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The Structure and Reproduction of the Genera *Ceramium* and *Campylaephora* in Japan with special Reference to Criteria of Classification

By

YOSITERU NAKAMURA

The status of the generic name *Ceramium* is very complicated. The retention of *Ceramium* (Roth) Lyngbye as a *nomen conservandum* has, however, been sanctioned by the International Botanical Congress (Briquet, 1935, p. 85). Lyngbye (1819, p. 117) enumerated the following six species and four forms: (1) *Ceramium elongatum*; (2) *Cer. brachygonium*; (3) *Cer. rubrum*, *β. proliferum*; (4) *Cer. secundatum*; (5) *Cer. diaphanum*, *β. hyalinum*, *γ. tenuissimum*, *δ. virescens*; (6) *Cer. ciliatum*.

Kützing (1841, 1847, 1849) made a revision of the genus *Ceramium* and proposed the ten following genera: *Hormoceras*, *Gongroceras*, *Echinoceras*, *Acanthoceras*, *Chaetoceras*, *Trichoceras*, *Celeceras*, *Pteroceras*, *Ceramium*, and *Centroceras*. This method of classification is based largely upon the gross structure of the cortex, the disposition of tetrasporangia, and the presence or absence of hairs and spines. Further, Cramer established a new genus *Herpoceras* in his 1863 work.

J. G. Agardh revised the genus *Ceramium* in 1851, distinguishing from it a new genus *Campylaephora* on the basis of the material collected by Tilesius from Japan, which was described by C. A. Agardh as *Ceramium rubrum* var. *firmum*. He assigned 56 species to *Ceramium* and in 1894 made his final revision, division into series, tribes, etc., and brought the number of species up to 63. He was followed by various investigators, Kylin (1907, 1944), H. E. Petersen (1908, 1911, 1923–24, 1929), Feldmann-Mazoyer (1940), Dawson (1950), and others. *Ceramium* as understood by the majority of the investigators contains more than one hundred species and is divided into the three following groups: (1) Cortication interrupted, (2) cortication partly continuous, and (3) cortication entirely continuous.

The late Professor K. Okamura applied himself to the problems of *Ceramium* in Japan at various times throughout his career, and rather steadily for several years before his death in 1935. At the time of his death the greater part of his results were still unpublished, being in the form of a copy of his lecture at the meeting, or of notes written on the sheet of herbarium specimens. Okamura (1927, 1930) revived C. A. Agardh's conception of *Ceramium,* recombining the genus *Campylaephora* in *Ceramium.* In 1934 he made his final revision (unprinted) of the genus in Japan and assigned 12 species to our coasts. Thus the genus *Ceramium* was divided by Okamura mainly on the basis of microscopic structure of the cortex into the three following types: (1) *Tenerrimum*-type, (2) *Rubrum*-type, and (3) *Crassum*-type. This scheme of Okamura materially is not in serious disagreement with the one which the writer has worked out, except the intrageneric position of the *Crassum*-type. The clarification of the origin and development of the rhizoidal cells has necessiated the elevation of the Okamura's *Crassum*-type to the level of genus, refounding the genus *Campylaephora.*

In the preceding paper, New *Ceramiums* and *Campylaephoras* from Japan (1950), the writer made several emendations of the genera and species concerned and proposed the following tentative arrangement:

I. Frond corticated with minute cells only around the nodes or throughout; rhizoidal cells in the cortex absent; frond-base composed of a cluster of rhizoids ··· ··· ··· ··· ··· ··· ··· ··· ··· ··· ··· ··· ··· ··· Genus *Ceramium* (Roth) Lyngbye.

1. Subgenus *Hormoceras* (Kützing) Nakamura ··· ··· ··· ··· ··· ··· ··· ···
   Frond corticated only around the nodes, forming a distinct band.
2. Subgenus *Mesoceramium* Nakamura ··· ··· ··· ··· ··· ··· ··· ··· ···
   Frond corticated only around the nodes in the greater part or in the upper part of a frond, and the remaining part of the frond corticated throughout.
3. Subgenus *Euceramium* De Toni ··· ··· ··· ··· ··· ··· ··· ··· ··· ··· ··· ···
   Frond corticated throughout.

II. Frond corticated with minute cells throughout; rhizoidal cells in the cortex present, frond-base forming a distinct conical disc, composed of rhizoidal cells ··· ··· ··· ··· ··· ··· ··· ··· ··· ··· ··· ··· ··· ··· Genus *Campylaephora* J. Agardh.

The main features of the arrangement presented earlier, to serve as a guide in the attempt to subdivide the genus *Ceramium* (*in sensu amplissimo*) into practical units and seemingly reasonable groups of cleavage, indicate that the chief reliance has been placed mainly on the details of microscopic structure of the cortex, on the disposition of tetrasporangia, and on the presence or absence of spines. The characters concerned have been ascertained from the work of every student of the genus from J. G. Agardh and Kützing down to Okamura, but other features, especially anatomical details of the frond-base and reproductive organs have not been fully studied. The writer's *Ceramium*-studies of Japan which are successive of Okamura's were undertaken as an attempt to fill this gap, so far as the present circumstances permit, and to reexamine the previous taxonomic results with special reference to the Japanese species. Thus the present study has been carried out on the following principles: (1) Systematic investigations of the material accumulated in herbaria, (2) anatomical studies of vegetative and reproductive organs of the fresh material, (3) culture experiments in the laboratory, and (4) ecological observations during field investigations.

The discussion of the subgeneric classification from a phylogenetic point of view, however, has not been fully realized owing to a limited collection of the material, especially to lack of the subgenus *Mesoceramium* species in the investigated waters. In delimiting the species of *Ceramium* which occur in Japan, the writer at first followed the species concept, guided by the OKAMURA's copy and notes. Various emendations have been necessary, however, owing to the discovery of certain new formae and to differences in opinion regarding the relative diagnostic value of particular characters, especially those in the mode of ramification. OKAMURA recognized twelve species in Japan mainly on the basis of the material in the YENDO Herbarium of the Tokyo University, of which seven species are new to science. Certain species of them are not so clear-cut and need the confirmation of observations of fresh or liquid-preserved material, especially as regards the expected range of variability in the microscopic structure of the cortex, in the mode of ramification, and in habitation. In the previous paper (1950) the writer has given preliminarily a part of the taxonomic results of his study from this point of view.

The present article as well as the preceding paper (1950), is a series of the studies on the *Ceramium* complex of Japan. In the present paper it is the purpose of the writer to describe the structure and development of vegetative and reproductive organs especially concerning the species of northern Japan in some details and to discuss the characters which have been used as the basis for the separation of the genera *Ceramium* and *Campylaephora* as well as of the subgenera and species. The systematic part of this study will be continuously published.

Sincere thanks are expressed to Prof. Y. YAMADA for his kind guidance during the course of the present study. The expense incurred in collecting a part of the material for the present study was covered by a grant of the Ministry of Education.

I. Structure and development of the frond

1. Spores and their germination

The germination of spores of *Ceramium* and its related genera has been studied by various authors, DERICK, (1899), LEWIS (1909), KILLIAN (1914), KYLIN (1917), ROSENVINGE (1923–24), CHEMIN (1937), FELDMANN-MAZOYER (1940), and INOH (1944, 1947). To the writer's knowledge, no records exist of differences in both dimension and mode of germination between tetraspores and carpospores of the same species. The results obtained from the present study show, however, that the tetraspore of the species examined is smaller than the carpospore in the mean diameter. The mode of spore-germination of certain species is described in some details in the present chapter.

The following species were dealt with in the present culture experiments.

TABLE 1. Date of culture and locality of the species examined

Species	Locality	Date of Culture
Cer. cimbricum	Muroran	Oct. 3, 1947
Cer. aduncum	Osyoro	Oct. 9, 1948
Cer. paniculatum	Yoiti	Oct. 10, 1948
Cer. japonicum	Muroran	Oct. 3, 1947; Sept. 1, 1948
Cer. Kondoi	Muroran	June 24, July 5, 1948
Camp. crassa		
f. *cymosa*	Muroran	Oct. 30, 1946
f. *borealis*	Muroran	July 5, 1948

Cultures were carried out mainly at the Muroran Seaside Laboratory of the Institute of Algological Research, Hokkaido University. Culture methods applied in the present study are almost similar to those employed by KANDA (1936, etc.) during the course of culture experiments of Laminariales. The material was left in the solution within a day while the spores were allowed to settle on the slide-glasses which had been previously placed on the bottom of the vessels. When the spores had settled on the slide-glasses, the frond was removed, as quickly as possible, out of the solution. The spores were measured statistically with an ocular micrometer under a microscope, exclusive of apparently immature or irregular ones, just after the liberation of spores on the slide-glasses.

Dimension of Spores

When liberated, both tetraspores and carpospores usually assume a perfect globular shape. They are voluminous and of dark brownish red colour, containing a nucleus and numerous chloroplasts. Excepting their dimensions, no differences can be found between tetraspores and carpospores in the species examined. The measurements of both spores are given in the Table 2.

As clarified from the Table 2, the difference in the diameter between tetraspores and carpospores of the same species, according to the SNEDECOR'S F-test, is statistically significant. Consequently, the mean diameter of the tetraspores of the genera concerned seems to be always smaller than that of the carpospores. Further, the mean diameter of both spores of *Ceramium* seems to be smaller than that of *Campylaephora* respectively (cf. Tab. 7).

TABLE 2. Dimensions of tetraspores and carpospores

Species	Diameters (μ)								F	n
	Tetraspores				Carpospores					
	Min.	Max.	Mean	U_{α}^2	Min.	Max.	Mean.	U_{α}^2		
Cer. paniculatum	26	40	30.2	0.41	30	43	34.9	0.70	1.77	200
Cer. aduncum	—	—	—	—	30	50	36.8	10.31	—	500
Cer. japonicum	31	41	35.4	4.09	32	45	38.2	5.54	1.35	500
Cer. Kondoi	30	45	35.4	3.98	30	47	40.1	8.79	2.21	500
Camp. crassa f. *borealis*	49	65	56.9	9.05	56	80	63.4	19.28	2.13	500

Mode of spore germination

After liberation, the spores fasten to the substratum, usually assuming a globular shape. They are not infrequently attached by means of a thick mucilaginous membrane (fig. 2, 10–12). There are found structurally two types in the mode of germination of spore cells; one is regular development, the other is irregular. The former usually takes place more rapidly than the latter. The regular development begins to occur within a 12 hour cultivation and reaches a height of six or more cells even within a 24 hour cultivation. On the other hand, in the irregular development, the spore cell remains to rest for a fairly long time and often gives rise to the erect frond after about a 30 day cultivation.

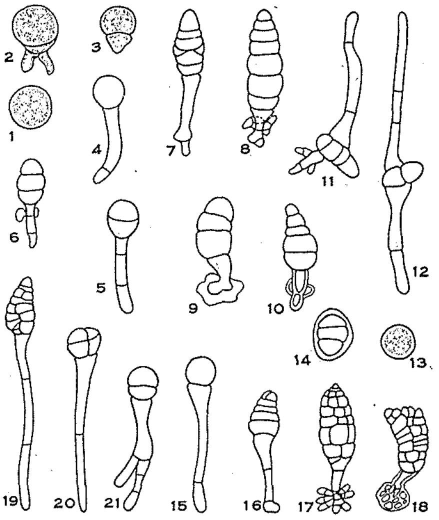

Fig. 1.

Ceramium cimbricum: 1–10, A series of various stages in the regular development of germinating tetraspores. × 100; 11–12, Irregular development of germinating tetraspores. ×100; *Ceramium japonicum*: 13–18, A series of various stages in the regular development of germinating tetraspores, ×100; 19–21, Irregular development of germinating tetraspores. ×100.

(1) Regular development

A series of various stages in the germination of a tetraspore of *Cer. cimbricum* are shown in fig. 1, 1–12. A spore cell is primarily divided into two parts of almost equal size. The lower half is of somewhat lighter colour and usually slightly protrudes. This protuberance appears mostly just after the first division of spore cells but often occurs earlier (fig. 1, 4).

The second cell-division subsequently takes place in both upper and lower halves of the spore cell by a parallel wall to the first septum (transverse division; fig. 1, 8).

In the lower half of the spore cell, transverse divisions usually occur no more. The elongated protuberance mostly expands into a small adhesive disc at the tip. The adhesive disc is primarily unicellular and irregularly lobed (fig. 1, 9). Later it becomes multicellular, forming a minute conical disc (fig. 1, 18). Sometimes the adhesive disc is irregularly branched (fig. 1, 8).

In the upper half of the spore cell, further successive transverse cell-divisions occur. When the third or the fifth division took place, the perpendicular division to the first septum (longitudinal division) occurs primarily in the cells formed by the first cell-division of spores, and both divisions subsequently take place. Then cortical cells are cut off by successive longitudinal divisions at the upper end of central cells (fig. 1, 7) in a remarkable order of succession (cf. p. 25).

In *Cer. japonicum*, *Cer. Kondoi*, and *Camp. crassa* f. *cymosa* and f. *borealis*, the mode of germination of spores is similar to *Cer. cimbricum*, as shown in figs. 1-2.

Judging from the writer's figures and FELDMANN-MAZOYER's illustrations (1940, p. 115, fig. 34), both erect and discal erect types of spore-germination which were proposed by INOH (1944) are apparently observed within the same species. Moreover, it is of interest that the species examined in the subgenus *Hormoceras* represent more abundantly the erect type than the discal erect type while those in the genus *Campylaephora* vice versa, and that those in the subgenus *Euceramium* exhibit an intermediate condition between *Hormoceras* and *Campylaephora*.

(2) Irregular development

In all the species examined, some spore cells remain unchanged for a fairly long time and issue primarily one or more long monosiphonous fibres, sometimes from one end, sometimes from both ends of a spore cell, or often more irregularly. Some of these monosiphonous fibres are unseptate, and some are divided into several segments. Most of them are simple and some are branched. They end in a blunt apex or expand into a small conical disc at their tips, adhering to the substratum (fig. 1, 11-12).

In the tetrasporic culture of *Camp. crassa* f. *borealis*, the division of spore cells often takes place successively two times by the perpendicular walls to each other, forming a tetrad (fig. 2, 13). After about 60 days it was found that these tetrads had given rise to the erect fronds (fig. 2, 14). Such an irregular development, however, could not be observed in the carposporic culture of the species concerned. Further, the more irregular divisions of spore cells were frequently obesrved (fig. 2, 15–16). Generally speaking, the irregular development of germination of spores is far more abundantly found in the tetrasporic culture than in the carposporic.

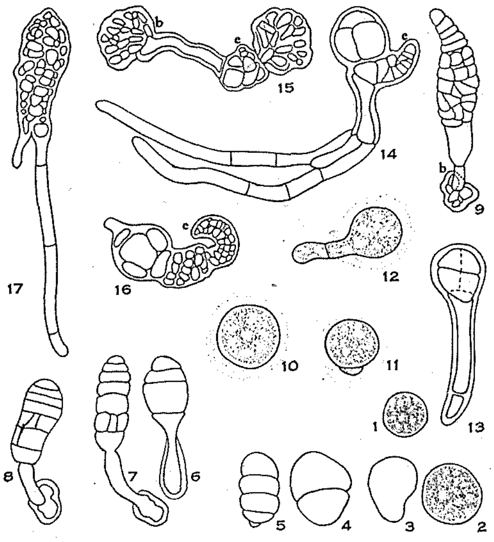

Fig. 2.
Campylaephora crassa f. *borealis*. 1, A tetraspore. ×100 ; A carpospore, × 100 ; 3–9, A series of various stages in the regular development of germinating carpospores. ×100 ; 10–12, Germinating carpospores attached by means of a thick mucilaginous membrane. ×100 ; 13–16, Irregular development of germinating tetraspores, forming a tetrad. ×100 ; 17, Irregular development of germinating carpospore. ×100 ; b, Basal adhesive disc. e, Erect filament.

2. Frond-bases

The gross structure of the frond-base of the genera concerned has been recorded by various authors. HARVEY describes in his "Phycologia Britanica" as follows: In *Cer. rubrum* root is scutate; in *Cer. botryocarpum* scutate with imperfect fibres; in *Cer. diaphanum* discoid; in *Cer. Deslongchampii* discoid, occasionally giving off short fibres. ROSENVINGE and OKAMURA mention on certain species that the frond-base is composed of rhizoids, expanding into a conical disc at their tips. Moreover, OKAMURA has pointed out in his "On *Campylaephora hypnaeoides* J. AG. (1927)" as follows: "It makes its appearance on the frond of species of *Sargassum*, never on stones forming a small disc from which a single frond stands erect." His attention, however, was not payed to the anatomical study of the basal structure.

(1) Genus *Ceramium*

Subgenus *Hormoceras*

The frond-base of the species examined in *Hormoceras* is composed of rhizoids which expand into a small conical disc at their tips or end in a blunt apex (fig. 3, 1–2). Thus the basal attachment-rhizoid is structurally not different from that of the sporelings. It is now simple, now branched and composed of one to three or more cells, measuring about 20–50 μ in diameter.

Some adhesive discs of the basal rhizoids are irregularly lobed and some of them assume a stellate outline. Not only the two forms of the adhesive discs, but also intermediate forms between the two are found within the same species.

The basal rhizoid is primarily given off from the node of the lowermost portion of the frond. It is apparently initiated by cortical cells, and one to three rhizoids are usually given arise from each node. The rhizoids not infrequently are issued from the nodes of the upper portion of the frond, and some of them develop into attachment-rhizoids. As a result of this the plant becomes decumbent as in *Cer. cimbricum*. The basal portion of the frond usually creeps on the substratum and somewhat intricates with the basal rhizoids. Moreover, it seems that when the basal rhizoid is endophytic (fig. 3, 2) or does not reach to the preferable substratum, it does not expand into a conical disc at the tip, but ends in a blunt apex.

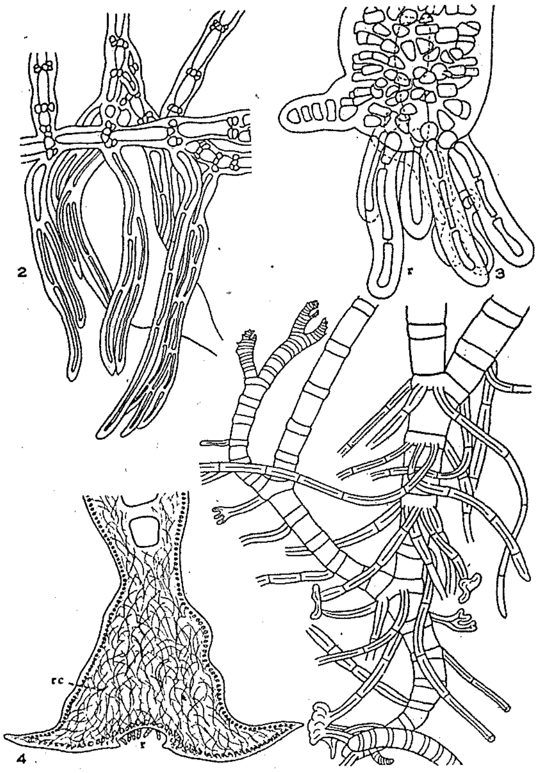

Fig. 3.

Frond-bases. 1, *Ceramium paniculatum*. ×40; 2, *Ceramium Codii*. ×75; 3–4, *Campylaephora crassa* f. *elongata*. 3, Basal part of a sporeling, issuing several rhizoids instead of the primary attachment-disc. ×235; 4, Longitudinal section of a frond-base, showing several rhizoids (r) in a minute cavity of the adherent side of the basal disc. × ca. 15; rc, Rhizoidal cells.

Subgenus *Euceramium*

The structure and development of the frond-base of the species examined in *Euceramium* are essentially not different from those of the species examined in *Hormoceras*. A series of various stages in the development of a frond-base of *Cer. Kondoi* are shown in fig. 1V, 1–5. The frond-base is composed of a cluster of rhizoids. The basal rhizoid is issued numerously from the lowermost portion of the frond and also from the branchlets close to the frond-base. Thus the basal portion of the frond creeps for a short distance, often assuming a disc-like appearance.

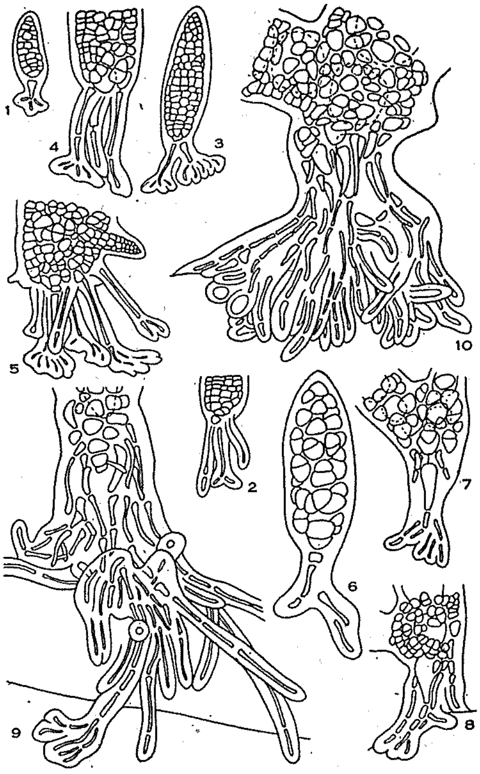

Fig. 4.

A series of various stages in the development of the frond-base. 1–5, *Ceramium Kondoi.* × 100; 6–10, *Ceramium Boydenii,* 6, × 250; 7–10, × 100; 10, Frond-base of a young plant, forming a conical disc surrounded by a cluster of rhizoids.

(2) Genus *Campylaephora*

The frond-base of the species examined in *Campylaephora* is composed of a distinct conical disc, and no basal rhizoids develop in general. The basal disc is about 2.0–2.5 mm. in diameter and usually entire in its margin, but sometimes irregularly lobed. It is composed of rhizoidal cells branched somewhat dichotomously (NAKAMURA, 1950, p. 166, fig. 6, a–e). In rare instances, several basal rhizoids were found in the centre of the adherent side of the basal disc (fig. 3, 4).

The development of the frond-base could be learned from materials in both culture and nature. The attachment-organs of sporelings are similar to those of *Cer. Kondoi.* A sporeling primarily gives off downwards several elongated rhizoidal cells from the cortical cells of the lowermost segment around the axial cell (NAKAMURA, 1950, p. 166, fig. 6, a). The formation of these rhizoidal cells extends gradually to cortical cells of the upper segments. The rhizoidal cell increases more and more, surrounding the primary attachment-disc of the sporeling and finally develops into a conical disc (NAKAMURA, 1950, p. 166, fig. 6, b).

There is found a minute cavity in the centre of the adherent side of the basal disc (fig. 3, 4). This is the vestige of the primary attachment-disc of the sporeling. In some sporelings, several basal rhizoids develop instead of the primary attachment-disc, as shown in fig. 3, 3. It is doubtless that these sporelings may acquire such a basal development as illustrated in fig. 3, 4.

(3) *Ceramium Boydenii*

The frond-base of *Cer. Boydenii* is composed of a minute conical disc surrounded by a cluster of rhizoids (fig. 4, 10). The development of the frond-base could be learned from materials in nature, as shown in fig. 4, 6–10. The attachment-organ of the sporeling is quite similar to that of the other *Ceramium* species examined and *Camp. crassa*. The sporeling primarily gives off downwards several elongated rhizoidal cells from the lowermost segment as in *Camp. crassa* (fig. 4. 7). The formation of these rhizoidal cells, however, is very much meager and extends no more to the upper segments, resulting a minute conical disc (fig. 4, 9–10).

3. Cortex of the fornd

The cortex of the genera concerned is equivalent to the determinate branchlet of *Crouania* etc., and the mode of cortication is more peculiar than that of other genera in the Ceramiaceae.

(1) Genus *Ceramium*

Subgenus *Hormoceras*

The frond of *Hormoceras* is zonately corticated only around the nodes, leaving hyaline interstices all over the frond. This character is designated as "Zonate. corticating band is present."

Cer. Codii shows the most simple and primitive development of the cortex, forming a distinct corticating band which is composed of 1–2 transverse rows of cells (fig. 3, 2). The corticating band of *Cer. cimbricum* consists of 2–3 transverse rows of cells. In *Cer. gracillimum* it is composed of 3–6 (usually 5) transverse rows of cells, and the lower end of each corticating band is somewhat narrower than the upper end of it. The former consists of 1–2 series of transversely elongated cells passing around an axial cell and the latter constitutes 2–4 series of somewhat irregularly disposed, roundish cells (fig. 5, 4). The corticating bands of *Cer. tenuissimum* and *Cer. tenerrimum* are broader, but sharply limited at both upper and lower boaders, forming a distinct band, although they rarely become slightly decurrent by upward proliferations (fig. 5, 7). With regard to the development of corticating bands, *Cer. aduncum* is one of the most advanced species belonging to this subgenus in the investigated waters. Its corticating band usually consists of several rows of irregularly disposed, somewhat roundish cells and slightly separates from each other in the centre of internodes leaving a very narrow interstice (Nakamura, 1950, p. 159, fig. 3, c, f, g).

Fig. 5, 8 represents a cross-section of a corticating band of *Cer. tenerrimum*. The corticating band is composed of both pericentral and outer cortical cells surrounding an axial cell.

The chromatophore is numerous and parietal laminate or more or less discoid in the cortical and the pericentral cells, and filiform in the central axial cells.

The frond develops from a nearly hemispherical apical cell, from which cells are cut off by successive horizontal partitions. Vertically oblique walls, in turn, cut off lateral cells, and these give rise in turn to outer cortical cells (fig. 5, 1–3). From the row of apical cells back to the older part, every step in the mode of cortication may be made out. The resulting plant has a monosiphonous axis issuing large globular pericentral cells from which outer cortical cells are given off. The outer cortical cell is usually unistratose or often bistratose, forming a distinct corticating band around each node.

Typical pericentral cells, which are as long as the central axial cells from the beginning, however, are not observed except in the sporelings. The number of pericentral cells is originally seven in all the species examined in this subgenus (fig. 5, 8). From this fact it may be suggested that an adjacent cell of the apical cell cuts off seven pericentral cells surrounding itself by successive, vertically oblique walls in a remarkable order of succession, right and left of the first segment, until the whole periphery is covered with the pericentral cells, as shown diagrammatically in fig. 5, 9.

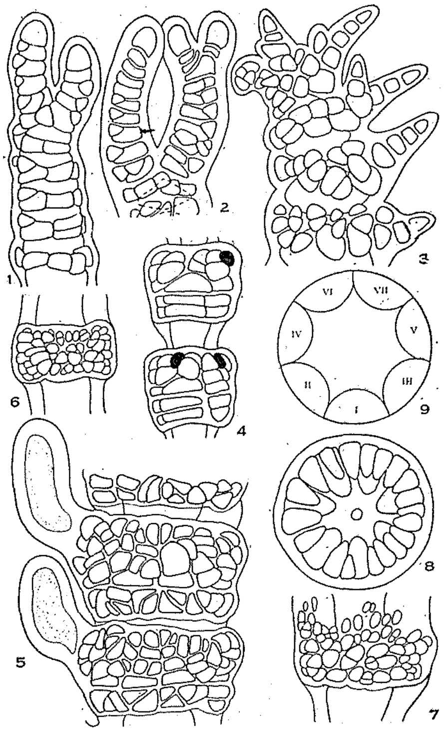

Fig. 5.

1–3, Frond-apices showing the development of corticating bands and branching. 1, *Ceramium cimbricum.* × 250 ; 2, *Ceramium fastigiatum.* × 250 ; 3, *Ceramium paniculatum.* Frond-apex with spines, × 235 ; 4, *Ceramium gracillimum,* The corticating bands showing three gland cells. × 250 ; 5, *Ceramium fimbriatum.* Corticating bands showing the arrangement of cortical cells and two thumb-like processes. × 200 ; 6–8, *Ceramium tenerrimum* : corticating bands. 6–7, × 100 ; 8, cross-section, of a frond, × 250 ; 9, diagram of supposed development of pericentral cells.

In certain species the growth of corticating bands at the nodes occurs in an upward direction (acropetal development) as shown in fig. 5, 5, while in others vice versa (basipetal development). In most species, however, it takes place in both upward and downward directions (acro-basipetal development).

Subgenus *Mesoceramium*

The species belonging to the subgenus *Mesoceramium* have a distinct corticating band as in the subgenus *Hormoceras* in the greater part or in the upper part of a frond, and the remaining part of the frond is furnished with a continuous cortex as in the subgenus *Euceramium*. In certain species the corticating band, however, becomes decurrent by acropetal, basipetal, or acro-basipetal proliferations respectively.

Regarding the development of cortication of *Mesoceramium* species, it is impossible for the writer at present to state in detail, since no species of this subgenus has as yet been discovered in the investigated waters. No additional descriptions, however, will be required, since H. E. PETERSEN (1908, 1911, 1929), KYLIN (1907), NEWTON (1931) and others have reported on it in some details.

Subgenus *Euceramium*

The development of cortication of the species examined in this subgenus is primarily quite similar to that of the species in *Hormoceras*. The frond of *Euceramium*, however, is composed of a central axis, enveloped by a continuous cortex instead of the zonate corticating band at each node in *Hormoceras*. It is not infrequently found a slight interruption in the cortex at the uppermost part of the frond, but it never forms such a distinct zonate corticating band as in *Hormoceras* (fig. 8, 1).

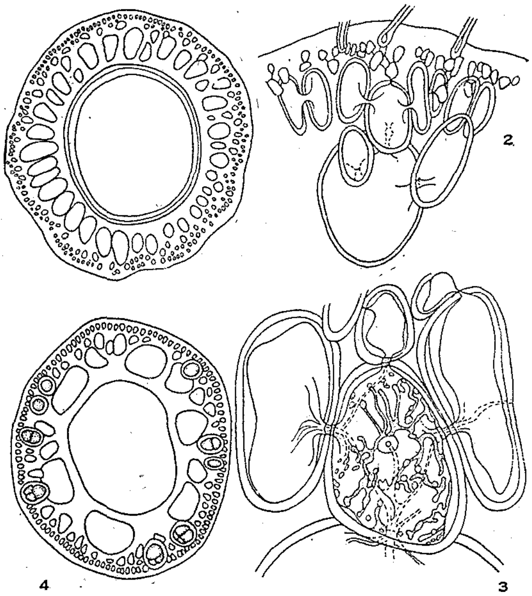

Fig. 6.

Ceramium Kondoi f. *ambiguum*: 1, Cross-section of a lower portion of a frond. × 40; 2, A portion of a cross-section of a frond, × 100; 3, The filiform chromatophores are indicated in a pericentral cell. × 300; 4, *Ceramium japonicum*. Cross-section of a frond. × 100.

Fig. 6 represents cross-sections of the fronds of *Cer. japonicum* and *Cer. Kondoi*. The central axial cell is cylindrical and contains numerous filiform chromatophores. The pericentral cell is large, globular and primarily seven in number, though it becomes much obscure in the older part of the frond. It is arranged in a whorl around an axial cell and contains more or less filiform chromatophores (fig. 6, 3). The inner cortical cell arising from the pericentral cell, is medium-sized and irregular in shape, containing more or less filiform chromatophores. The outer cortical cell is minute and deeply coloured, sometimes angular, sometimes globular or elongated, containing parietal laminate chromatophores. The outer cortical layer is unistratose or bistratose.

In *Cer. japonicum* the outer cortical cell is angular and arranged in a parenchymatous order (fig. 7, 1), giving a reticulate appearance in a lower magnification of surface view, while in *Cer. Kondoi* f. *typicum* it is somewhat elongated and arranged in longitudinal chains, showing a parallel arrangement to the long axis of the frond (fig. 7, 3). When young, however, the outer cortical cells of *Cer. Kondoi* are always angular and give a reticulate appearance in surface view as in *Cer. japonicum.* As it grows, various transitional stages ranging from angular to elongated in shape and those between a reticulate appearance and a parallel arrangement to the long axis of the frond in longitudinal chains (fig. 7, 1–4) are commonly found on the same individual.

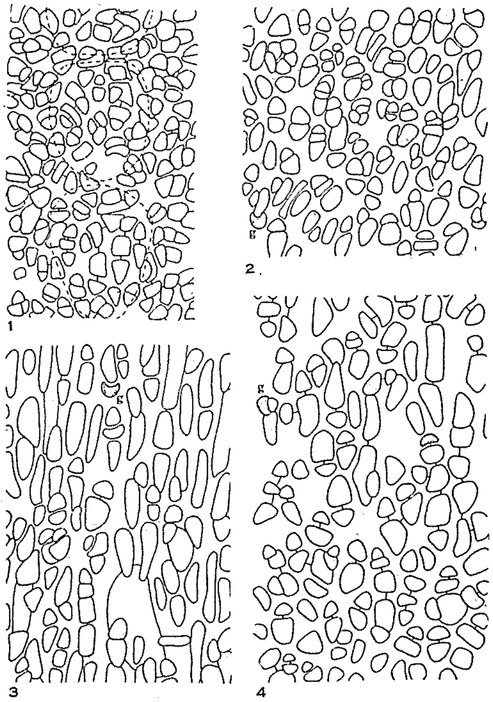

Fig. 7.

Ceramium Kondoi: 1–4, Surface view of the middle portion of a frond, showing the shape and arrangement of cortical cells; 1, f. *ambiguum*; 2, f. *trichotomum*; 3, f. *typicum*; 4, f. *abbreviatum*; g, Lenticular cells; × 250.

In *Cer. Boydenii*, the cortex is very thin, and the cortical layer is usually unistratose except at the nodes of the frond. Further, internal rhizoids were abundantly observed in the cortex, as have been recorded by PHILLIPS in *Cer. rubrum* and by FELDMANN-MAZOYER in *Cer. diaphanum* var. *zostericola*, etc. They primarily descend from pericentral cells surrounding an axial cell (fig. 8, 2). Fig. 8, 3 represents a cross-section of a frond whose central axial cell is compactly filled with the internal rhizoids. It is very interesting that *Cer. Boydenii* and *Camp. hypnaeoides*, which possess the internal rhizoid and the rhizoidal cell in the cortex respectively, are utilized as a "Kanten-material".

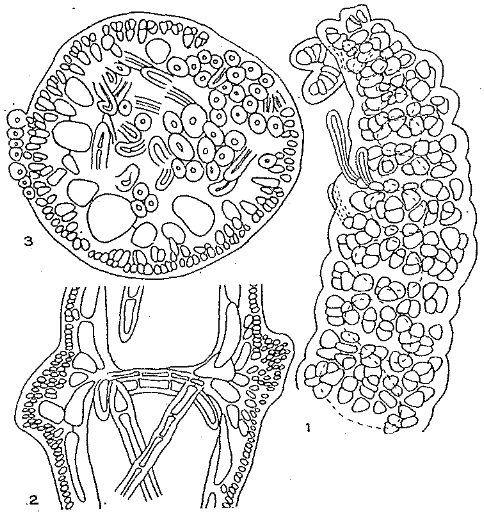

Fig. 8.

1, *Ceramium Kondoi* f. *ambiguum*. Frond-apex showing a slight interruption of the cortex. × 250; 2–3, *Ceramium Boydenii*: 2, Longitudinal section of a frond showing internal rhizoids, × 75; 3, Cross-section of a frond filled with internal rhizoids. × 75.

A cross-section of a frond (fig. 9, 2) shows a central cell which is surrounded by a cortex, consisting of three layers: (1) A pericentral layer, (2) an infra cortical layer, composed of larger, irregular cells and rhizoidal ones, and (3) an outer cortical layer.

The chromatophore is filiform in shape in the central axial cells, discoid in both preicentral and infra cortical cells, and parietal laminate in the outer cortical cells (Nakamura, 1950, p. 168, fig. 7, e).

The development of cortication of the species examined in *Campylaephora* is primarily not different from that of the *Ceramium* species examined. A cross-

(2) Genus *Campylaephora*

Fig. 7, b of the writer's 1950 work represents a longitudinal section parallel to the surface of a frond of *Camp. crassa*. There is a central axis, composed of large cylindrical cells. Outside of the axis, there are long, narrow, rhizoidal cells, running in a generally parallel direction with reference to the surface of the frond, often interlacing and connecting among themselves by short cross-branches. They occasionally branch off dichotomously. Interspersed among these rhizoidal cells, there are numerous, large, oblong or spheroidal cells which have granular contents and are connected with each other by pits. The outer cortical layer is unistratose or bistratose.

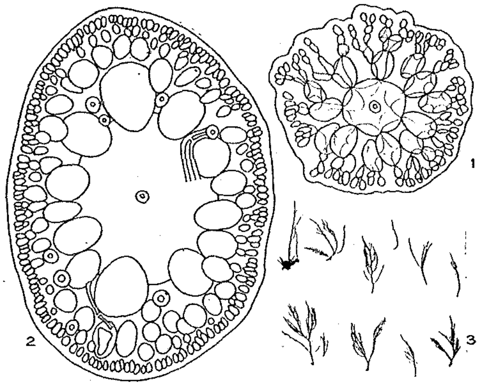

Fig. 9.

1–2, Cross-section of a frond. 1, *Campylaephora hypnaeoides* f. *typica*. Upper part of a frond showing seven pericentral cells around an axial cell. × 100; 2, *Campylaephora crassa* f. *typica*. × 75; 3, *Ceramium japonicum*. Young plants showing the method of the primary branching. × 1/3.

section of a node of a young frond is shown in Fig. 9, 1. A central cell gives rise to seven globular pericentral cells, arranged in a whorl surrounding their mother-cell. The pericentral cell issues infra cortical cells which bear distally by a dichotomous branching a number of branches fitting compactly together to form a firm cortex. The cortical layer is primarily unistratose or bistratose, and at the same time the rhizoidal cell does not develop there (NAKAMURA, 1950, p. 168, fig. 7, c), As it grows, both cortical and rhizoidal cells, especially the latter continue to grow actively, developing into the infra and the outer cortical layers. The first stage of cortication becomes much obscure in the older part of the frond by a copious growth of rhizoidal cells which arise from the infra cortical cells.

The incipient stage of rhizoidal cells occurs in the lowermost segment of the sporelings and it gradually extends upwards as stated in the chapter of the development of the frond-base (cf. p. 23). Thus the rhizoidal cell considerably develops in the lower portion of the frond, especially near the frond-base and hardly develops in the uppermost portion.

4. Ramification

The growth of the frond of the species examined in the genera concerned is apical and monopodial. A branch develops from the cell which is produced from one of the adjacent cells of the apical cell by vertically oblique partitions. The ramification of the main axis of all the species examined is primarily pseudodichotomous (fig. 5, 1). Sooner or later, however, the branch becomes upwardly displaced and subsequently lies on the same level as the continuation of the parent-axis, so that an appearance of dichotomy results (fig. 5, 2). Repeatedly dichotomous ramification is to be seen regularly developed throughout the frond in certain species, but often may be expressed only in the younger frond. In certain species, one fork of the presumable dichotomy overtops the other and as a result a subdichotomous or an alternate branching is produced. Consequently, it is not rare that the ramification of the main axis is alternate, subsecund, or pinnate (fig. 9, 3). Further, in certain species, one or two branchlets are given off at each axil of the dichotomous branching (NAKAMURA, 1950, p. 161, fig. 4). Thus trichotomy or tetrachotomy may be derived from dichotomy.

The ramification of the main axis occurs primarily in the same plane. This is to be seen regularly developed throughout the frond in certain species, but sometimes may be expressed only in the younger plant and often becomes obscure, occurring in various directions. In *Cer. Kondoi*, the main axis usually gives off two main branches. The main branch is repeatedly dichotomous and bears a branchlet at each axil in opposite directions by turns (f. *ambiguum*). The branchlet may often grow up to a normal branch, assuming a main branch, and as a result the main branch becomes trichotomous (f. *typicum*). When the main branch gives off simultaneously two branchlets at each axil (f. *trichotomum*), the tetrachotomy results in the same manner as in the trichotomy. In *Camp. hypnaeoides* the main axis gives off primarily two main branches and also subsequently issues two main branches, occurring in the perpendicularly crossed plane to the first branching plane. Thus the ramification of the main branch occurs in all directions.

A lateral branchlet now develops considerably well, now is almost absent. If the lateral branchlet is simple or once or twice forked, it is described as a proliferous branchlet or proliferation, and if several times repeatedly forked, it is designated as a corymboso-fasciculate branchlet. It may often grow up to a normal branch. The proliferous branchlet is secundly seriated or arises on all sides of a branch. Further, various transitional conditions between the two are abundantly found.

The entire ramification is, of course, characterized by the number of axial cells between the bifurcations, by the angle of branching (axil), and by the branching-plane. Above all, the pseudodichotomy, dichotomy, alternacy, and panicle are characterized mainly by an interval between the bifurcations.

(1) Genus *Ceramium*

Subgenus *Hormoceras*

The ramification of *Cer. cimbricum* is usually pseudodichotomous and that of *Cer. fastigiatum* is regularly dichotomous. *Cer. tenerrimum* branches on all sides, and as a result it represents an appearance of deliquescent dichotomy. The main branch of *Cer. paniculatum* is divided by alternate branchlets mostly every fourth axial cell and thus it shows an outline of regular panicle. In general, the ramification of the species examined in the subgenus *Hormoceras* is pseudodichotomous or dichotomous, and the lateral branchlet hardly develops.

Subgenus *Euceramium*

In *Cer. japonicum* the ramification is somewhat pinnate. In *Cer. rubrum* it is dichotomous, and in *Cer. Kondoi* f. *ambiguum* dichotomous in the lower portion

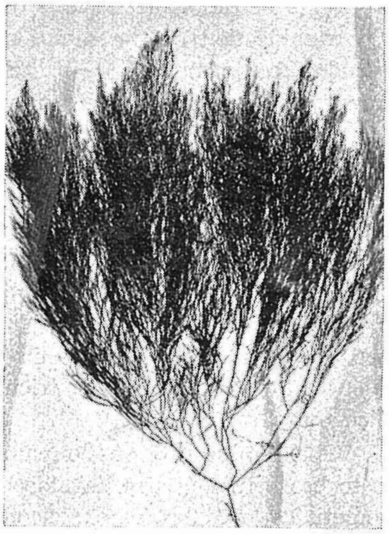

Fig. 10.
Ceramium Kondoi f. *trichotomum*. Entangled habit. × $^1/_2$; Loc. Akkesi, Hokkaido.

of the frond, but trichotomous in the upper portion. *Cer. Kondoi* f. *trichotomum* is generally trichotomous in branching and not infrequently tetrachotomous (fig. 10). The ramification of the species examined in the subgenus *Euceramium* shows mainly a progression from dichotomy to tetrachotomy through trichotomy, and the lateral branchlet develops now scarcely, now considerably well.

(2) Genus *Cmpylaephora*

Camp. crassa f. *cymosa* may possibly represent a simple, even primitive type of the species of *Campylaephora*. It assumes an outline ovate or flabellate, and the ramification occurs in the same plane in a regularly dichotomous manner (fig. 11). In *Camp. hypnaeoides*, the vegetative growth is very vigorous, and the ramification of the main axis occurs in all directions (cf. p. 30). It takes primarily an arbuscular appearance and gradually becomes entangled into a globular mass.

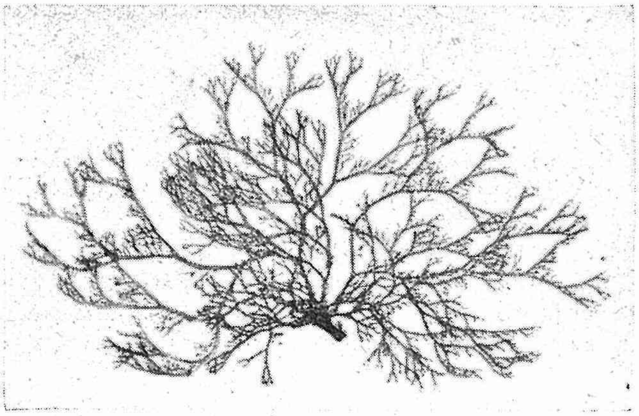

Fig. 11.

Campylaephora crassa f. *cymosa*. Showing secundly seriated proliferous branchlets. × 1 ; Loc. Syôbuta, Rikuzen Prov. (YENDO Herb., Tokyo Univ.)

With regard to the development of lateral branchlets, *Camp. crassa* shows a progressive advance from the simplest type which bears the secundly seriated, proliferous branchlets (f. *cymosa*, fig. 11) through the intermediate types (f. *typica* and f. *elongata*) to the ultimate development as in f. *borealis* which is furnished with the corymboso-fasciculate branchlets (fig. 12).

5. Frond-apices

The frond-apex is very characteristic in certain species of the genera concerned. It is now straight (*Cer. cimbricum*, *Cer. japonicum*), now incurved

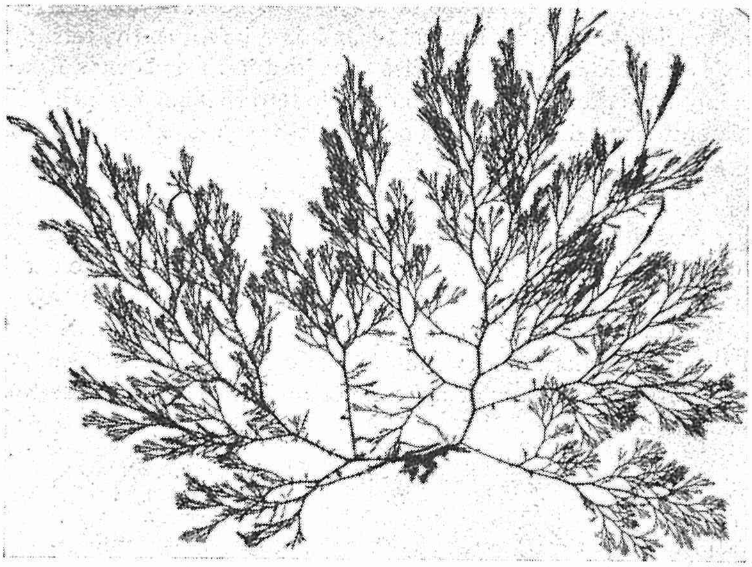

Fig. 12.
Campylaephora crassa f. *borealis*. Showing corymboso-fasciculate branchlets. × ½; Loc. Muroran, Hokkaido.

(*Cer. Kondoi*), now rolls inwards (*Cer. aduncum*). It is mostly forcipated or often simple (*Cer. Kondoi*). When the forcipe of the apex is very short, it is described as emarginated (*Cer. fastigiatum*, (fig. 5, 2). The outer edge of the apex is mostly even, but often dentate (*Cer. tenerrimum*).

6. Supporting-rhizoids and sickle-shaped portions of the frond

Most species examined in the subgenus *Hormoceras* issue numerous rhizoids not only from near the frond-base, but also from the upper portion of the erect frond as in *Cer. fastigiatum*. The rhizoid which is given off from the upper erect frond functions as a supporting-rhizoid in general. The supporting-rhizoid is structurally indistinct from the basal attachment-rhizoid, but both are functionally distinguishable. It is very commonly found in the species examined in *Hormoceras*, but not so commonly found in those of *Euceramium*, further never found in *Campylaephora*.

The sickle-shaped portion of the frond in *Camp. hypnaeoides* is apparently initiated by an usual branchlet (NAKAMURA, 1950, p. 166, fig. 6, b). The rhizoidal cells in the cortex of a branchlet continue to develop far more actively on one side of its upper portion than on another side of it, and thus the branchlet crooks, forming a sickle-shape. Not infrequently this crooked portion of the frond is furnished with a minute adhesive disc which grows out at the point of intersection.

7. Gland cells, hairs, and spines

Gland cells, hairs, and spines in the Ceramiaceae were fully reviewed by FELDMANN-MAZOYER (1940).

The gland cell develops from outer cortical cells of the frond. It is globular and voluminous. It may be clearly distinguished from the other cortical cells by its bright, highly refractive contents. In the glycerine preparations stained with erythrosin, it is easily recognizable by its bright denseness of staining. In *Cer. aduncum* it is mostly seriated on the outer side of the frond-apex and not infrequently scattered in the lower corticating bands (NAKAMURA, 1950, p. 159, fig. 3, a–b).

According to PETERSEN and FELDMANN-MAZOYER, the gland cell occurs very commonly in various species. In the investigated waters, it was found only in *Cer. gracillimum* and *Cer. aduncum*. Such a peculiar lenticular cell as shown in fig. 7, 2–4, g, however, is abundantly found in *Camp. crassa* and *Cer. Kondoi*. This lenticular cell is colourless and quite agrees with PETERSEN's illustration (1929, p. 398, fig. 2, b) of the gland cell in *Cer. vendlicum*. Since it is not stained with erythrosin, however, it appears to be different in nature from the genuine gland cell. To the writer's knowledge, it seems to be a scar of fallen hairs. Accordingly, it is not described as a gland cell in the present study.

The hair is apparently initiated by outer cortical cells of the frond and it is hyaline unicellular. When the plant is young, the hair is commonly found in all the species examined in the genera concerned. As it gorws, the hair becomes scarce and is often almost destitute of. In the subgenus *Hormoceras*, as far as the writer observed, the hair does not so well develop in general. *Cer. cimbricum* possesses hairs in the youngest portion of the frond only. In the subgenus *Euceramium* it is commonly found, especially in the youngest portion of the frond. In *Campylaephora*, however, it develops considerably well, covering the whole frond.

In *Cer. fimbriatum*, thumb-like unicellular processes are seriated longitudinally on the outer side of each node almost all over the frond (fig. 5, 5). This outstanding character is designated by SETCHELL and GARDNER as "the presence of a single row of thicker, short, unseptate hair". In the writer's opinion, however, it is rather to be described as "processes" instead of "hairs", because hyaline, elongated, unicellular hairs are present in this species and these peculiar structures appear to correspond to the spines in certain species of *Ceramium*.

The spine develops from outer cortical cells of the frond. It is separable structurally into two forms; one is unicellular as in *Cer. echinotum*, the other multicellular and mostly three jointed as in *Cer. paniculatum* (fig. 5, 3). There are found several species with the spines in *Ceramium*, but never found in *Campylaephora*, as far as the writer observed.

II. Structure and development of reproductive organs

1. Tetrasporangia

The structure of the tetrasporangia in the genus *Ceramium* has been studied by various investigators. The division of the sporangia in the genus is triangular in most species, and it is cruciate in certain species (*Cer. cruciatum*). With regard to the division of the sporangia ROSENVINGE (1923–24, pp. 372–374, figs. 310–312) has pointed out that in *Cer. diaphanum* and *Cer. rubrum* both triangular and rectangular divisions are ascertained in different sporangia of the same plant, and the spore-mother-cell divides into four cells by walls growing gradually from the periphery toward the centre of the cell without a bipartition of the spore-mother-cell into two cells, each of which subsequently divides into two. The development and arrangement of the tetrasporangia of the species examined are described in some details in the following pages.

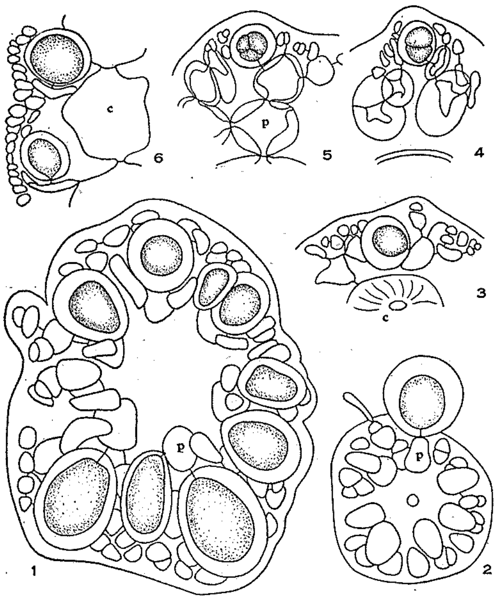

Fig. 13.

1–5, Transverse section of a tetrasporic frond. p, Pericentral cell; c, Central cell. 1, *Ceramium paniculatum*. × 250; 2, *Ceramium aduncum*. × 250; 3, *Campylaephora crassa*. × 100; 4, *Ceramium japonicum*. × 100; 5, *Ceramium Kondoi*. × 100; 6, *Campylaephora crassa*. Longitudinal section of a tetrasporic frond. × 100.

(1) Genus *Ceramium*

Subgenus *Hormoceras*

In *Cer. aduncum* the tetrasporangia are formed at the nodes of the upper part of the frond. They are primarily formed on the adaxial side of branches and gradually become whorled around the nodes (NAKAMURA, 1950, p. 159, fig. 3, c, f, d). The method by which the tetrasporangia are initiated is best observed in a cross-section of a young fertile frond. Fig. 13, 2 represent a cross section of a young tetrasporangium-bearing corticating band of *Cer. aduncum*. It can be seen that a tetrasporangium is cut off distally from a pericentral cell. Each pericentral cell usually forms a single tetrasporangium and thus each corticating band may contain sporangia as many as pericentral cells, surrounding an axial cell. Since some of the pericentral cells may, however, fail to form tetrasporangia, less than seven sporangia usually occur on each corticating band. As the tetrasporangia mature, there are formed no additional layers of cortical cells, and the tetrasporangia thus are erumpent (not bracteated). They are divided triangularly and attached only to the stalk cell.

In *Cer. Codii*, *Cer. cimbricum*, and *Cer. fastigiatum*, the development of the tetrasporangia is similar to that of *Cer. aduncum*, but the sporangia are mostly solitary at each node. Thus the sporangia are seriated on the adaxial side of branches. They are erumpent and rarely slightly bracteated. The bracts often develop seemingly within the sporangial wall. The tetrasporangia are divided triangularly in a regular manner.

In *Cer. paniculatum* each pericentral cell may form one to three tetrasporangia, surrounding an axial cell in a whorl, as shown in fig. 13, 1. From the figure, it will be seen that a pericentral cell initiates 1–3 sporangia and also cuts off crotical cells. The primarily formed cortical cell gives rise to an additional layer of cortical cells and as a result the tetrasporangium becomes bracteated, being somewhat immersed in a cortical layer. The structure, development and arrangement of the tetrasporangia of *Cer. tenerrimum* are essentially not different from those of *Cer.*

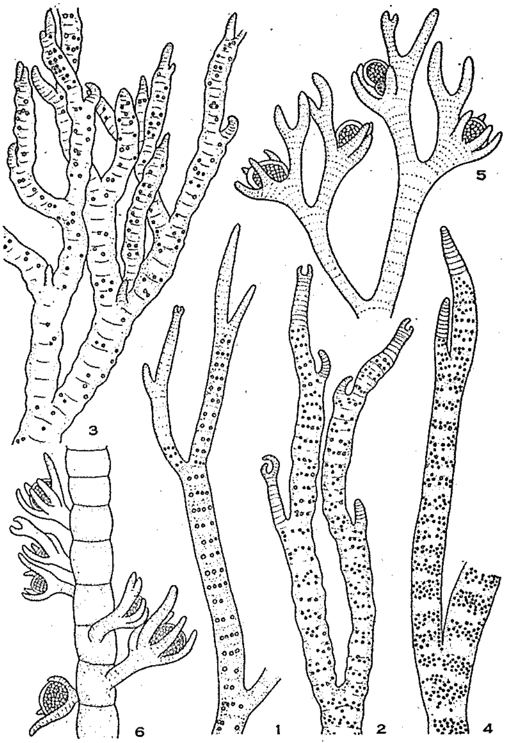

Fig. 14.
Ceramium Kondoi: 1–4, Tetrasporic fronds showing the arrangement of tetrasporangia. × ca. 15. 1, f. *ambiguum*. Note the whorled arrangement at the nodes. 2, f. *typicum*. Note the somewhat disturbed arrangement. 3, f. *abbreviatum*. Note the somewhat disturbed arrangement. 4, f. *trichotomum*. Note the scattered arrangement extending over the internodes 5, Lateral cystocarps of f. *ambiguum*. × ca. 15. 6, Terminal cystocarps of f. *ambiguum*. × ca. 15.

paniculatum.

Subgenus *Euceramium*

The tetrasporangia of the species examined in the subgenus *Euceramium* are primarily formed around the nodes in the upper part of the frond, and the sorus gradually extends to internodes almost all over the frond (fig. 14, 1–4). The method by which the tetrasporangia are initiated will be seen in fig. 13, 4–6. A pericentral cell cuts off laterally tetrasporangia toward the frond-apex. The tetrasporangia are formed from cortical cells in various orders as well as from the pericentral cells in the same manner. When the sporangia are initiated only by pericentral cells, the tetrasporangia are whorled around the nodes in a single transverse row (fig. 14, 1). If the sporangia are also initiated by cells other than the pericentral cells, they become scattered, extending to the internodes (fig. 14, 4). The tetrasporangia are apparently immersed within the cortex and are divided mostly triangularly, often cruciately.

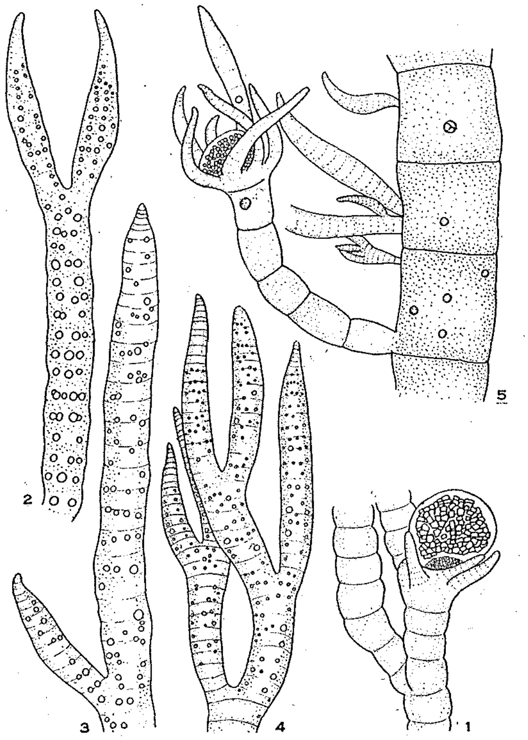

Fig. 15.

1, *Ceramium japonicum.* A cystocarp showing a single, large gonimolobe and a rudimentary one. × 55. 2–5, *Campylaephora crassa.* 2–4, Tetrasporic fronds showing the arrangement of tetrasporangia. × ca. 15. 2, f. *cymosa.* 3, f. *elongata.* 4, f. *borealis.* 5, f. *elongata.* Tetrasporic frond bearing a cystocarp. × ca. 15.

(2) Genus *Campylaephora*

The structure, development and arrangement of the tetrasporangia of the species examined in the genus *Campylaephora* are quite similar to those of the subgenus *Euceramium.* They are shown in fig. 13, 3, 6; fig. 15, 2–4.

(3) *Ceramium Boydenii*

Cer. Boydenii is very characteristic in the formation and arrangement of the tetrasporangia. The tetrasporangium is initiated by a single pericentral cell in each segment as shown in fig. 16, 3–4. Each pericentral cell which lies on the abaxial side of branchlets cuts off laterally 1–2 sporangia toward the frond-apex. The tetrasporangia slightly protrude along the outer margin of branchlets, and thus the branchlets are bent inwardly. They are borne only on the upper portion of branches or on proliferous branchlets in the material examined (fig. 16, 1-2). They are divided triangularly or cruciately. According to OKAMURA (1909, pl. 50, fig. 17), the tetrasporangia are initiated by the central cells. They, however, are always formed from the pericentral cells, as far as the writer observed.

2. Parasporangia

The paraspore has not been observed during the present study. It was, however, recorded by the following authors: By H. E. PETERSEN (1908) in *Cer. diaphanum* f. *strictum*, by ROSENVINGE (1924) in *Cer. strictum*, by SJÖSTEDT (1929) in *Cer. diaphanum* f. *corticatum*, and by FELDMANN-MAZOYER in both *Cer. rubrum* var. *barbatum* and *Cer. diaphanum* var. *zostericola*.

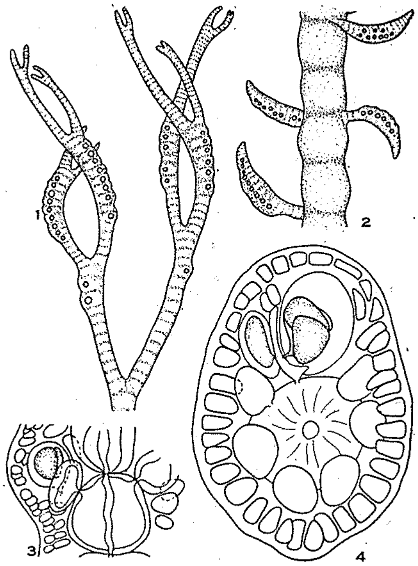

Fig. 16.

Ceramium Boydenii: Upper portion of a frond showing an arrangement of tetrasporangia along the outer margin of branches. × ca. 15; 2, Portion of a frond issuing proliferous branchlets with tetrasporangia. × ca. 15; 3, Longitudinal section of a tetrasporic frond. × 100; 4, Transverse section of a tetrasporic frond. × 250.

3. Spermatangia.

The spermatangia of *Cer. diaphanum* and *Cer. tenuissimum* were recorded by CRAMER (1857) and BUFFHAM (1884, 1888), those of *Cer. rubrum* by DERBÈS and SOLIER (1850), H. E. PETERSEN (1908), and V. GRUBB (1925), in *Cer. procumbens, Cer. bicorne, Cer. interruptum*, and *Cer. clarionensis* by SETCHELL and GARDNER (1930, 1937), in *Cer. Codii* by FELDMANN-MAZOYER (1940), and in *Cer. Masonii* and *Cer. Taylorii* by DAWSON (1950) respectively.

In the present study, the writer observed spermatangia in *Cer. Codii, Cer. cimbricum, Cer. gracillimum, Cer. aduncum, Cer. paniculatum, Cer. Kondoi, Cer. Boydenii, Camp. crassa*, and *Camp. hypnaeoides*.

In general, the male plant is often far smaller than both tetrasporic and cystocarpic plants, and the former matures earlier than the latter two. In all the species examined the spermatangia form sessile patches covering the whole area of the upper portion of the frond and assume a whitish, minutely dotted

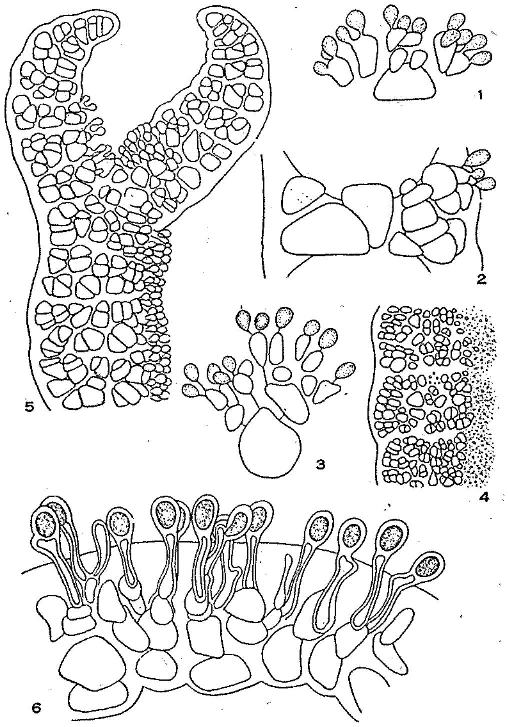

Fig. 17.

1–2, *Ceramium cimbricum*: 1, Portion of a transverse section of spermatangia-bearing corticating band. × 600; 2, Surface view of a young spermatangia-bearing corticating band. × 600. 3, *Ceramium paniculatum*. Portion of a transverse section of spermatangia-bearing corticating band. × 600. 4. *Ceramium aduncum*. Portion of an antheridial plant. × 100. 5, *Campylaephora hypnaeoides* f. *hamata*. Frond-apex bearing spermatangia. × 250. 6, *Campylaephora crassa* f. *cymosa*. Transverse section of a frond with spermatanigia. × 600.

appearance (fig. 17, 4). The spermatangia are produced from outer cortical cells of the frond. They are whitish in colour, elliptical in shape and measure about 4 μ by 6 μ in dimension. They are attached to the more or less elongated stalk cell (fig. 17, 6).

A series of various stages in the development of the spermatangia are shown in fig. 17. The first step in the development of spermatangia is the formation of cortical cells. The cortical cells are cut off in turn by walls which are parallel or somewhat perpendicular to the frond (fig. 17, 2). The cells so formed are spermatangium-mother-cells. They do not become connected by secondary pit-connections. The spermatangia are formed as protuberances which are budded off from the external surface of the spermatangium-mother-cells. Each spermatangium-mother-cell may form one to three spermatangia (fig. 17, 1). The spermatangium is primarily formed on the adaxial side of the upper branches (fig. 17, 5) and gradually spreads over the whole area of the frond (Nakamura, 1950, p. 159, fig. 3, g).

4. Procarps and cystocarps

The development of the procarp and cystocarp of the genus *Ceramium* has been described by Janczewski (1876), Phillips (1897), Rosenvinge, (1923–24), Miranda (1929), and Feldmann-Mazoyer (1940). In *Cer. tenuissimum* by Janczewski and Phillips, and in *Cer. fruticulosum* by Rosenvinge, two carpogonial branches were observed on each side of a single supporting-cell, while KYLIN only one carpogonial branch there in *Cer. rubrum*.

In all the materials examined by the writer, however, each supporting-cell always bears only one carpogonial branch. Further, from the present study, it has been found that the species examined in *Hormoceras* are distinct from those in both *Euceramium* and *Campylaephora* in the development of gonimolobes of cystocarps.

The cystocarp of the genera concerned is composed of a berry-like nucleus surrounded by several involucral ramuli. The cystocarp is borne now laterally on branches and branchlets; now terminally on proliferous branchlets (fig. 14, 5–6).

(1) Genus *Ceramium*

Subgenus *Hormoceras*

In *Cer. paniculatum* the procarp occurs always close to the apex on the abaxial side of branchlets. The procarp develops from the pericentral cell of fertile segments. A fertile pericentral cell can be distinguished at an early stage from a sterile pericentral cell by its denser cytoplasmic contents. In the glycerine preparations stained with erythrosin, it is easily recognizable by the denseness of staining.

The carpogonial branch is composed of four cells and bent characteristically toward the frond-apex in such a manner that the carpogonium lies lateral to the supporting-cell. The basal cell of the carpogonial branch is the largest while the carpogonium is the smallest. The trichogyne is narrow, comparatively long and usually a little swollen up close to the carpogonium (fig. 18, 1).

While the carpogonial branch is in process of development, the supporting-cell (s) cuts off another cell, namely, a group of sterile cells usually on the same side or very rarely on the side opposite to the carpogonial branch.

Previous to fertilization of the carpogonium, the procarp is thus composed of: (a) A supporting-cell, (b) a four-celled carpogonial branch, and (c) a group of sterile cells. The cells of the carpogonial branch, the supporting-cell, and the central cell of the segment have a dense cytoplasmic content, that of the central cell and the supporting-cell being the densest, while the cytoplasm of the group of sterile cells is more or less of the same density as that of the vegetative cells of the frond.

Each fertile branchlet as a rule bears two to three procarps, which develop commonly from consecutive pericentral cells in acropetal succession. The position of the carpogonial branch with relation to the supporting-cell is not always in regular order. Sometimes the carpogonial branches diverge to the right and left of the supporting-cell in alternating order, sometimes they arise from the same side of the supporting-cell in consecutive segments (fig. 20, 1).

In *Cer. paniculatum* each supporting-cell bears only one carpogonial branch as recorded by KYLIN in *Cer. rubrum*. As far as the writer observed, in *Cer. cimbricum*, *Cer. Kondoi*, *Cer. japonicum*, and *Camp. crassa*, the supporting-cell bears usually no cells on the side opposite to the carpogonial branch, though it is rarely not the case.

After a carpogonium has been fertilized, the carpogonium, the supporting cell, and the central cell acquire a denser cytoplasm. Shortly afterwards the supporting-cell enlarge considerably and as far as the writer examined, it appears to be immediately converted itself into an auxiliary cell without any cell divisions (fig. 18, 1–2), though it is unable to detect it clearly owing to the lack of cytological evidences.

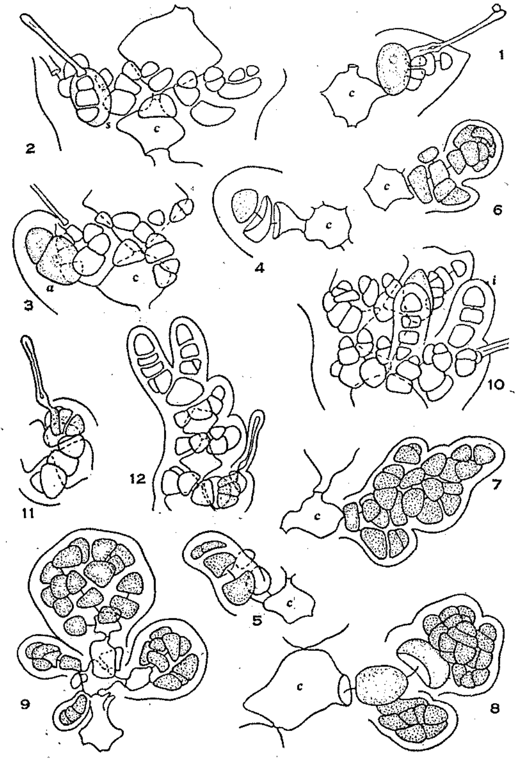

Fig. 18.

1–10, *Ceramium paniculatum*: Various stages in the development of a procarp and cystocarp. c, Central cell; a, Auxiliary cell; s, Supporting-cell; i, Involucre. 1, Stage just after the fertilization of an auxiliary cell. × 300. 2, Young procarp. × 300. 3, The first cell-division of an auxiliary cell. × 300. 4–8, Formation of the gonimoblast. × 300. 9. Nucleus of a cystocarp containing four gonimolobes. × 350. 10, Formation of an involucre. × 300. 11–12, *Ceramium cimbricum*. Young procarp showing three celled carpogonial branch. × 300.

Subsequent to the formation of the auxiliary cell, the carpogonium and the auxiliary cell both enlarge and come to lie close to each other. The fusion of the carpogonium with the auxiliary cell was not observed. It may be suggested, however, that the carpogonium fuses directly with the wall of the auxiliary cell without any intermediary connecting-cells as in *Camp. crassa.*

Concurrently with the enlargement of the auxiliary cell and the carpogonium, there is a further increase in the number of cortical cells of the segment next to a fertile segment, and thus the involucre is formed there (fig. 18, 10). At the time of the fertilization of the auxiliary cell and the early development of the gonimoblast, there is an increase in the density of the cytoplasm of the fertile central cell, but no further growth in its size. The central cells in the neighbourhood of the fertile segment, however, enlarge considerably, and accordingly, the fertile central cell can be easily distinguished from the sterile ones by its smaller size as well as by its denser cytoplasm.

The development of the cystocarp begins with the fertilization of the auxiliary cell and its subsequent division to form the first cell of the gonimoblast. The latter cell is cut off by a concave wall mostly from the anterior part of the auxiliary cell (fig. 18, 3) and in volume constitutes about one-third of the fertilized auxiliary cell. The early divisions of the gonimoblast initial and its daughter-cells are also made by concave walls. Fig. 18, 5 represents an auxiliary cell and a three-celled gonimoblast. In fig. 18, 4–9 are shown a series of various stages in the development of a cystocarp. Subsequent to the formation of the primary gonimoblast initial, one to three gonimoblast initials are cut off in succession from the remaining two-thirds of the auxiliary cell (fig. 18, 4–6). Thus the cystocarp consists of two to four gonimolobes. Fig. 18, 9 shows a fairly advanced cystocarp. It can be seen that there are four gonimolobes in various stages developing from an auxiliary cell. The carpospore is formed from each cell of the gonimoblast.

While the gonimoblast is in process of development, the branchlets which are formed in consequence of outgrowths of cortical cells in the segment next to the fertile segment, continue to grow actively and develop into the involucral ramuli of the cystocarp.

In *Cer. paniculatum* the cystocarp is mostly composed of two to four gonimolobes and surrounded by four to five involucral ramuli. A comparison of the structure and development of the procarp and cystocarp of *Cer. paniculatum*, *Cer. cimbricum*, and *Cer. aduncum*, (NAKAMURA, 1950, p. 158, fig. 2, b) shows no essential differences. In *Cer. cimbricum*, however, the carpogonial branch is composed of three cells, whereas in others it consists of four cells (fig. 18, 11–12).

Subgenus *Euceramium*

In *Cer. Kondoi* the procarp occurs close to the apex on the abaxial side of branchlets. The structure and development of the procarp are quite similar to those of *Cer. paniculatum*, as shown fig. 19, 1–2.

The structure and development of the cystocarp, however, somewhat differ those of *Cer. paniculatum*. In *Cer. Kondoi*, at the beginning of the development of the cystocarp, the first division of the auxiliary cell to form the primary gonimoblast initial takes place usually at its posterior part by a concave wall (fig. 19, 3), while in *Cer. paniculatum* it occurs mostly at the anterior part of the auxiliary cell. Thus in *Cer. Kondoi* the volume of the primary gonimoblast initial is about two-thirds of the auxiliary cell, whereas in *Cer. paniculatum* it is about one-third of the auxiliary cell.

The early divisions of the primary gonimoblast initial and its daughter-cells are also made by concave walls. Fig. 19, 4 represents an auxiliary cell and a two-celled gonimoblast. While the gonimoblast is in process of development, the changes in a fertile central cell and its neighbouring central cells, and the formation of the involucre continue to occur actively as in *Cer. paniculatum.*

A series of various stages in the development of a cystocarp are illustrated in fig. 19, 5–8. Fig. 19, 8 represents a central part of an advanced cystocarp. The figure shows a large, globular, mature gonimolobe and a rudimentary one. The primary gonimoblast initial which is about two-thirds of the auxiliary cell, develops actively into a large globular gonimolobe. The secondary gonimoblast initial is successively cut off from the remaining one-third of the auxiliary cell, but it does not develop into a full-grown gonimolobe. Thus the cystocarp consists of a single gonimolobe and a rudimentary one (fig. 14, 5). Not infrequently no vestige of the rudimentary gonimolobe can be seen.

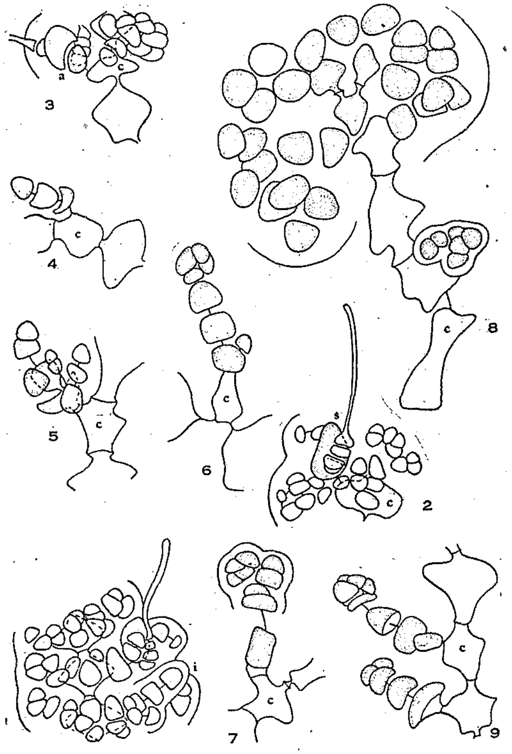

Fig. 19.

Ceramium Kondoi: Various stages in the development of a procarp and cystocarp. c, Central cell; a, Auxiliary cell; s, Supporting-cell; i, Involucre. 1, Formation of an involucre. × 300. 2, Young procarp. × 300. 3, The first cell-division of an auxiliary cell. × 300. 4-7, Formation of the gonimoblast. 4, 5. × 300; 6, 7. × 250. 8, Nucleus of a cystocarp containing a single, large gonimolobe and a rudimentary one. × 250. 9, Two young cystocarps produced simultaneously from two consecutive fertile segments. × 300.

The cystocarp of *Cer. Kondoi* often constitutes two or more gonimolobes and are seemingly quite like that of *Cer. paniculatum*. Both are, however, quite different in process of development. Fig. 19, 9 shows two young cystocarps produced simultaneously from two consecutive fertile segments. While the gonimoblast is in process of development, these two cystocarps are surrounded by the same involucre and thus assume an appearance of a single cystocarp which is initiated by the same segment.

In *Cer. japonicum* the structure and development of the procarp and cystocarp are similar to those of *Cer. Kondoi* (fig. 15, 1).

(2) Genus *Campylaephora*

The structure and development of the procarp and cystocarp of *Camp. crassa* f. *borealis* are quite similar to those of *Cer. Kondoi*. It requires no additional descriptions except the fusion of the carpogonium with the auxiliary cell.

A series of various stages in the development of a cystocarp are illustrated in fig. 20. Fig. 20, 1 shows the fusion of a carpogonium with an auxiliary cell. From the figure it may be assumed that a somewhat elongated carpogonium fuses directly at its distal end with the wall of an auxiliary cell without any intermediary connecting-cells.

In *Camp. hypnaeoides*, the cystocarps and the tetrasporangia both are rarely formed on the same individual, but in such cases the former is far less numerous than the latter, as already noticed by Okamura (1927, p. 366). It seems therefore that the cystocarps are borne on the tetrasporic plant (fig. 15, 5).

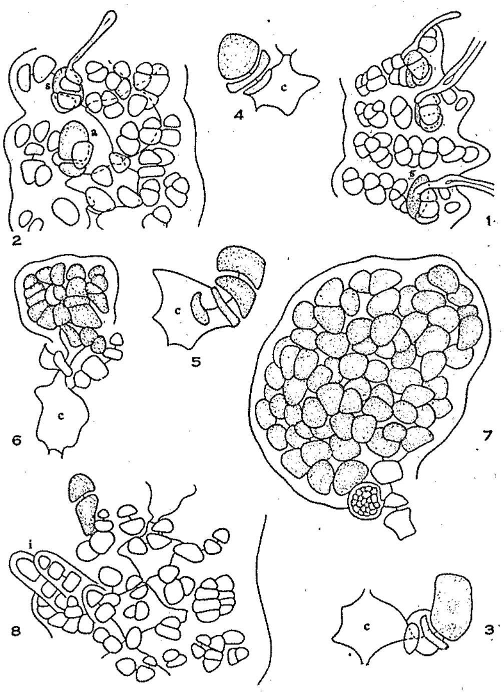

Fig. 20.

Campylaephora crassa f. *borealis*: Various stages in the development of a procarp and cystocarp. c, Central cell; a, Auxiliary cell; s, Supporting-cell; i, Involucre. 1, Fertile branchlet showing carpogonial branches given off from the same side of the suppoting-cells in consecutive segments. The fusion of a carpogonium with an auxiliary cell is indicated in the lowermost procarp. × 300. 2, A young procarp and an auxiliary cell just after the first cell-division. × 300. 3–6, Formation of the gonimoblast. × 300. 7, Nucleus of a cystocarp containing a single, large gonimolobe and a rudimentary one. × 100. 8, Formation of an involucre. × 300.

5. Vegetative Propagation

The frond of certain species of the subgenus *Hormoceras* may become secondarily attached by means of cellular rhizoids which are formed as outgrowths from cortical cells of the frond at the point of intersection. The evidence gained from the present study shows that the vegetative propagation can occur, when the secondarily attached part of the frond accidentally breaks away.

In *Cer. fastigiatum*, if the secondarily attached basal frond breaks away, it can give rise to a complete new frond. If only the secondarily attached portion of the frond is severed from the mother-plant, it can continue an independant existence, though it is unable to develop into a complete new plant unless it gives rise to a new frond. In *Cer. cimbricum* the fragmentary part of the frond which is severed from the mother-plant issues cellular rhizoids from its lower end. These rhizoids form disc-like attachment-organs by means of which the part concerned becomes firmly affixed to the substratum. The result obtained from the present culture experiment shows that this fragmentary part of the frond can continue an independant existence for about half a year in the SCHREIBER's culture solution. On the other hand, these fragmentary portions of the frond are commonly found in nature in *Cer. cimbricum* and *Cer. fastigiatum*. Such a regeneration as this is recorded by FELDMANN-MAZOYER (1940) in *Cer. tenerrimum*.

In certain species of the subgenus *Euceramium* the secondarily attached portion of the frond is not infrequently observed. The secondary attachment-rhizoids may be formed from cortical cells in any part of the frond, but they occur more frequently in the injured parts of the frond or in the older plant. The evidence that the secondarily attached portion of the frond can continue an independant existence when it is severed from the mother-plant, however, was not gained from the present study. In *Cer. Kondoi* it was observed at times that new fronds are budded off from the main branches of a older frond of the forgoing year.

In the genus *Campylaephora* the outgrowth of rhizoids does not occur in general, as already mentioned. In *Camp. hypnaeoides*, the frond is very often secondarily attached to the host by means of the sickle-shaped portions of the frond. It is commonly found that when the part concerned is severed from the mother-plant, it can continue an independant existence, often giving rise a new complete frond. On the other hand, *Camp. hypnaeoides* may bud off new fronds from a older frond of the forgoing year and thus the vegetative propagation may commonly occur by means of budding.

III. Evaluation of criteria for classification

Spores and their germination

The Table 3 was constructed on the basis of the results obtained from the present study. Judging from the Tables, 2, 3 and 7, the difference in the dimension of spores of the species examined in *Ceramium* and *Campylaephora* seems to be of generic value, but of little specific importance. The tetraspores of the species examined in *Ceramium* vary within 26–45 μ in diameter and the carpospores within 30–50 μ. In the species examined in *Campylaephora* the former varies within 49–65 μ in diameter and the latter within 56–80 μ respectively. The mode of germination of the spores, as far as the writer observed, is of no use in determining genus and species (cf. p. 19).

TABLE 3. Character in structure of vegetative and reproductive organs

Genera Characters		*Ceramium*			*Campylaephora*
		Hormoceras	*Mesoceramium*	*Euceramium*	
Frond-bases		a cluster of rhizoids			conical disc composed of rhizoidal cells
Cortication	Zonate corticating bands	present entirely	partly	absent	absent
	Rhizoidal cells	absent	absent	absent	present
Ramification of the main axes		pseudodichotomous dichotomous	dichotomous	simple dichotomous trichotomous tetrachotomous	dichotomous
Supporting-rhizoids		numerous	?	scarce	absent
Sickle-shaped portions of the frond		absent	?	absent	present
Gland cells		present	?	absent	absent
Spines		present	?	absent	absent
Hairs		scarce	?	numerous	very numerous
Tetrasporangia	Initials	pericentral cells	?	pericentral cells and cortical cells in various orders	pericentral cells and cortical cells in various orders
	Arrangement	erumpent or bracteated, seriated or whorled	?	immersed, whorled	immersed, whorled
Cystocarps	Diameter of spores	26–45 μ	?	26–45 μ	49–65 μ
	Gonimolobes	2-4	?	1	1
	Involucral ramuli	3-5	?	3–6	4–9
	Diameter of spores	30–50 μ	?	30–50 μ	56–80 μ

Frond-bases

From the Table 3, in regard to the structure of the frond-base, the genus *Campylaephora* seems to depart considerably from the line represented by the genus *Ceramium*. Thus it is found a distinct cleavage between *Campylaephora* and *Ceramium*. No essential differences, however, are found in the structure of the frond-base of the species examined between the subgenera *Hormoceras* and *Euceramium*.

A separation based on the structure of the frond-base is in accordance with a segregation by the presence of rhizoidal cells in the cortex and by the ramification of the main axis. This is the most significant fact supporting that this method of separation of the writer may suggest a generic cleavage. Consequently, the structure of the frond-base is of a diagnostic importance in separating genus, but of no use in determning species (cf. p. 21).

Regarding the structure of the frond-base, *Cer. Boydenii* appears to link the two genera, *Ceramium* and *Campylaephora* (cf. p. 24). It therefore may require another genus for itself. Other peculiarities of this species supporting this suggestion are in the development and arrangement of the tetrasporangia. A further critical study concerning this problem has been carried on by Prof. YAMADA and the writer.

Cortex of the frond

From the Table 3 it may be made a clear distinction between *Campylaephora* and *Ceramium* on account of the presence or absence of the rhizoidal cells in the cortex, while it is unable to draw a line among the subgenera, *Hormoceras*, *Mesoceramium*, and *Euceramium* by the character concerned. *Hormoceras* and *Mesoceramium*, however, may be clearly distinguished from *Euceramium* and *Campylaephora* by the presence of the zonate corticating bands.

In *Hormoceras*, the microscopic structure of corticating bands of the species examined is sufficiently characteristic and invariable to warrent its use in separating species, as already mentioned in detail (cf. p. 24). Another evidence in support of this opinion lies in the fact that the character concerned is mostly correlated with the disposition of tetrasporangia (p. 50, Tab. 4). It is first utilized by H. E. PETERSEN to the determination of species.

On the other hand, in both *Euceramium* and *Campylaephora* the microscopic structure of the cortex, as far as the writer examined, is not so valuable in separating species, but it may be useful in distinguishing formae. The evidences supporting this view are: (1) The shape and the arrangement of the outer cortical cells, the developmental degree of the rhizoidal cells in the cortex, and the thickness of the cortex are variable according to the age of the plant (cf. p. 27). (2) The characters concerned, especially the latter two are also strongly influenced by external conditions, namely, habitat and growing season.

For example, in *Camp. crassa* the plant growing on *Rhodomela*, *Ptilota*, etc. exhibits a greater development of the rhizoidal cells in the cortex than the plant growing on *Phyllospadix*. The plant thriving in the earlier season (from April to July) also possesses the rhizoidal cells in the cortex more abundantly than the plant growing in the later season (from August to November). In *Camp. hypnaeoides*, the plant from the Japan Sea coast shows a comparatively greater development of the cortex than that from the Pacific coast of Japan. In addition, as far as the writer examined, in the species of *Euceramium* and *Campylaephora* the cortex of the plant growing in a rough sea develops better than that in a calm sea. From these facts it is apparent that the characters under discussion have a strong bearig upon ecological factors.

Ramification

Broadly speaking, the ramification of the genera concerned is fundamentally pseudodichotomous. If the axil is between 45° and 90°, it is patent, if narrower than 45°, acute. The terms divaricate or furcate are used when the axil is broader than the right angle. These characters may be often utilized as a diagnostic criterion.

In the subgenus *Hormoceras* the ramification of the species examined is usually dichotomous and the trichotomous branching is never found, although the pseudodichotomy is often seen throughout the life. The variance in the entire ramification is a useful aid to the determination of species in this subgenus, as already mentioned in detail (cf. p. 30).

In the subgenus *Euceramium* the main axis now simple (*Cer. japonicum*), now dichotomous (*Cer. rubrum*), now trichotomous (*Cer. Kondoi*), exhibiting a progresssive sequence from simple to tetrachotomous through dichotomous and trichotomous. These variations in the ramification of the main axis are sufficiently evident to warrent its use in distinguishing species, since they are correlated mainly with characters in the structure of the cortex.

In the genus *Campylaephora* the ramification of the main axis is always dichotomous and occurs now in the same plane (*Camp. crassa*), now in all directions (*Camp. hypnaeoides*). Regarding the ramification, *Campylaephora* is thus more closely related to *Hormoceras* than to *Euceramium*. In *Campylaephora*, whether the ramification occurs in the same plane or in all directions offers a reasonably satisfactory basis for separating species, since the presence of sickle-shaped portions of the frond is an invariable concomitant of the latter condition.

In the genera concerned other features in the mode of ramification, e. g. the development of the main axes and lateral branchlets are altogether not always available in determining species. The evidences supporting this view are as follows:

According to H. E. Petersen (1911), the forms with the percurrent main axes are commonly found on the fixed substratum in shallow waters where a great movement of waves prevails, while the pure dichotomous forms occur in more or less quiet conditions or as epiphytes in the living, often flexible substratum. From these facts H. E. PETERSEN considers that the development of the main axes and lateral branchlets seems to be influenced by various external conditions.

This view of PETERSEN is supported by the following facts obtained from the present observations: (1) *Campylaephora* which is always epiphytic, is in general more regularly dichotomous than *Ceramium* which is saxicolous or often epiphytic. (2) *Camp. crassa* f. *cymosa* epiphytic on *Phyllospadix* is regularly dichotomous (fig. 11), while f. *borealis* of the same species growing on *Rhodomela*, *Ptilota*, etc. has a percurrent axis (fig. 12). (3) *Camp. hypnaeoides* f. *hamata* usually occurs on *Laminaria* in a calm sea, while f. *typica* grows mostly on *Sargassum* in a rough sea. Thus the former is regularly dichotomous, taking an elegant arbuscular appearance, while the latter is irregularly dichotomous and much entangled. (4) *Cer. Kondoi* usually occurs on the comparatively fixed substratum facing to the surfs and it has mostly a percurrent axis. Further, *Cer. Kondoi* does not show usually such a regularly dichotomous form as f. *modificata* of *Cer. rubrum*.

Regarding the lateral branchlets, they bevelop better in the older plant than in the younger one. The cystocarpic plant bears them more dominantly than the tetrasporic. Further, the plant growing on the fixed substratum facing to the surfs is furnished numerously with the lateral branchlets (*Camp. crassa* f. *borealis*), while the plant growing in a comparatively quiet condition as an epiphyte vice versa (*Camp. crassa* f. *cymosa*). In general, the lateral branchlets are more abundant in *Ceramium* than in *Campylaephora*, as far as the writer examined.

As above mentioned in detail, it is apparent that the development of the main axes and lateral branchlets are strongly influenced by ecological factors. This is the most significant fact that the characters concerned are utilized by the writer in distinguishing formae.

Frond-apices

Cer. cimbricum is always furnished with the straight frond-apices, and its ramification shows the pseudodichotomy. In *Cer. tenerrimum* the frond-apices strongly roll inwards and their outer edges are dentate. It would seem that the characters concerned are correlated with a deliquescently dichotomous ramification. In *Cer. japonicum* the frond-apices are always not forcipated and the ramification is pinnato-decompound which is peculiar to this species. Judging from these facts, the characters of the frond-apex are certainly of significance in separating species.

On the other hand, there are evidences that whether the frond-apex is rolled inwards or straight depends mainly upon the age of the plant and the growing season. When young, the plant is always furnished with the frond-apices which roll inwards, especially in the growing part of the frond (NAKAMURA, 1950, p. 161, fig. 4). In the older plant the frond-apices, however, are mostly slightly incurved or straight (NAKAMURA, 1950, p. 162, fig. 5). Further, the forms with the frond-apices which strongly roll inwards are more commonly found in the earlier season than in the later season, and also in colder waters than in warmer waters. Consequently, the characters of the frond-apex, unless correlated with other definite characters, seem to be of little importance in distinguishing species.

Supporting-rhizoids and sickle-shaped portions of the frond

The presence or absence of supporting-rhizoids appears to be closely correlated with peculiarities in the mode of cortication of the frond, since in the materials examined the supporting-rhizoid is very commonly found in *Hormoceras*, not so commonly in *Euceramium*, but never found in *Campylaephora*. For instance, *Cer. Boydenii* (the subgenus *Euceramium*) which possesses very thin cortex bears abundantly the supporting-rhizoids.

On the other hand, in the subgenus *Euceramium* the supporting-rhizoid is more commonly found in such a vigorous form as *Cer. Kondoi* f. *trichotomum*. From this fact it may be suggested that the occurrence of supporting-rhizoids is closely correlated with the mode of ramification. Further, *Cer. Kondoi* f. *trichotomum* is very characteristic in habit, forming a large entangled mass by means of numerous supporting-rhizoids (fig. X), reminiscent of a similar condition of *Camp. hypnaeoides* on account of the presence of sickle-shaped portions of the frond. Accordingly, it may be also suggested that the occurrence of supporting-rhizoids in *Ceramium* corresponds to that of sickle-shaped portions of the frond in *Campylaephora*.

In fact, the sickle-shaped portion of the frond occurs only in *Camp. hypnaeoides* whose ramification takes place in all directions, whereas it lacks in *Camp. crassa* whose ramification occurs in the same plane. Moreover, in the sexual plant of *Camp. hypnaeoides* f. *hamata* it hardly develops with the exception of the older plant.

Judging from the results obtained from the present study, the supporting-rhizoid in *Ceramium* is, of course, an undependable character as a diagnostic criterion. It is apparent, however, that the presence of sickle-shaped portions of the frond in *Campylaephora*, is sufficiently enough to warrent its use in separating species, but of no use in determining genus, although the genus *Campylaephora* was established by J. AGARDH on the basis of the character concerned.

Gland cells, hairs and spines

Since the presence of gland cells and spines is very characteristic, as already mentioned in detail (cf. p. 33), it is, of course, a useful aid to the deter-

TABLE 4. Arrangement of tetrasporangia of *Hormoceras*

Species	Arrangement		Corticating Band (Height)
Cer. Codii	erumpent	seriated	20-26 μ
Cer. cimbricum	erumpent	seriated	20-60-(100) μ
Cer. fastigiatum	erumpent	seriated	80-130 μ
Cer. aduncum	erumpent	seriated or whorled	50-130 μ
Cer. tenuissimum	{erumpent or {bracteated	seriated	60-108 μ
Cer. gracillimum	{erumpent or {slightly bracteated	seriated or whorled	30-140 μ
Cer tenerrimum	bracteated	whorled	50-80 μ
Cer. paniculatum	bracteated	whorled	50-70 μ

TABLE 5. Arrangement of tetrasporangia of *Euceramium*

Species	Arrangement	Cortex
Cer. Kondoi	whorled around the nodes	thin
f. *ambiguum*		
f. *typicum*	↓	↓
f. *abbreviatum*		
f. *trichotomum*		
Cer. japonicum	scattered beyond the nodes	thick

TABLE 6. Arrangement of tetrasporangia of *Campylaephora*

Species	Arrangement	Cortex
Camp. crassa	whorled around the nodes	thin
f. *cymosa*		
f. *borealis*		
f. *elongata*	↓	↓
f. *typica*		
Camp. hypnaeoides		
(f. *hamata*)		
f. *typica*	scattered beyond the nodes	thick

mination of species.

The hair, however, is not sufficiently enough to warrent its use in determining species and genus in the genera concerned, since the presence or absence of hairs in the species examined is nothing but a dependant character upon the age of the plant or upon the development of the cortex of the frond (cf. p. 33).

Tetrasporangia

A comparison of the process of formation of tetrasporangia of the species examined in the subgenera *Hormoceras* and *Euceramium* and in the genus *Campylaephora* may suggest the following major differences: (1) In *Hormoceras* the tetrasporangia are formed from pericentral cells, so each corticating band may contain only several sporangia, while in both *Euceramium* and *Campylaephora* the tetrasporangia are initiated by cortical cells in various orders as well as from the pericentral cells, and thus the greater part of a frond may be converted into a sorus. (2) In *Hormoceras* the tetrasporangia are erumpent or bracteated, being somewhat immersed in the cortex, whereas in both *Euceramium* and *Campylaephora* they are apparently immersed within the cortex. If the above differences in process of formation of tetrasporangia shall be ascertained for each and every one of the species, a generic cleavage may appear between *Hormoceras* and *Euceramium*.

From the Table 4 it will be seen that the arrangement of tetrasporangia of the species examined in *Hormoceras* is correlated with the structure of corticating bands which is a useful aid to the determination of species (cf. p. 34). If the corticating band is very narrow and thin, the tetrasporangia are erumpent and seriated as in *Cer. cimbricum*, and that as cortication advances, the tetrasporangia progressively show an arrangement, ranging from erumpent and seriated to somewhat immersed (bracteated) and whorled through intermediate conditions. Accordingly, the characters concerned are certainly of specific value in *Hormoceras*, but seem to be of no generic importance (cf. p. 36).

The arrangement of the tetrasporangia of the species examined in *Euceramium* and *Campylaephora* exhibits progressively an advance from "whorled around the nodes" to "scattered beyond the nodes", as cortication advances (Tabs. 5–6). Thus it is unable to draw a clear line among the species on the basis of the characters concerned.

With regard to the formation and arrangement of the tetrasporangia, *Cer. Boydenii* apparently belongs to the subgenus *Hormoceras*.

Spermatangia

The structure and development of spermatangia are quite like in all the species examined in the genera concerned. Consequently, it is unable to utilize them in determining genus or species.

Procarps and Cystocarps

In *Hormoceras*, as far as the writer examined, a cystocarp consists of two to four gonimolobes, while in *Euceramium* and *Campylaephora* it constitutes a single, large, globular gonimolobe, usually accompanied by a rudimentary one. As previously mentioned (cf. pp. 41–42), the difference in the number of gonimolobes of the cystocarp between *Hormoceras* and both *Euceramium* and *Campylaephora* is initiated by the first division of the auxiliary cell to form the primary gonimoblast initial. Not infrequently the cystocarps of the species

TABLE 7. Measurements of terminal cystocarps

Species	Involucral ramuli				Carposporangia	
	Number	Breadth (B)	Length (L)	$\frac{L}{B}$	Nucleus	Spores
Cer. cimbricum	3–4	55 μ	500 μ	9.1	240–360 μ	24–42 μ × 40–60
		60	750	12.0		
		60	780	13.0		
		60	960	16.0		
Cer. aduncum	3–4	96	660	6.9	144–321	28–40 × 40–50
		108	540	5.0		
		108	600	5.5		
		?	?	?		
Cer. paniculatum	4–5	72	420	5.8	240–360	16–24 × 36–54
		72	300	4.1		
		72	180	2.5		
		84	216	2.5		
		96	360	3.7		
Cer. japonicum	3–6	120	420	3.5	164–344	20–32 × 36–54
		132	300	2.3		
		140	480	3.4		
		240	780	3.3		
Cer. Kondoi f. *typicum*	4–5	36	150	4.2	540–600	30–42 × 44–74
		84	264	3.2		
		84	264	3.2		
		96	360	3.7		
Camp. crassa f. *borealis*	4–9	72	300	4.2	240–360	40–70 × 64–90
		96	420	4.4		
		96	420	4.4		
		96	480	5.0		
		108	480	4.4		
		120	480	4.0		
		?	?	?		
Camp. hypnaeoides	5–6	50	300	6.0		44–50 × 60–84
		60	240	4.0		
		60	300	5.0		
		60	300	5.0		
		72	360	5.0		
		72	400	5.6		

examined in *Euceramium* and *Campylaephora* consist of more than two gonimolobes. It is, however, quite different in process of development from the case of the *Hormoceras* species examined (cf. p. 42). From the writer's observations, it may be suggested that this distinction in the gross structure of the cystocarp is of great significance in determining genus.

Another outstanding features in the development of the cystocarp of the species examined lie in the formation of the auxiliary cell (cf. p. 40) and the fusion of the carpogonium with the auxiliary cell (cf. p. 43). It is of course that both are the most significant facts to the determination of the systematic position of the genera concerned.

The number of involucral ramuli is of no diagnostic value to the determination of genus and species (Tab.. 7). From the Table 7 it will be seen that the shape of the involucral ramuli is of some value in determining species, although it is of no use in separating genus.

IV. Some remarks on the revision of the genera and subgenera

Although every student of the genus *Ceramium* from J. G. AGARDH and KÜTZING down to OKAMURA has made various divisions, none, other than J. G. AGARDH and KÜTZING, has brought forward any definite generic suggestions. The genera of KÜTZING excepting *Centroceras* do not seem to obtain approval in general, and J. G. AGARDH's *Campylaephora* was recombined by OKAMURA in *Ceramium*. In the previous paper (1950, pp. 155–157), however, the writer refounded the genus *Campylaephora* and made a division of the genus *Ceramium* into three subgenera (cf. p. 16).

Ceramium as understood by the majority of the investigators is separated by the structure of the cortex into three groups (H. E. PETERSEN, 1908): (1) The frond is corticated only around the nodes. (2) The greater part or the upper part of a frond is corticated only around the nodes, and the remaining part of the frond is completely corticated throughout. (3) The frond is completely corticated throughout. According to the writer's arrangement, the first group is the subgenus *Hormoceras*, the second the subgenus *Mesoceramium*, and the third the subgenus *Euceramium*, respectively. This subgeneric classification of the writer based on the structure of the cortex seems to be phylogenetical as discussed in the next chapter (cf. p. 55).

When KÜTZING (1841) established the genus *Hormoceras*, he characterized it as consisting of a jointed axis which is corticated only at the joints in transverse zones and the tetrasporangia being immersed in the cortex. He included thirteen species in the genus, viz., *Hormoceras diaphanum* and twelve others. In the same paper, KÜTZING proposed five other genera and later (1847, 1849) he added to them three new genera. The characters attributed to the KÜTZING's genera are here given.

(1) *Hormoceras*. Frond jointed; cortical cells collected at the dissepiments in transverse zones; tetrasporangia immersed (*H. diaphanum*).

(2) *Gongroceras*. Frond jointed; cortical cells collected at the dissepiments in transverse zones; tetrasporangia erumpent (*G. Deslongchampii*).

(3) *Trichoceras*. Frond jointed; cortical cells collected at the dissepiments in transverse zones and clothed with hyaline flexible hairs; tetrasporangia immersed (*Tr. villosum*).

(4) *Echinoceras* Frond jointed, zoned and aculeated at the joints; tetrasporangia immersed (*E. ciliatum*).

(5) *Celeceras*. Frond as in *Hormoceras*; tetrasporangia globose or subglobose and lateral sessile, forming peculiar tumour (*Cel. monile*).

(6) *Acanthoceras*. Frond jointed, zoned and aculeated at the joints; tetrasporangia erumpent (*A. acanthonotum*).

(7) *Ceramium*. Frond filiform, consisting of a jointed central axis and cortical, continuous layer of cells, destitute of cilia or spines; tetrasporangia immersed in the cortical layer (*Cer. rubrum*).

(8) *Centroceras*. Frond as in *Ceramium*, but furnished at the joints with prickles or spikes; tetrasporangia erumpent (*Cen. clavulatum*).

(9) *Pteroceras*. Frond corticated throughout; branched pinnately; tetrasporangia prominent on pinnulated branchlets (*Pt. cancellatum*).

(10) *Chaetoceras*. This genus was erected in 1847 on the basis of *Cer. echinotum*, but it postdates *Chaetoceras* EHRENBERG (1844). Accordingly it was merged by KÜTZING with *Trichoceras* in 1849.

This method of separation of KÜTZING is based apparently upon the structure of the cortex, the arrangement of tetrasporangia, and the presence or absence of hairs or spines.

The presence or absence of hairs has proved to be an undependable character, since the species under discussion possess altogether hairs at least in the youngest stages. Thus the genus *Trichoceras* is to be merged with *Hormoceras*.

The presence or absence of spines is untenable as a generic criterion, since there is no evidence in support of it. The spines are, however, nothing but such an appendage as hairs or gland cells to which the cortical cells transformed. Consequently, the presence or absence of spines seems to be of importance in determining rather species than genus. Thus the genus *Echinoceras* should be combined in *Hormoceras*, and *Acanthoceras* in *Gongroceras* respectively.

According to the KÜTZING's diagnoses, the primary feature which distinguishes *Hormoceras*, *Gongroceras*, and *Celeceras*, is the arrangement of the tetrasporangia. As previously noted (cf. p. 51), the arrangement of tetrasporangia depends mainly upon the development of the cortication, ranging from erumpent and seriated to bracteated and whorled through intermediate conditions. Furthermore, such a variance in the arrangement of tetrasporangia often occurs within the same species. *Hormoceras*, *Gongroceras*, and *Celeceras* are also linked by so many intermediate species that it seems best to unite them under the name *Hormoceras*.

The subgenus *Hormoceras* of the writer thus includes the KÜTZING's genera just considered, *Gongroceras*, *Trichoceras*, *Echinoceras*, *Celeceras*, and *Acanthoceras*. KÜTZING, however, has made no mention of the species belonging to the subgenus *Mesoceramium*. The writer's subgenus *Euceramium* receives apparently the KÜTZING's two genera, *Ceramium* and *Pteroceras*.

OKAMURA (1934, unprinted) divided the genus *Ceramium* (*in sensu amplissimo*) in Japan by differences in the microscopic structure of the cortex of the frond as follows: (1) *Tenerrimum*-type. Frond corticated only around the nodes, forming a distinct band. (2) *Rubrum*-type. Frond throughout corticated with minute cells; cortication thin, consisting of unistratose inner cortical cells and unistratose or bistratose outer cortical cells. (3) *Crassum*-type. Frond throughout corticated with minute cells; cortication thick, consisting of several layers of inner cortical cells and unistratose or bistratose outer cortical cells.

According to the writer's classification, the *Tenerrimum*-type corresponds to the subgenus *Hormoceras* and the *Rubrum*-type to the subgenus *Euceramium*. Regarding the intrageneric position of the *Crassum*-type, however, the results obtained from the present study disaccord with the OKAMURA's. This disagreement is apparently caused by the clarification of the origin and development of the rhizoidal cells in the cortex (cf. p. 23). It seems thus to be logical to elevate the OKAMURA's *Crassum*-type to the level of genus as has been discussed in the writer's previous paper (1950, pp. 165–166).

V. Relationships between *Ceramium* and *Campylaephora*, and their systematic positions

From the preceding accounts of the structure of the frond and the development of procarps and cystocarps, it is clear that *Ceramium* and *Campylaephora* belong to the Ceramiaceae. Within this family the two genera belong to the subfamily Ceramiae. A comparison with other genera within the subfamily shows that the subgenus *Hormoceras* is the simplest of known Ceramiae. This is shown by the structure of the frond and by a partially exposed condition of tetrasporangia. Another feature supporting this view lies in the formation of the tetrasporangia (cf. p. 34). Within the Ceramiae the initiation of tetrasporangia only by pericentral cells probably is a feature which in itself is indicative of a primitive condition. As to the development of procarps and cystocarps, however, it is difficult to evaluate whether *Hormoceras* exhibits a more primitive condition than *Euceramium* or *Campylaephora*.

A question which may here be considered is whether *Hormoceras* exhibits a primarily simple or a reduced condition. The partially exposed state of tetrasporangia, coupled with the simplicity of structure of the frond, favours the view that *Hormoceras* actually represents a primitive condition within the Ceramiae. Moreover, another evidence in support of this view lies in the fact that the cortex of the frond shows a progressive sequence from the simplest type, *Hormoceras* to the highly evolved *Euceramium* and *Campylaephora* through the intermediate type, *Mesoceramium*.

From the results of the present study it is apparent that *Hormoceras* phylogenetically lower than *Euceramium* and *Campylaephora*. Certain facts furthermore suggest that *Hormoceras* would evolve from *Crouania*-like ancestor, and that *Mesoceramium*, *Euceramium*, and *Campylaephora* from *Hormoceras*-like plant.

Hormoceras is closely connected with *Crouania* on account of the fact that the procarps are borne on the basal cells of the determinate branchlets. Another evidence supporting this view lies in the fact that in *Crouania* the determinate branchlets are erect at each node while in *Hormoceras* they adhere to the central axis, forming a corticating band at each node.

As above mentioned, it is doubtless that *Euceramium* evolved from *Hormoceras*. It may thus be noted that the frond of *Euceramium* is structurally more complex than that of *Hormoceras*, exhibiting a progressive advance from *Hormoceras* to *Euceramium* through *Mesoceramium*.

As to the probable ancestors of *Campylaephora*, there is a reason to believe that it may evolve as an off-shoot from the subgenus *Mesoceramium*. Two facts especially may be cited in support of this view: (1) In the branching *Campylaephora* is always dichotomous in connection with *Mesoceramium* which is dichotomous, whereas *Euceramium* exhibits an independant peculiar development (cf. p 30). (2) With regard to the development of the cortication *Campylaephora* is more closely related to *Mesoceramium* than to *Euceramium*. In fact, *Camp. crassa* f. *cymosa* exhibits a far more primitive condition in the structure of the frond than *Cer. Kondoi*.

Regarding the relative position of the genera, *Ceramium* and *Campylaephora*, the available facts favour the conclusion that *Euceramium* and *Campylaephora* represent two parallel lines of evolution, with *Campylaephora* occupying a somewhat higher level than *Euceramium*. The evidences in support of this view are: (1) In *Campylaephora* the rhizoidal cells develop in the cortex instead of outgrowth of the rhizoids. (2) *Campylaephora* fastens to the substratum with a conical basal disc composed of the rhizoidal cells, while *Ceramium* attaches by means of a cluster of the rhizoids. (3) In *Campylaephora* the sickle-shaped portions of the frond occur instead of the supporting-rhizoids in *Ceramium*. (4) The attachment-organs of the sporelings of *Campylaephora* exhibit more abundantly the discal erect type than those of *Ceramium*. (5) The mean diameter of both spores of *Campylaephora* is larger than that of

Ceramium.

On the other hand, as previously mentioned (cf. p. 43), it is assumed that in the species examined of the genera concerned the auxiliary cell may possibly receive a diploid nucleus directly from a fertilized carpogonium without any intermediary connecting-cells, as in *Griffithsia*. From this point of view, it may be suggested that the genera concerned are highly evolved groups in the Ceramiaceae. Furthermore, from the writer's observations (cf. p. 40), it is supposed that the species examined of the genera concerned appear to be different in the formation of the auxiliary cells from other genera of the Ceramiaceae. A thorough revision as to the relative position of the genera concerned in the Ceramiaceae should, however, await further results obtained from a detailed cytological study of the development of the procarp and cystocarp.

VI. Summary

1. In the species examined, the mean diameter of the tetraspore is smaller than that of the carpospore, and both spores of *Ceramium* are smaller than those of *Campylaephora* in the mean diameter respectively. The mode of germination of the spores shows both erect and discal erect types.

2. The frond-base consists of a cluster of the rhizoids in *Ceramium*, while in *Campylaephora* it forms a distinct conical disc, composed of the rhizoidal cells.

3. In *Ceramium*, the cortication of the frond consists of a zonate corticating band at each node or a continuous layer of cortical cells, and the rhizoidal cells are absent in the cortex, while in *Campylaephora* it is composed of a continuous layer of cortical cells, containing numerous rhizoidal cells in the cortex.

4. In *Ceramium*, the ramification of the main axis shows a progressive sequence from simple to tetrachotomous through dichotomous and trichotomous, while in *Campylaephora* it is always dichotomous.

5. The supporting-rhizoids are abundantly found in *Ceramium*, while in *Campylaephora* the sickle-shaped portions of the frond occur instead of them.

6. The tetrasporangia are initiated by the pericentral cells and erumpent or somewhat immersed in the cortex in *Hormoceras*, while in *Euceramium* and *Campylaephora* they are initiated by cortical cells in various orders as well as the pericentral cells and immersed within the cortex.

7. The spermatangia are produced one to three from each cortical cell and form sessile patches on the frond in all the species examined.

8. The procarps are formed in acropetal succession close to the frond-apex. Their development and that of the cystocarps is described and figured. The number of gonimolobes of the cystocarp of *Hormoceras* mostly differs from that of *Euceramium* and *Campylaephora*. The above difference is initiated by

the first division of the auxiliary cell to form the primary gonimoblast initial.

9. The diagnostic value of criteria to the determination of genus, subgenus, species, and forma in the genera concerned are discussed in some details.

10. Regarding the relative position of *Ceramium* and *Campylaephora*, the results of the present study show that *Campylaephora* is more highly evolved than *Ceramium*, and that *Hormoceras* evolve from *Crouania*-like, *Mesoceramium* and *Euceramium* from *Hormoceras*-like, and *Campylaephora* from *Mesoceramium*-like ancestors respectively.

Literature Cited

AGARDH, C. A.
1817. Synopsis Algarum Scandinaviae. Lundae.
1824. Systema Algarum. 130–142. Lundae.
1828. Species Algarum. **2** : 138–156. Grifswald.
AGARDH, J. G.
1844. In systemata algarum hodierna adversaria. 19–29. Lundae.
1851. Species Genera et Ordines Algarum. **2** (1) : 113–150.
1894. Analecta Algologica, Contr. II : 3–48. Lundae.
ARDISSONE, Fr.
1871. Revista dei Ceramii della Flora italiana. N. Giorn. bot. it., **3** : 32.
1883. Phycologia Mediterranea, 1, Floridee 98–120. Varese.
BOERGESEN. F.
1918. The Marine Algae of the Danish West Indies. Dansk. Bot. Arkiv., **3** : 241–244. Copenhagen.
BUFFHAM, T. H.
1884. Notes on the Florideae and some newly-found Antheridia. Journ. of the Quekett microscop. Club., **1** : 337. London.
1888. On the reproductive Organs, especially the Antheridia. Ibid., **3** : 237.
1893. On the Antheridia of some Florideae. Ibid., **4** : 183–190.
CHEMIN, E.
1937. Le développement des spores chez les Rhodophycées. Rev. generale de Bot., **49** : 445–448, 478–491. Paris.
CRAMER, C.
1863. Physiologische-systematische Untersuchungen über die Ceramiaceen. Zürlich.
DAMMANN, H.
1932. Beitrag zur Kenntnis der Zentralzellen der Gattung *Ceramium*. Ber. deutsch. bot. Ges., **50** : 68–72. Berlin.
DAWSON, E. Y.
1950. A Review of *Ceramium* along the Pacific Coast of North America with special Reference to its Mexican Representatives. Farlowia, **4** (1) : 113–138.
DERBÈS, P. and SOLIER, A.
1850. Sur les organis reproducteurs des algues. Ann. Sc. Nat., Bot., **14** : Paris.
DERICK, C. M.
1899. Notes on the Development of the Holdfasts of certain Florideae. Bot. Gaz.,

28 : 246–263. Chicago.

DE TONI, J. B.

1903. Sylloge Algarum. 4 (3) : 1443–1504. Patavii.

1924. Ibid. 6 : 504–521, 526. Patavii.

DU RIETZ, G.

* 1930. Studies in the Taxonomy and Ecology of *Ceramium diaphanum* in the Baltic. Bot. Notiser, 433, Lund.

FELDMANN, J. and MAZOYER, G.

1937. Sur la structure et les affinitées du *Ceramium Poeppigianum* GRUNOW (*Reinboldiella Poeppigianum*). Bull. Soc. Hist. Nat. Afrique du Nord, 28 : 213–223.

FELDMANN-MAZOYER, G.

1939. Sur quelque Céramiacées de la rade de Villefranche. Bull. Soc. Bot. de France, 86 : 7–12. Paris.

1940. Recherches sur le Ceramiacées de la Méditerranée Occidentale. Alger.

FOSLIE, M.

* 1893. The Norwegian Forms of *Ceramium*. Norske Vidensk. Selsk. Skrifter. Trondhjem.

GEPP, E. S.

1904. Chinese Marine Algae. Journ. of Bot., 42 : 193–198. London.

GRUBB, V. M.

1925. The male Organs of the Florideae. Journ. Linn. Soc. Bot., 47 (314) : 228–233. London.

HARVEY, W. H.

1849. A Manual of British Marine Algae. ed 2, 161–166. London.

1846–1851. Phycologia Britanica. London.

1853. Nereis Boreali-Americana. 2. Washington.

HAUCK, F.

1885. Die Meeresalgen Deutschlands und Oesterreichs. Rabenhorst's Kryptogamenflora von Deutschland, 2 : 102–115. Leipzig.

HOWE, M. A.

1914. Marine Algae of Peru. Mem. Torrey Bot. Club., 15 : 155–158. New York.

INOH, S.

1944. Sinsei Kôsôrui no hikaku-hasseigakuteki Kenkyu. Igaku to Seibutugaku, 5 : 441–447. Tokyo.

1947. Kaiso no Hassei. Tokyo.

JANCZEWSKI, E.

1876. Notes sur le développement du cystocarpe dans les Floridées. Mem. Sc. nat. de Cherbourg, 20 : 120. Paris.

KILLIAN, K.

1914. Ueber die Entwickelung einiger Florideen. Zeitsch. für Bot. Jahrb. 6 : 221–222. Jena.

KÜTZING, F. T.

1841. Ueber *Ceramium* AG., Linnaea, 15 : 727. Halle.

1843. Phycologia generalis. 378–382. Leipzig.

1845. Phycologia germanica. 289–293. Nordhausen.

1847. Diagnosen und Bemerkungen zu neuen oder kritischen Algen, Bot. Zeit.

5 : 34.

1849. Species Algarum. 674–690. Lipsiae.

1862-1863. Tablulae Phycologicae. **11–13**. Nordhausen.

KYLIN, H.

1907. Studien über die Algenflora der Schwedischen Westküste. 174–187. Upsala.

* 1909. Studien öfver nagra svenska *Ceramium* former. Svensk. Bot. Tidskrift, **3** : Stockholm.

* 1917. Ueber die Keimung der Florideensporen. Arkiv för Botanik, **14** (25) : Stockholm.

1923. Studien über die Entwickelungsgeschichte der Florideen. Vet. Acad. Handl., **63** : 62–63. Stockholm.

1937. Anatomie der Rhodophyceen. Hand. der Pflanzen-anatomie **4** : 261–269. Berlin.

1944. Die Rhodophyceen der Schwedischen Westküste. Lunds Univ. Arsskrift, N. F. Avd. 2, **40** : 64–70.

LEWIS, I. F.

1909. The Life-history of *Griffithsia Bornetiana*. Ann. of Bot., **13** : 639-690. London.

1912. Alternation of Generations in certain Florideae. Bot. Gaz., **53** : 236–242. Chicago.

LYNGBYE, H. Ch.

1819. Tentamen Hydrophytologiae Danicae. 117–122. Hafniae.

MARTENS, G.

1866. Die preussische Expedition nach Ostasien, Bot. Theil. Die Tange, **8** : 117, 120, 124, 130. Berlin.

MAZOYER, G.

1937. Sur la présence du *Ceramium tenerrimum* (MARTENS) OKAMURA sur les cotes nord-africaines. Bull. Soc. d'Hist. nat. Afrique du Nord, **28** : 510–512. Alger.

1938. Sur une nouvelle espéce de *Ceramium* des cotes marocaines : *Ceramium callipterum*. l. c. **29** : 14–18.

1938. Les Céramiées de l'Afrique du Nord. Bull. Soc. d'Hist. nat. Afrique du Nord, **29** : 317–331. Alger.

MENEGHINI, G.

1844. Del genere *Ceramium* e di alcune sue specie. Giorn. bot. ital., **1** : 178, Firenze.

MIRANDA, F.

* 1929. El desarrollo del cistocarpio en una Ceramiaceae (*Ceramium flabelligerum* J. AG.), Bolt. Real Soc. Esp. Hist. Nat. **29** : 47–52. Madrid.

NAKAMURA, Y.

1948. Kôsô-rui no ryôsei Hôsi no Hatuga ni tuite. Kagaku, **18** (10) : 470–471. Tokyo.

1950. New *Ceramiums* and *Campylaephoras* from Japan. Sci. Pap. Inst. Algol. Res., Fac. Sci., Hokkaido Univ., **3** (2) : 155–172. Sapporo.

NEWTON, L.

1931. Handbook of British Seaweeds. 395–403. London.

OKAMURA, K.

1896. Contributions to the Knowledge of the Marine Algae of Japan II. Bot. Mag. Tokyo, **10** : 36.

1901. Illustrations of the Marine Algae of Japan. **1** (4) : 47. Tokyo.

1902. Nippon Sôrui-Meii 1st. ed. 82. Tokyo.

1909–1930. Icones of Japanese Algae. **1–6**. Tokyo.

1914. Igisu no wamei ni tuite. Bot. Mag. Tokyo, **28** : 233

1916. Nippon Sôrui-Meii 2nd. ed. 97. Tokyo.

1922. Report of the Experiments of the Propagation of *Ceramium hypnaeoides*. Journ. Imp. Fisheries Inst., **18** (1) : 45. Tokyo.

1927. On *Campylaephora hypnaeoides* J. AG. Bot. Mag. Tokyo. **41** : 365–368. Tokyo.

1935. *Ceramium rubrum*-rui ni tuite, Bulletin Jap. Soc. Sci. Fisheries, **3** : 302 (Abstract). 735–742. Tokyo.

1936. Nippon Kaisôsi. 736–742. Tokyo.

OLTMANNS, Fr.

1922–1923. Morphologie und Biologie der Algen. Jena.

PAPENFUSS G. F.

1944. Structure and Taxonomy of *Taenioma*, including a Discussion on the Phylogeny of the Ceramiales. Madrono, **7** : 193–214.

PETERSEN, H. E.

1908. Danske Arter af Slaegten *Ceramium* (ROTH) LYNGBYE. Danske Vidensk. Selsk. Skrifter, 7 Raekke, Naturv. og Mathem. Afd., **5** : 41–96. Köbenhavn.

1911. *Ceramium* Studies I and II. Bot. Tidskrift, **31** : 97–120 Köbenhavn.

* 1925. Norwische *Ceramium* Arten. Hyt Mag. for Natur. **63**. Oslo.

* 1928. Nolge Jagttagelser over Cellekerne hos *Ceramium* (ROTH) LYNGBYE, Danske bot. Arkiv. **5** : 1–5. Köbenhavn.

1929. Oversigt over de i det nordvestilige Kattegat forkommende *Ceramium*-Arter. Bot. Tidskrift, **40** : 390–407. Köbenhavn.

PHILLIPS, R. W.

1897. On the Development of the Cystocarps in certain Rhodymeniales I. Ann. of Bot., **11** : 361. London.

RICHARDS, H. H.

1901. *Ceramothamnion Codii*, a new Rhodophyceous Algae. Bull. Torrey Bot. Club, **28** : 257–265. New York.

ROSENVINGE, L. K.

1923–1924. The Marine Algae of Denmark, Mam. Acad. Roy. Sc. et lettres de Danemark. 371–387. Köbenhavn.

ROTH, A. G.

1797–1806. Catalecta botanica quibus plantae novae et minus cognitae describuntur atque illustrantur. 146–156. Leipsiae.

SCHMITZ, Fr. and HAUPTFLEISCH, P.

1897. Rhodophyceae. In ENGLER und PRANTL, Die natürlichen Pflanzenfamilien, **1** (2) : 485, 502. Leipzig.

SCHUSSNIG, Br.

1914. Bemerkungen über die Rotalge *Ceramothamnion adriaticum* SCHILLER. Oesterreich. Bot. Zeitschr., **64** : 85–93. Wien.

SETCHELL, W. A. and GARDNER, N. L.

1930. Marine Algae of the Revillagigedo Islands Expedition in 1925., Proceed. Calif. Acad. of Sci., **19** (11) : 169–174. Sanfrancisco.

1937. The Templeton Crocker Expedition of the California Academy of Science, 1932, A preliminary Report on the Algae. l. c., **22** : 90.

SEGI, T.

1944. Some Marine Algae from Ise Bay and adjacent Waters I. Bot. Mag. Tokyo, 58 : 33. Tokyo.

SINOVA, E. S.

1940, The Algae of the Commander Islands, 121–124.

SJÖSTEDT, L. G.

* 1928. Revision of some dubious Swedish *Ceramium*-types, their Classification and Ecology. Lunds Univ. Arsskrift, N. F. Avd. 2, **23** : Lund.

SVEDELIUS, N.

* 1927 The seasonal alternation of generations of *Ceramium corticatulum* in the Baltic. Nova Acta Soc. Scient. Vol. extra ord. editum. Upsala.

* 1929. The seasonal alternation of generations of *Ceramium corticatulum* : some anticlinal Remarks. Svensk Bot. Tidskrift, **23**. Stockholm.

TOKIDA, J.

1948. Notes on new or little known marine algae 3. Journ. Jap. Bot., **22** : 100–103. Tokyo.

WEBER VAN BOSSE, A.

1923. Liste des algues de Siboga. II Rhodophyceae. 320–335. Leiden.

YAMADA. Y.

1928. Marine Algae of Mutsu Bay and Adjacent Waters II. Sci. Rep. Tohoku Imp. University, Biology, **3** : 497. Sendai.

YENDO, K.

1911. Kaisan-Syokubutugaku. 676–692. Tokyo.

1917. Notes on Algae New to Japan. VI. Bot. Mag. Tokyo, **31** : 92–93. Tokyo.

1918. l. c. VIII. Bot. Mag. Tokyo, **32** : 79–81. Tokyo.

1920. Novae Algae Japonicae Decas I–III. Bot. Mag. Tokyo, **34** : 9. Tokyo.