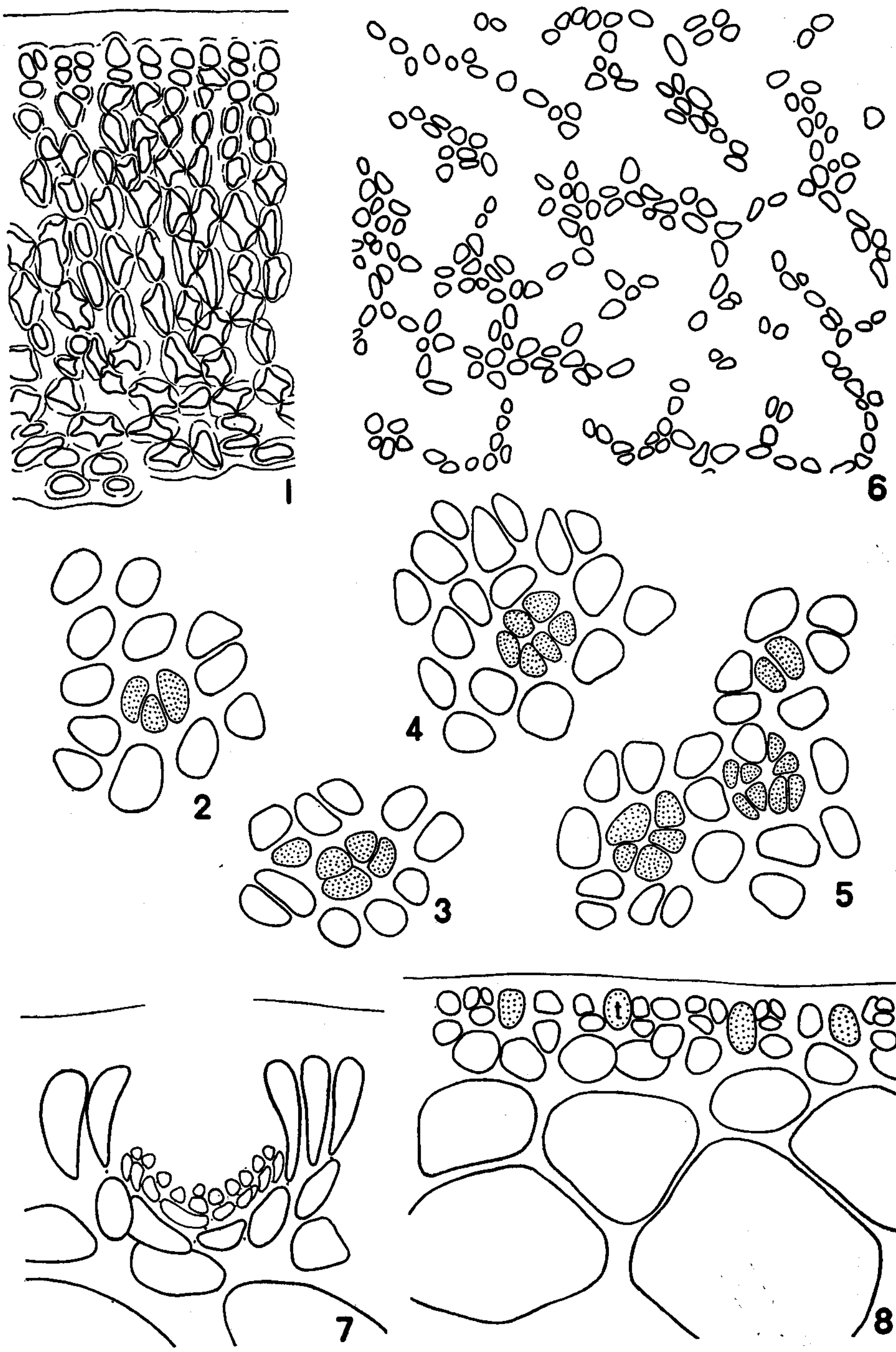

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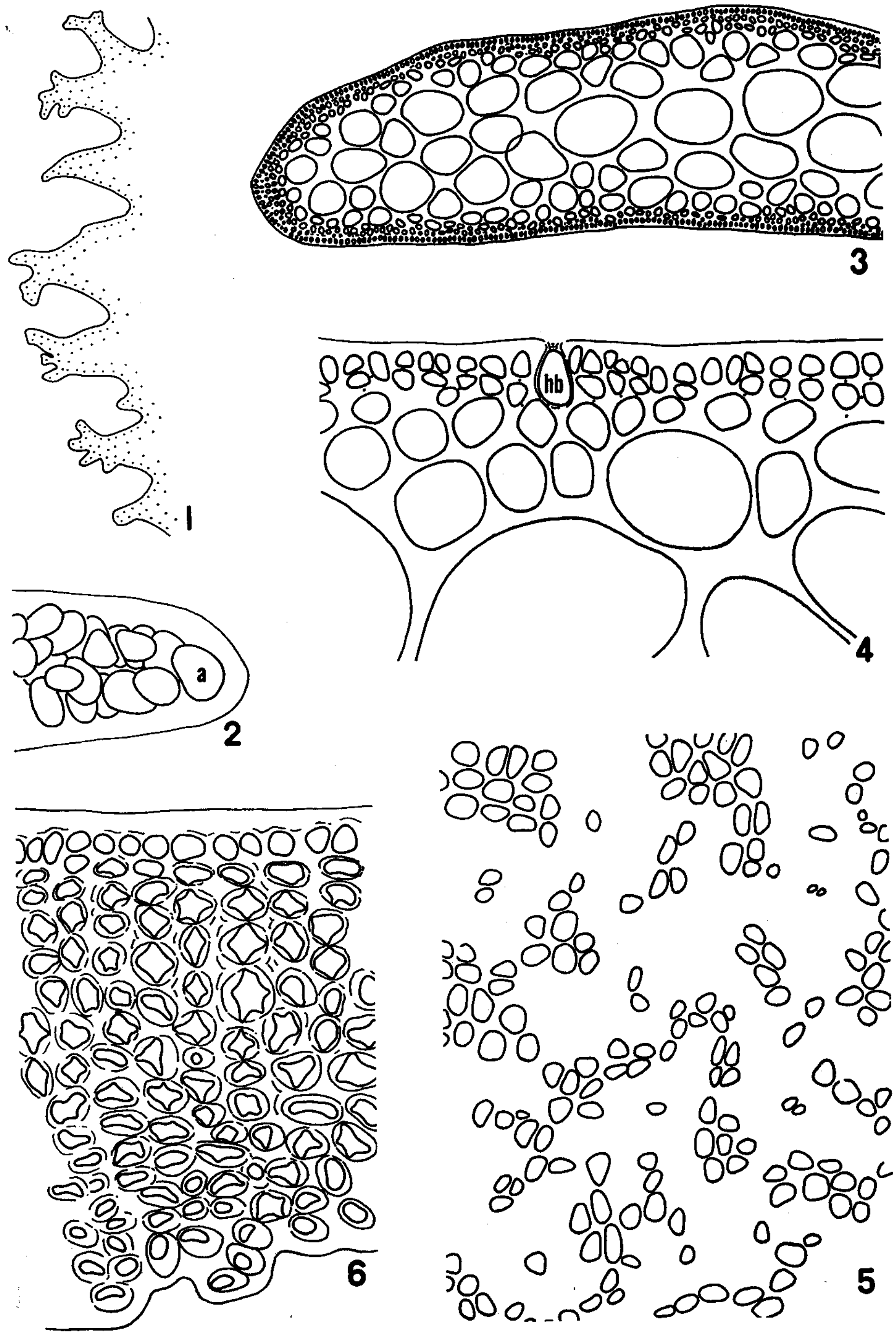

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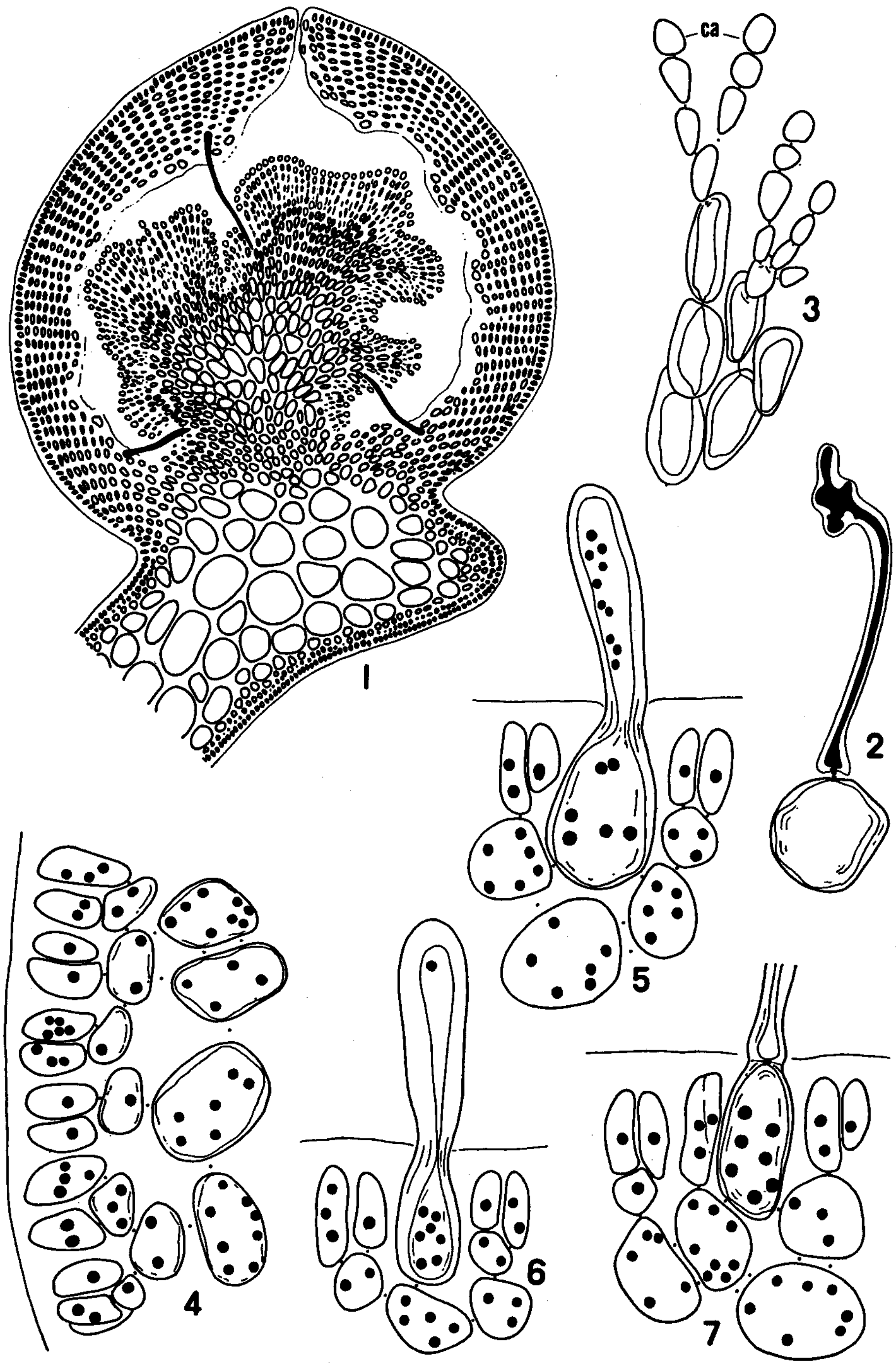

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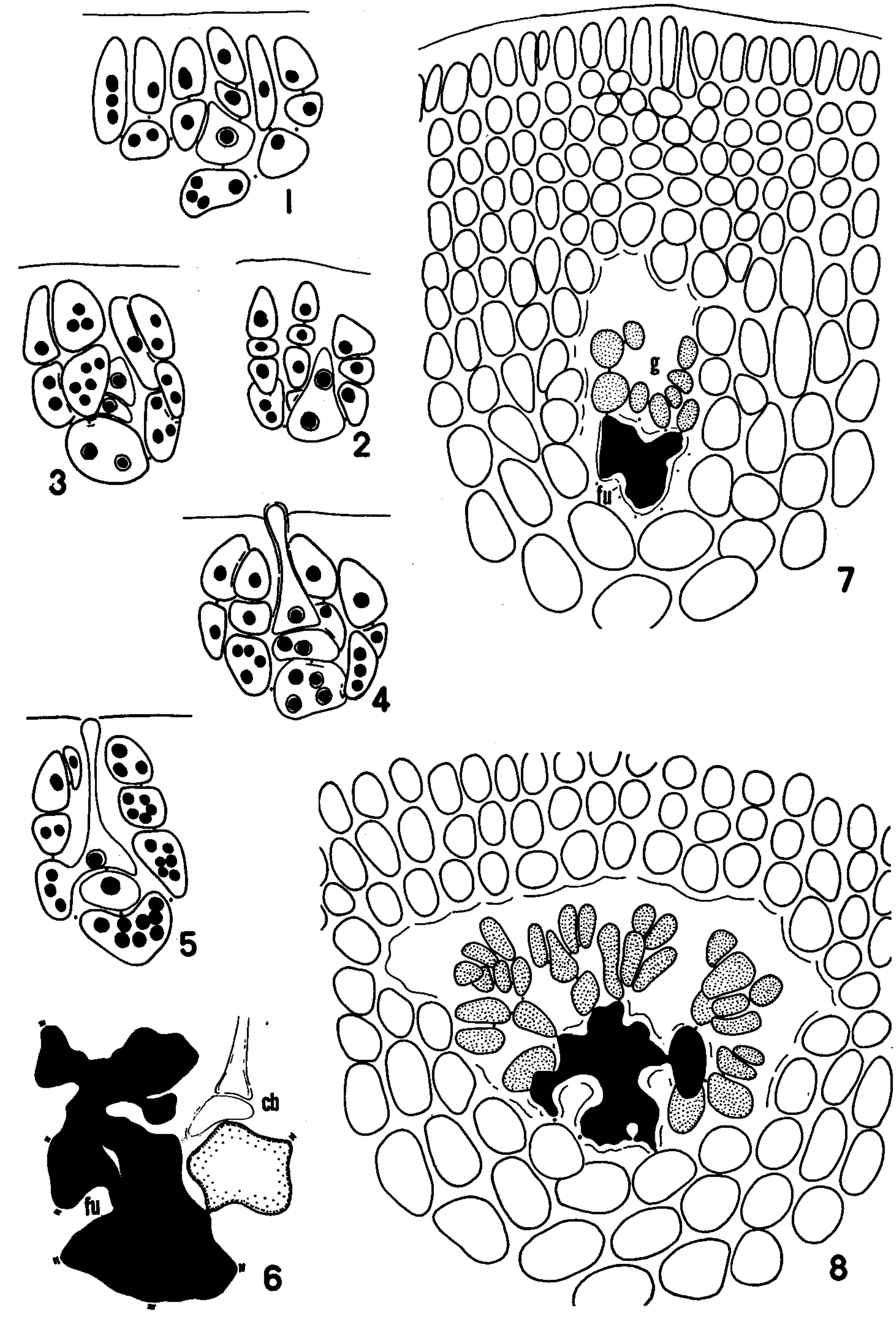
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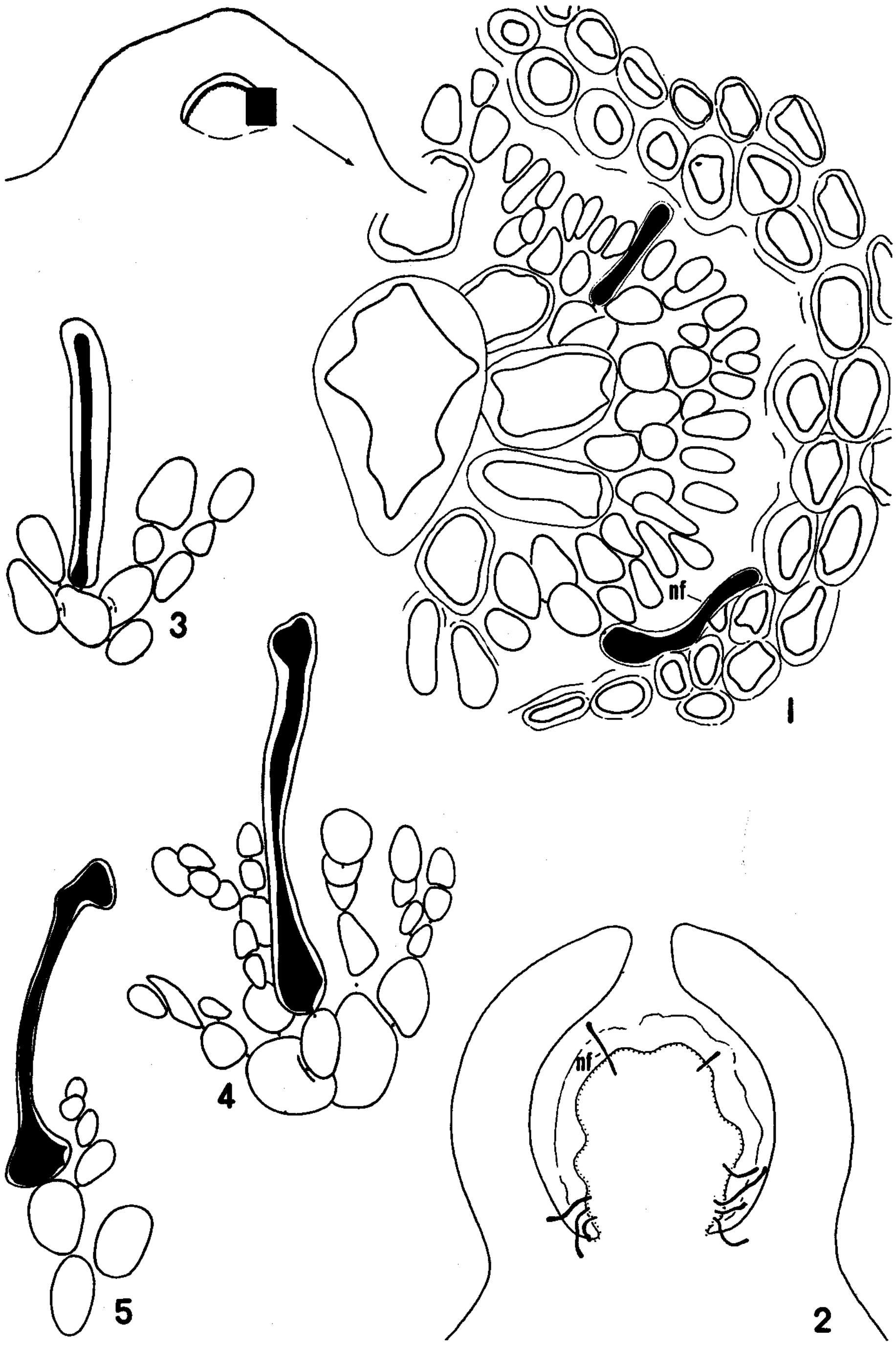

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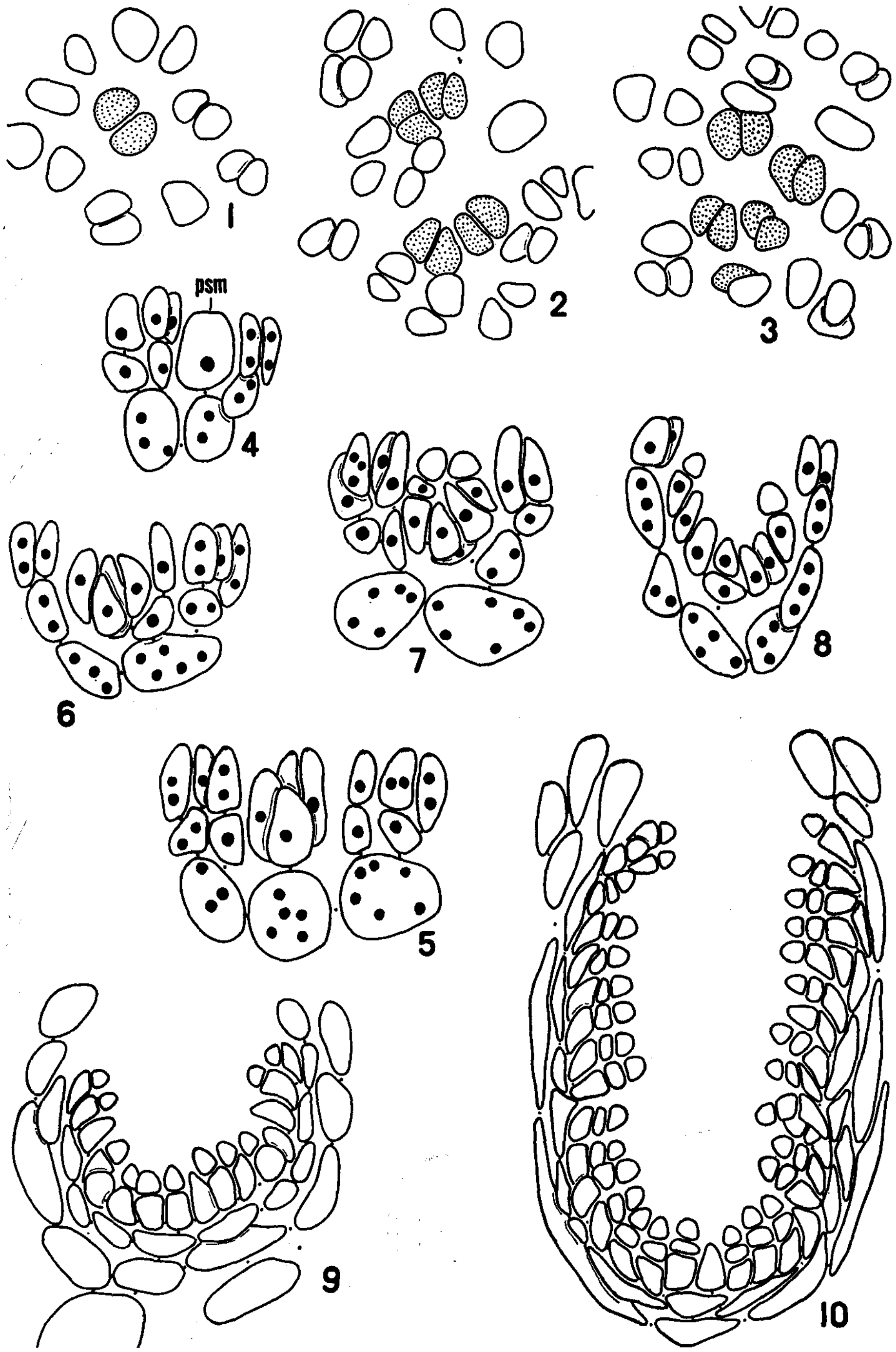

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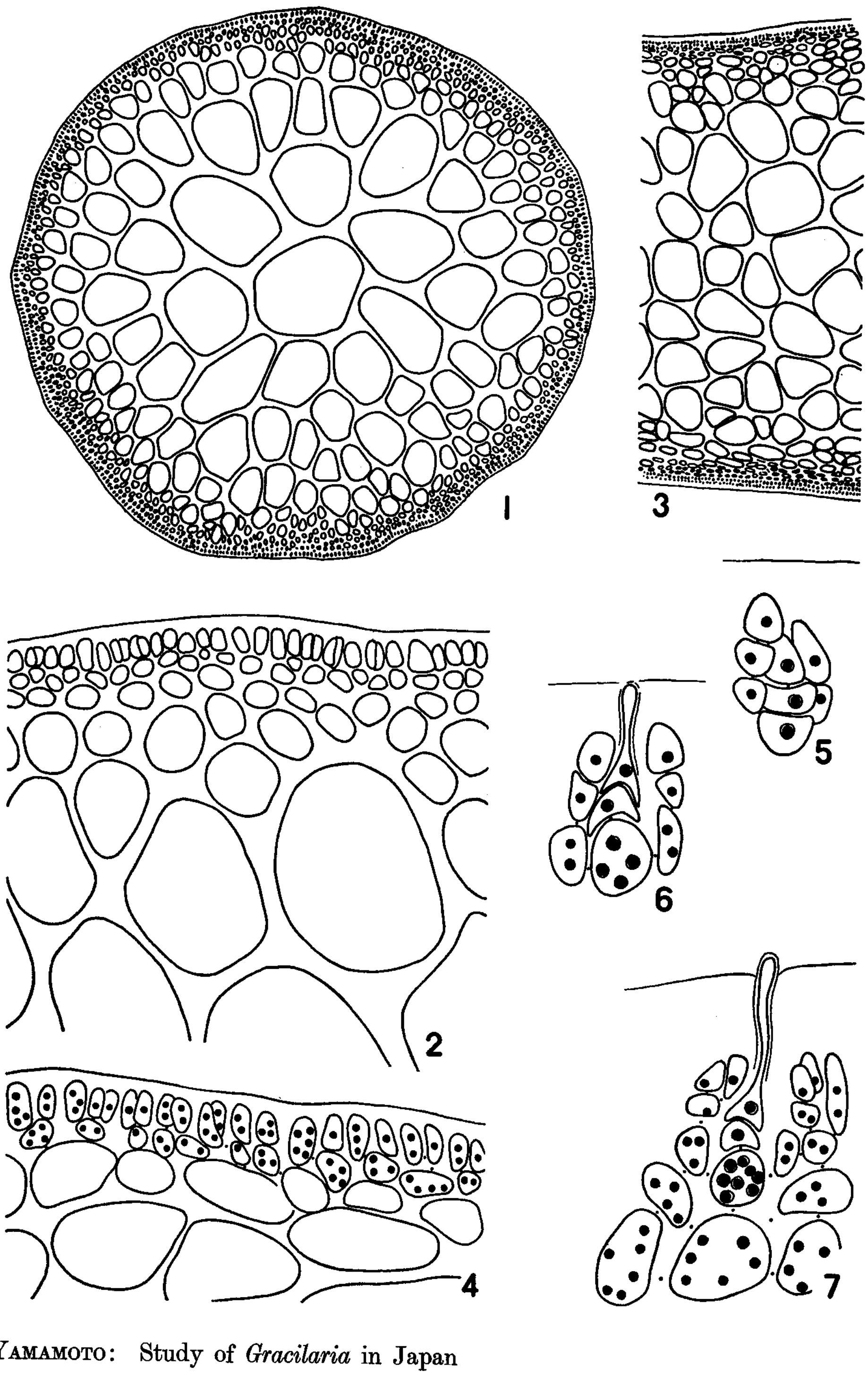

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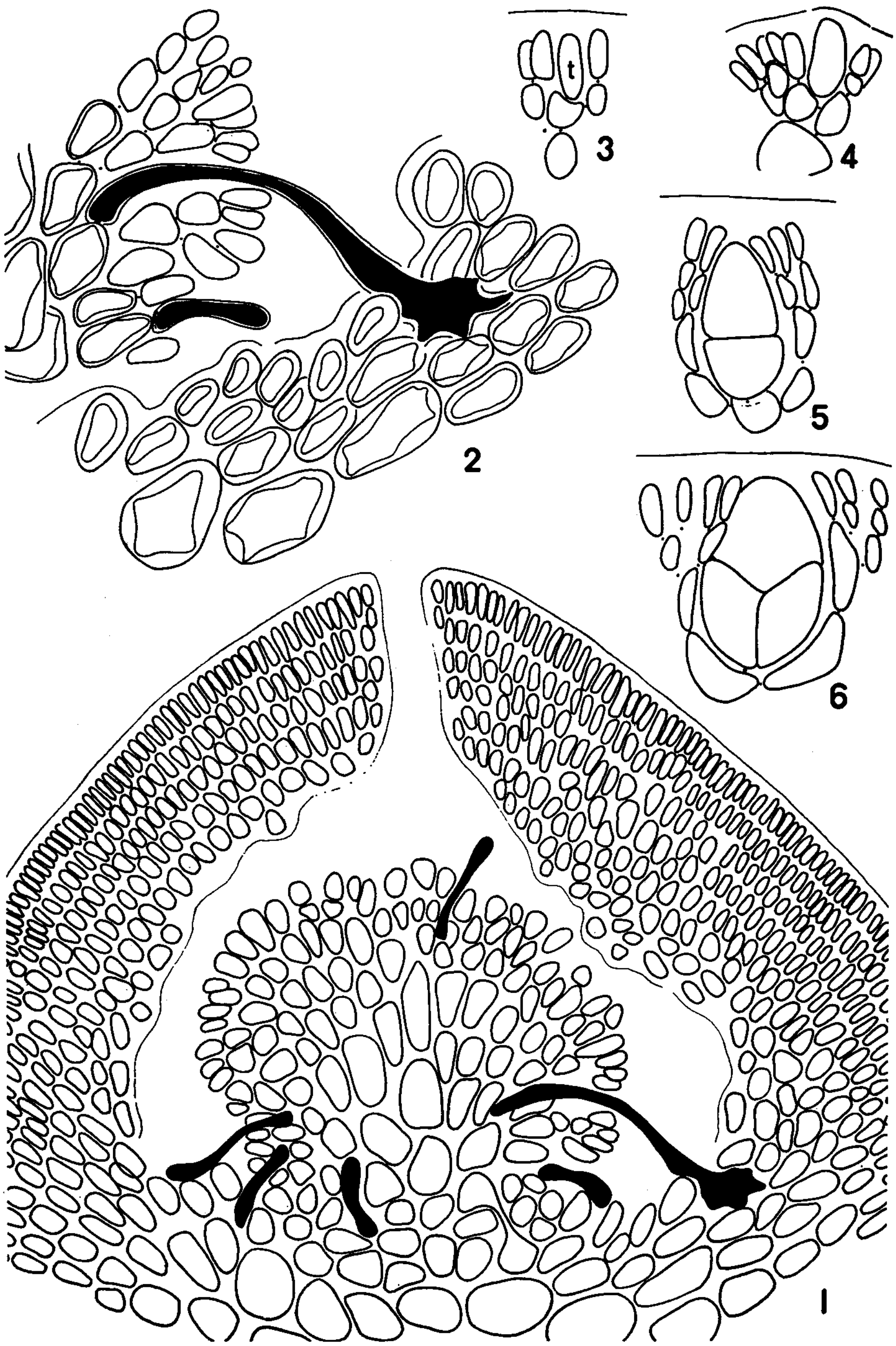

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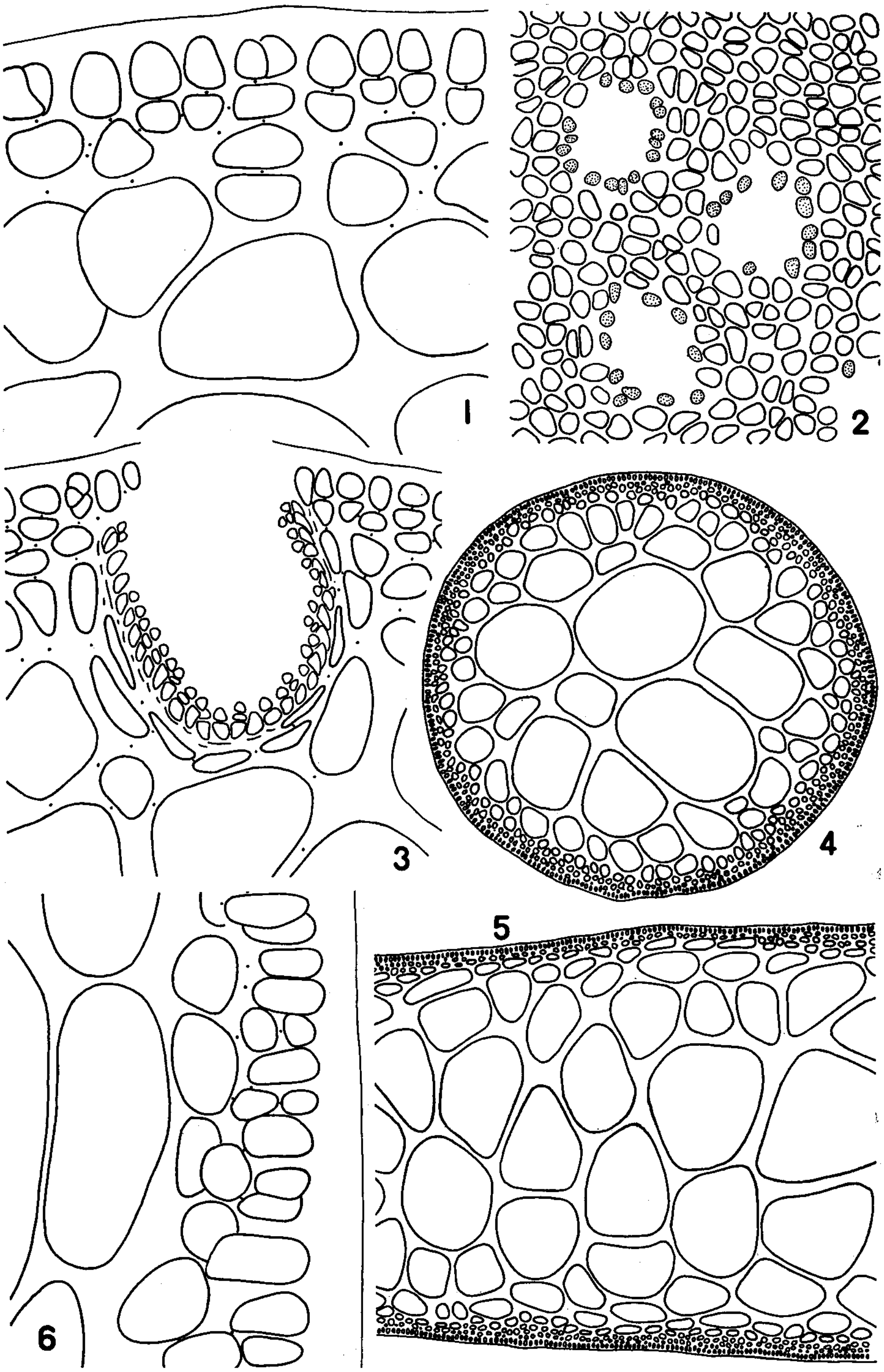

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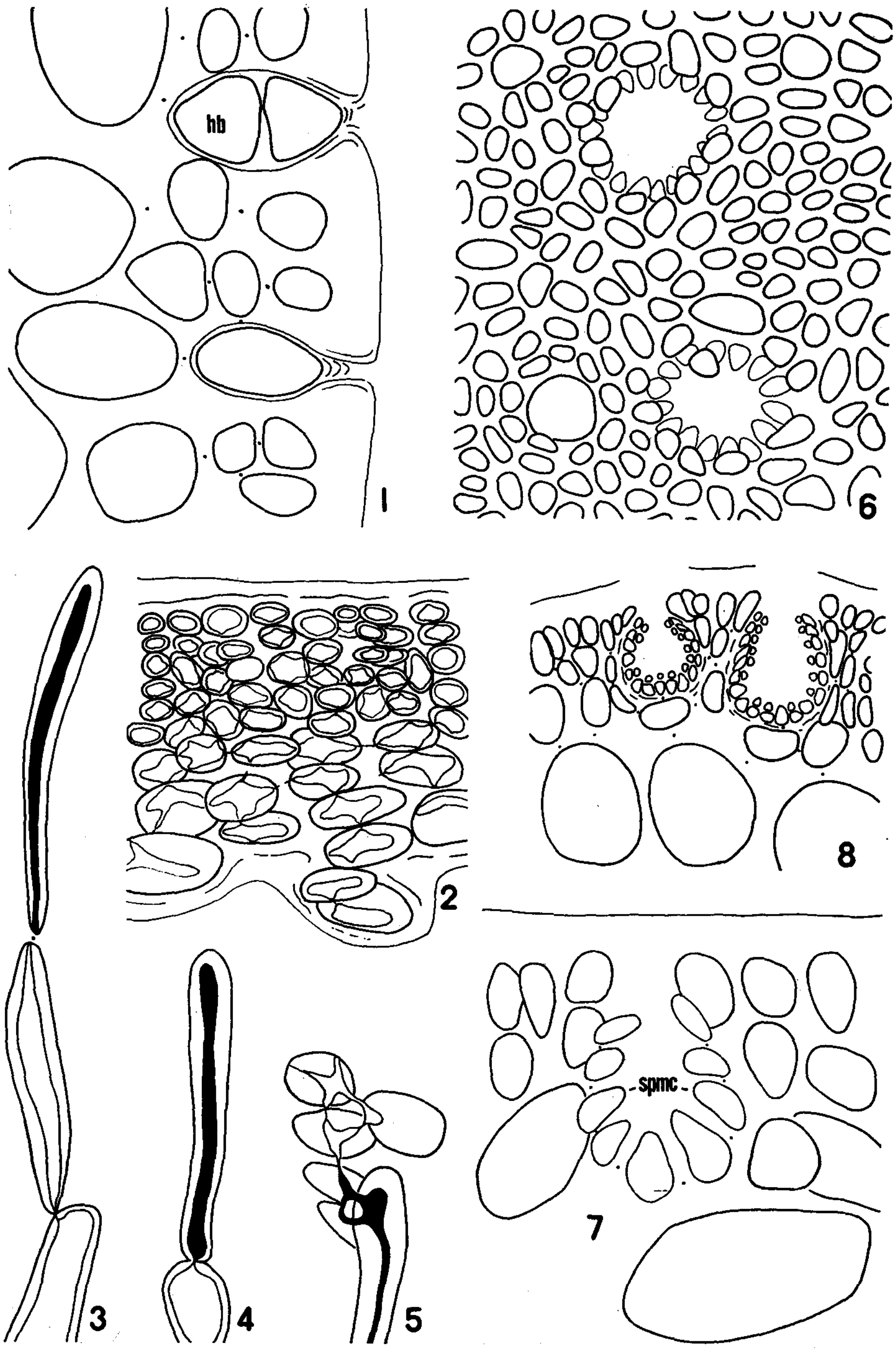

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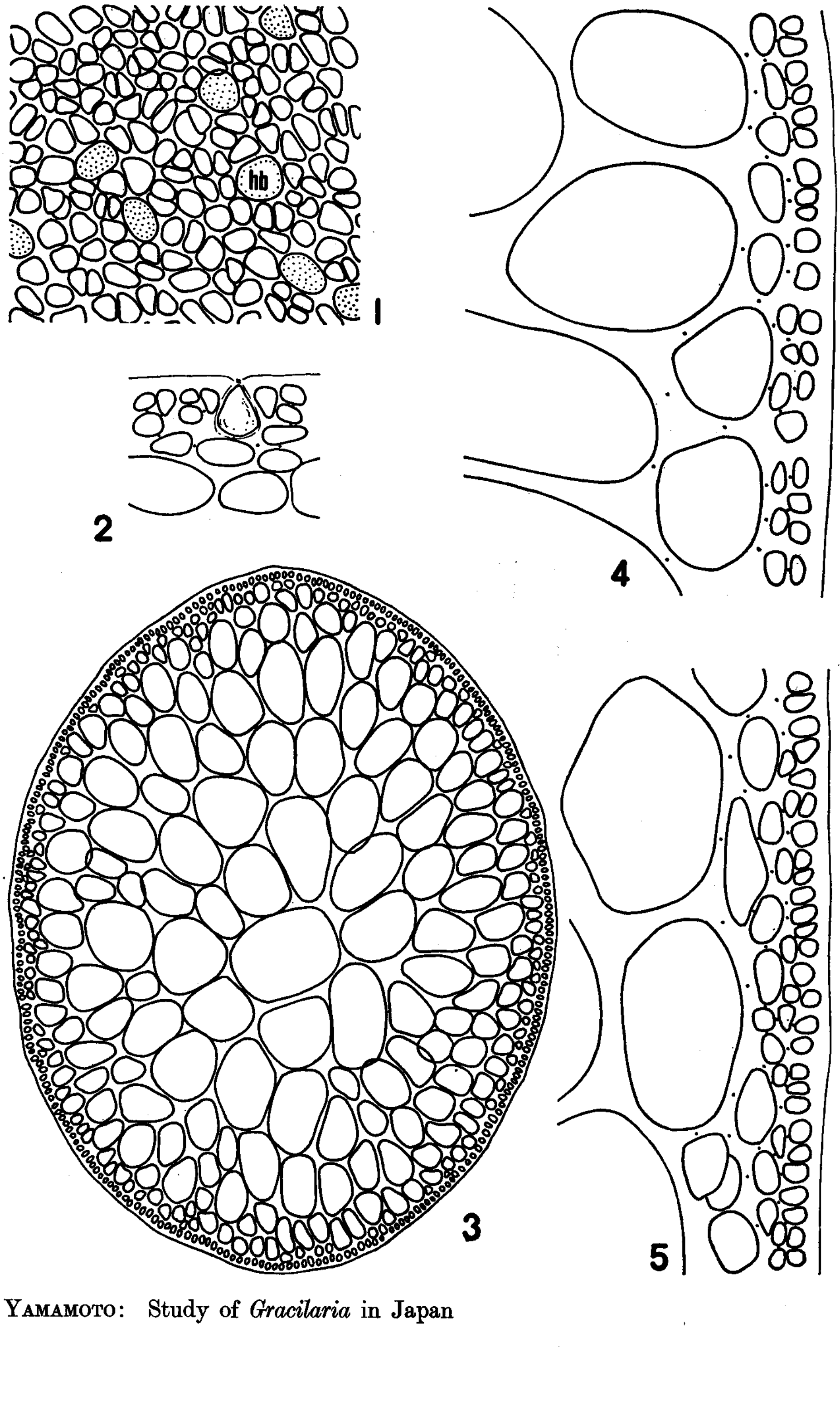

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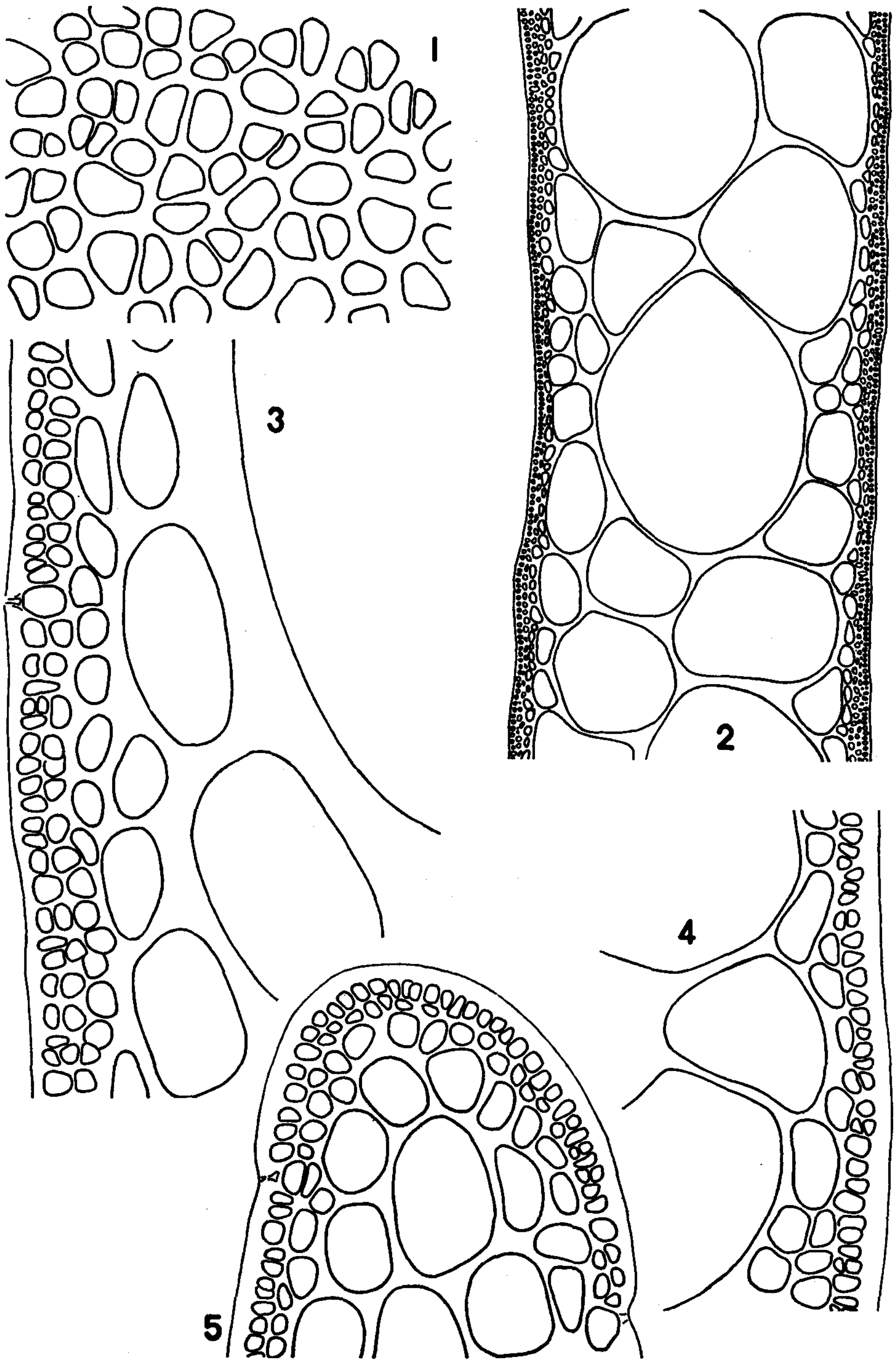

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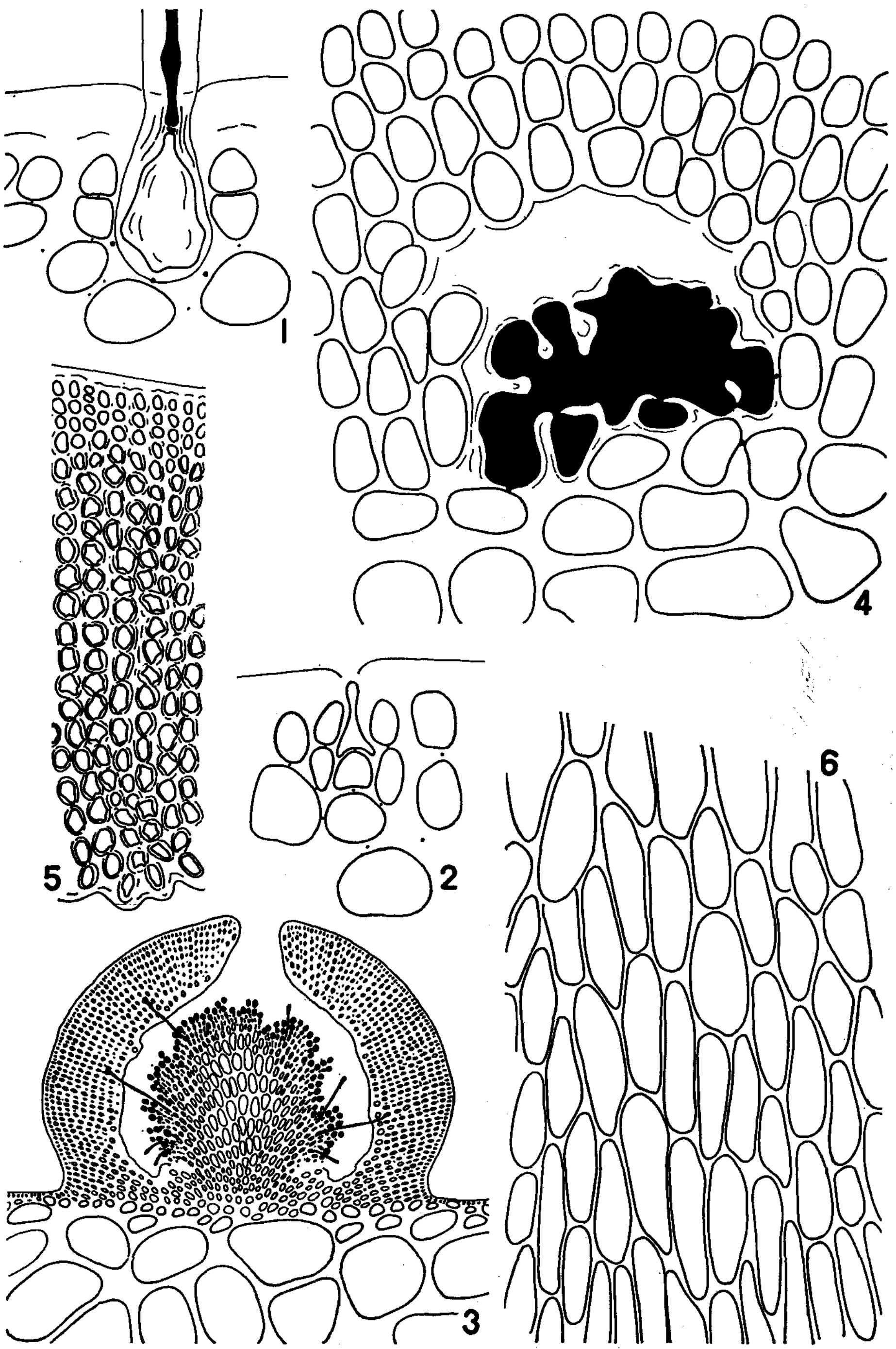

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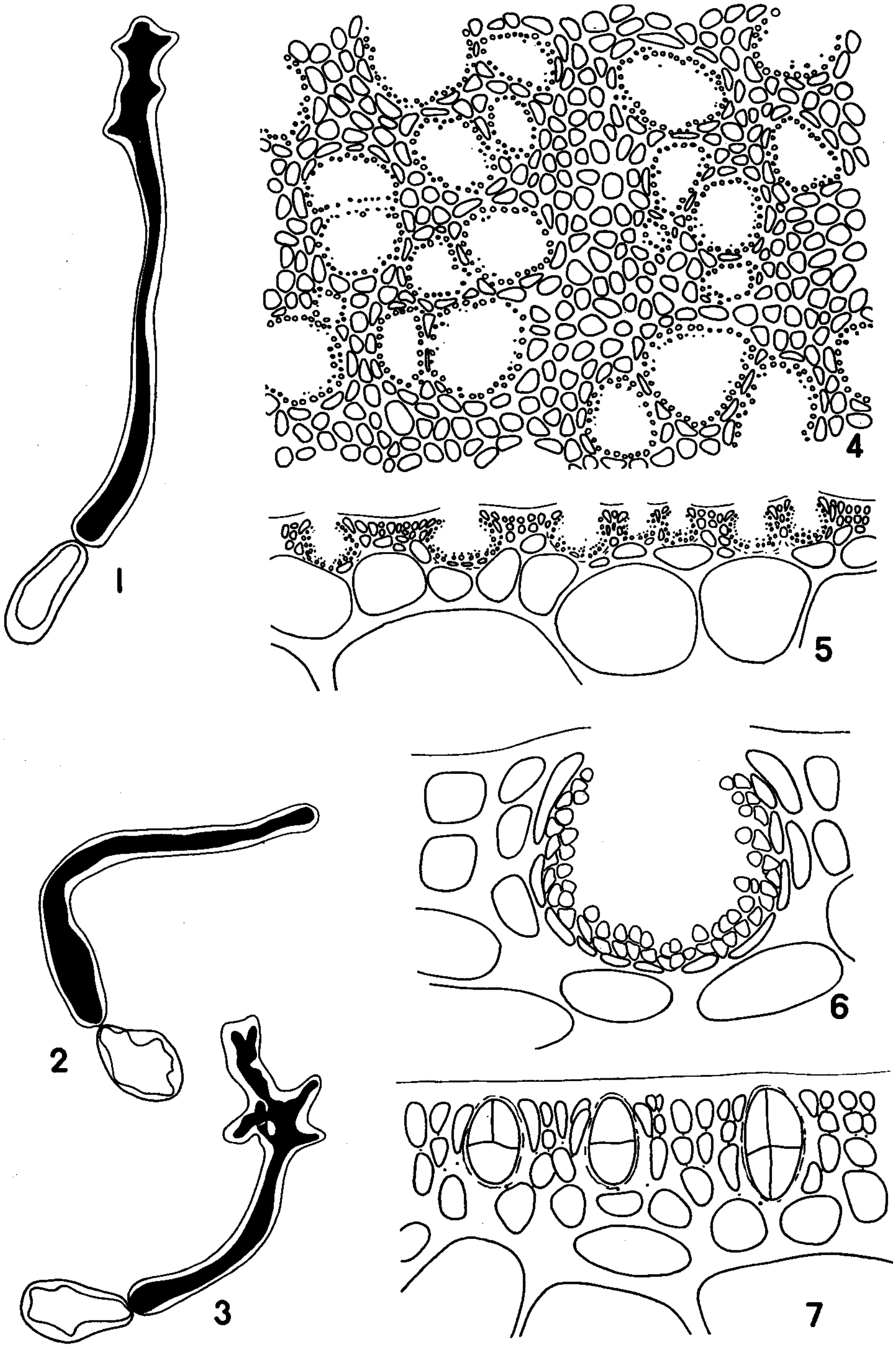

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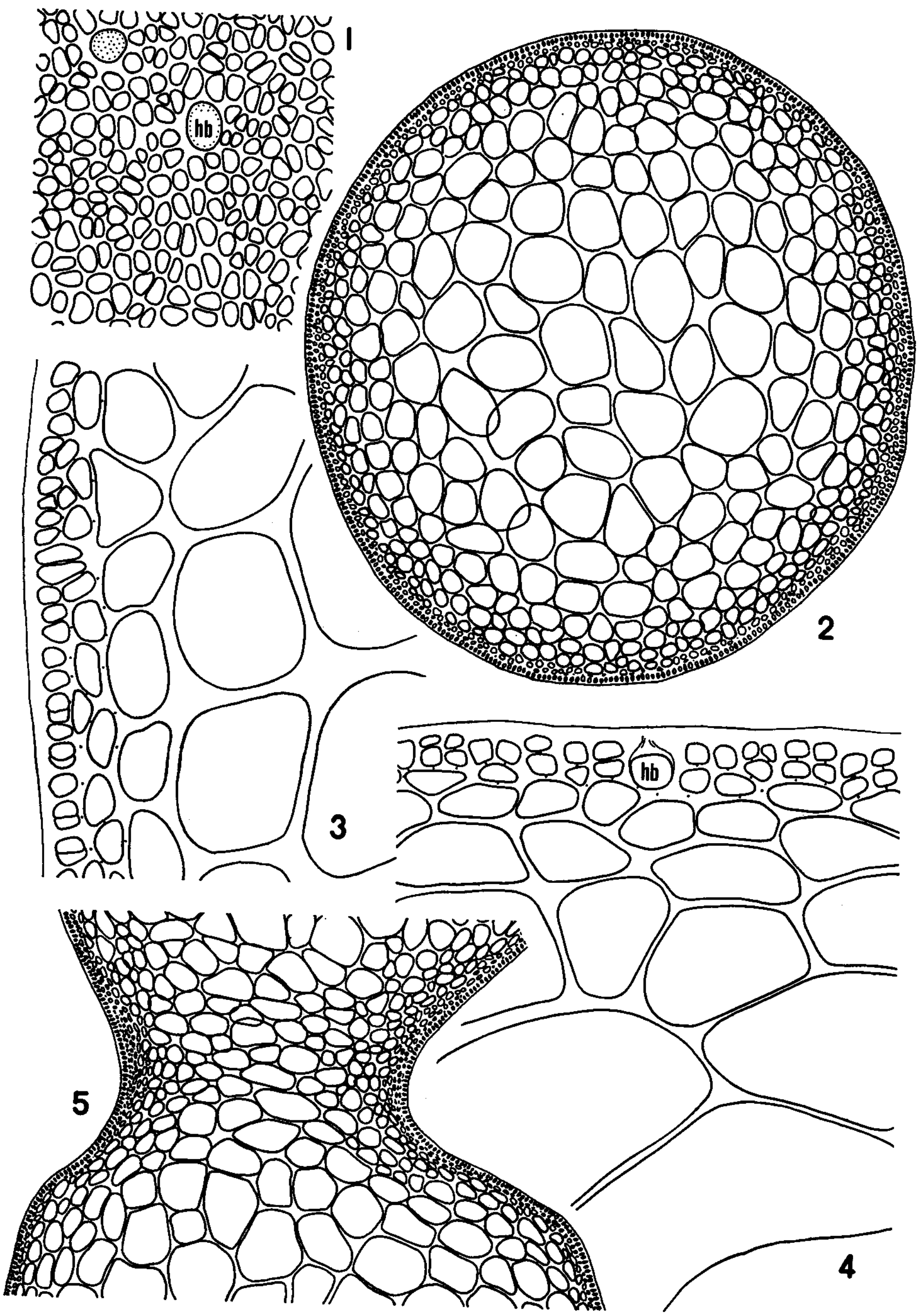

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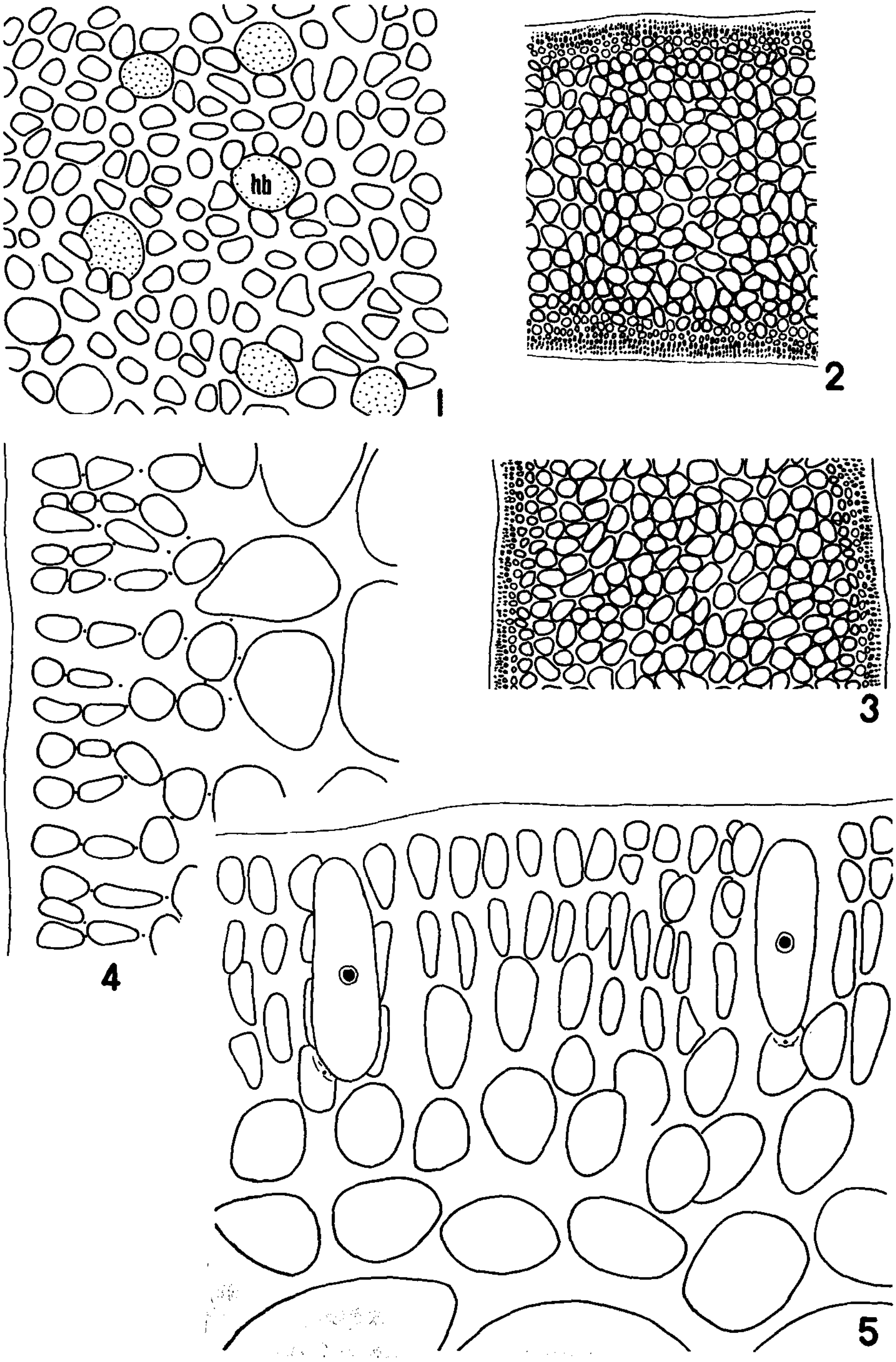
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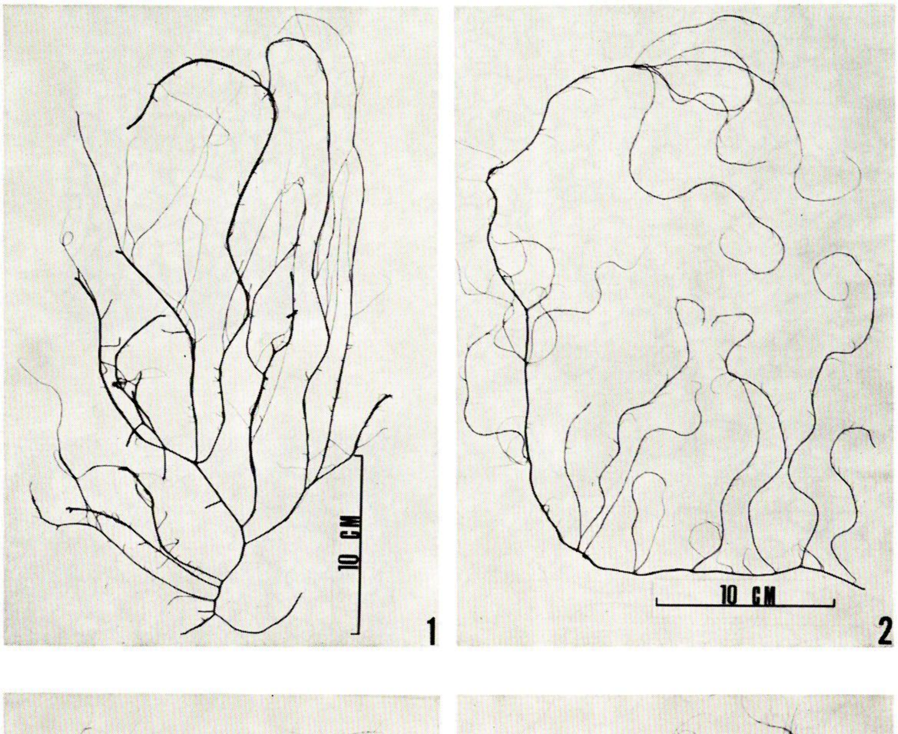

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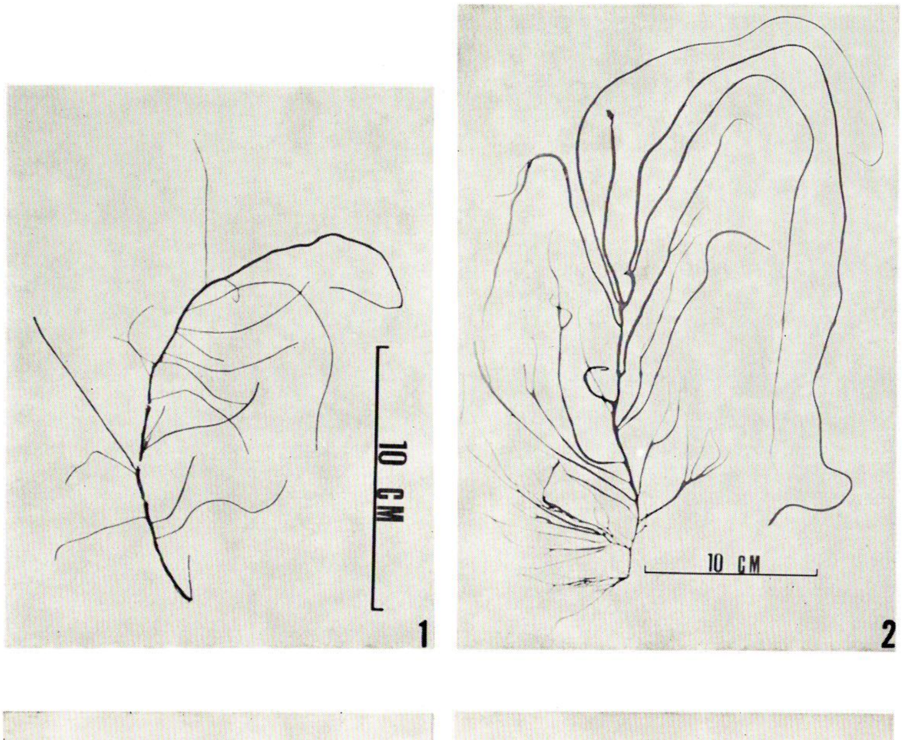

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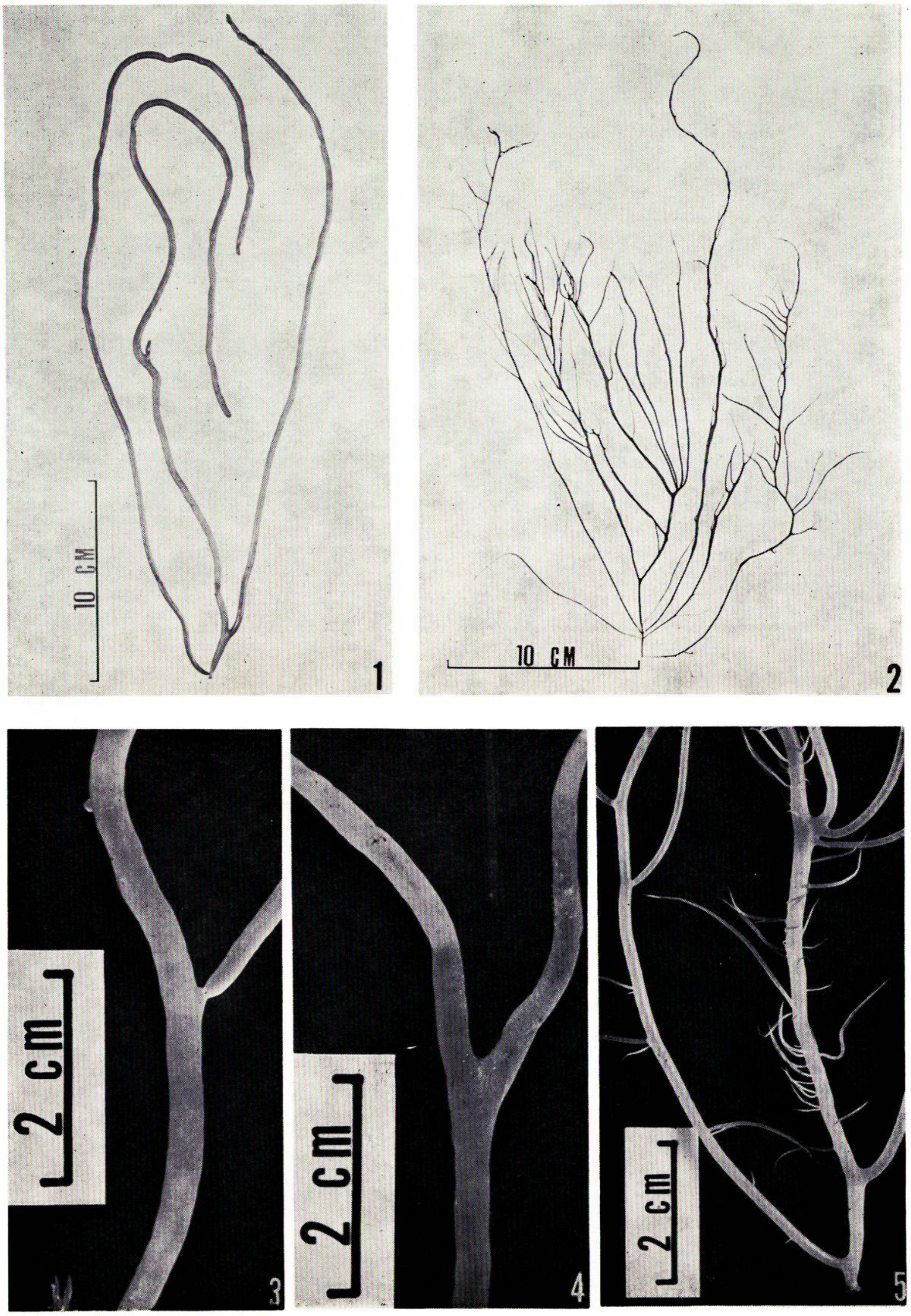

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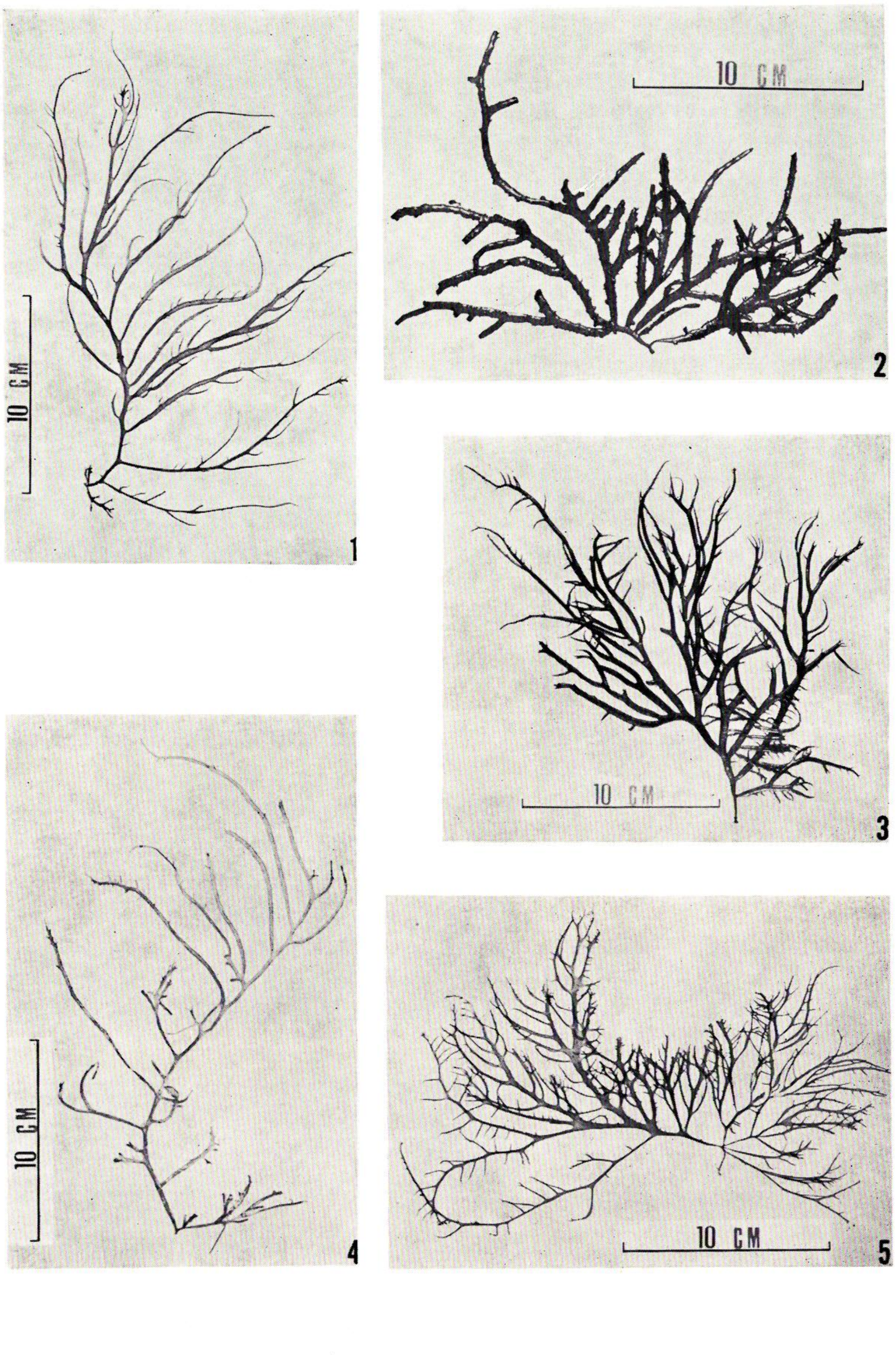

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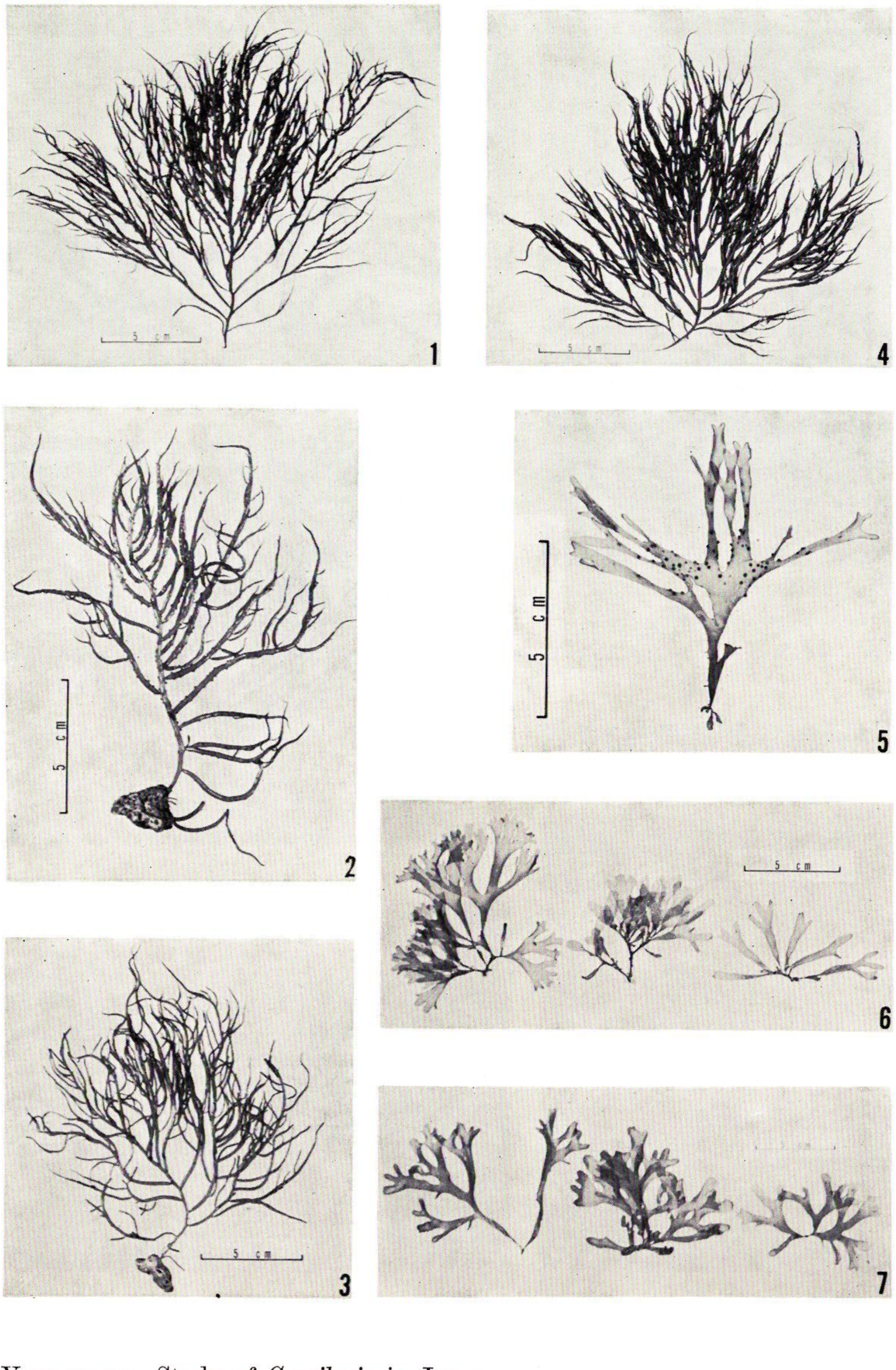

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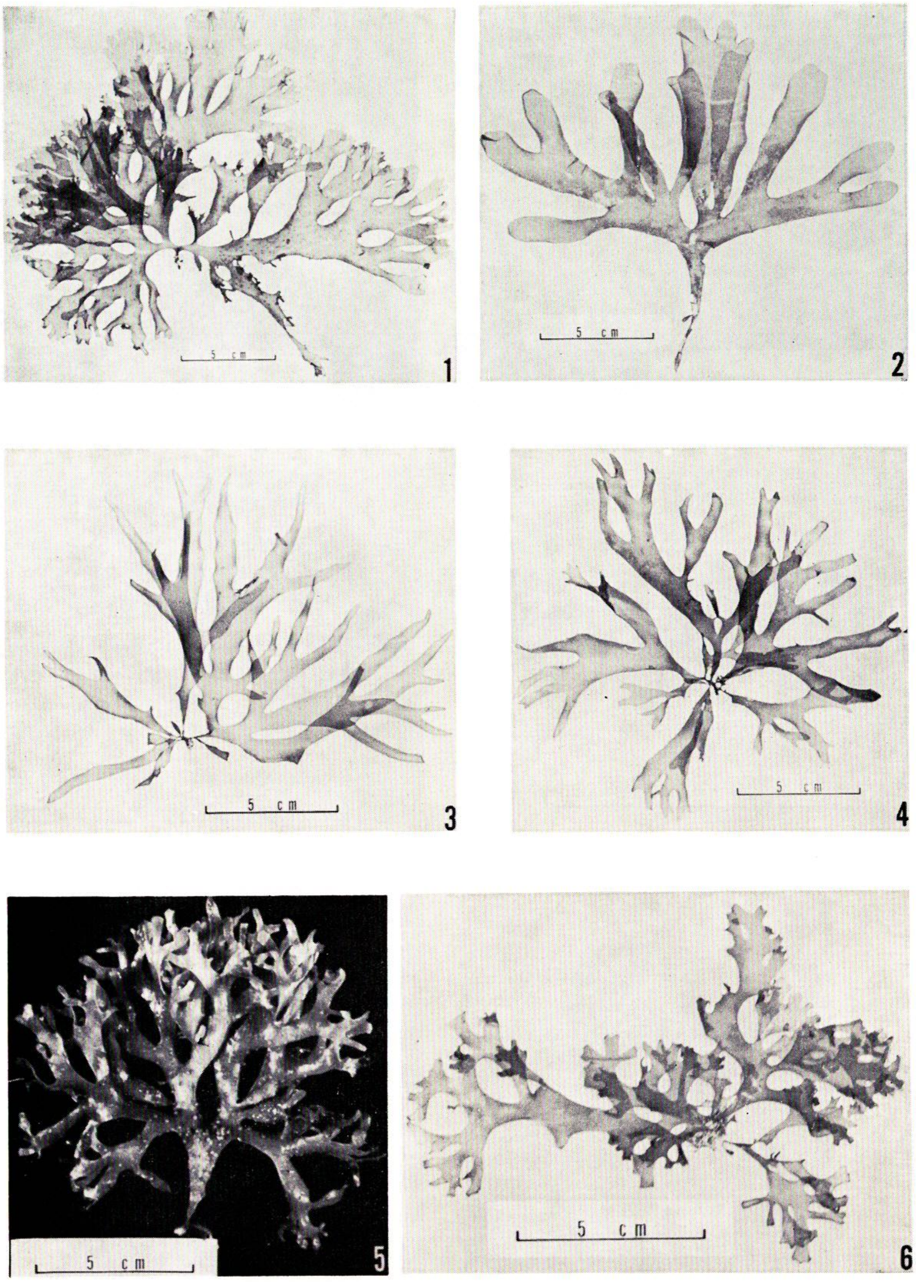

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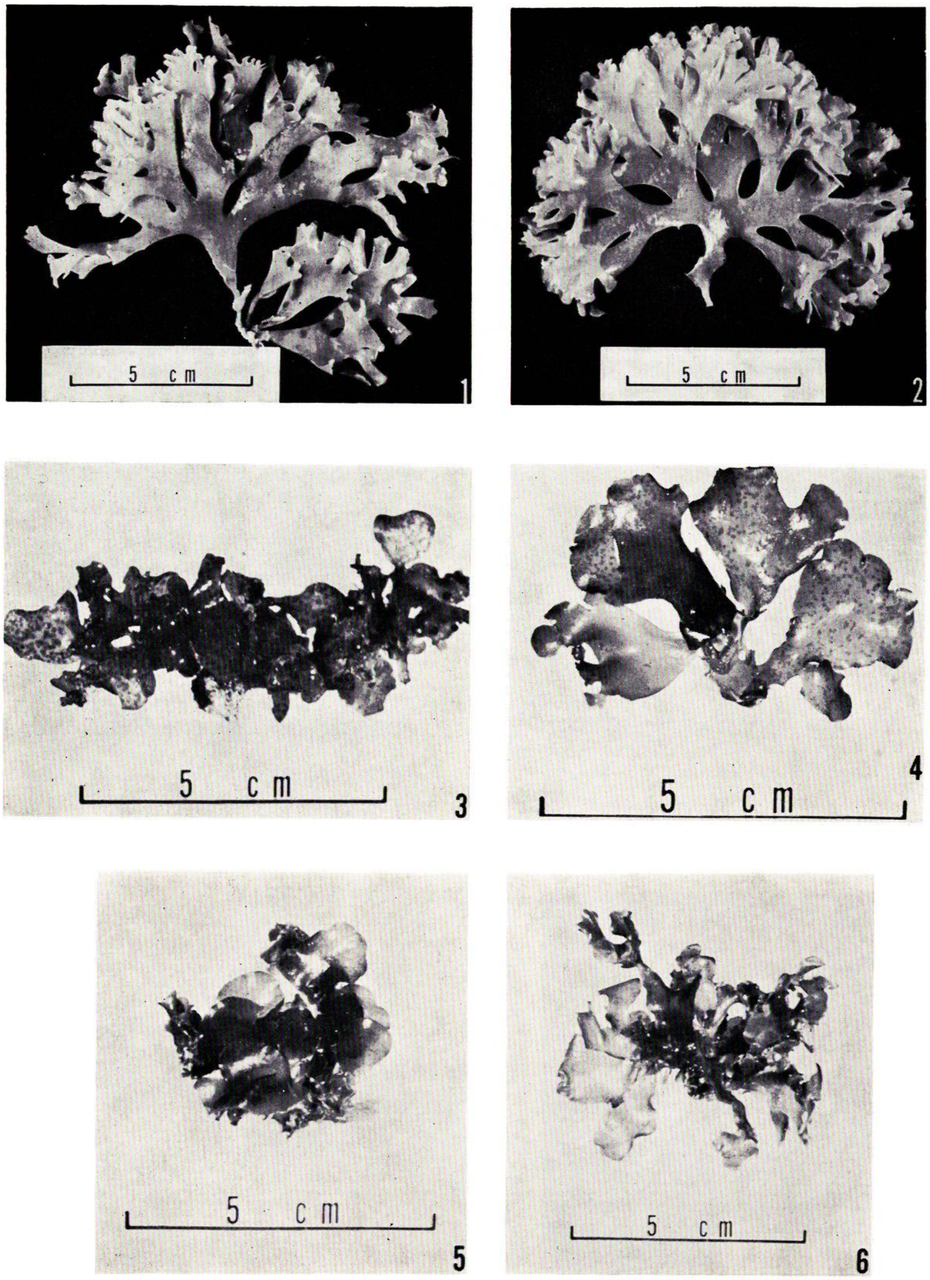

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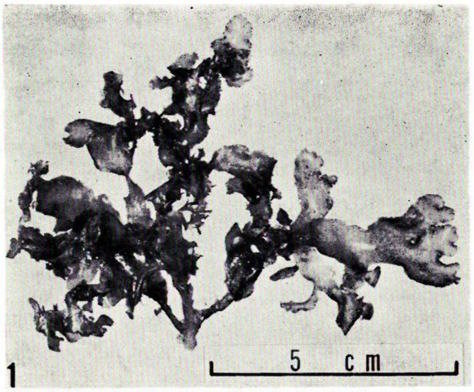

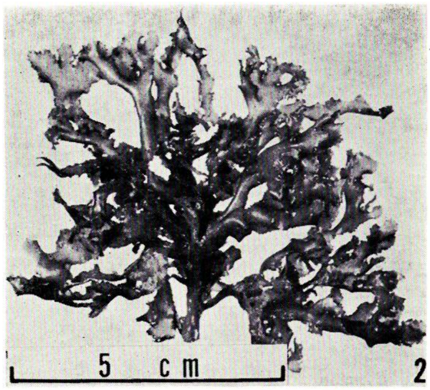

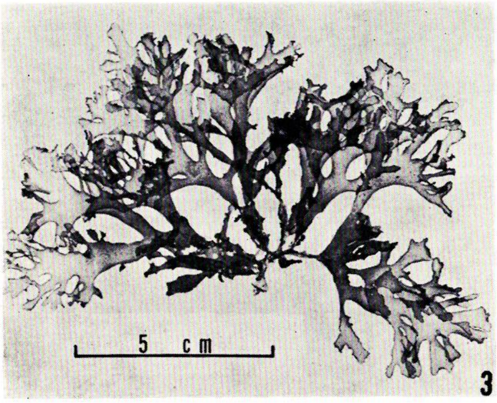

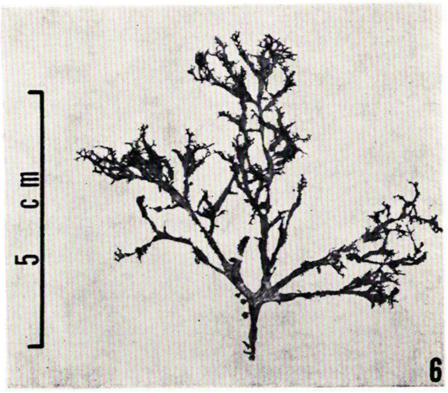

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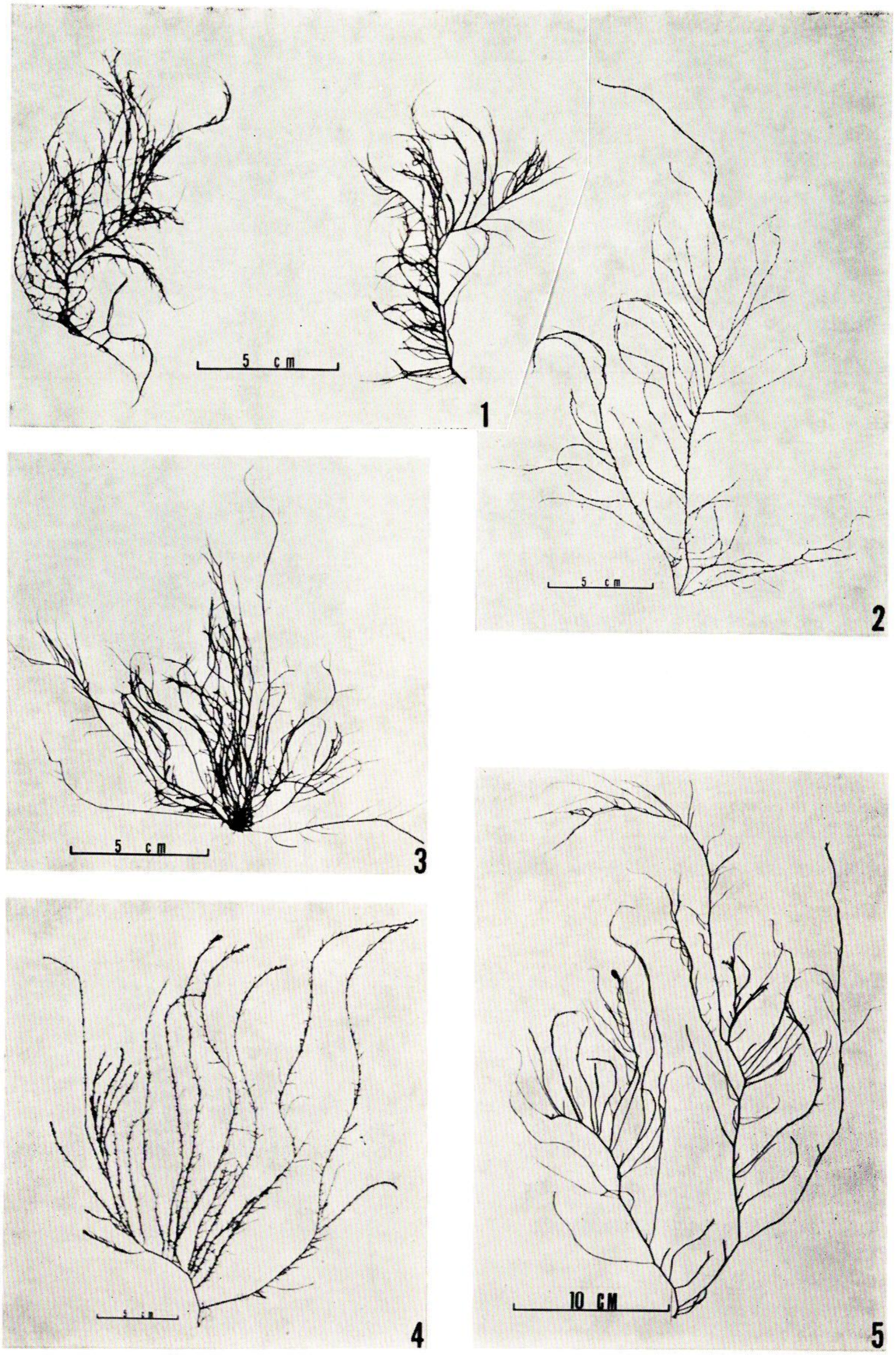

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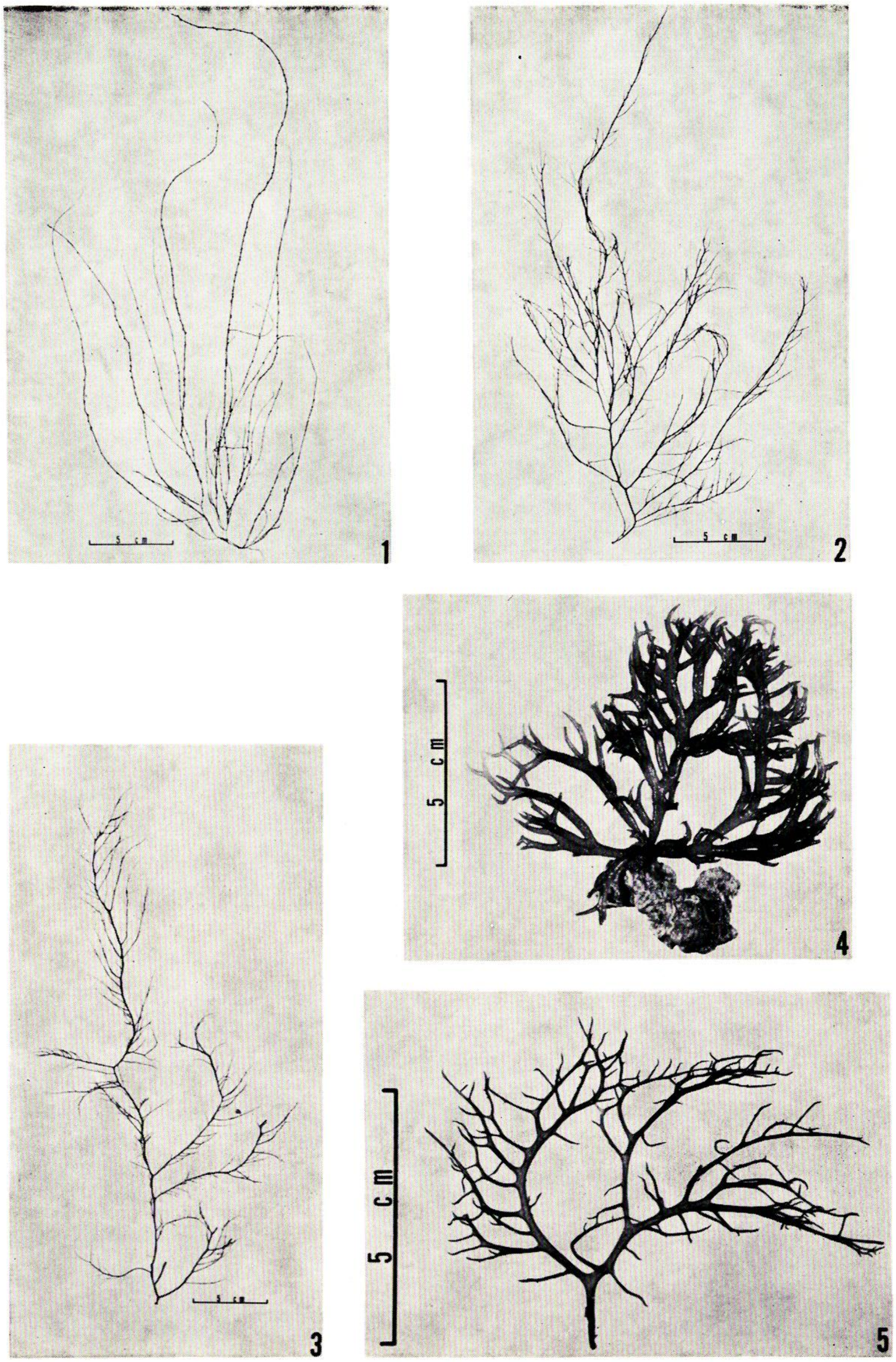

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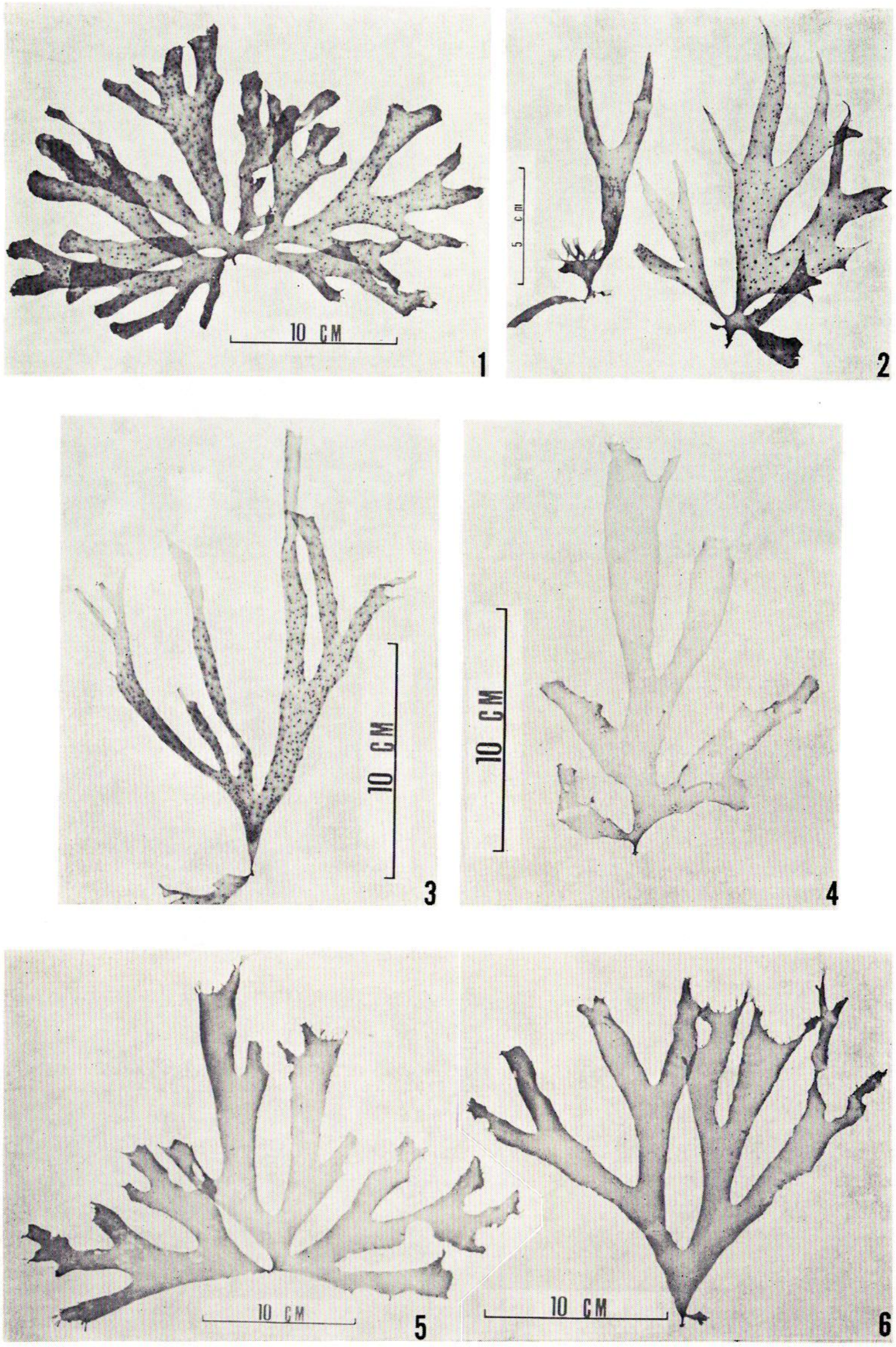

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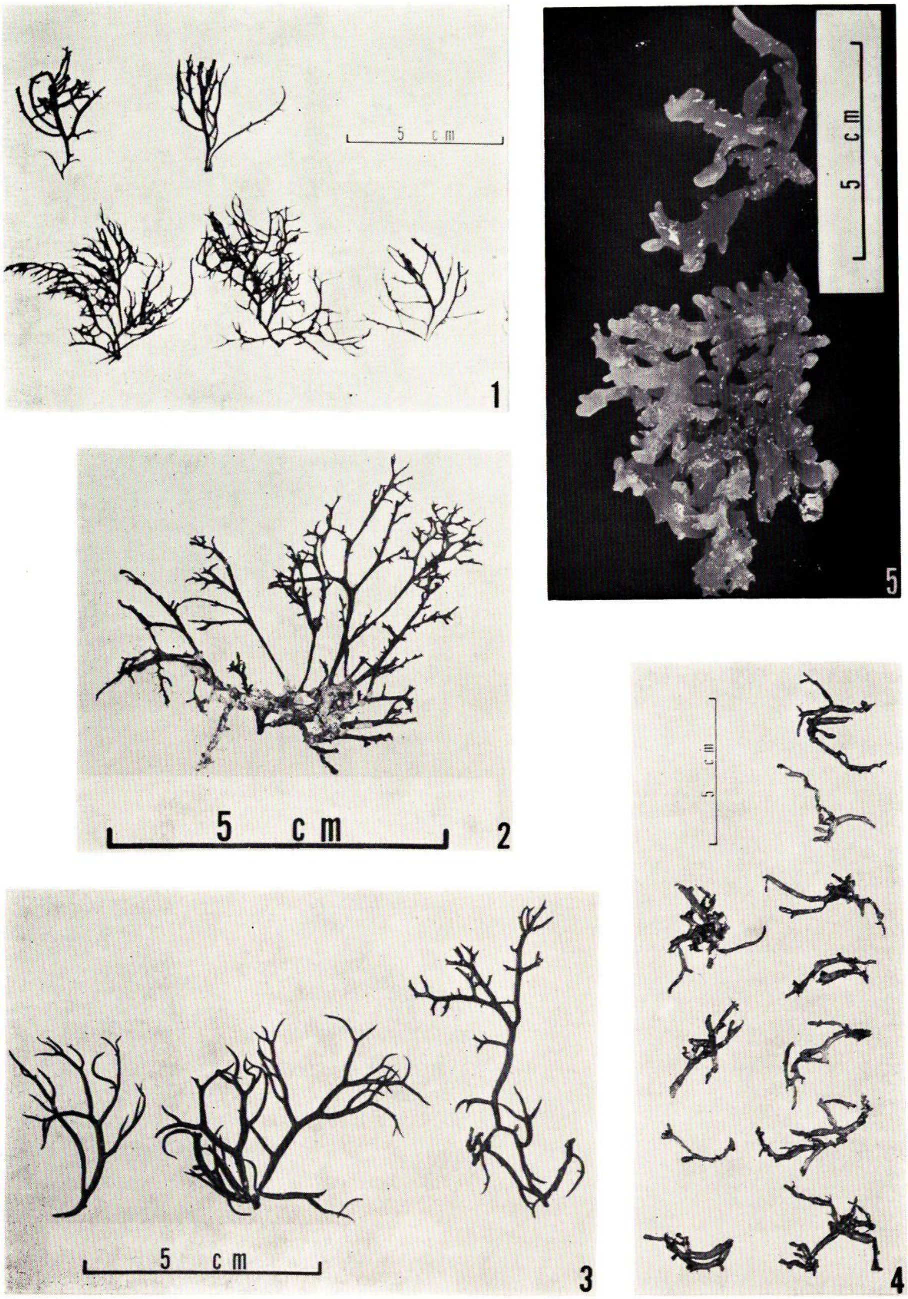

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