Systematic Anatomy of the Red Algal Genus *Rhodopeltis*[1]

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AT PRESENT five species are known in the genus *Rhodopeltis*, which belongs to the red algal order, Cryptonemiales. Of these, *Rhodopeltis australis* was first found in Australia, and the other four species, *R. borealis*, *R. setchelliae*, *R. liagoroides*, and *R. gracilis* all grow in the southern islands of Japan and were described by Yamada.

The first description of a species of the genus *Rhodopeltis* was made by Harvey (1859, 1863), when he described a red alga, *Amphiroa australis* Sond., with a tiny red alga, *Rhodopeltis australis* Harv., parasitic on it. This description was accompanied by a beautifully colored illustration. In that illustration, on the heart-shaped segment of *Amphiroa australis*, an elliptical, dense, scarlet-colored part was delineated as a parasitic alga. About this parasitic red alga he said, "I have puzzled where to place the curious little parasite here represented. In the structure of the skin-like frond there is a near agreement with *Cruoria*, so much so that at first I referred it to that genus." *Amphiroa australis*, which was regarded as a host plant by Harvey, had been described by Sonder (1845), and this was followed by Harvey. Kützing (1858) treated this as a new genus different from *Amphiroa*. Weber van Bosse (1904), who agreed with Kützing, made a new genus for it called *Lithartheron*, while Schmitz (1889) published the assertion that *Rhodopeltis australis* is not a parasite but only nemathecia of *Amphiroa australis*, which was taken for a host plant.

Since 1892, when Schmitz mentioned that the genus *Rhodopeltis* contains only one species, *R. australis*, no new species was discovered until 1931, when among specimens collected at Ryūsensui and Kōtōsho, Formosa, one quite similar to *R. australis* but smaller was found

by Yamada (1931). He compared it with Harvey's type specimen, determined that it belonged to the genus *Rhodopeltis*, and named it *R. borealis* Yamada. Later, from specimens collected at Kōtōsho, Formosa, and on Chichi-jima, another was detected which was dissimilar to *R. australis* and *R. borealis* in that it had a quite slender frond and in its structure, which was similar to the subgenus *Eugalaxaura* of the genus *Galaxaura*. This was named *R. gracilis* Yamada et Tanaka (1935).

After that, from the specimens collected in Kasyō-tō of Formosa, a kind having the outermost layer of the frond uncalcified was found and, in memory of Mrs. W. A. Setchell, this was named *R. setchelliae* Yamada (1935a). In *R. borealis* and *R. gracilis*, the reproductive organs were too dubious to fix their relationship, but in this last species the tetrasporangial nemathecia could be seen clearly, and they were characteristic of the genus *Rhodopeltis*. From specimens collected in Nawa and Koshiki-jima another new species, *R. liagoroides* Yamada was described (1935a).

The above-mentioned four species are those which were classified *Rhodopeltis* by Yamada a long time after the exposition of *R. australis* (Harv.) Schmitz. For details, reference should be made to Yamada's publication (1935b). This paper reminds us of the effort and insight needed to get a clear picture of the uncalcified nemathecia, which when not clear is baffling in the determination of species belonging to this genus.

Although Harvey put the genus *Rhodopeltis* into the Squamariaceae, Schmitz put it into Rhizophyllidaceae, and Yamada did likewise. Kylin (1956) separated *Polyides* and *Rhodopeltis* from the Rhizophyllidaceae and put them into a new family, Polyideaceae.

Since the descriptions of the four species by Yamada, there has been no exposition of new species nor any detailed report about the formal characteristics of the genus. Reports of collections, but without descriptions, include

Yamada and Tanaka (1938), Tanaka (1950), Tanaka (1956), and Segawa and Kamura (1960). According to the investigation made by Tanaka, *Rhodopeltis* seems to cover a rather wide area extending from Formosa, to Ryūkū, through the Amami Islands, and to many islands scattered around Kagoshima Prefecture.

As described above, both in its generic peculiarities and in determining the family to which it belongs, the genus *Rhodopeltis* is of great interest. It is especially interesting that this genus is characterized clearly by its distributional area being confined, with the exception only of *R. australis,* to the southwestern islands of Japan. The characteristics of the genus are further clarified by minute examination of the process of nemathecia formation and the manner of development of the reproductive organs. The results thus obtained are expected to offer a clue to determining its position in the classification scheme.

This study was commenced on the advice of Dr. Takesi Tanaka who possesses a great many specimens of *Rhodopeltis.* An additional collection was made by the author in the Amami Islands, Mageshima and others. In addition to these, Dr. Yukio Yamada kindly allowed me to borrow not only the specimens belonging to Hokkaido University, but also the priceless specimen of *R. australis.* Thus I have had an opportunity to examine each of the five known species. The total number of individual specimens examined was 192.

Detailed observations were made of the inner structure of these specimens, with special attention being given to the examination of the reproductive organs, to the clarification of species characteristics, and to a comparative examination of the genus as a whole. Fortunately, through the study of the four species, *R. borealis, R. setchelliae, R. liagoroides,* and *R. gracilis,* the development of the cystocarp and the antheridia was brought out. Therefore, this study of *Rhodopeltis* has contributed to the appraisal of its systematic position.

METHODS

In the study of *Rhodopeltis,* decalcification is necessary. In this process care must be taken not to injure the uncalcified nemathecia. The most common method of decalcification is the use of 2–10 percent hydrochloric acid. There is also another method in which the specimen is fixed in formalin-alcohol and then decalcified with alcohol to which has been added a certain amount of acetic acid. Though the methods of Inoh (1948) for fixation and decalcification of Corallinaceae are good, these methods cannot be used in investigating the development of the cystocarp of *Rhodopeltis* because the nemathecia of this genus are uncalcified.

As a decalcifying fixation medium, then, Perenyi's solution was found to be most favorable. As a staining medium lactic acid with anilin blue is suitable. With materials stained in this medium it is easy to distinguish the vegetative and reproductive cells. As a mounting medium glycerin or malt jelly with antiseptic is suitable.

All the specimens used in this study were dried. Many of them were put fresh into 10 percent formalin seawater immediately after the collection, and then later they were water-washed and stored in the form of dry herbarium specimens.

SYSTEMATIC REVIEW OF THE GENUS *Rhodopeltis*

The genus has been enlarged from time to time without any critical review of its characteristics. The author examined the attributes of each species to facilitate such a review. The

details in reference to each species are given, following the key that may be used to distinguish them, on a practical basis, as the author distinguished them for this project.

KEY TO THE SPECIES OF *Rhodopeltis*

1. Growing points in the terminal notches in tips of the flattened terminal segments; cortical cells round in all 7 to 9 layers 2
    2. Australian .... *R. australis*
    2. Japanese and Philippine .... *R. borealis*
1. Growing points at the tip of the cylindrical tapered terminal segments; cortical cells elliptical in all 4 to 5 layers 3
    3. Surface not zonate .... *R. gracilis*
    3. Surface faintly zonate 4
    4. Lower dichotomies at the basal part complanate and broad .... *R. liagoroides*
    4. Lower dichotomies at the basal part showing cylindrical tendency .... *R. setchelliae*
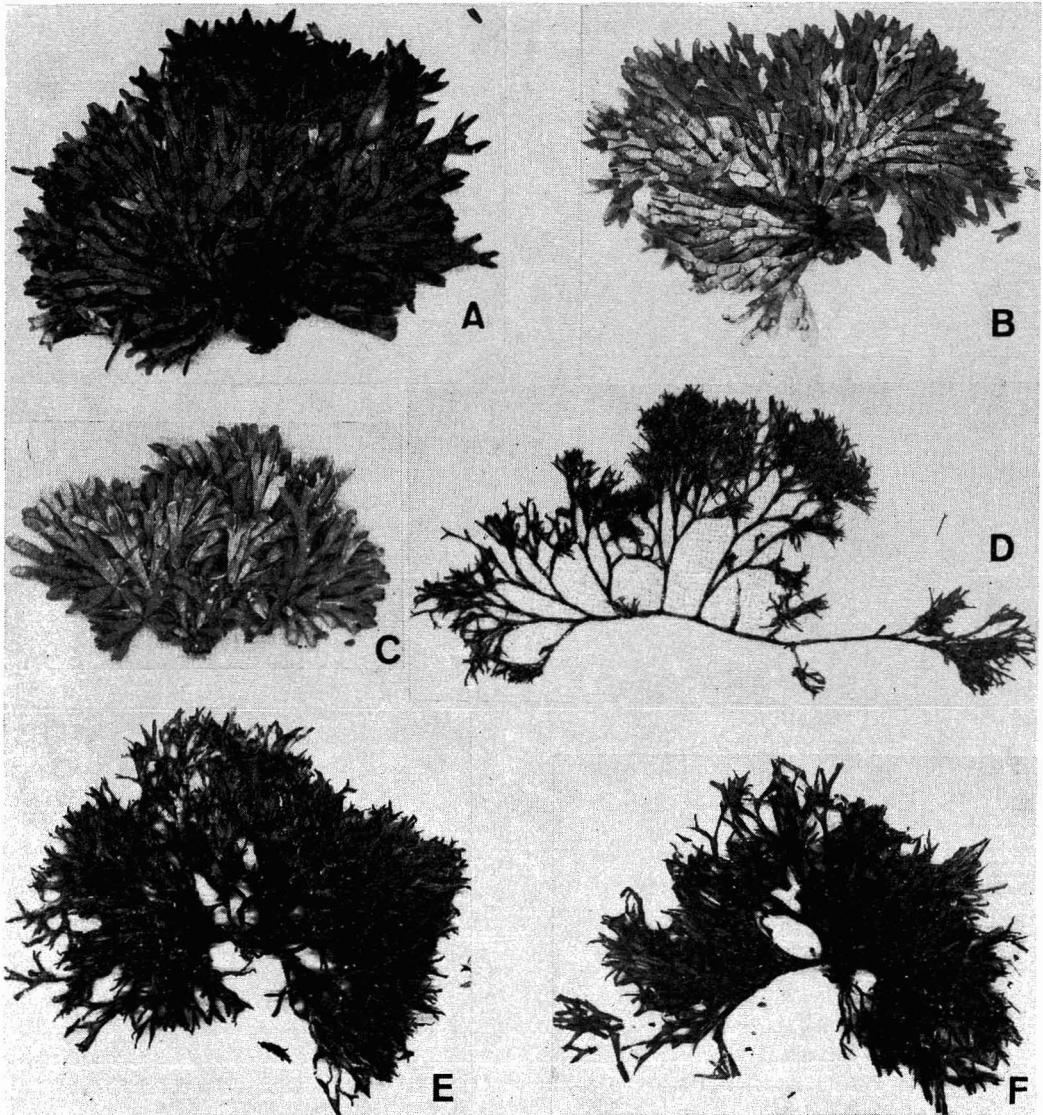

FIG. 1. *A–C, Rhodopeltis borealis* Yam. *A*, Tetrasporophyte (Amami-Ōshima); *B*, female (Amami-Ōshima); *C*, male (Amami-Ōshima). *D–F, Rhodopeltis setchelliae* Yam. *D*, Tetrasporophyte (Nakano-shima); *E*, female (Kasyo-jima); *F*, male (Kasyo-jima).

Rhodopeltis borealis YAMADA

The original description of *Rhodopeltis bore-alis* was made by Yamada from specimens collected at Ryūsensui and Kōtōsho in Formosa, and at Naha in Okinawa (Yamada, 1931). This was followed by the reports made concerning the specimens collected in Yonakuni Jima (Yamada and Tanaka, 1938), Mageshima (Tanaka, 1950), Amami Oshima (Tanaka, 1956), and the Ryūkyū Islands (Segawa and Kamura, 1960). According to further investigations made by Tanaka it seems that this species is widely distributed over the area extending from Formosa, the Ryūkyū Islands, through the Amami Islands, the Tokara Islands, and to Mageshima.

In this study 86 specimens of *R. borealis* were used, all of which were dried (Fig. 1 *A–C*).

Structure of Thallus

OUTER STRUCTURE: Usually the frond is 4–5 cm high, but occasionally some are found which are as large as 7 cm. The frond grows fasciculately from a short stem and branches densely and dichotomously. Each branch consists of an obconical or oval complanate segment which is nearly 500μ thick, 2–3 mm wide, and 4–7 mm long. Branching is repeated regularly from the base of the frond to the top. The size of the segment remains comparatively uniform to the tip. The frond periphery is strongly calcified and smooth. The color is light purplish red. Sometimes orange colored specimens are seen. This is due to the coloring of the carbonate deposited over the periphery. At a branch base, lime is exfoliated, hence this part becomes slightly constricted forming a node (Fig. 2 *C, G*). In some young branches no node formation can be seen. When dried, the thallus becomes very brittle and tends not to adhere to paper. The branchlet is slightly swollen on its surface and, in the dried state, the marginal part is slightly revolute and a dorsiventral tendency can be recognized. The stem is cartilaginous, blackish brown, and cylindrical, and the lower end is turned into a discoid root with irregular margins (Fig. 2 *H*). Irregular branchlets are sometimes produced from the dorsal side of the lower node (Fig. 2 *G*). The tip of the growing

branchlet is uncalcified, shows a blood-red color, and is slightly curved toward the ventral side. In the mature frond nemathecia may be seen on the ventral side of the segment at the tip of the branch. It is not rare for nemathecia to be produced on the ventral side of the second or third segment from the tip. Nemathecia are uncalcified, and so they can be distinguished easily from other parts even with the naked eye (Fig. 2 *C*). They are described in detail in the paragraph treating the reproductive organs.

INNER STRUCTURE: The frond consists of two parts—the medullary layer composed of numerous filamentous cells running longitudinally, and the cortical layer composed of spherical or elliptical cells. The difference between the dorsal side and the ventral side does not appear in the inner structure.

Cortical layer: As seen in a cross section of the frond, a cell-row of the cortical layer consists of 8 to 9 cells and can be divided into outer and inner cortical layers. The cell-rows of the outer cortical layer usually consist of three small cells supplied with assimilatory pigments. Small round cells, 4–5μ in diameter, are arranged in a file in the outermost and sub-outermost layer. The inner cortical layer consists of large cells containing no assimilatory pigments. Those innermost are the largest and are round cells, 40–50μ in diameter, which gradually become smaller toward the outer side (Fig. 2 *A, B, D*). Often many oil-drop-like granules are contained in these cells (Fig. 2 *B, I*). These granules do not stain with anilin blue. A limey precipitation can be observed in all parts of the cortical layer.

Medullary layer: The filamentous cells forming the medullary layer are 4–8μ thick, run longitudinally, and are ramified. The medullary filaments, stretching outward at a right angle, branch several times dichotomously, and the tip of each leads to a row of cortical cells. The connection of the cortical layer cells to the medullary filaments is not obvious except in that portion near the growing point. The ramifying part of the medullary filaments near the cortical layer is enlarged like the node and is stained quite easily with anilin blue. No limey precipitation can be seen in the medullary layer (Fig. 2 *L*).

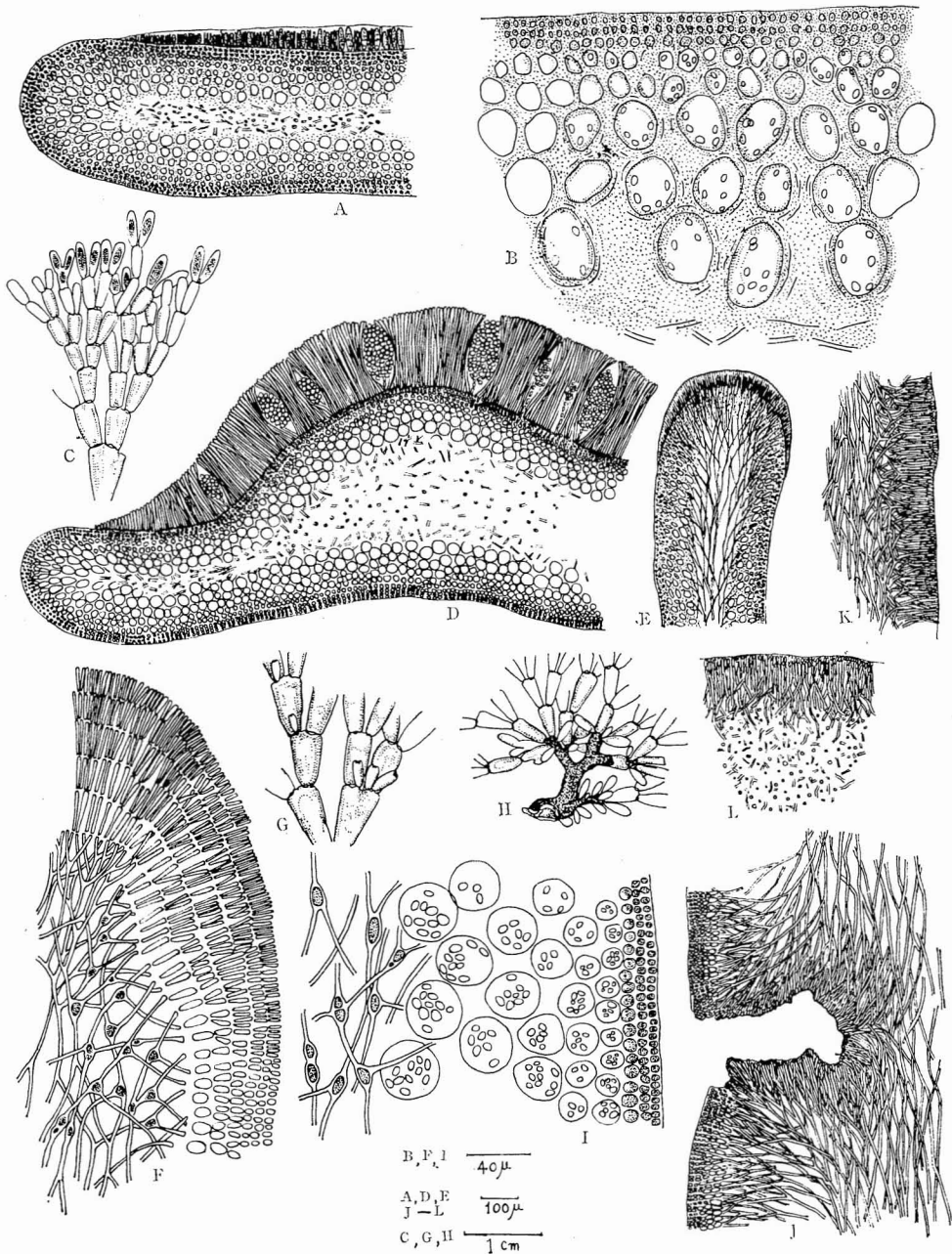*Node*: The node is uncalcified and is com-

FIG. 2. *Rhodopeltis borealis*. *A*, Cross section of the the tetrasporangial nemathecium, before decalcification; *B*, cross section of the cortical layer of the frond, before decalcification; *C*, dorsal side of the branch with carpogonial nemathecia; *D*, cross section of the female branch with a mature carpogonial nemathecium; *E*, longitudinal section of a portion of the vegetative point; *F*, magnified longitudinal section of *E; G*, branchlets proliferating out of the lower segment of the frond, front side; *H*, basal part of the frond; *I*, longitudinal section of the frond; *J*, longitudinal section of the node; *K*, longitudinal section of the root; *L*, cross section of the root.
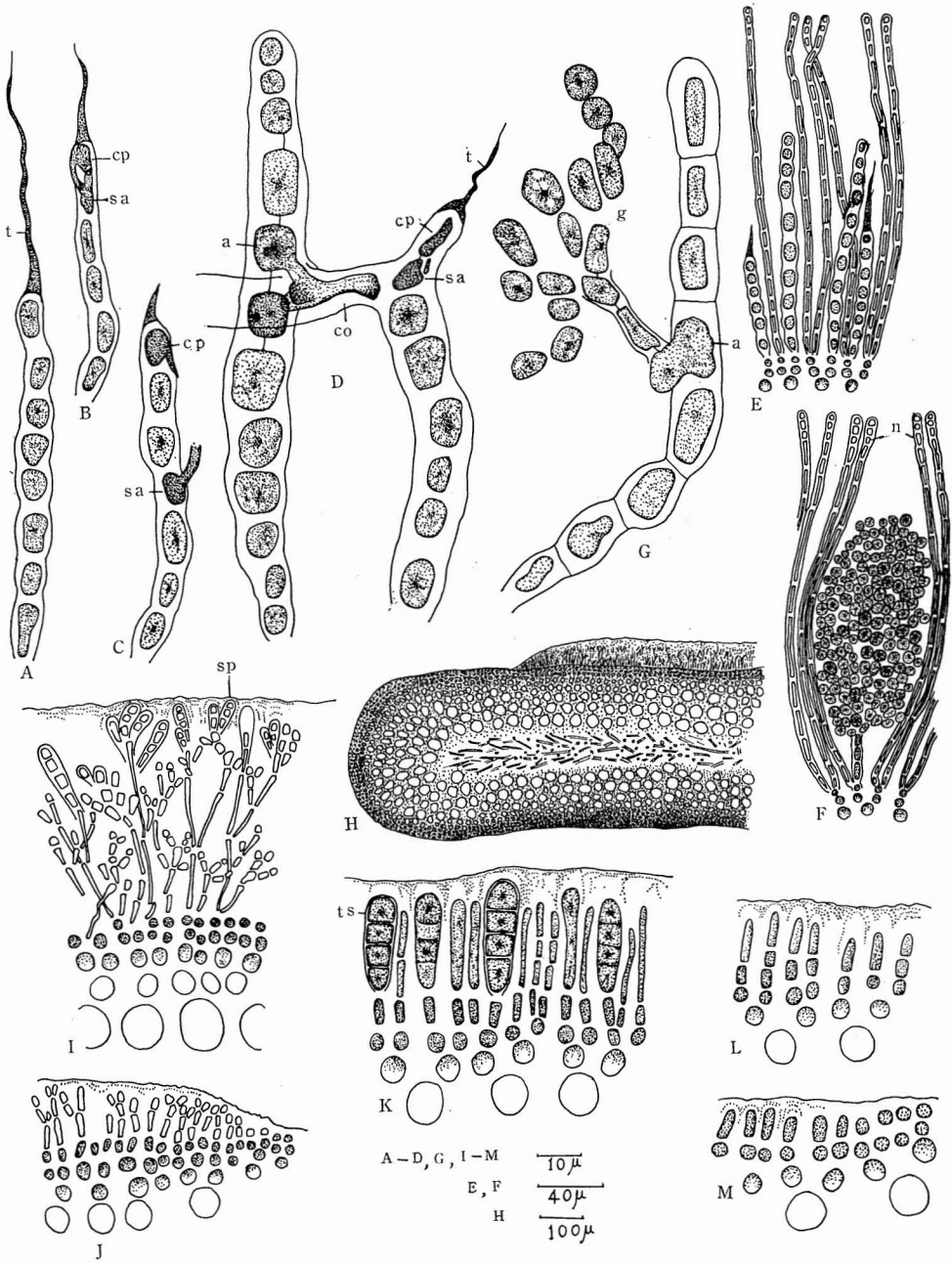
FIG. 3. *Rhodopeltis borealis.* A, Unfertilized carpogonial branch; B, connection between the fertilized car-
pogonium and the adjoining sterile auxiliary cell; C, same as B, the sterile auxiliary cell is the 4th cell in the
carpogonial branch; D, connection between the fertilized carpogonium which fused with the adjoining sterile
auxiliary cell and the auxiliary cell; E, auxiliary cell branches, carpogonial branches, and cell-rows of nema-
thecia; F, mature cystocarp; G, auxiliary cell and gonimoblast; H, cross section of the frond with the sperma-
tangial nemathecium; I, cross section of the spermatangial nemathecium; J, young stage of the spermatangial
nemathecium; K, tetrasporangial nemathecium; L–M, young stage of the tetrasporangial nemathecium.

a, Auxiliary cell; co, connecting filament; cp, carpogonium; g, gonimoblast; n, nemathecial cell-row; sa, sterile
auxiliary cell; sp, spermatangium; t, trichogyne; ts, tetrasporangium.

posed of ramified medullary filaments of small size, forming a compact tissue. At first glance, the node of *Rhodopeltis borealis* resembles the geniculum of *Amphiroa,* but, judging from the inner structure, no special cell arrangement like the one seen in the node of *Amphiroa* is observable (Fig. 2 *J*).

Stem: As in the structure of the node, tough cartilaginous tissue is formed by a large number of medullary filaments running both longitudinally and horizontally in the stem (Fig. 2 *K, L*).

Tip-end: No calcification can be seen near the vegetative (growing) point of the young branchlet, and sections of the dichotomously branching filaments show a typical multiaxial structure. In relation to the distance from the vegetative point, these filamentous cells become gradually spherical, and in forming the cortex there is a simultaneous precipitation of lime (Fig. 2 *E, F*).

Reproductive Organs

DEVELOPMENT OF CYSTOCARP: Carpogonial nemathecia are sometimes about 1.5 × 3–4 mm in diameter and elliptical, and sometimes they are about 2 × 2 mm in diameter and round. They appear on the surface of the frond as reddish brown dots, and are uncalcified. The nemathecia grow out of the ventral side of the segment either at the top of the frond or at the second or third segment of that frond. The nemathecia, however, do not grow from young branchlets or from the branchlets growing from the basal part of the branch. Usually one nemathecium is attached to one segment, but rarely two small nemathecia are seen. Mature nemathecia may be 200μ in diameter and project from the surface (Fig. 2 *D*).

The cell-rows of the nemathecia are produced from the outermost cells of the cortical layer, each cortical cell producing two rows. The cell-row consists of 13 to 15 cells and is not ramified. In the mature cell-rows, the middle cells of each row are elongate and stretched; the terminal cells are round and small, with a thick cell membrane. Both carpogonial and auxiliary cell branches grow interspersed among the nemathecia cell-rows. The carpogonial branch usually consists of 6 to 8 cells, rarely of 5. As in the case of the vegetative cell-rows, the carpo-

gonial branch is derived from the apical cell of the outermost cortical layer. Usually one carpogonial branch is produced from one cell of the outermost cortical layer, but sometimes this is also accompanied by one cell-row of sterile cells. The carpogonial branch stands straight, and the trichogyne grows straight upward, reaching 50–60μ in length (Fig. 3 *A*). The auxiliary cell branch of 9 to 12 cells grows in the same way as the carpogonial branch. Both the carpogonial branch and the auxiliary cell branch are rich in contents, and prior to fertilization both of them can easily be distinguished from the cell-rows of the nemathecia (Fig. 3 *E*). There are far more auxiliary cell branches than carpogonial branches.

After fertilization, the carpogonium fuses with the sterile auxiliary cell (or nutritive cell) of the same carpogonial branch. The sterile auxiliary cell is usually the cell next to the carpogonium but may be the third or fourth cell back from the carpogonium (Fig. 3 *B, C*). Where the cell next to the carpogonium is the sterile auxiliary cell, there is an immediate disappearance of the cell membrane between these two cells (Fig. 3 *D*). Compared with other cells in the carpogonial branch no notable difference can be seen in the sterile auxiliary cell. The carpogonium, after fusing with the sterile auxiliary cell, dispatches a connecting filament toward the auxiliary cell of the auxiliary cell branch. The position of the auxiliary cell is not fixed, but generally it appears in the center of the cell-row, the fourth or fifth cell from the tip. When the connecting filament reaches the auxiliary cell, its tip enlarges, and from this enlarged end a long cell is cut off and fuses with the auxiliary cell, forming a process which extends out of the auxiliary cell-row. From this enlarged fusion cell the several primary gonimoblast cells are separately divided toward the surface (Figs. 3 *D* and 4 *A–F*). Each gonimoblast initial continues to divide and produces a single carpospore terminally (Figs. 3 *G* and 4 *G, H*). Each carpospore is 6–8 × 12–15μ. The cystocarp has no pericarp. Connecting filaments may branch repeatedly, seeking other auxiliary cells. Occasionally a continuation of the connecting filament is seen, presumably to other auxiliary cells (Fig. 4 *A*).
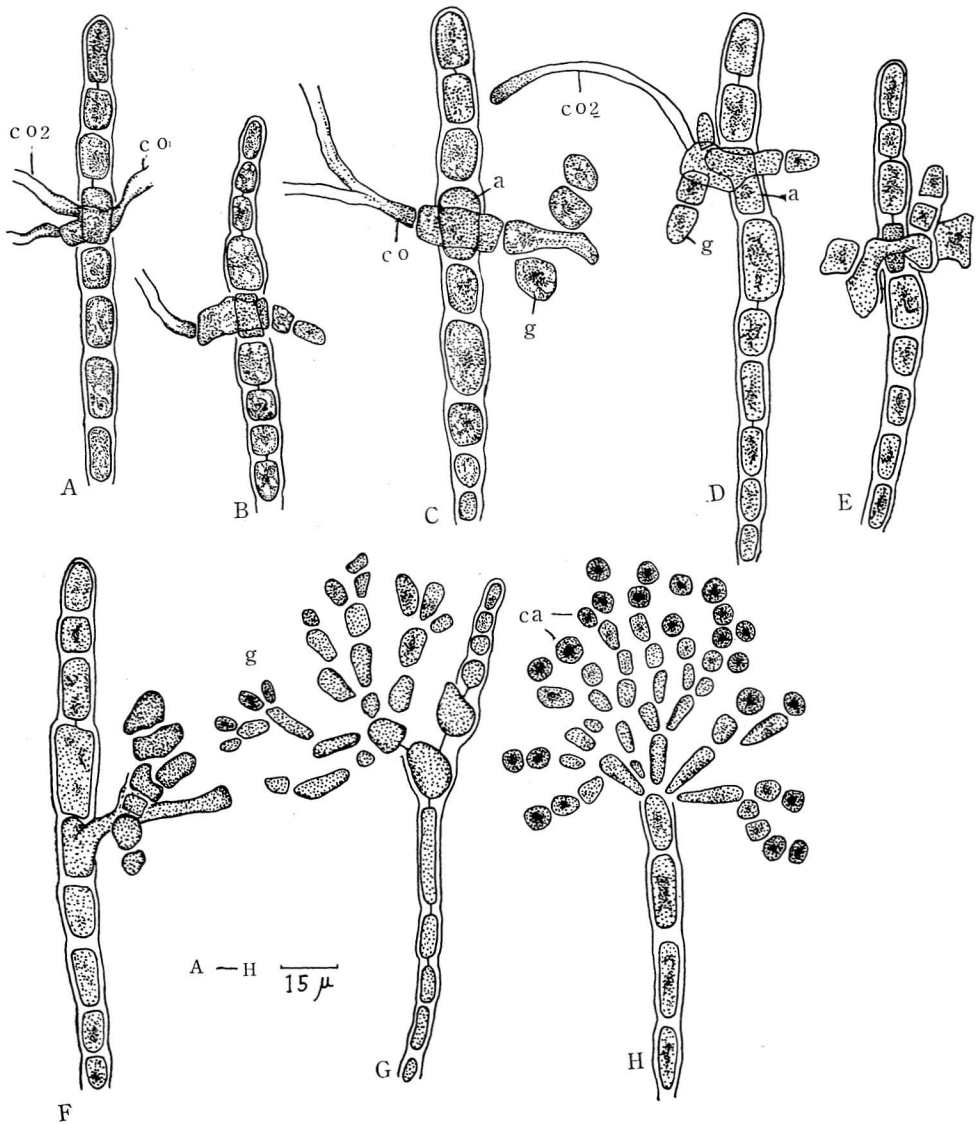
DEVELOPMENT OF SPERMATANGIUM: Sper-

FIG. 4. *Rhodopeltis borealis. A,* auxiliary cell which fused with a first connecting filament and two secondary connecting filaments; *B–F,* young stages of the gonimoblast; *G,* a more advanced stage of *F; H,* gonimoblast producing carpospores.

a, Auxiliary cell; *co,* connecting filament; *co2,* second connecting filament; *ca,* carpospore; *g,* gonimoblast.

matangial nemathecia are 1–2 mm in diameter, elliptical, somewhat smaller than the female nemathecia, 70–100μ thick, uncalcified, and colorless. In the dried specimen its slight luster is the sole clue for distinguishing it from other parts. Nemathecia are produced in a similar way to that of the carpogonial ones (Fig. 3 *H*). The formation of this structure is as follows: Cells

in the outermost periphery of the cortical layer become elongated vertically, and then this is divided into the two parts, upper and lower, by horizontal division. The upper one is uncalcified, and becomes the original cell of a nemathecium. It contains no pigments. After irregular dichotomous divisions, a nemathecium consisting of slender colorless branchlets, with mi-

nutely ramified tip-ends is formed. Several cells in a row at the tip-end of the respective branches become spermatangia. The periphery of nemathecia is covered with the transparent cuticle-like layer, and spermatangia lie buried in the layer (Fig. 3 *I*, *J*).

DEVELOPMENT OF TETRASPORANGIUM: Tetrasporangial nemathecia are nearly 1.5 × 3 mm in diameter, elliptical, and appear at similar locations to those seen in male and female thalli. They are reddish brown in color, uncalcified, and at first glance are barely distinguishable from the carpogonial nemathecia. Tetrasporangial nemathecia are usually 50–60μ, sometimes 70μ, and are far thinner than carpogonial nemathecia (Fig. 2 *A*). They are formed in the following way: At first, the cell in the outermost periphery of the cortical layer assumes an elliptical shape, pointed at its tip-end; then it is divided into two parts by horizontal division. The lower cells remain part of the cortical layer and become calcified, but these cells are somewhat longer than the ordinary frond cells and are arranged in a palisade row. The upper cell is uncalcified, and after stretching out through the cortical layer becomes the original cell of a nemathecium. This is either elongated in accordance with this original shape or forms unbranched cell-rows consisting of 2 to 4 cells. Sometimes two nemathecia-generating cells grow from one outermost cortical cell. The first cell of the nemathecium is directly turned into a tetrasporangium by enlarging, and the contents become rich and zonately divided. A tetrasporangium measures 8–12 × 30μ, and they are arranged in a single row within the nemathecium. The periphery of the nemathecium is covered with a colorless cuticle-like layer (Fig. 3 *L*, *M*).

Rhodopeltis setchelliae YAMADA

A study of *Rhodopeltis setchelliae* was made from specimens collected at Kasyō-tō, Formosa, by Yamada (1935*a*). This was followed by a report of specimens collected in the Ryūkyū Islands (Segawa and Kamura, 1960), and since then a collection of this species was also made at Nakanoshima and Takara Jima in Kagoshima Prefecture. Twenty-two dried specimens were used in this study (Fig. 1 *D–F*).

Structure of Thallus

OUTER STRUCTURE: Some external differences can be seen between the specimens collected at Kasyō-tō in Formosa and at Nakanoshima in Kagoshima Prefecture, but no difference is observed in the internal structure. The specimen collected in Kasyō-tō may be described as follows: Frond 5–7 cm high, from a short stem, branching densely, fasciculately, and dichotomously. Lower branches of the frond complanate, being 1.8–2 mm wide, nearly 5 mm long, about 800μ thick, and at the dichotomies they may be 3–4 mm wide. The branches taper toward their tips, becoming cylindrical, the ultimate branchlets 2–3 mm long with somewhat sharpened apex. In dried specimens the cylindrical branchlets are furrowed longitudinally (Fig. 5 *A*). In the specimen collected in Nakanoshima the basal part of the frond is less densely branched than those collected in Kasyō-tō. Some of these fronds are 10 cm high, and the branching angle at the basal part is wider than in those from Kasyō-tō (Fig. 5 *B*, *C*).

The periphery of the fronds is covered with lime, but the precipitation of lime is not as abundant as in *R. borealis*. The lime is richer in the upper part of the frond than in the lower. The color is scarlet purple. The thalli are brittle and do not adhere to paper. Weak transverse striations can be seen on the surface of the frond. The stem is 1–2 mm long, and nearly 600μ–1 mm in diameter basally, forming an irregular disclike holdfast (Fig. 5 *C*). Nodes are formed irregularly. The growing tips are slightly sharpened, show a somewhat dense color, and are uncalcified. Nemathecia are dark purple and uncalcified and grow at random on the upper branchlets. Details concerning nemathecia are explained in the paragraph describing the reproductive organs.

INNER STRUCTURE: The frond can be divided into the medullary layer consisting of many longitudinal filaments, and the cortical layer consisting of spherical or elliptical cells.

Cortex: The cortical layer is usually composed of 4 to 5 cells and can be roughly divided into an outer layer consisting of small cells containing assimilatory pigments and an inner layer of large cells containing no assimilatory pigments. The outer cortex usually consists of 2
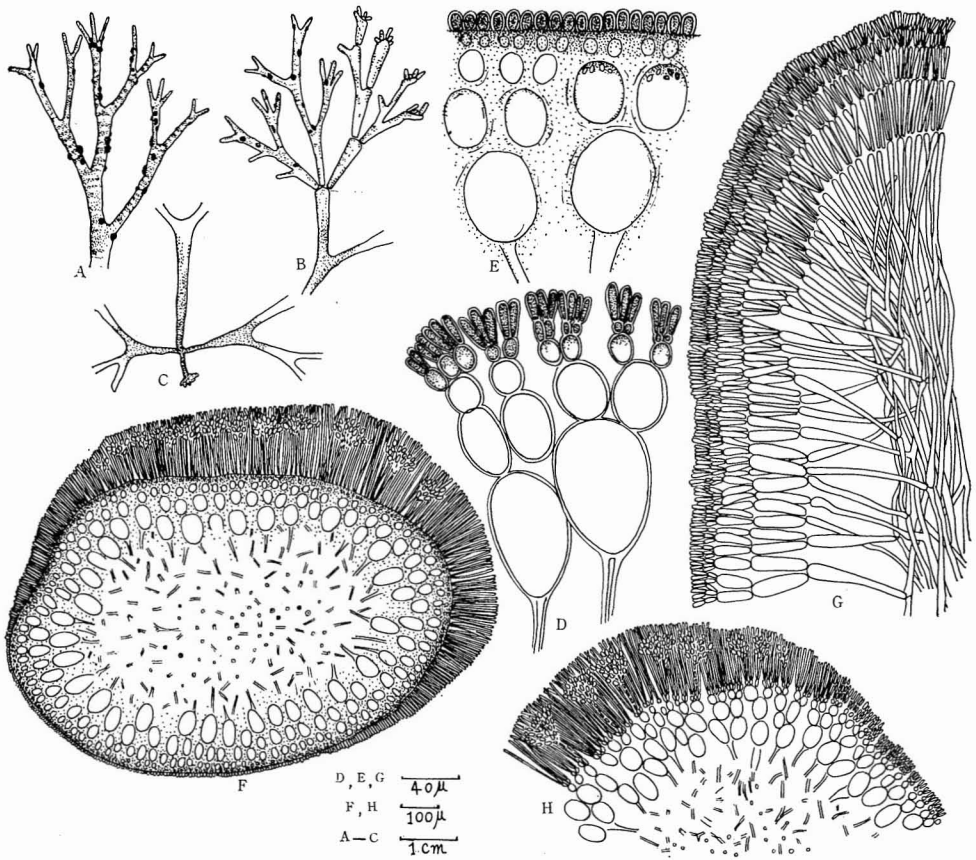
FIG. 5. *Rhodopeltis setchelliae.* *A,* Branch with carpogonial nemathecia; *B,* branch with tetrasporangial nemathecia; *C,* root part of the tetrasporangial frond; *D,* cortical layer cells of the frond; *E,* same as *D,* before decalcification; *F,* cross section of branch with a carpogonial nemathecium, before decalcification; *G,* longitudinal section of the tip-end of a branchlet; *H,* cross section of the carpogonial nemathecium.

cell-rows, the outermost being uncalcified and consisting of oblong, elliptical, or obconical cells $5-6 \times 15\mu$ in size. The cell membrane is thickened and supplied with a lot of assimilatory red pigments (Fig. 5 *E*). The 2 to 3 outermost cortical cells are borne on a layer of calcified cells (Fig. 5 *D*). These calcified cells are of various sizes and shapes, being spherical, with a diameter of 4μ, to elliptical, measuring $10 \times 20\mu$. More abundant assimilatory pigments and lime precipitation can be seen in the smaller spherical cells than in the large elliptical ones. The inner cortical layer consists of 2 to 3 cells, usually 3, the innermost being $50-60 \times 60-80\mu$ and elliptical. The slight transverse striations may be due, perhaps, to the difference in

the cell sizes observable in the calcified outer cortical layer. Lime precipitation decreases toward the center of the inner layer (Fig. 5 *D,* *E, F*) and disappears completely in the medulla.

Medulla: The medullary layer consists of branched filaments, $6-8\mu$ thick, intertwined, and directed periclinally. The medullary filaments branch anticlinally, and the cells assume a different shape as they become part of the cortex. The transition between the medullary filaments and cortical cells is more obvious than in the case of *R. borealis* (Fig. 5 *D, F*).

As in *R. borealis* the node consists of the minute entanglements of medullary filaments.

The growing portion of the young branches
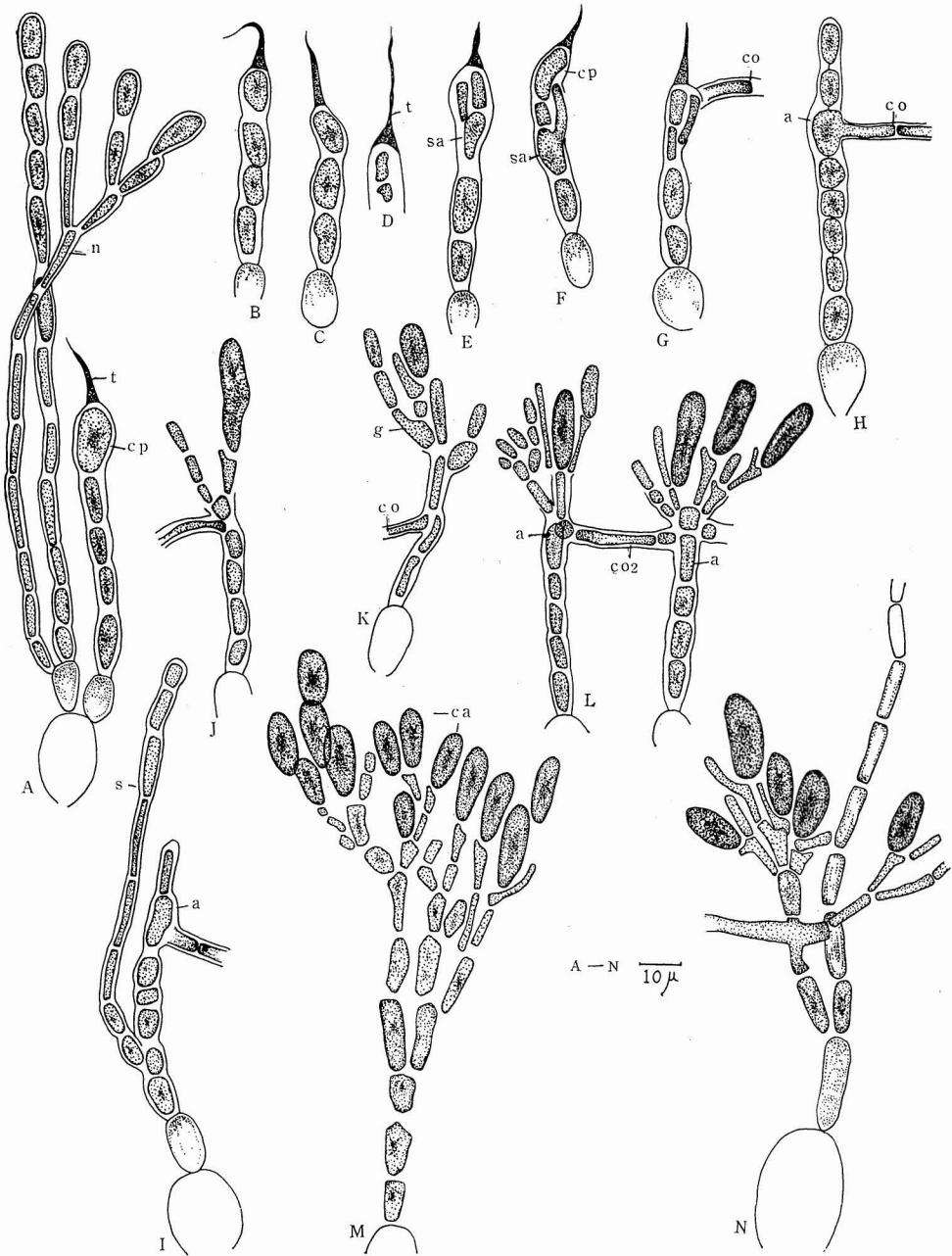
FIG. 6. *Rhodopeltis setchelliae*. *A*, Unfertilized carpogonial branch and nemathecial cell-row; *B*, carpogonial branch consisting of four cells; *C*, carpogonial branch consisting of three cells; *D*, a trichogyne; *E–F*, connection between the carpogonium and the sterile auxiliary cell; *G*, same as *F*, showing formation of the connecting filament; *H*, fusion between the connecting filament and the auxiliary cell; *I*, auxiliary cell-row with a sterile branch; *J–K*, young stage of the gonimoblast; *L*, connection between two auxiliary cells; *M–N*, mature cystocarp.

a, Auxiliary cell; *co*, connecting filament; *co2*, second connecting filament; *cp*, carpogonium; *g*, gonimoblast cell; *n*, nemathecial cell-row; *sa*, sterile auxiliary cell; *t*, trichogyne.

is uncalcified, and the 3- or 4-times dichotomously branched filaments show in section a multiaxial type of construction (Fig. 5 G).

Reproductive Organs

DEVELOPMENT OF CYSTOCARP: Carpogonial nemathecia are 500–800μ in diameter, dark brown, wartlike, and irregular, and grow on the upper part of the frond (Fig. 5 A). The mature nemathecium is 160–200μ thick and uncalcified (Fig. 5 H). Occasionally as many as 20–30 nemathecia are produced on segments 3 cm in length. The cell-rows composing the nemathecia are formed on the calcified outer cortical cells, each cortical cell producing 2 to 3 cell-rows. Each cell-row is composed of nearly 12 cells and the tip is sometimes dichotomously divided. The terminal cell is more or less spherical. The cell-rows of the nemathecia are loosely arranged and each row is separated from the other. They are not as slender as in *R. borealis* (Fig. 6 A). The carpogonial branch is produced terminally on a calcified cell of the outer cortical layer, growing parallel to the nemathecia cell-row (Fig. 6 A). The number of cells in the carpogonial branch is 4 to 5, sometimes 3. The trichogyne stands straight upward, the longest was about 20μ (Fig. 6 D). The auxiliary cell branch, also terminal, consists of 6 to 9 cells. Sometimes a sterile cell-row is found from the basal part of the auxiliary cell branch (Fig. 6 I).

The fertilized carpogonium immediately connects with the sterile auxiliary cell in the same carpogonial branch. It is usually the cell lying next to the carpogonium. The carpogonium, after connecting with the sterile auxiliary cell, produces a connecting filament which grows toward the auxiliary cell (Fig. 6 G). An intercalary cell of the auxiliary cell branch becomes the auxiliary cell. Its content is not exceptionally rich, and before the fusion no distinction can be made from other cells in the auxiliary cell branch. The position of the cell is not fixed; it may be the second, third, or fourth cell from the tip (Fig. 6 H, I). The gonimoblast is produced distally assuming a dendroid shape. Only the terminal cells of the gonimoblast produce carpospores (Fig. 6 J–N). No sterile branchlets are to be found among any gonimoblast branches. Carpospores are oblong-elliptical and measure 4–5 $\times$ 6–20μ. In the mature cystocarp of this species there can be observed no such massive cystocarp as was seen in *R. borealis,* but it consists of 10 to 20 carpospores scattered at the tips of the dendroid gonimoblast. A case was found in which the connecting filament from one auxiliary cell fused directly with an adjacent auxiliary cell and produced a gonimoblast there (Fig. 6 L). In the ripened nemathecia the cystocarps are scattered among the nemathecial cell-rows (Fig. 5 H).

DEVELOPMENT OF SPERMATANGIUM: The male organs may be found on any part of the frond. That is, they form on any surface of the frond from the basal part to the tip-end. Seen with the naked eye, the male frond shows nothing especially characteristic, but it feels rather rough on its surface. The internal structure shows uncalcified layers, 50–60μ in diameter, and containing assimilatory pigments. The cell-rows in this layer are ramified 3 to 4 times and are produced from the outermost cortical cells. The terminal portions of the cell-rows are modified into small spherical colorless cells, 1.0–1.5μ in diameter, which are the spermatangia (Fig. 7 E, G). Often the basal-most cell of these modified portions becomes more or less elongated into a stalk. Spermatangia may be formed singly on these (Fig. 7 F).

DEVELOPMENT OF TETRASPORANGIUM: Externally, both with regard to location and shape, tetrasporangial nemathecia are very similar to the carpogonial nemathecia; this is especially true of dried specimens where one is unable to distinguish the two kinds of thalli (Fig. 5 B). Tetrasporangial nemathecia are nearly 80–160μ thick, and uncalcified. Nemathecial cell-rows consist of those cells which were produced, in 2 to 3 rows, from a single cell of the calcified outer layer. Each row consists of 10 to 15 cells. Among those cell-rows, some are ramified rather compactly from the basal part and are shorter than the ordinary cell-rows of the nemathecia. Tetrasporangia are formed at the tips of these short branches. Some of these branchlets remain sterile and appear to serve a nutritive role as nourishment-cell-rows (Fig. 7 A, B). Each tetrasporangium is 4–8 $\times$ 15–25μ in size, elliptical or oblong obconical. They are
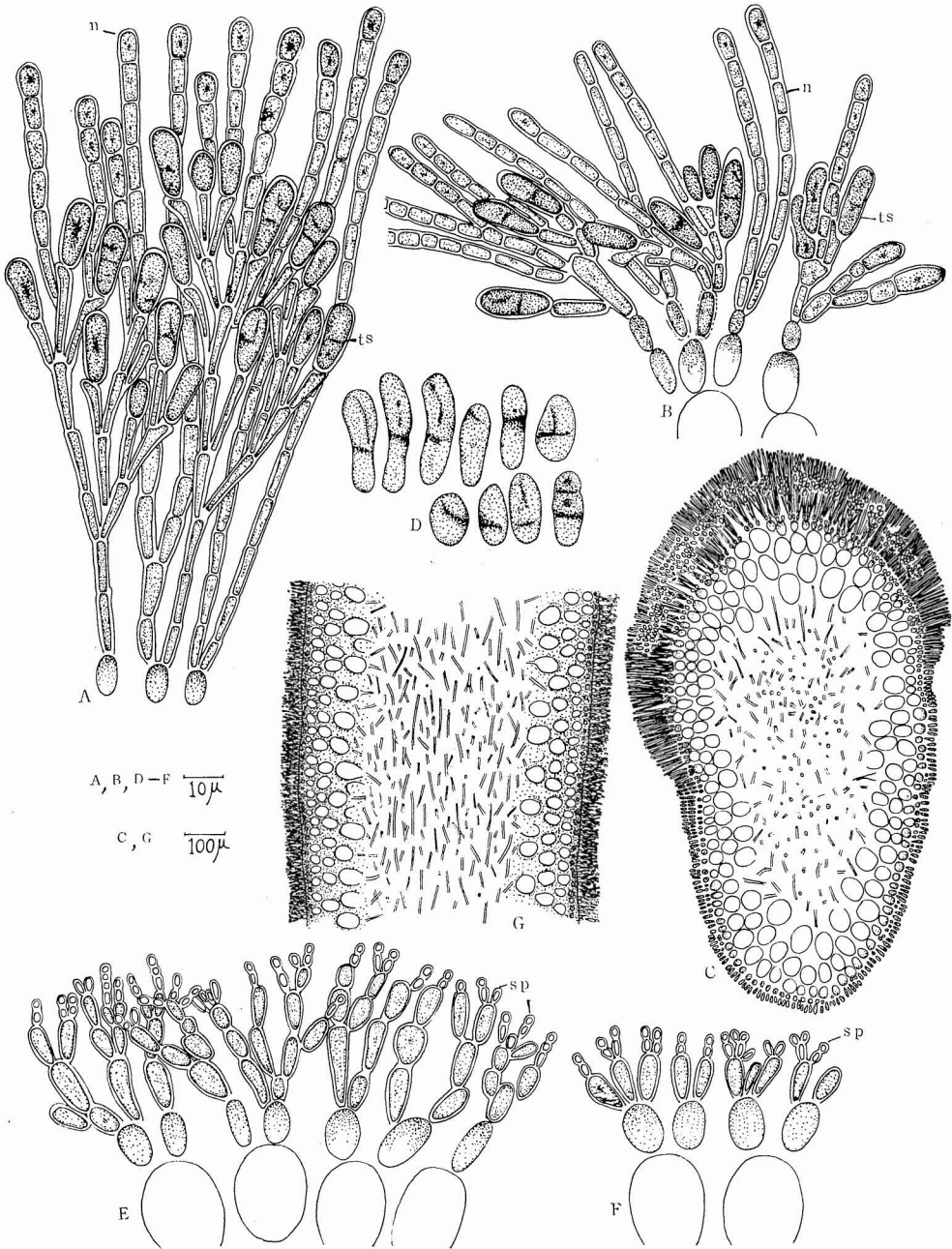
FIG. 7. *Rhodopeltis setchelliae. A,* Mature tetrasporangial nemathecium; *B,* same as *A,* but comparatively short; *C,* cross section of branch with a tetrasporangial nemathecium; *D,* manner of division of the tetrasporangium; *E–F,* spermatangial nemathecia; *G,* longitudinal section of a male frond.

n, Nemathecial cell-row; *sp,* spermatangium; *ts,* tetrasporangium.

irregularly zonately to cruciately divided (Fig. 7 *D*). No cuticle-like layer can be seen on the surface of the nemathecia.

Rhodopeltis liagoroides YAMADA

The description of *Rhodopeltis liagoroides* was made from specimens collected in Naha, Ryūkyū, and Koshiki Jima by Yamada (1935*a*).

Later, more specimens were collected in the Uji Islands and Mageshima. Twenty-nine individual specimens were used in this study, all of them dried (Fig. 8 *A–C*).

Structure of Thallus

OUTER STRUCTURE: Generally the frond is 5–7 cm high, the dichotomous branches arising from a horizontal slender stem. The upper
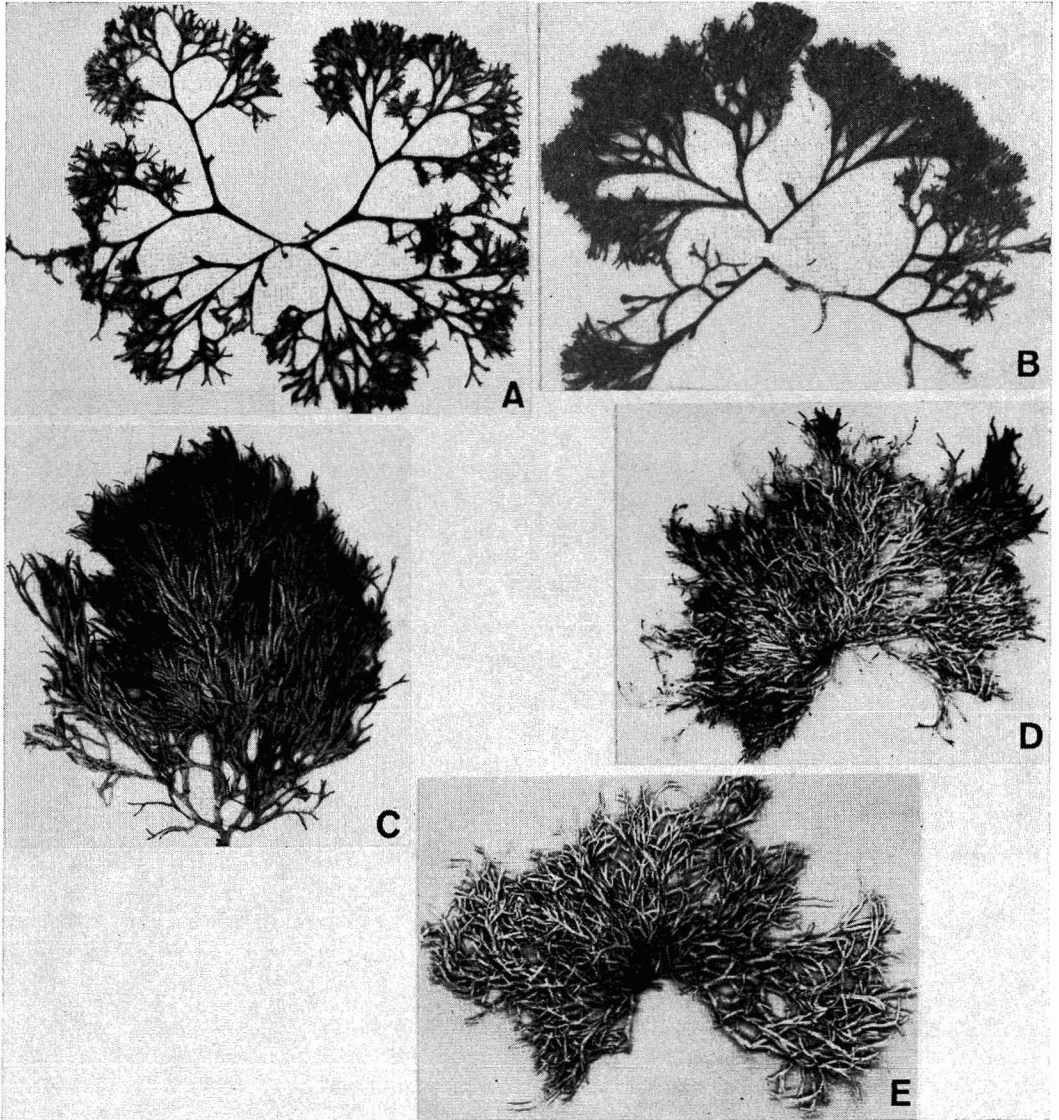

FIG. 8. *A–C, Rhodopeltis liagoroides* Yam. *A,* Tetrasporophyte (Yoron-jima); *B,* female (Mage-shima); *C,* male (Mage-shima). *D–E, Rhodopeltis gracilis* Yamada et Tanaka. *D,* Female (Mage-shima); *E,* male (Mage-shima).
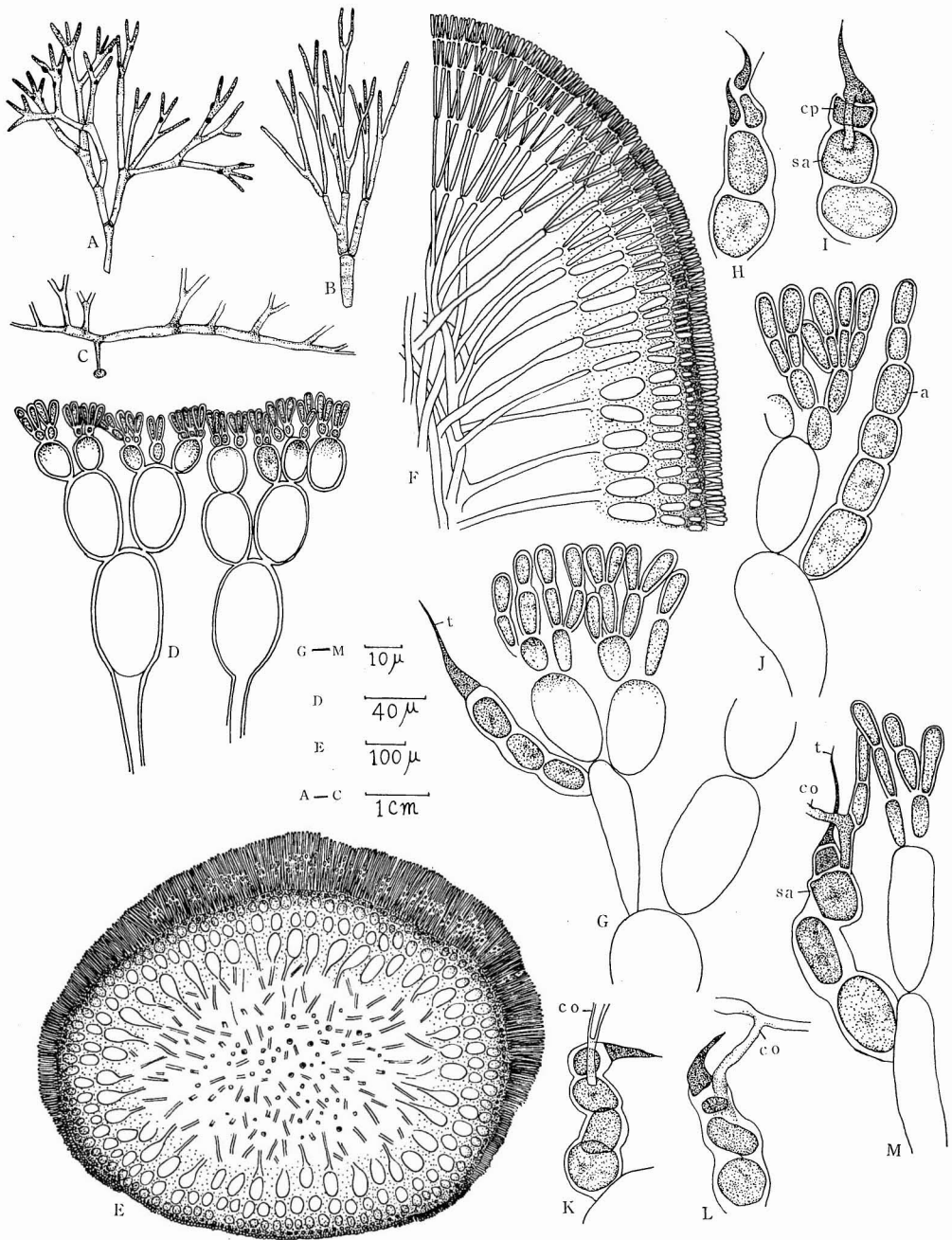
FIG. 9. *Rhodopeltis liagoroides. A*, Branch with carpogonial nemathecia; *B*, male branch; *C*, an example of ramification of the basal part; *D*, cortical layer of frond; *E*, cross section of branch with carpogonial nemathecia, before decalcification; *F*, longitudinal section of tip-end of branchlet; *G*, cortical layer cells with an unfertilized carpogonial branch; *H–I*, connection between fertilized carpogonium and sterile auxiliary cell; *G*, cortical layer cells with auxiliary cell; *K*, formation of connecting filament from sterile auxiliary cell; *L*, a connecting filament which is ramified; *M*, a connecting filament with sterile cell-row.

a, Auxiliary cell; *co*, connecting filament; *cp*, carpogonium; *sa*, sterile auxiliary cell; *t*, trichogyne.

branches are densely fasciculate. Sometimes the first ramification is elongated like a creeping main axis, and branches borne on it are pectinate (Fig. 9 C). The branchlet at the lower part of the frond is 1–2 cm long and 1–2 mm wide, and is flat. The branches taper toward the tips and become cylindrical. The branchlet at the tip-end is 2–3 mm long, about 400–500μ in diameter, and is acute (Fig. 9 A). The periphery is calcified and not smooth. The degree of calcification is slightly different in each individual, but generally the cylindrical branchlet in the upper part of the frond is more calcified. In some specimens the precipitated lime makes it look as if sprinkled with white powder. The growing point of each branchlet is uncalcified. The color of the dried specimens is scarlet purple or reddish brown. In some specimens a slight transverse striation can be observed. The stem is 0.5–2 mm long, nearly 800μ in diameter, and more or less complanate. The holdfast is small, discoid, and nearly 1.5 mm in diameter (Fig. 9 C). Branch segments are irregular in length, and in many cases show a node. Nemathecia are dark brown, uncalcified, and scattered upon the upper branchlets (Fig. 9 A). Details will be described in the paragraph on reproductive organs.

Some specimens collected in Mageshima are somewhat different from others in appearance. These are nearly 10 cm high and comparatively large; the branches at the upper parts of the frond are very densely fasciculate. The branchlets are somewhat longer than those collected from elsewhere, about 5 mm long at the tips and less than 500μ in diameter. Transverse striations can be seen on the surface. There were three such specimens, each of which was male. They were not otherwise different from the ordinary specimens (Fig. 9 B).

INNER STRUCTURE: The frond can be divided into the medullary layer consisting of many longitudinally running filaments, and the cortical layer consisting of spherical to oblong-elliptical cells.

Cortical layer: The cortical layer is usually composed of 4 to 5 cells which can be roughly divided into an outer cortical layer consisting of small cells containing assimilatory pigments, and an inner cortical layer consisting of large

cells containing no assimilatory pigments. The cells of the inner and outer cortical layers grade more gradually into each other than is true of *R. setchelliae*. The outer cortical layer consists of 2 cells, the outer of which is uncalcified, 3–4 × 10μ, and oblong-obconical. The calcified inner cell is spherical and small, 3–4μ or 6μ. The cell-rows of the inner cortical layer are made up of 2 to 3 cells. The innermost cell measures about 40 × 70μ, oblong-elliptical. The cell lying in the outermost side of the inner layer is smaller and of irregular size, covering the range from 6 × 10μ to 20 × 30μ; it is rich in assimilatory pigments. This size relationship is reversed in *R. setchelliae* where the size of the cell lying in the inner side of the outer layer is irregular (Fig. 9 D). Sometimes it appears that the uncalcified cell in the outer layer is divided into two rows, but in many cases this is nothing but a primary stage of nemathecia (Fig. 9 G). The precipitation of lime becomes gradually thinner toward the inner side of the cortical layer (Fig. 9 E).

Medullary layer: The medullary layer consists of longitudinally directed filaments. No lime precipitation can be seen. The filaments are 8–10μ thick and little branched. The axial filaments turn outward to form a cortical layer. In cross section, the medulla, consisting of longitudinally directed filaments surrounded by radially ramifying cortical filaments, can be distinguished comparatively clearly (Fig. 9 E).

The lime-free portions of the segments consist of compact cartilaginous tissue composed of filamentous cells.

The growing tip is uncalcified and shows a multiaxial construction (Fig. 9 F).

Reproductive Organs

DEVELOPMENT OF CYSTOCARP: Carpogonial nemathecia are brown, wartlike, about 500μ in diameter, scattered at the tips of branches, and 120–150μ thick; unripened nemathecia are indistinct to the naked eye (Fig. 9 A, E). In *R. borealis* and *R. setchelliae,* female organs are first formed where nemathecial cell-rows are more or less well developed, but in this species the development of cell-rows of the nemathecia starts after cystocarp formation following fertilization. The carpogonial branch consists usually of 3 cells, rarely of 4. The
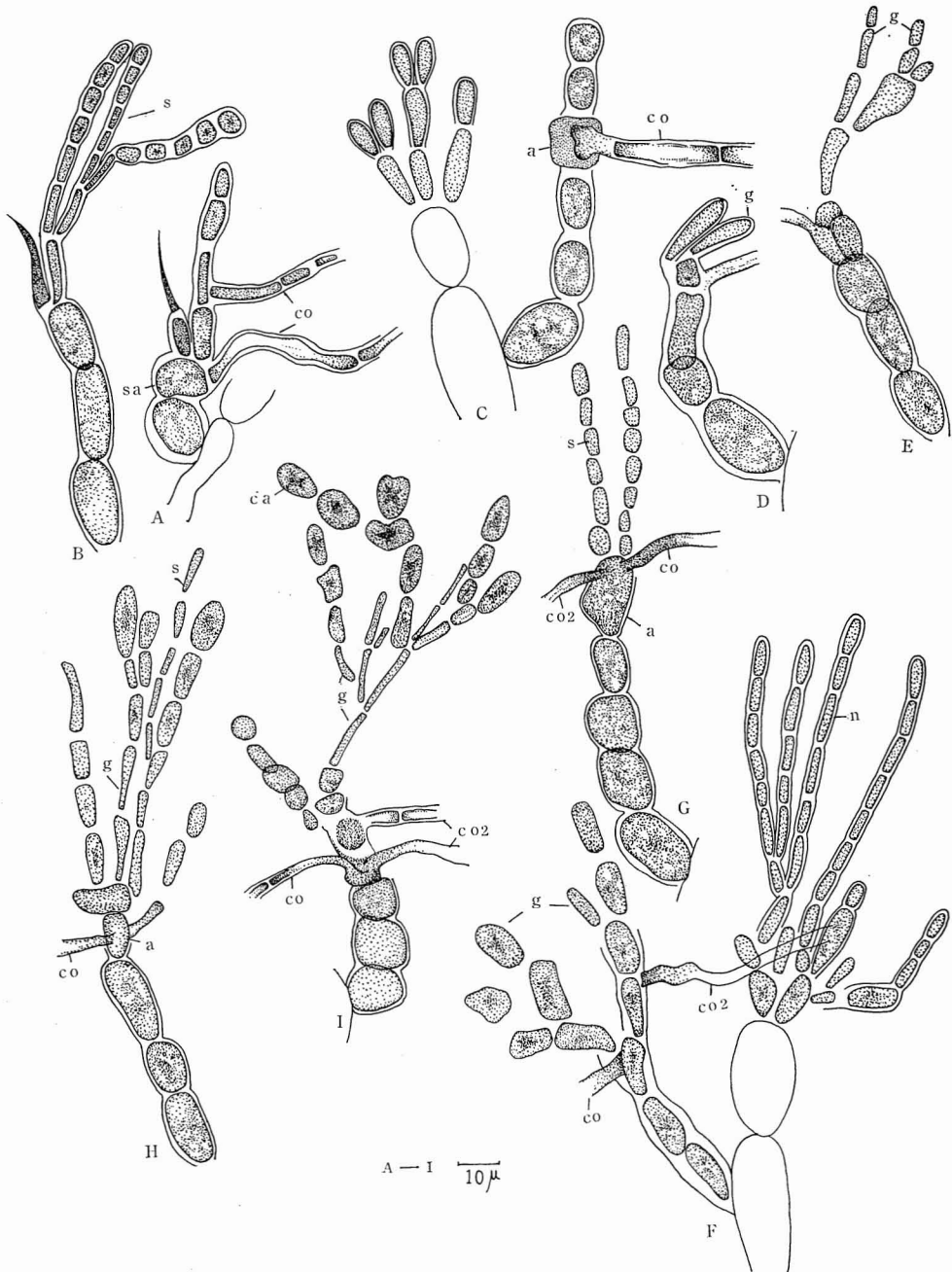
FIG. 10. *Rhodopeltis liagoroides*. A, Forming of two connecting filaments; B, sterile cell-rows produced from the carpogonium without fertilization; C, fusion between auxiliary cell and connecting filament; D–E, young gonimoblast; F–I, gonimoblast and primary and secondary connecting filaments.

a, Auxiliary cell; co, connecting filament; co2, second connecting filament; g, gonimoblast cell; n, nemathecial cell-row; s, sterile cell-row.

place where the carpogonial branch is formed differs markedly from those seen in *R. borealis* or *R. setchelliae*. In the latter two species the carpogonial branch is produced from the cells of the outer layer of the cortex, but in *R. liagoroides* the carpogonial branch is formed from the lateral side of an inner cortical cell (Fig. 9 *G*). The carpogonial branch curves toward the thallus surface with an upright trichogyne, nearly 20μ long. Before fertilization the cell-rows of the nemathecia remain undeveloped (Fig. 9 *G*). The auxiliary-cell branch is also developed laterally on a cell of the inner cortex and consists of 3 or 6 cells. Neither by contents nor by position can the auxiliary cell be distinguished before fertilization (Fig. 9 *J*).

The fertilized carpogonium makes a connection with the sterile auxiliary cell, which is the cell adjoining the carpogonium in the same carpogonial branch (Fig. 9 *H, I*). Usually the sterile auxiliary cell cuts off a nourishment cell-row upward (Fig. 9 *M*), and 1 to 2 connecting filaments are produced directly or from this cell-row, and grow toward auxiliary cells (Figs. 9 *K, L* and 10 *A*). Sterile cell-rows appear to be produced from unfertilized carpogonia at times (Fig. 10 *B*). Connecting filaments pass horizontally through the nemathecia and fuse with the auxiliary cell, which lies near the tip of the auxiliary cell branch. The fused auxiliary cell becomes somewhat swollen and cuts off gonimoblast initials on its distal surface (Fig. 10 *C, D, E*). The gonimoblast consists of irregular treelike cell-rows, and carpospores are produced in short chains at the tips (Fig. 10 *F, H, I*). Gonimoblasts are not so dense as in *R. setchelliae*, and the gonimoblast threads are spreading. In the gonimoblast there are some erect sterile branches. Carpospores are 6–7 × 12–13μ and elliptical.

In many cases an auxiliary cell reached by a connecting filament immediately cuts off another connecting filament toward another auxiliary cell (Fig. 10 *G*). In the mature nemathecium the cell-rows containing nearly 15 cells are mixed with short branchlets consisting of a few cells. The dendroid gonimoblasts are shorter than the cell-rows of the nemathecia, and are buried among them, as are carpospores (Fig. 11 *B*).

DEVELOPMENT OF SPERMATANGIUM: As mentioned above, the male frond shows slight external differences, but in its inner structure there is a loss of one layer of the cortical cells. Male nemathecia may occur anywhere on the whole periphery of the thallus. From a single calcified outer cortical layer, 1 or 2 rows of uncalcified cells are produced. Each row consists of 1 or 2 cells, each cell oblong-obconical, the rows not ramified or dichotomous. At the terminal portions of that layer are formed 2 to 4 rows of colorless small cells, each row consisting of 3 to 4 cells. Those cells lying at the basal part of this row of small cells are somewhat long, but the upper ones are spherical, 0.8–1.0μ in diameter, and they become spermatia. The surface of the spermatangia-producing layer is covered with a cuticular layer (Fig. 11 *F, G, H*).

DEVELOPMENT OF TETRASPORANGIUM: Externally, the tetrasporangial and carpogonial nemathecia resemble each other closely. The nemathecia appear at random on the upper part of the frond. A mature one is nearly 120–150μ thick. Cell-rows of the nemathecia are more orderly than those in the carpogonial nemathecia (Fig. 11 *D*). Each usually unbranched row consists of about 10 cells. Fertile filaments are branched and clustered, and can therefore be distinguished among the nemathecial cell-rows. Tetrasporangia are produced terminally. They are similar in appearance to those of *R. setchelliae*, but each branchlet is comparatively long, and the terminal tetrasporangia lie at the same level as the tips of the nourishment-cell-rows (Fig. 11 *C*). Tetrasporangia are 5–7 × 20–25μ, dividing zonately but irregularly (Fig. 11 *E*).

Rhodopeltis gracilis YAMADA ET TANAKA

The description of *Rhodopeltis gracilis* was made from specimens collected at Kōtōsho (Formosa) and Ogasawara-chichi Jima by Tanaka (1935*a*). Since then, the species has been collected in the Amami Islands (by Tanaka) and Mageshima (by Nozawa). Forty-eight individual specimens were used in this study, all of them dried except those collected in Mageshima (Fig. 8 *D, E*).
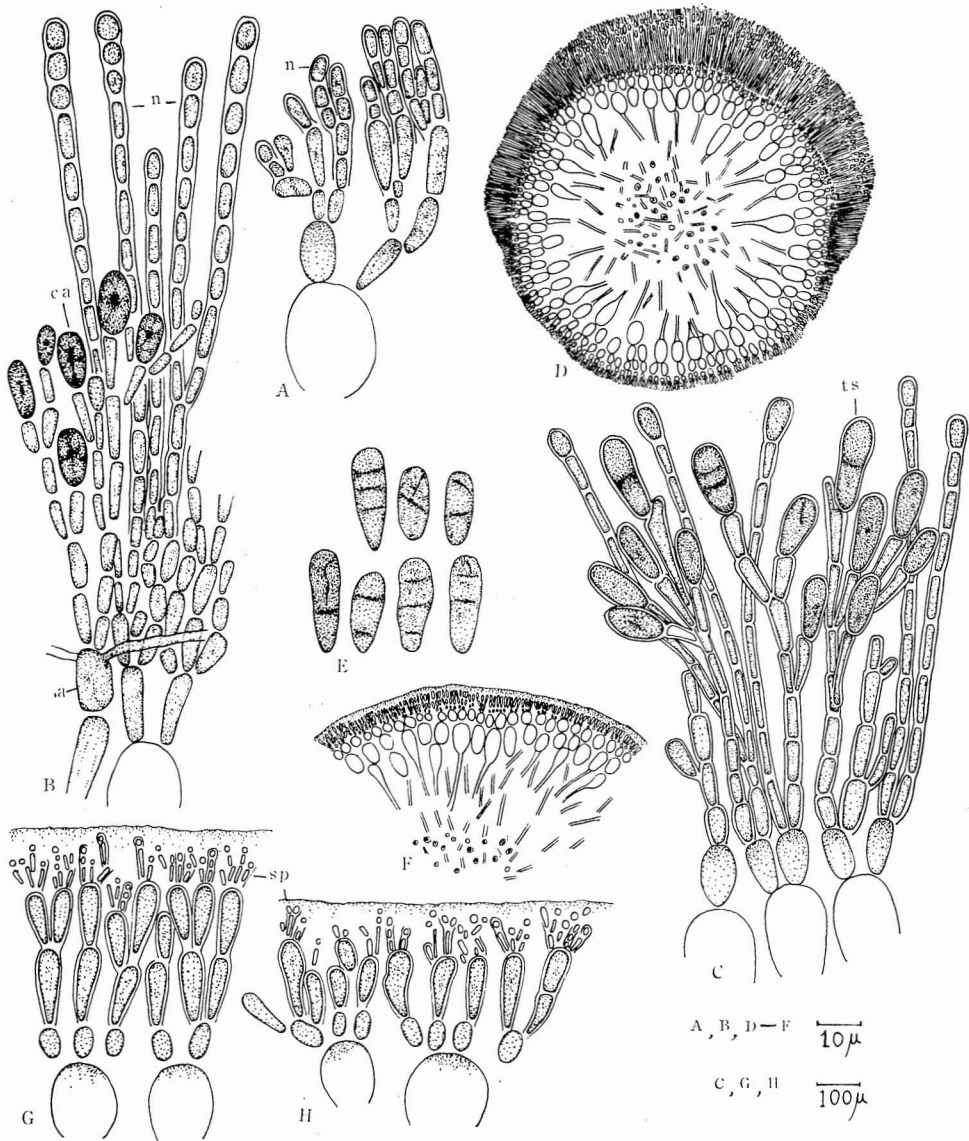
FIG. 11. *Rhodopeltis liagoroides. A,* Primary formation of cell-rows of carpogonial nemathecium; *B,* mature carpogonial nemathecium; *C,* tetrasporangial nemathecium; *D,* cross section of tetrasporangial nemathecium; *E,* manner of division of tetrasporangium; *F–H,* cross section of male branch.

a, Auxiliary cell; *co,* connecting filament; *cp,* carpogonium; *n,* nemathecial cell-row; *s,* sterile cell-row; *sa,* sterile auxiliary cell; *t,* trichogyne.

Structure of Thallus

OUTER STRUCTURE: The frond is usually 5–7 cm high, with dense, fasciculate branches, and a small short stem. The branches at the lower part of the frond are complanate or cylindrical, 800μ–1 mm wide, 300–500μ thick.

The upper part is somewhat complanate to cylindrical with a diameter of nearly 300μ, the tips delicate and acute (Fig. 12 *A*). Branches are dichotomously divided, but the length of the dichotomies is irregular. The peripheral calcification is irregular. Specimens are red-
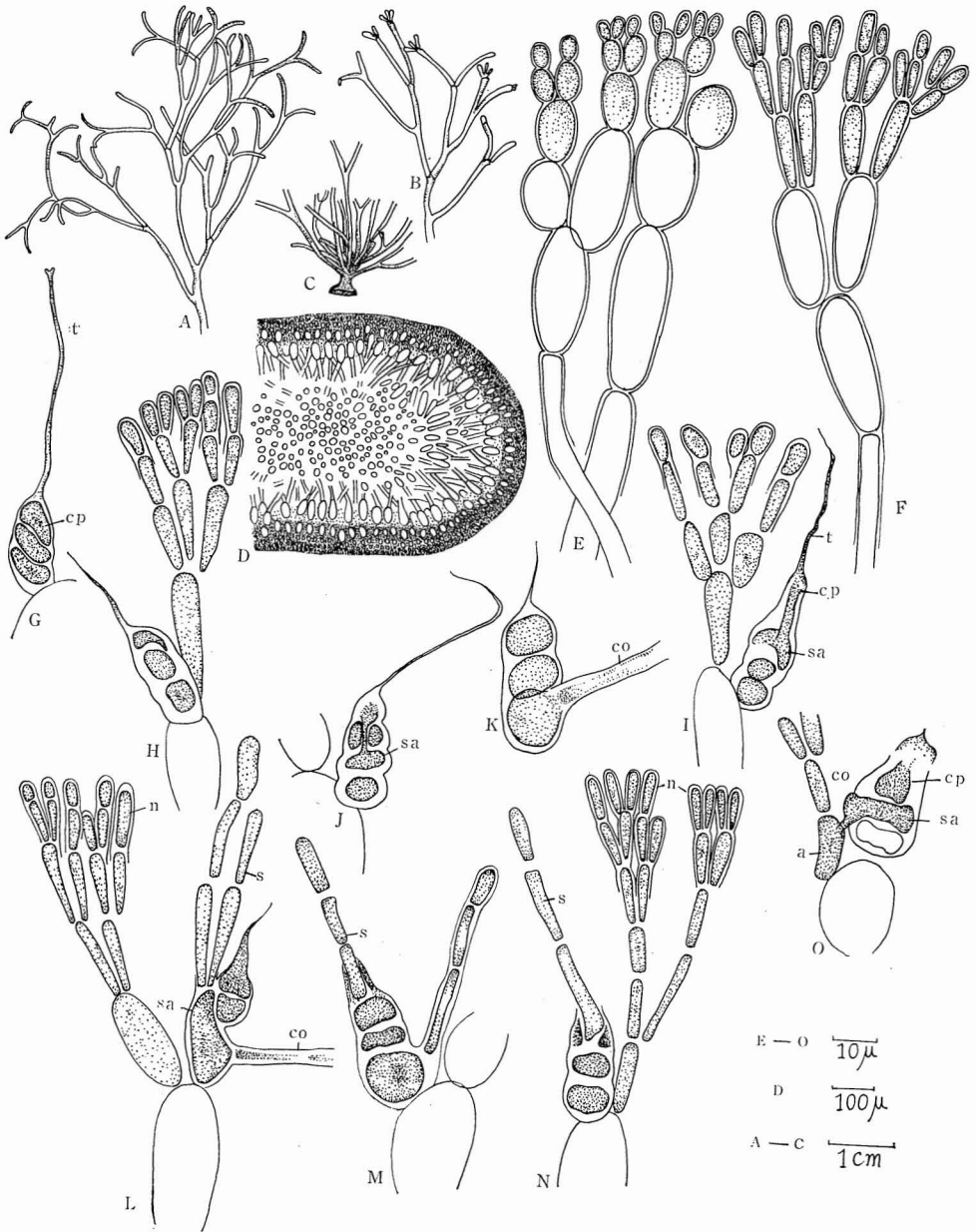
FIG. 12. *Rhodopeltis gracilis*. *A*, Female branch; *B*, male branch; *C*, root part of frond; *D*, cross section of frond, before decalcification; *E*, cortical layer cells and medullary filaments; *F*, same as *E*, tip-end; *G*, unfertilized carpogonial branch; *H–J*, connection between carpogonium and sterile auxiliary cell; *K*, formation of connecting filament from the sterile auxiliary cell; *L*, connecting filament and sterile cell-rows; *M–N*, sterile cell-row being produced from the carpogonial branch; *O*, connection between adjoining auxiliary cell and sterile auxiliary cell.

a, Auxiliary cell; *co*, connecting filament; *cp*, carpogonium; *n*, nemathecial cell-row; *s*, sterile cell-row; *sa*, sterile auxiliary cell; *t*, trichogyne.

dish purple, with the tips of the delicate un-calcified branchlets densely colored. The stem, 4–5 mm long, consists of compact cartilaginous filaments and a discoid holdfast nearly 1.5 mm in diameter (Fig. 12 C).

INNER STRUCTURE: The frond can be di-vided into a medullary layer consisting of the longitudinally running filaments, and a cortical layer consisting of oblong-elliptical cells.

Cortical layer: The cortical layer consists of 4 to 5 cells and usually can be divided into two parts, one consisting of three outer layers containing assimilatory pigments, and the other consisting of two inner layers composed of large cells containing no assimilatory pigments. The outermost cells of the cortical layer are $3–4 \times 4–5\mu$ and elliptical or obconical. The cells in the innermost cortical layer are $12–15 \times 30–40\mu$, oblong-elliptical, and are connected with medullary filaments directly. Lime deposits, $80–100\mu$ thick, are present in the entire cortex, but the largest amounts occur on the outward side of the inner cortical layer. The inner side of this layer of the innermost cortical cells is wholly uncalcified (Fig. 12 D). In proportion as it approaches the tips of the branchlets, the outer cortical layer cell becomes more slender and changes from somewhat clavate to somewhat cylindrical; the lime also becomes thinner (Fig. 12 F).

Medullary layer: Medullary filaments are $8–15\mu$ thick and run longitudinally along the central part of the frond. Medullary filaments in the lower part of the frond are thick, and so in cross section the central medulla looks paren-chymatous (Fig. 12 D).

Cartilaginous portions of segments and stem are composed of the filamentous cells united together compactly.

Reproductive Organs

DEVELOPMENT OF CYSTOCARP: Carpogonial nemathecia are scattered on the upper parts of the uncalcified frond, in the form of specks $60–80\mu$ thick and nearly $160–200\mu$ in diame-ter. Although there are some parts where these specks are gathered compactly, they are not dense enough to distinguish with the naked eye. The branchlet, however, is colored dark brownish, and by means of its uneven surface

the existence of nemathecia can be confirmed (Figs. 12 A and 13 H). In this species, the nemathecial cell-rows remain undeveloped, and only the parts surrounding the carpogonia have rare, irregularly produced nemathecial cell-rows. Moreover, the growth of these nemathe-cial cell-rows gradually accompanies the growth of the cystocarps. Accordingly, there is only one row of cells in the region of the unfer-tilized carpogonial branches. The carpogonial branch usually consists of 3 cells, rarely of 4 or 2 cells, with a prominent trichogyne about 50μ long (Fig. 12 G). The carpogonial branch is produced laterally from a cell lying at the inner side of the cortical layer (Fig. 12 H). Often the carpogonial branch may be produced in a terminal position together with the outer cortical layer cell. The auxiliary cell branch (Fig. 13 A) is also produced from the top of the same inner cortical layer cell and adjacent to the carpogonial branch (Fig. 13 A, B). In this species the auxiliary cell branch is not com-posed of a single row, but is composed of ramifying 3 cell-rows. The auxiliary cell is the basal cell of such a branched filament and occupies the same position as the innermost cell of the outer layer of the cortex. Before fer-tilization no especially rich cell content is to be seen, and so it is almost impossible to dis-tinguish the auxiliary cell branches among the vegetative branches of the cortical outer layer.

Fertilized carpogonia fuse with a sterile auxil-iary cell lying in the same carpogonial branch. The sterile auxiliary cell may be the one adjoin-ing the carpogonium or the lowest cell of the carpogonial branch. Connection is made chiefly through protoplasmic extensions in the carpo-gonial branch (Fig. 12 I, J). The fused cell produces a connecting filament which seeks the adjacent auxiliary cell (Fig. 13 K, L). The connecting filament may be very short if the carpogonium and auxiliary cell are very close (Fig. 12 O). The fused auxiliary cell cuts off a cell rich in contents, which produces a rami-fied gonimoblast bearing terminal carpospores (Fig. 13 A, D). Carpospores are $4 \times 15–20\mu$, oblong-elliptical, and few in number (Fig. 13 A, D, E, F). Because of the shortness of the nemathecial cell-rows, the carpospores are ex-posed to the periphery of the nemathecia (Fig. 13 G). From the primary gonimoblast initial,
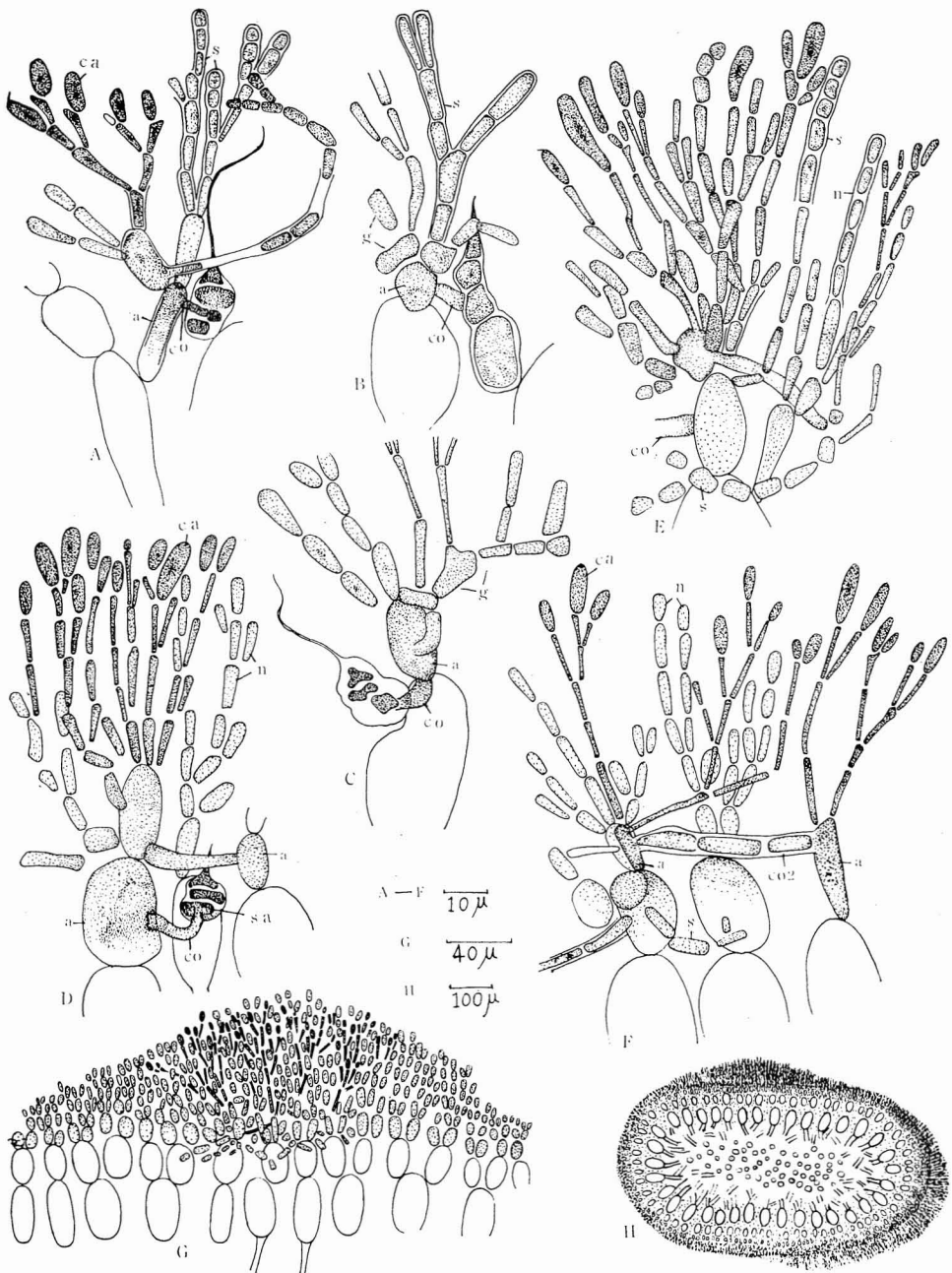
FIG. 13. *Rhodopeltis gracilis*. *A*, Formation of the gonimoblast; *B–D*, same as *A*, showing the additional formation of sterile branches; *E*, same as *A*, showing the sterile branchlet of the gonimoblast produced toward the inner part of the cortical layer; *F*, showing the connection between two auxiliary cells and the relationships with the surrounding cortical layer cells; *G*, mature carpogonial nemathecium; *H*, cross section of branchlet with carpogonial nemathecia, before decalcification.

a, Auxiliary cell; *ca*, carpospore; *co*, connecting filament; *co2*, second connecting filament; *g*, gonimoblast cell; *n*, nemathecial cell-row; *s*, sterile cell-row of gonimoblast; *sa*, sterile auxiliary cell.

a new connecting filament is sent forth toward another auxiliary cell, and another gonimoblast can be seen forming there (Fig. 13 *D, F*). Sterile branches are also produced from the gonimoblast initial. Some of these resemble vegetative cell-rows of the nemathecia and are erect, while others appear to run downward (Fig. 13 *E, F*). The mature nemathecium therefore looks somewhat complicated at first glance, with the downward sterile filaments giving the appearance of the gonimoblasts being parasitic. The production of the sterile cell-rows from the cells of the carpogonial branch irrespective of fertilization was observed in this species (Fig. 12 *L, M, N*), as in *R. liagoroides*.

DEVELOPMENT OF SPERMATANGIUM: No special nemathecia formation can be seen in the male frond, the whole periphery of the terminal tips being involved in spermatangia production (Fig. 12 *B*). Male organs are produced from the cells of the outer cortical layer of these parts, which are composed of 3 to 4 layers and branched somewhat more densely than vegetative cell layers. One to two rows of small cells are produced external to the cortical layer. The small cells are somewhat long at the base of the rows and are supplied with assimilatory pigments, but the ones at the top of the rows are spherical and nearly $0.8-1.0\mu$ in diameter, and these are converted into spermatangial cells. A thin cuticular layer lies over the surface (Fig. 14 *A, B*).

DEVELOPMENT OF TETRASPORANGIUM: In this species no tetrasporangial specimens were obtained. Observations carried out by Inoh (1947) on specimens collected at Chichi Jima in the Ogasawara Islands showed tetrasporangial nemathecia as warts on the segments, oval in outline and producing globelike tetrasporangia $12-14\mu$ in diameter. Detailed information regarding structure is lacking.

Rhodopeltis australis HARVEY

This is the type species of *Rhodopeltis* and the only species of the genus known to occur outside of Japan. Comparative examination of the four Japanese species with this one is therefore very important. The author was fortunate in being allowed by Dr. Yamada to study an authentic specimen of *R. australis*. The specimen used in this study was sent by Dr. H. B. S. Womersley of Adelaide University, and was collected in the drift at Port Eliot, South Australia.

Structure of Thallus

OUTER STRUCTURE: The scarlet calcified segment is complanate; the periphery is smooth and shows a slight dorsiventral tendency. The internode is 5–6 mm long, heart-shaped, with an indented tip and thin winglike margins. The growing point is in the indented part. The incomplete specimen shows a dark brownish, cartilaginous node (Fig. 14 *D*).

INNER STRUCTURE: The frond consists of a medullary layer of longitudinally running filaments and a cortex of variously shaped, radially directed filaments, and is about $500-600\mu$ thick.

Cortical layer: The cortex is nearly $80-200\mu$ thick, with thinner portions lying in the tips and margins. The cortex consists of 7 to 8 layers of cells, and 2 to 3 layers among the outer layers contained assimilatory pigments. They are small, the outermost ones being $3-4\mu$ in diameter. The inner cortical layers are not supplied with assimilatory pigments; the innermost cells are $40-50\mu$ in diameter, approximately round in shape. The inner layer cells contain a lot of oil-drop-like granules similar to those seen in *R. borealis*. In the old segment, calcification is most abundant in the outermost layer and decreases toward the inner layer. But in the case of a young segment which was about 200μ thick, the periphery of the outermost layer was observed to be wholly uncalcified. In *R. borealis*, even the young segments are wholly calcified (Fig. 14 *E*).

Medullary layer: The medullary layer is uncalcified, and medullary filaments are about $3-4\mu$ thick. The filaments branch little. The connection with the cortical layer is not so obvious as in *R. borealis*. The growing point is uncalcified and shows a multiaxial construction (Fig. 14 *F*).

Reproductive Organs

No female or male frond was observed in this species; only tetrasporangial nemathecia
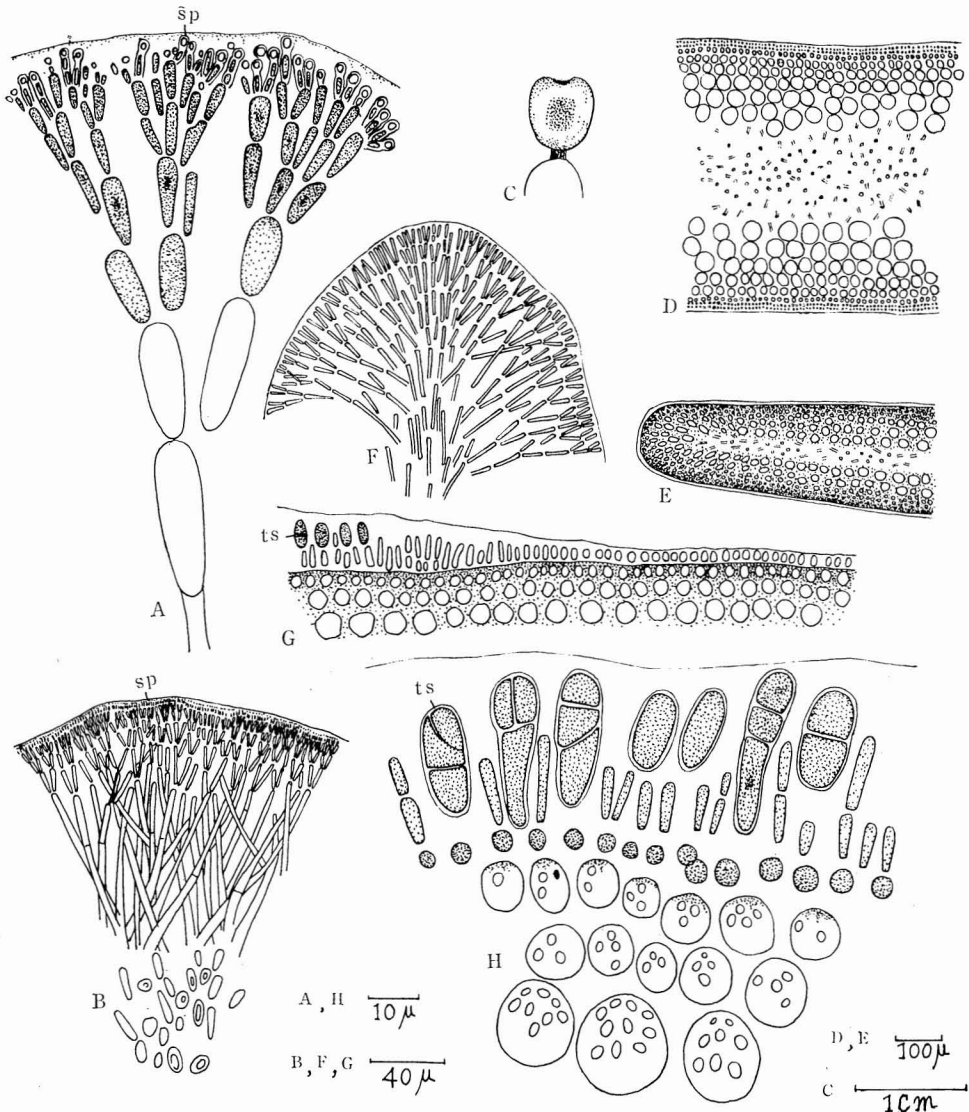
FIG. 14. *A–B, Rhodopeltis gracilis. A,* Cross section of cortical layer of male with spermatangia; *B,* cross section of tip-end part of male with spermatangia.

C–H, Rhodopeltis australis. C, Segment with a tetrasporangial nemathecium; *D,* cross section of frond; *E,* cross section of young segment, before decalcification; *F,* longitudinal section of apical portion; *G,* progressive formation of tetrasporangial nemathecium; *H,* tetrasporangial nemathecium.

sp, Spermatangium; *ts,* tetrasporangium.

were available for study. The tetrasporangial nemathecia lie at the tip of the frond, and are 1.5 × 1.5 mm square, dark brown, and about 40μ thick (Fig. 14 *C*). They are composed of uncalcified outermost cells of the cortical layer, transformed into cell-rows by direct elongation, and of the 2 to 3 cell-rows produced from this transformed layer. The cells lying at the tips of these cell-rows become the tetrasporangium (Fig. 14 *G*). Maturing tetrasporangia are

nearly 8–10 × 20–30μ, and divide irregularly. Some are divided into two by transverse walls and others by oblique walls; others appear to be irregularly cruciate or zonate. In the periphery of the nemathecia there is a cuticle-like layer (Fig. 14 H).

In Harvey's illustrations (1863), only carpogonial nemathecia, similar to those observed in *R. borealis*, are shown. The cystocarp seems to be buried in the nemathecia, and is elliptical or round; the gonimoblast is composed of brushlike filaments grouped together, and spreading radially from a central axis.

GENERAL CONCLUSIONS

The common characteristics of *Rhodopeltis* and the differences between the species are summarized as follows:

Distribution

All the species of *Rhodopeltis* from Japan are calcareous algae growing in tropical and subtropical zones. With the exception of *R. australis* from Australia, all are found in the southern islands of Kagoshima Prefecture, Chichi Jima of the Ogasawara (Bonin) Islands, the Amami Islands, the Ryūkyū Islands, and Formosa.

Outer Structure

The height of the fronds of all species except *R. australis* lies within the range of 4–10 cm, and all are branched dichotomously from a short erect stem, forming fasciculately shaped thalli. Observations on *R. australis* were confined to a frond segment. All the species belonging to this genus contain greater or smaller quantities of lime.

The branches are generally composed of segments, but within species there are two groups: one in which the node is conspicuous by its cartilaginous material, and the other in which nodes are scarcely noticeable. The formation of nodes in *Rhodopeltis* is brought about by secondary development of the medullary filaments exposed by the loss of lime in the cortical layer, and it seems that the structure of the node varies in accordance with the degree of precipitation of lime and with the variations in the shape of the segments. Clear segmenta-

tion, making the plants resemble *Amphiroa* (Corallinaceae), is shown by the specimens of *R. australis* and *R. borealis*. In the other species, segmentation is not as conspicuous as in these two species. However, a slight difference can be detected between segmentation in *R. setchelliae* and *R. liagoroides* where a considerable number of nodes can be seen, and in *R. gracilis* where very few are seen. *R. australis* and *R. borealis* segments are complanate and wide and heart- or oval-shaped, but in the other species they are complanate or cylindrical with slender branchlets.

In the four species growing around Japan, the holdfast is discoid and composed of cartilaginous material. In *R. australis* the holdfast is also assumed to be discoid, judging from the illustration of *Amphiroa australis* by Harvey. In *R. borealis* the holdfast is well developed and the species may be collected almost throughout the whole year, which suggests that it is perennial. In *R. gracilis* the holdfast is quite tough, even though the frond is delicate.

In these five species the vicinity of the growing point at the tips of the branchlets is uncalcified and is a deeper color than other vegetative parts. In *R. australis* and *R. borealis* the growing point lies in an indentation of the terminal segment. In others, the growing point lies at the pointed tip of the cylindrical branchlet.

Inner Structure

In the growing point of all of these species, the formation of filaments appears to be the same.

The inner structure of the ordinary frond can be divided into two parts: the cortex consisting of round or elliptical cells, and the medulla consisting of the longitudinal filaments. Lime precipitation is seen only in the cortical cells. These cortical cells are connected with the longitudinally running medullary filaments at right angles. At and around the growing point, the formation of the cortical layer can be clearly observed. The cortex can be divided into an outer layer consisting of small cells containing assimilatory pigments, and an inner layer consisting of cells enlarged toward the inner side. A comparative examination of

TABLE 1

CHARACTER COMPARED	R. australis	R. borealis	R. setchelliae	R. liagoroides	R. gracilis
Number of Cells in Cortical Layer	(7)*–8	(8)–9	4–(5)	4–(5)	4–(5)
Cells in Outer Layer of Cortical Layer	3	3	2	2	3
Cells in Inner Layer of Cortical Layer	4	5	3	3	2
Thickness of Cortical Layer	80–200μ	Nearly 200μ	160–200μ	160–200μ	80–100μ
Size and Shape of Cells in Outer Cortical Layer	3–4μ Round	4–5μ Round	5–6 × 15μ Oblong obconical, oblong elliptical	3–4 × 10μ Oblong obconical, oblong elliptical	3–4 × 4–5μ Obconical, elliptical
Size and Shape of Cells in Inner Cortical Layer	40–50μ in diam. Round	40–50μ in diam. Round or elliptical	50–60 × 60–80μ Elliptical	Nearly 40 × 70μ Oblong elliptical	12–15 × 30–40μ Oblong elliptical
Thickness of Medullary Filament	3–4μ	4–8μ	6–8μ	8–10μ	8–15μ
Lime Precipitation	From cortical layer periphery; in young branch one layer of outer layers is uncalcified	From periphery of cortical layer	The outermost layer is uncalcified	The outermost layer is uncalcified	From periphery; the exposure of outer layer increases toward upper part
Connection of Cortical Layer with Medullary Filament	Doubtful	Doubtful	Less doubtful	Less doubtful	Connected clearly
Cells of Irregular Size	None	None	Secondary cells in the outer layer irregular in size	Cells in outer part of cortical layer irregular in size	Some tendency toward irregular cell size
Size of Cells			Diam. 4–10 × 20μ	6 × 10–20 × 30μ	

* Numbers most usually found are shown in parentheses.

the cortex in regard to the number, shape and size of cells, lime precipitation, connection with medullary filaments, and thickness of the filament, is summarized in Table 1.

As seen from this table, *Rhodopeltis* can be divided into two groups according to the inner structure. Those belonging to one group are *R. australis* and *R. borealis,* in both of which the cortical cells are all round, and there are 7 to 9 layers of cells. In the other three species, forming a second group, almost all of the cortical cells are elliptical in shape, and occur in 4 or 5 layers.

There is also a distinct difference in the medullary filaments: in the first group the medullary filaments are slender and much ramified, and are not very clearly connected with the cortical layer; in the second group, the medullary filaments are thicker and less ramified, and the connection with the cortical layer is clear.

With regard to lime precipitation, generally speaking, in the first group calcification begins from the outermost layer, while in the second group the outermost layer remains uncalcified and is exposed. The distinctions in the first group are not, however, so sharp, for the younger segments of *R. australis* have an uncalcified outermost layer, and in the second group, although the mature frond of *R. gracilis* is calcified all over, in the younger branches an irregular exposure of the outermost layer can easily be seen. In short, lime precipitation shows intermediate types.

R. gracilis exhibits unusually thick medullary filaments, and in cross section of the lower part of the frond, they sometimes look like parenchyma. No other species show this. In addition, those in the second group show some slight transverse striations over the periphery. In these specimens some notable irregularities in the size of the inner cells of the outer layer of the cortex and in the cells of the outer layer of the inner cortex can be detected. In these cells of irregular size, the quantity of the assimilatory pigments varies also. The formation of the transverse striations observable from the surface may be due to the slight unevenness of lime precipitation caused by the existence of these irregularly sized cells. Other inner structural differences cannot be seen in the regions of transverse striations.

Reproductive Organs

The reproductive organs of *Rhodopeltis* are formed in nemathecia or distributed in the uncalcified layer of the periphery of the frond. The reproductive organs occur in carpogonial, spermatangial, and tetrasporangial groups.

FEMALE ORGANS: In *Rhodopeltis* carpogonial and auxiliary cell branches are two separate branches formed from the outer cortical cells. Carpogonial branches are straight, as are trichogynes, the latter never spiraling as is common in many other Cryptonemiales. The fertilized carpogonium first makes a connection with the sterile auxiliary cell in the same carpogonial branch, and from there, by means of a connective filament, it makes contact with an intercalary auxiliary cell in the auxiliary cell branch. The fused cells produce a gonimoblast. Gonimoblast filaments are ramified umbellate or dendroid, and carpospores are formed at the ends of the filaments except in *R. borealis* where they are in chains. Sterile branches may or may not occur in the gonimoblasts. The mature cystocarp is elliptical or oval in shape, or it is simply a thickly branched gonimoblast which has scattered carpospores. They lie buried in the cell-rows of the nemathecia, and are not covered with a pericarp. Comparative examination results obtained from observations of the female organ of each species are summarized in Table 2.

As may be seen from this table, admitting a slight difference in detail, these species may be divided into two groups based on the shape of the mature cystocarp. The first group consists of those species in which the cystocarp is umbellate—*R. australis* and *R. borealis.* All cells of the cystocarp except for those at the basal part of the gonimoblast become carpospores. The second group consists of those in which carpospore production can be seen only at the tip-end of the dendroid gonimoblast; *R. setchelliae, R. liagoroides,* and *R. gracilis* belong to this group.

Furthermore, these species can also be divided into two groups depending on the location of the carpogonial branch. In the case

TABLE 2

CHARACTER COMPARED	R. australis	R. borealis	R. setchelliae	R. liagoroides	R. gracilis
Number of Carpogonial Branch Cells		6–8	4–5, rarely 3	3, rarely 4	3, rarely 4 or 2
Length of Trichogyne		50–60μ	20μ	20μ	50μ
Number of Cells in Auxiliary Cell Branch		9–12	6–9	3–6	3 cell-rows, ramified in same manner as outer cortical layer cells
Position of the Sterile Auxiliary Cell in the Carpogonial Branch		Adjacent to cell of carpogonium	Adjacent to cell of carpogonium	Adjacent to cell of carpogonium	Adjacent to cell of carpogonium
Position of the Auxiliary Cell in the Auxiliary Cell Branch		Intercalary, central part	Intercalary, central part	Intercalary, tip-end	Intercalary or basal, lower part
Shape of Gonimoblast		Umbellate	Dendroid	Dendroid	Dendroid
Shape of the Mature Cystocarp	Long, elliptical, massive	Long, elliptical, massive	Small, spreading, fan-shaped	Same as R. setchelliae	Same as R. setchelliae
Presence of Sterile Branch in Gonimoblast		None	None	Present in upper part only	Present in upper part and stretching downward
Size of Carpospore		6–8 × 12–15μ	4–5 × 16–20μ	6–7 × 12–13μ	4 × 15–20μ
Size of Carpogonial Nemathecia		1.5 × 3–4mm	500–800μ in diam.	nearly 500μ in diam.	160–200μ in diam.
Thickness of Carpogonial Nemathecia		nearly 200μ	160–200μ	120–150μ	nearly 60μ
Number of Cells in Nemathecial Cell-Row		13–15, unramified	12–13, twice dichotomous near the tip	12–13, irregular branch in its basal part	3–4, ramified dichotomously
Origin of Carpogonial Branch in Cortical Layer		From the outermost cell of the cortical layer, terminal	From the calcified outer-layer cell, terminal	From the 2nd cell from the innermost cortical layer, laterally inserted	From the 2nd cell from the innermost cortical layer, terminally or laterally inserted
Manner of Attachment of Carpospore to the Gonimoblast Branch		Except basal part all cells are carpospores	Tip-end only become carpospores	Tip-end only	Tip-end only
Manner of Formation of Gonimoblast		From the protruding part in which auxiliary cell and connecting filament fused	Directly from auxiliary cell, with some exceptions	Same as R. setchelliae	Same as R. setchelliae

of *R. borealis* and *R. setchelliae,* the carpogonial branch is produced from the outermost cell of the calcified cortical layer, and lies parallel with the nemathecial cell-rows. But in *R. liagoroides* and *R. gracilis,* the carpogonial branch is lateral or terminal to a subcortical cell lying below the surface, and not in nemathecia organized like those in the other species.

Moreover, the difference in the location of carpogonial branches is generally paralleled by differences in the developmental processes of the connecting filaments. In the first group the connection to the auxiliary cell branch is carried out by the connecting filament running transversely only within the nemathecia. In the second group there are at least two cases: one, in *R. liagoroides,* provides that the connecting filament is produced from a cell in a sterile branch associated with the fertilized carpogonium, and then runs transversely along the basal part of the nemathecia; in the other, as was seen in *R. gracilis,* only a short connecting filament is sent forth to the auxiliary cell lying comparatively close to the sterile auxiliary cell. A secondary connecting filament from the fused auxiliary cell may be longer than the primary filament and may run transversely along the basal part of the nemathecia.

In another respect, also, *R. gracilis* is quite different from the other species. In all other species known the auxiliary cell branch consists of a single cell-row, but in *R. gracilis* the auxiliary cell branch consists of three ramified layers arising from the outer cortical cells, and

it is not easy to distinguish them from ordinary vegetative cortical cells lying nearby. The lowest cell serves as the auxiliary cell. Moreover, in the formation of the gonimoblast, all species show branching in an outward direction without any exceptions, but in *R. gracilis,* sterile branches are also formed toward the inner sides. On these two points *R. gracilis* may be clearly distinguished from the other species.

In both *R. liagoroides* and *R. gracilis,* sterile cell-rows arise from cells of the carpogonial branch whether the carpogonium has been fertilized or not. The formation of assimilatory filaments from the carpogonial branch cells is similar to that in *Liagora* reported by Börgesen (1915) and Yamada (1938), and in *Helminthocladia* by Doty and Abbott (1961).

SPERMATANGIA: In this genus the formation of spermatangia is carried out on the periphery of the thallus, in the outermost cells of the uncalcified layer. Two groups may be distinguished: one in which the fertile structures are concentrated in a special part on the periphery forming the nemathecia, and the other in which the male organs are formed at random throughout the periphery without forming any nemathecia. The first type is shown by *R. borealis,* and the second by *R. setchelliae, R. liagoroides,* and *R. gracilis.* (Spermatia have not been reported in *R. australis.*) The differences between these species are summarized in Table 3.

In *R. borealis* the nemathecium consists of a row of slender branched colorless filamentous cells, and spermatangia are formed at the tips

TABLE 3

CHARACTER COMPARED	R. borealis	R. setchelliae	R. liagoroides	R. gracilis
Origin of Male Organ	Nemathecia, on terminal segment of frond	Whole periphery	Whole periphery	Whole periphery of a branchlet
Thickness of Uncalcified Layer	70–100μ	50–60μ	40–50μ	30–40μ
Whether Spermatium is Directly Borne on Vegetative Cell	On the branchlet of a colorless filamentous cell-row	Direct formation is possible	On small stalk cell	On small stalk cell
Presence of Cuticula-like Layer in the Periphery	Yes	No	Yes	Yes
Diameter of Antheridial Cell	1–1.5μ	0.8–1μ	0.8–1μ	0.8–1μ
Number of the Uncalcified Cell Layers	Ramified irregularly	1–3	1–3	1–2

of these cell-rows. In the other species sper-matangia are produced from the top of the cells belonging to the outermost cortical layer among 1 to 3 layers of uncalcified cells which are exposed at the periphery. The manner of spermatangial cell attachment also appears to differ slightly. In the case of *R. liagoroides* and *R. gracilis,* a small stalk cell is formed on the outermost cells, and the spermatia are borne on the stalks. In *R. setchelliae,* spermatangia for-mation sometimes occurs directly on the cells of the outer cortical layer. In *R. liagoroides* and *R. gracilis,* the periphery is covered with a cuticle-like layer, but in *R. setchelliae* there is no such covering membrane, and the cell membrane of the spermatangial cell is more or less thick.

TETRASPORANGIA: Nemathecia formation over the periphery can be seen throughout the genus *Rhodopeltis,* with the exception of *R. gracilis,* in which tetrasporangia are not known. The division of the tetrasporangium is either zonate, irregularly zonate, or irregularly cru-ciate. The species can be clearly divided into two groups according to the formation of tetrasporangia. In one group, the tetrasporan-gium is formed from an elongated outermost cell of the cortex, or from a terminal cell of the 1- or 2-layered nemathecial cell-row which in turn was produced by transverse division of a cell in the outermost layer. In these situations the tetrasporangium lies parallel with the nemathecial cell-row, forming a single file over the periphery. *R. australis* and *R. borealis* be-long to this group. In the other group, the cell-rows are longer, and between the cell-rows lie branched filaments which bear the tetra-sporangia at their tips. To this group belong *R. setchelliae* and *R. liagoroides.* Observations on tetrasporangia of the respective species are summarized in Table 4.

Division of the Genus

So far, through a study of five species, com-parative evaluations have been made on some characteristics shown by them. The present de-tailed study of this genus adds much new in-formation on the segmental form of the frond, the number and shape of the cortical cell layers, the thickness of the medullary layer, shape of the cystocarp, whether the sperma-tangia occur in nemathecia or not, and the manner of formation of the tetrasporangia. An evaluation of these characters suggests that this genus can be divided into two groups with *R. australis* and *R. borealis* in one, and all other species in the other. Among the latter, *R. gracilis* shows a notable difference in the development of the female reproductive struc-tures. Observations on tetrasporangia in *R. gracilis* are absolutely necessary in order to determine how this species differs from *R.*

TABLE 4

CHARACTER COMPARED	R. australis	R. borealis	R. setchelliae	R. liagoroides
Size and thickness of Nemathecia	1.5 × 1.5 mm 40μ	1.5 × 3 mm 50–70μ	500–800μ in diam. 80–160μ	Nearly 500μ in di-am. 120–150μ
Manner of Forma-tion of Nemathe-cial Cell-Row	Direct or trans-verse division of the outer-most cortical layer	Transverse division of outermost cor-tical layer; rarely 2 rows	From calcified cor-tical layer cell; 2–3 rows	From calcified cor-tical layer cell; 2 rows
Number of Nema-thecial Cells	2–3 cells	2–4 cells	10–15 cells, unram-ified	Nearly 10 cells, un-ramified
Formation of Tetra-sporangia	Terminal cell of nemathecia	Terminal cell of ne-mathecia	Tips of branched fil-aments	Tips of branched fil-aments
Manner of Division	Irregular	Zonate	Irregular	Irregular
Size of Tetraspuoran-gium	8–10 × 20–30μ (Young)	8–12 × 30–40μ	4–8 × 15–25μ	5–7 × 20–25μ

setchelliae and *R. liagoroides*. Much to the author's regret, tetrasporangial specimens were lacking. If more numerous specimens belonging to this genus should later supply us with enough materials to justify subdivision, it seems possible that this genus might later be divided into two or three sections.

DISCUSSION

Hitherto, in the order Cryptonemiales the presence of a sterile auxiliary cell in the carpogonial branch has been regarded as a chief clue for determining the position of the species in a system of classification. The families Dumontiaceae, Rhizophyllidaceae, Squamariaceae, and Corallinaceae have been enumerated as the ones possessing sterile auxiliary cells. Among these, the Rhizophyllidaceae and Squamariaceae are assumed to be closely related because they have exposed nemathecia. *R. australis* was first placed in the Squamariaceae by Harvey, while Schmitz, having perceived that *R. australis* is nothing but the nemathecia of Harvey's *Amphiroa australis,* put it into the Rhizophyllidaceae. Yamada also classified it in the same way. Afterwards, *Polyides* and *Rhodopeltis* were separated from the Rhizophyllidaceae by Kylin (1956), as a new family, Polyideaceae. Kylin at this time contributed information on *Polyides,* but some conflicting studies have since been made (Rao, 1956). *Rhodopeltis* was clarified very little. Characteristics of the Rhizophyllidaceae, Squamariaceae, and the genus *Polyides,* following Kylin, are reviewed here with the intention of finding a clue to the classification of the genus *Rhodopeltis.*

1. Rhizophyllidaceae

The family Rhizophyllidaceae contains three genera: *Rhizophyllis, Desmia,* and *Ochtodes.* In these genera the fronds are creeping, have a leaflike appearance, and branch dichotomously; some possess a dorsiventral structure and others are erect, showing complanate or columnar shape, but all of them have a uniaxial construction. The cortical layer of these genera is supplied with gland cells filled with yellow matter of a special kind. Most cells in the gonimoblast become carpospores. In *Desmia* an auxiliary cell branch consisting of three cells

was observed by Kylin (1956), and it was ascertained that the one lying at the middle was to become the auxiliary cell. Tetrasporangium division is zonate, and tetrasporangia occur in a special sorus at the periphery of the frond. Between the tetrasporangia no sterile filaments are present. The spermatangia are cut off by cells lying in the upper part of the nemathecia.

2. Squamariaceae

The Squamariaceae contain nine genera: *Peyssonelia, Rhododermis, Ethelia, Coriophyllum, Herpophyllon, Contarinia, Rhododiscus, Erythrodermis,* and *Porphyrodiscus.* In general appearance nearly all are encrusting, although some species are leaflike. Some are encrusted with lime, and are more or less creeping and attached firmly to the substratum. The inner structure formation is as follows: first, a single group of cells (hypothallus) is formed. On the periphery of this layer, the vertically ramifying cell filaments (perithallus) are produced. These are fused into parenchyma tissue. Some genera have rhizoids, others do not. Kylin (1925, 1928) has described sexual reproduction in *Peyssonelia.* According to his study, female nemathecial cell-rows consist of 6 to 8 cells, and the carpogonial branch and auxiliary cell branch are formed laterally from these cells. The reproductive branches consist of 4 to 5 cells each. After fertilization the carpogonium is connected with the adjoining sterile auxiliary cell, and from there a connecting filament is sent forth to the auxiliary cell. The auxiliary cell is an intercalary cell in the auxiliary cell branch. The gonimoblast is produced from the part where this cell is connected to the connecting filament. The gonimoblast consists of 8 to 12 cells, and, except for those lying at the lowest part, all the other cells become carpospores. The ripened gonimoblasts lie in nemathecia. Spermatangial branches are produced in a special nemathecium. The branch is first divided into 2 or 3 pericentral cells, and these become spermatangial mother cells. According to available information, tetrasporangia are produced in specific nemathecia and have sterile filaments (paraphyses). Generally, the manner of tetraspore division is cruciate, but in *Porphyrodiscus* it is zonate.

3. *Polyides*

In this genus sexual reproduction was observed by Thuret and Bornet (1878). Anatomical studies were made by Kylin (1923) and Rao (1956). According to those studies, fronds of *Polyides* stand erect and have columnar stems; they branch dichotomously, and are cartilaginous and uncalcified. The vegetative structure is multiaxial. The inner part is composed of medullary tissue consisting of long cell filaments and many rhizoids, while the outer layer consists of cortical tissue composed of cells which are thick and densely connected, small on the outer side and large on the inner side. In the female nemathecia there are carpogonial branches and auxiliary cell-rows among the many sterile filaments. Carpogonial branches consist of 5 to 7 cells with dense contents, and each bears a spirally twisted trichogyne. The auxiliary cell branch is a little longer than the carpogonial branch and usually produces 2 or 3 short side branches. The cells of the auxiliary cell branch are not very well filled, and therefore the auxiliary cell is not very noticeable. The gonimoblast is not produced directly from the auxiliary cell but is produced indirectly from the connecting filament. After fusion with the auxiliary cell the connecting filament divides itself into many cells in a ring which branch densely, forming a bushy gonimoblast; the terminal cells become carpospores. The ripened cystocarps are scattered in nemathecia. The spermatangia are formed in nemathecia on the periphery of the frond. Nemathecia consist of many parallel filamentous cells growing upon the cortical layer, and these filamentous cells are divided into many pericentral cells. These pericentral cells become the spermatangia mother cells. Tetrasporangia are produced in the outermost layer of the cortical layer and are divided cruciately.

Table 5 shows a comparison of *Rhodopeltis* with the Rhizophyllidaceae, the Squamariaceae, and *Polyides* in regard to the above features. As the table shows, when seen from the point of view of vegetative structure *Rhodopeltis* seems to be most similar to *Polyides,* but when the development of the female reproductive structures is considered, *Rhodopeltis* seems to be notably similar to the two genera, *Polyides*

and *Peyssonelia*. The spermatangia and tetrasporangia of *Rhodopeltis* are quite unique and wholly different from those of *Polyides*. The suitability of placing both *Polyides* and *Rhodopeltis* in one family should be further considered. From the present information, *Rhodopeltis* seems to be as similar to *Peyssonelia* of the Squamariaceae as it is to *Polyides,* and it seems also to be somewhat alien to the Rhizophyllidaceae. But sufficient information has not yet been obtained on the sexual reproductive organs of the Rhizophyllidaceae and the Squamariaceae, and more thorough study will be necessary in order to establish the relationships of *Rhodopeltis*.

SUMMARY

The calcareous red alga *Rhodopeltis* of Japan is distributed also in tropical and subtropical regions. There are five known species in the world, four of which are found in Japan.

The frond of this genus is 4 to 10 cm high. It has a short erect stem, branching dichotomously from the stem and growing fasciculately. The branch is complanate or columnar, with segments in the upper parts especially. The holdfast is cartilaginous and discoid.

The structure of the frond is multiaxial and consists of a filamentous medullary layer and a cortical layer. The latter is composed of round or elliptical cells. Precipitation of lime is observed in the cortical layer. The cortical layer consists of 4 to 9 layers of cells. These cells become small toward the outer side. The outermost layer of some species contains lime but in others it does not.

All of the female organs are in nemathecia. The nemathecia are in the periphery of the end of the branches. The carpogonial branch consists of 3 to 8 cells. In some species it is produced from the outer cells of the calcified outer cortical layer. The trichogyne grows erect. The auxiliary cell branch consists of 3 to 12 cells and is produced from the same part as the carpogonial branch. Some difference in the location of the auxiliary cell in the auxiliary cell branch is observed in the various species. The adjoining cell of the carpogonium, known as the hypogynous cell, usually becomes the sterile auxiliary cell. The fertilized carpogonium con-

TABLE 5

CHARACTER COMPARED	Rhizophyllidaceae	Squamariaceae	*Polyides*	*Rhodopeltis*
Outer Appearance of Frond	Leaflike, creeping dorsi-ventral structure, or stand erect and compla-nate or columnar, branch dichotomously	Creeping, leaflike or crustose	Stand erect, branch dichoto-mously, cartilaginous	Stand erect, branch dichoto-mously, columnar or com-planate branches
Lime Precipitation	None	Some are calcified	None	Present
Inner Anatomy	Uniaxial type	Modified multiaxial	Multiaxial type	Multiaxial type
Carpogonial Branch and Auxiliary Cell Branch	3 cells (*Desmia*)	Both 4–5 cells (*Peyssonelia*)	5–7 cells Comparatively long	3–8 cells 3–12 cells
Place where Gonimoblast is Produced		Fusion position of auxiliary cell	Connecting filament near aux-iliary cell	Fusion position of auxiliary cell, or near it
Manner of Production of Carpospores from Goni-moblast	Most of the cells of goni-moblast become carpo-spores	Gonimoblast consists of 8–12 cells, all except the lowest one become carpospores	Gonimoblast forms a bush; only the terminal cells be-come carpospores	Umbel-like gonimoblast, all except basal cells become carpospores; or treelike gonimoblast, only the ter-minal cells become carpo-spores
Trichogyne		Stands erect	Coils spirally	Stands erect
Manner of Production of Spermatangia	Cells at the upper part of nemathecia are divided directly into spermatium	Nemathecia with spermatan-gial branch; 2–3 pericentral cells of that branch become spermatangial mother cell	Nemathecia; many pericentral cells of the nemathecia cell-row become spermatangial mother cell	Nemathecia, or all over the periphery; spermatangium and its stalk cell terminal on the outermost cortical cell
Formation of Tetrasporan-gial Organ	At sorus upon the frond surface, with no sterile filament	Nemathecia with sterile fila-ment; or sorus with no sterile filament	In the outermost layer of the cortical layer	Nemathecia with sterile fila-ment; tetrasporangial branches straight or treelike
Division of Tetraspores	Zonate	Generally cruciate, or zonate (*Porphyrodiscus*)	Cruciate	Zonate (irregular)
Gland Cell	In the cortical layer	None	None	None

nects with the sterile auxiliary cell, and the connecting filament is produced from that connecting part. The connecting filament tip fuses with the auxiliary cell. The gonimoblast is produced from that fused part and ramifies in an umbellate or dendroid manner. In the umbellate ramification the cystocarp is oblong-pyriform, and carpospores are formed from all of the gonimoblast cells except the basal cells. In other species carpospore formation is limited to the terminal cells of the gonimoblast. The gonimoblast of some species has sterile branches but that of other species does not. Carpospores are either elliptical or oblong-elliptical.

The spermatangia are formed in nemathecia or on the whole surface of the outermost uncalcified layer. The small cells produced from the tip-end of the outermost layer or of the nemathecial cell-row become spermatangia.

Tetrasporophytes form nemathecia. Tetrasporangia lie scattered among the nemathecial cells. Uniseriate and branched cell-rows produce tetrasporangia. The division of the tetrasporangium is usually zonate or irregular.

Rhodopeltis can be divided into two groups using morphological differences shown by the outer structures, inner structures, female organs, male organs, and tetrasporangia. One group includes *R. australis* and *R. borealis,* and the other group, *R. setchelliae, R. liagoroides,* and *R. gracilis.* The shape of the auxiliary cell branch in *R. gracilis* is characteristic; the tetrasporophyte is unknown.

Some similarities in female reproductive structures are observed in the genera *Rhodopeltis, Polyides,* and *Peyssonelia.* But there are distinctive differences in male and tetrasporangial organs between *Rhodopeltis* and other genera, such as *Polyides* and the many genera of the Rhizophyllidaceae and Squamariaceae.

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