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### HELMINTHOCLADIA FROM INDIA AND NEW ZEALAND

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THE genus, *Helminthocladia* J. Ag., includes at the present day about eight species. The ontogeny of the cystocarp has been studied in only three species, viz., *H. calvadosii* (Schmitz, 1896; Kylin, 1930; Rosenvinge, 1909; Hamel, 1930), *H. papenfussii* (Kylin, 1938; Martin, 1939), and *H. hudsoni* (Feldmann, 1939). Even then there are quite a few points and doubts to be cleared (see Papenfuss, 1946, p. 433). There is a definite need for studying as many species as possible of this genus with the help of fluid preserved material.

The writer collected a species of *Helminthocladia* at Okha (see also Boergesen, 1931, p. 7) in January 1955. He has also good material of *H. australis* collected from different parts of New Zealand and the neighbouring islands. He has also with him material of *H. papenfussii* which Prof. Papenfuss had lent him for purposes of comparison. The present paper is based mainly on a study of these materials.

#### *Helminthocladia* from India

This form resembled very closely in habit *Helminthocladia calvadosii*. It attains a length of 18–20 inches and its main axis is about  $\frac{1}{2}$ –1.5 cm. in diam. The alga is highly mucilaginous and sticks to paper. This alga has been collected freshly washed ashore and has not been collected *in situ* (see also Boergesen, 1931). In the present case the writer collected the plant with the attachment intact. The alga is attached by a basal disc and grows on corals, probably in deeper waters (Plate XV, Fig. 1). The branching is pinnate and secondary branches are common. Proliferations were, however, not seen in any great abundance.

The structure of the thallus is as in the other *Helminthocladia* spp., consisting of a compact medulla and a cortex made of radially arranged assimilatory branches. The assimilatory branches are generally up to five times furcate (Text-Fig. 1). The terminal cells of the branches are large and pyriform (Text-Figs. 1, 2). They are 15.3–25.5  $\mu$  broad

and  $44.2-54.4 \mu$  long. Hairs are very common and their origin is similar to that described by Rosenvinge (1909) in *H. purpurea* and by Martin in *H. papenfussii*. The cells of assimilatory branches have the distinctly stellate chromatophore and a pyrenoid lodged in the upper end (Text-Fig. 2). The chromatophore and the pyrenoid are quite distinct especially in the terminal cells. From the lower cells of the assimilatory branches long narrow rhizoid-like filaments are given off (Text-Fig. 5). These rhizoids run parallel to the medulla and produce clusters resembling the cortical branches.

The alga is monœcious. Boergesen (1931) has observed only female plants. The writer also has collected female plants. Similar variation has been noted in many other species and genera of the Helminthocladaceæ by other workers.

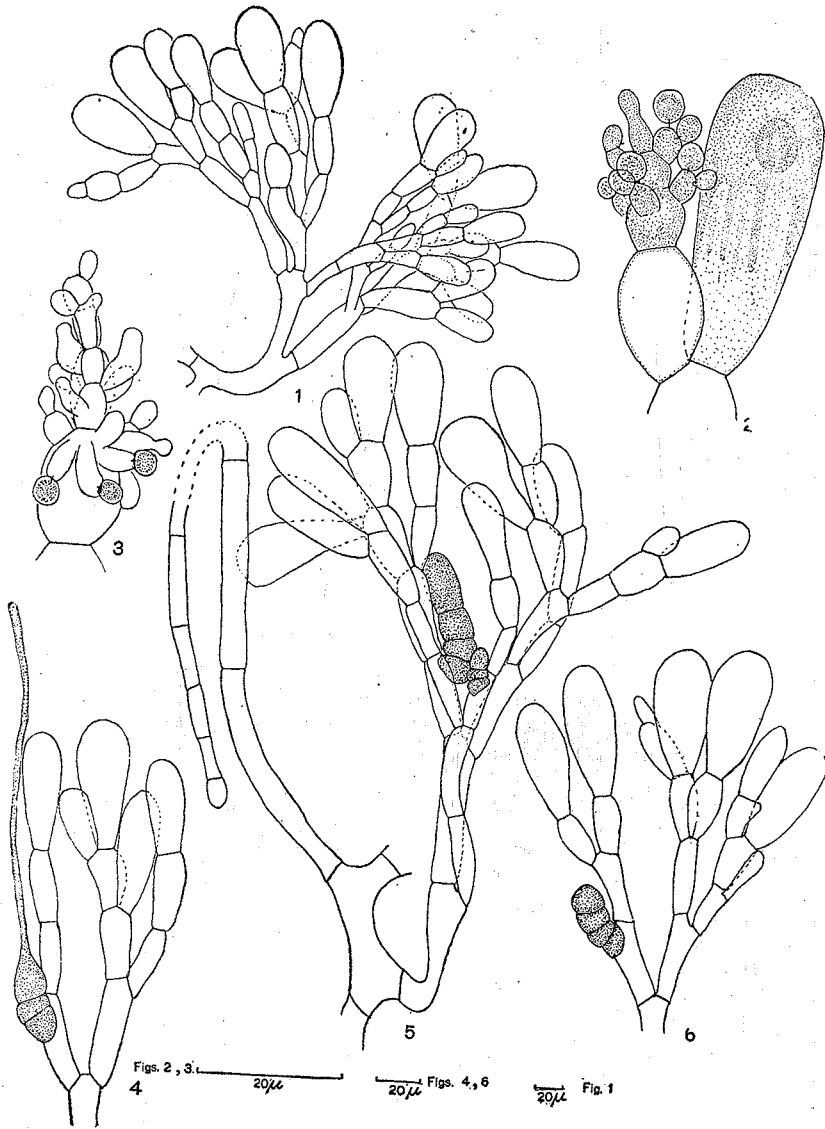
The antheridia are formed at the tips of assimilatory branches (Text-Figs. 2, 3). By repeated division a series of two or three very short cells are formed at the ends. From each of these cells one or more, usually many, antheridial mother cells are formed. From each antheridial mother cell, 2-3 antheridia are cut off, each antheridium producing a single spermatium which is  $2.8-3.5 \mu$  in diam.

The carpogonial branches are generally 3-celled (Text-Fig. 4); four-celled branches are also met with (Text-Fig. 6). These are formed laterally on the assimilatory branches below the second and the third furcations (Text-Fig. 5). The carpogonial branch initial is generally clearly seen even when quite young and is differentiated even before the pyriform end cells of the assimilatory branches are distinguishable or developed. The trichogynes are very long and protrude beyond the assimilatory branches. The carpogonial branches are  $8.5-11.2 \mu$  broad. Actual fertilization of the carpogonium was not observed.

The fertilized carpogonium at first cuts off the trichogyne (Text-Fig. 11). Then one or more longitudinal divisions take place (Text-Fig. 7). From the daughter cells are developed a number of gonimoblasts which remain very compact for a long time (Text-Figs. 8, 12). The filaments become much branched and produce terminally carpospores. After the formation of a carpospore, the cell below it gives forth a lateral branch which again forms a carpospore terminally. Thus a number of carpospores are formed by repeated branching of the gonimoblast filaments.

With the progress in the formation of the gonimoblast filaments there is a very clear enlargement of the protoplasmic connections between the carpogonial branch cells themselves and the supporting cell. Gradually this widens further and in many cases a fusion cell is ultimately formed (Text-Fig. 12).

Just at the same time as the trichogyne is cut off and the fertilized carpogonium undergoes division, a number of branches are initiated by the cells below and above the supporting cell and by the cells of the neighbouring assimilatory branches. These are the initials of involucrel



TEXT-FIGS. 1-6. *Helminthocladia* from India. Fig. 1. Assimilatory branches. Figs. 2, 3. Antheridia. Fig. 4. Carpogonial branch. Figs. 5, 6. Development of the carpogonial branch.

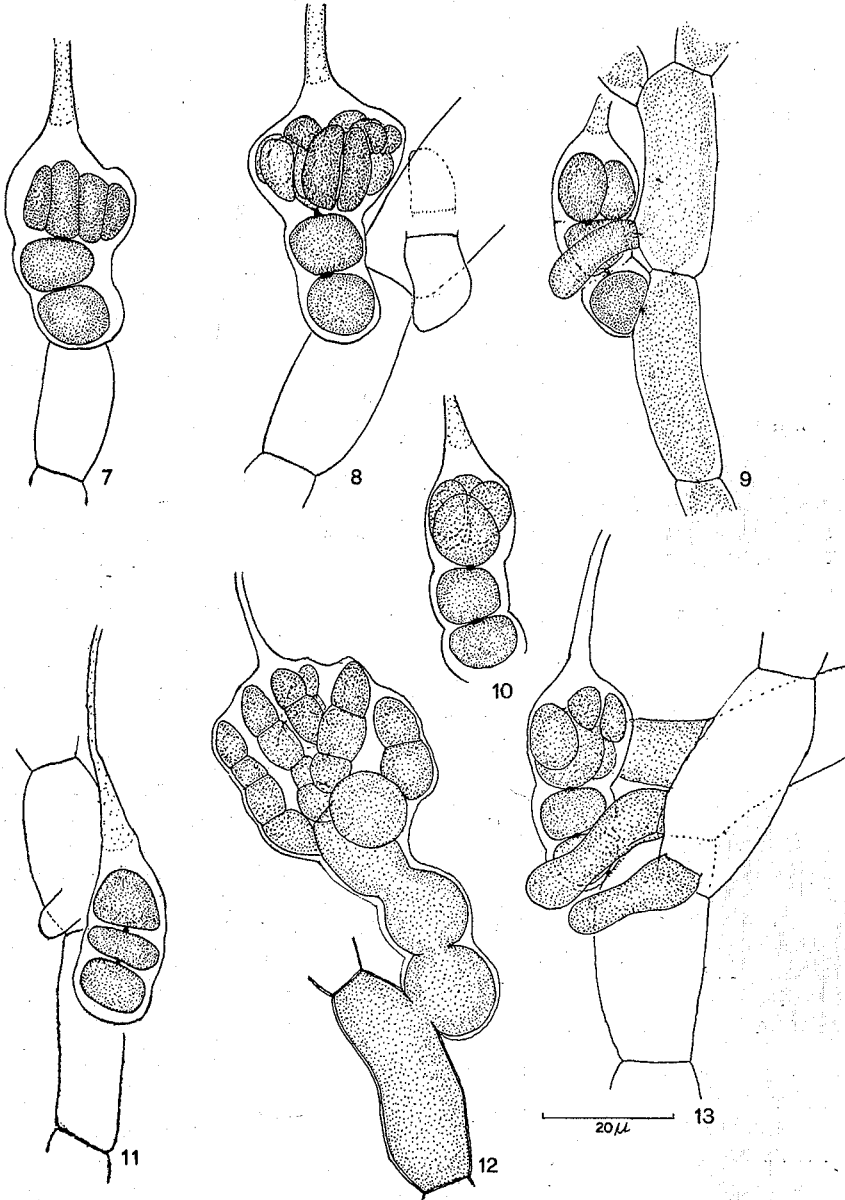
filaments (Text-Figs. 8, 9, 11, 13). Though the involucrel filaments are initiated, they are not developed in the Indian form in any great profusion as for instance, in *H. californica*.

Boergesen (1931, p. 7) has described this species as *Helminthocladia australis* and has pointed out its resemblance to *H. calvadosii*. He has also referred to the variation in the habit. Boergesen (1931) observed only female plants and hence separates the Indian plant from the European species.

The Indian plant has points of resemblance with *H. calvadosii*. In both there is a fusion cell. *Helminthocladia calvadosii* is monœcious. However, Rosenvinge (1909) also has observed plants which are either male or female only. In the Indian form also this character is variable. There has been difference of opinion on the presence of involucrel filaments. Rosenvinge (1909) and Hamel (1930) (see also Schmitz, 1896) describe the presence of involucrel filaments while Kylin (1930) denies the presence of any. Papenfuss (1946) suggests that one of these materials (?) may belong to another species, viz., *H. hudsoni*. *Helminthocladia hudsoni* has been clearly worked out by Feldmann (1939) and in it there is no fusion cell and the sterile filaments are completely lacking. Further, this species has carpotetraspores. Hence none of the material of Schmitz, Rosenvinge and Kylin can belong to *H. hudsoni* as none of these authors have described carpotetraspores and they have recorded a fusion cell. A reinvestigation of *H. calvadosii* is indicated. The Indian form has both involucrel filaments and the fusion cell.

The Indian form differs from *H. calvadosii* in one character, i.e., in the European form the first division of the fertilized carpogonium is oblique and is nearly longitudinal. In the Indian form the division is very clearly longitudinal. In view of this there is some doubt whether the Indian form is *H. calvadosii*.

Boergesen (1931, p. 7) identified it as *H. australis*. *H. australis* is abundantly found in Australia and New Zealand and varies very greatly in habit. Recently Levring (1953, 1955) has described this species based on his Australian and New Zealand collections. As Levring's study was based on herbarium material it was not possible for him to follow the development of the gonimoblasts properly (see Levring, 1953, p. 494). The writer visited New Zealand in 1955 under a Travel grant kindly given to him by the Nuffield Foundation, London. During this visit he studied extensive collections of this species. Having fixed material the writer has followed clearly the post-fertilization stages in the various forms of *H. australis* occurring in New Zealand. He has also studied a number of herbarium specimens of this species kindly lent to him by Mr. V. Lindauer of Russell, New Zealand. Mrs. E. Willa of Stewart Island has also kindly sent him a good amount of preserved material of this species. The writer is in agreement with Levring (1953) that this alga shows a large amount of variation in habit though in structure and reproduction there is a very large degree of similarity between the various plants. Hence a general description of the post-fertilization stages is given below and is substantiated by figures showing the various stages in each of the collections.



TEXT-FIGS. 7-13. *Helminthocladia* from India, post-fertilization stages. Figs. 7, 10. Division of fertilized carpoogonium. Figs. 8, 9, 11, 13. Showing initiation of involucre branches. Fig. 12. Fusion cell.

*Helminthocladia* from New Zealand

Collections of *Helminthocladia* came from Stewart Island, Campbell Island and from Red Beach, Narrow Neck, St. Leonard's Beach, near Auckland. The Stewart Island alga had both male and female plants. The plant from St. Leonard's Beach was male while the rest were all female.

The construction of the thallus is typical of *Helminthocladia*. The assimilatory filaments in all the forms end in the characteristic large pyriform cells. Rhizoid-like branches are profusely formed from the lower cells of the assimilatory branches.

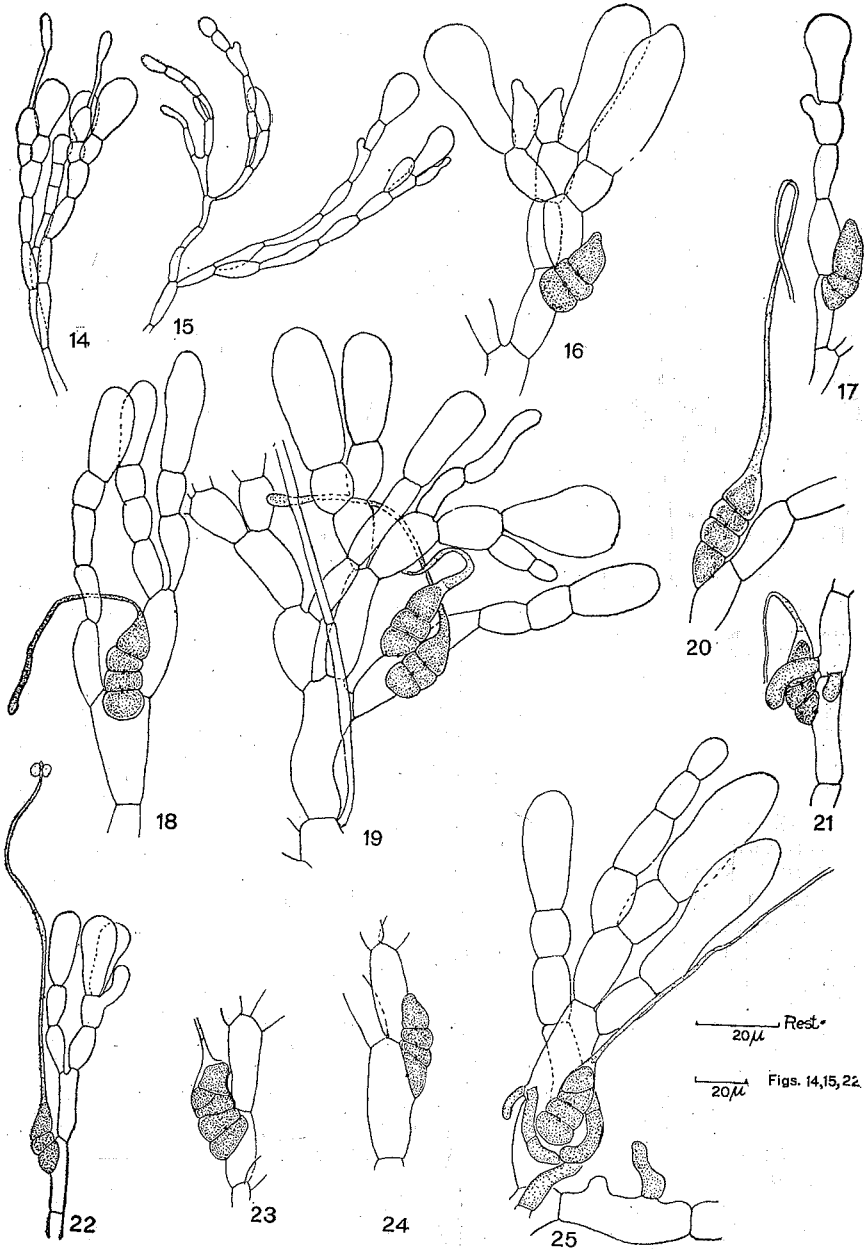
*Red Beach Material.*—The habit of this alga is typically that of *H. australis*. It is attached by a basal disc from which one or more main branches arise (Plate XVI, Fig. 3). The peripheral cells of the assimilatory branches are much smaller than those of all the other forms. They are  $14.0\text{--}22.4\ \mu$  broad and  $28.8\text{--}43.2\ \mu$  long (*cf.* Levring's measurements in 1953, p. 494). The carpogonial branches are about  $11.2\text{--}14.4\ \mu$  broad. These are generally three-celled (Text-Fig. 37). The first division of the fertilized carpogonium is obliquely transverse (Text-Figs. 27, 30, 36).

*Stewart Island Material.*—These plants agreed with *f. ramosissima* so well figured and described by Levring (1953). It has a pinnate habit and the secondary branches are very well developed (Plate XV, Fig. 2; Plate XVI, Fig. 4). The main axis is generally about 3–4 mm. when fluid preserved and less when dried. One or more branches are given from a common disc. The pyriform end cells of the assimilatory branches are  $21.6\text{--}25.2\ \mu$  broad, and  $54.0\text{--}64.8\ \mu$  long. The carpogonial branch is generally three-celled and sometimes four-celled (Text-Figs. 54, 55, 58, 59). The carpogonial branches are  $(12.6\text{--})\ 14\text{--}18\ \mu$  in diam. The first division of the fertilized carpogonium is obliquely transverse (Text-Figs. 58, 59). Involucral filaments are also formed (Text-Fig. 55).

*Narrow Neck Material.*—This plant shows a large amount of proliferations, even more than the '*H. tumens*' figured by Levring (Plate XVI, Fig. 6). The peripheral cells are  $14.8\text{--}25.9\ \mu$  broad and  $44.4\text{--}55.5\ \mu$  long while the carpogonial branches were about  $11\ \mu$  broad. The main axis is about 10 mm. broad.

The carpogonial branches are generally three-celled and sometimes four-celled (Text-Figs. 18, 22). The first division of the fertilized carpogonium is obliquely transverse (Text-Fig. 25). Involucral filaments are also formed (Text-Figs. 21, 25).

*Campbell Island Material.*—In habit the alga resembles the Red Beach material, though the main branches are thicker. Secondary branches are very common (Pl. XVI, Fig. 5). The peripheral cells of the assimilatory filaments are  $22.5\text{--}29.6\ \mu$  broad and  $55.5\text{--}74\ \mu$  long. The carpogonial branches are about  $10\ \mu$  broad. The carpogonial branches are three-celled (Text-Figs. 67, 70). The first division of the fertilized



TEXT-FIGS. 14-25. *Helminthocladia australis* from Narrow Neck. Fig. 14. Young assimilatory branch. Fig. 15. Apical portion of an axial filament. Figs. 16, 17, 24. Young carpegonial branches. Figs. 18, 19. Carpegonial branches. Figs. 19, 20, 22. Showing trichogyne being cut off after fertilization. Figs. 21, 23, 25. First division of the fertilized carpegonium and the initiation of the involucre branches.

carpogonium is obliquely transverse (Text-Figs. 65, 68). Involucral filaments are definitely formed (Text-Figs. 65, 66, 68, 69).

*St. Leonard's Beach Material.*—A number of main branches arise from a common basal disc. They are dichotomously branched (Pl. XVI, Fig. 7). The main branches are 40–56  $\mu$  long and 20.8–30.4  $\mu$  broad. Proliferations are commonly seen. Only male plants were observed.

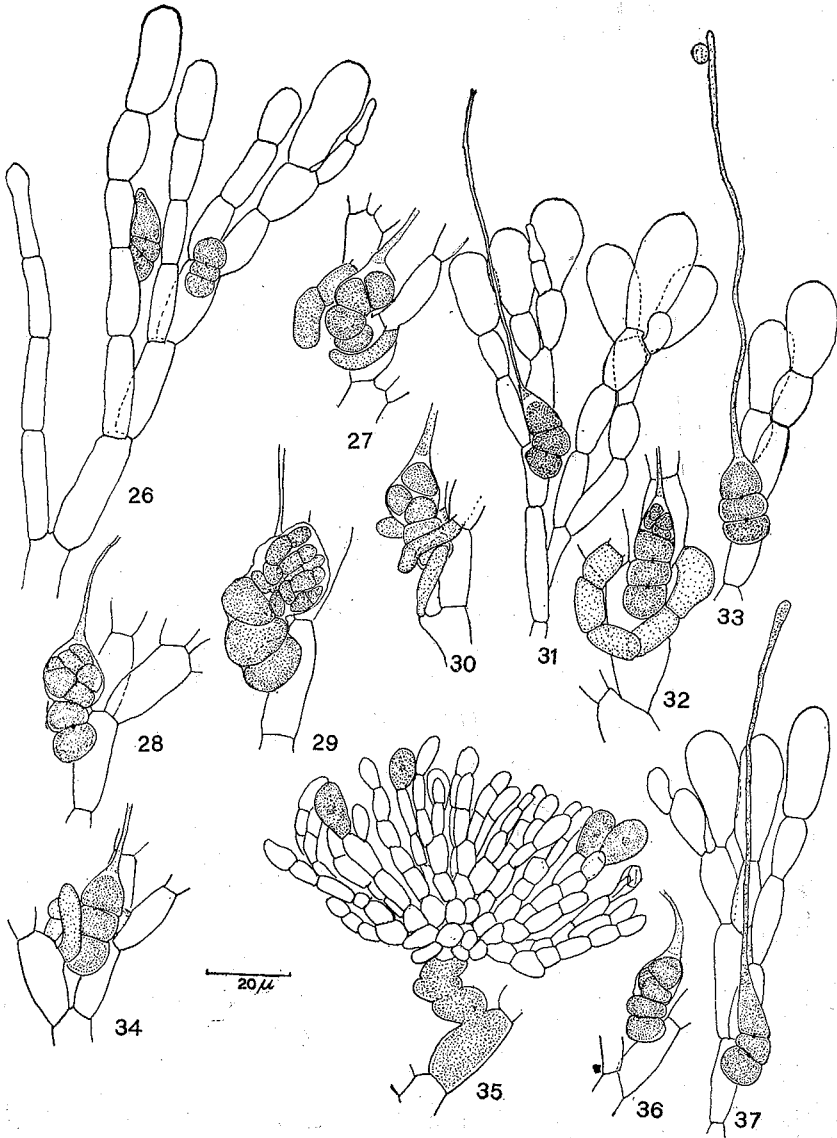
From the above it may be seen that in the various dimensions there is a very great range of variation and these cannot be conveniently used for separating them. In the post-fertilization stages there is a large amount of uniformity.

The carpogonial branches are generally three-celled. The fertilized carpogonium first cuts off the trichogyne and then divides by a transversely oblique wall. Both the daughter cells give rise to gonimoblast filaments. Enlargements of the protoplasmic connections between the cells of the carpogonial branches is very common and a distinct fusion cell is formed. Involucral filaments are definitely formed from the cells above and below the supporting cell and the neighbouring cells. The quantity of the involucral filaments developed is very variable.

The New Zealand alga resembles very much *H. papenfussii* in the ontogeny of the cystocarp. The possibility of these two southern species being closely related cannot be ruled out. When Kylin established the species it was essentially based on the obliquely transverse division of the fertilized carpogonium and with the discovery of a similar occurrence in the older member of the southern hemisphere, *H. australis*, one is prone to doubt on the validity of *H. papenfussii*. To this end the writer re-examined the South African material (see Text-Figs. 38–53). The writer's observations very well agree with those of Kylin (1938) and Martin (1939). The carpogonial branches are three-celled (Text-Figs. 40, 53). In *H. papenfussii* as in *H. australis*, the first division is obliquely transverse (Text-Figs. 41, 43, 45). The involucral filaments are similarly developed (Text-Figs. 46, 47, 49). They are better developed in the *H. papenfussii* than in the New Zealand plant. The fusion cell is better developed and more prominent in *H. papenfussii* (Text-Fig. 51). In the New Zealand plants, however, the fusion cell developed is very variable. *H. papenfussii* seems to be distinct for all appearances and the early stages of the cystocarp formation are quite characteristic.

According to Levring (1953) all the present material belongs to *H. australis*. Levring (1953) studied the type material and has identified his Australian and New Zealand material. His account of the post-fertilization stages in his material is, however, different. The first division of the fertilized carpogonium is according to him longitudinal. The writer has in no case observed longitudinal division in the New Zealand material. Levring himself states that he did not have fluid material and that he could not describe the early stages in gonimoblast development clearly. The writer is of the opinion that the Australian form of *H. australis* must be studied with the help of

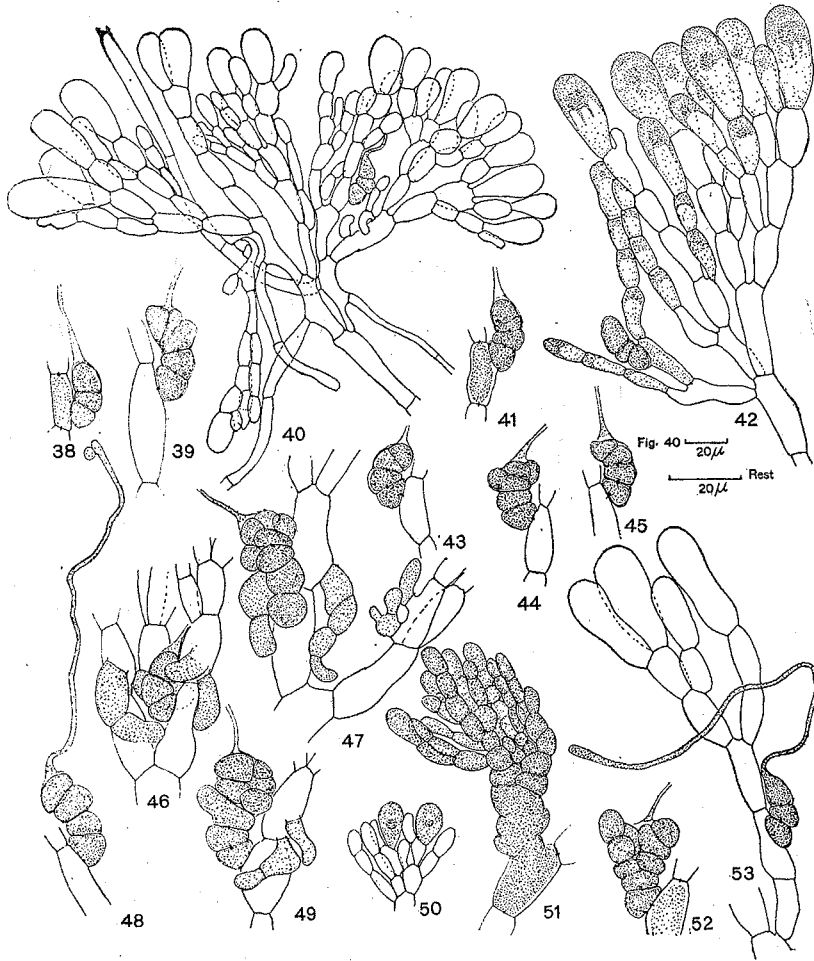




TEXT-FIGS. 26-37. *Helminthocladia australis* from Red Beach, New Zealand. Fig. 26. Formation of the carpoogonial branch. Figs. 27-34, 36. Post-fertilization changes in the carpoogonium and the initiation of the involucre filaments. Fig. 35. Cystocarp showing fusion cell. Fig. 37. Carpoogonial branch.

preserved material to settle this point. In the event of the longitudinal division being proved the rule in the Australian material, the New Zealand form must be separated from the Australian one. There is no

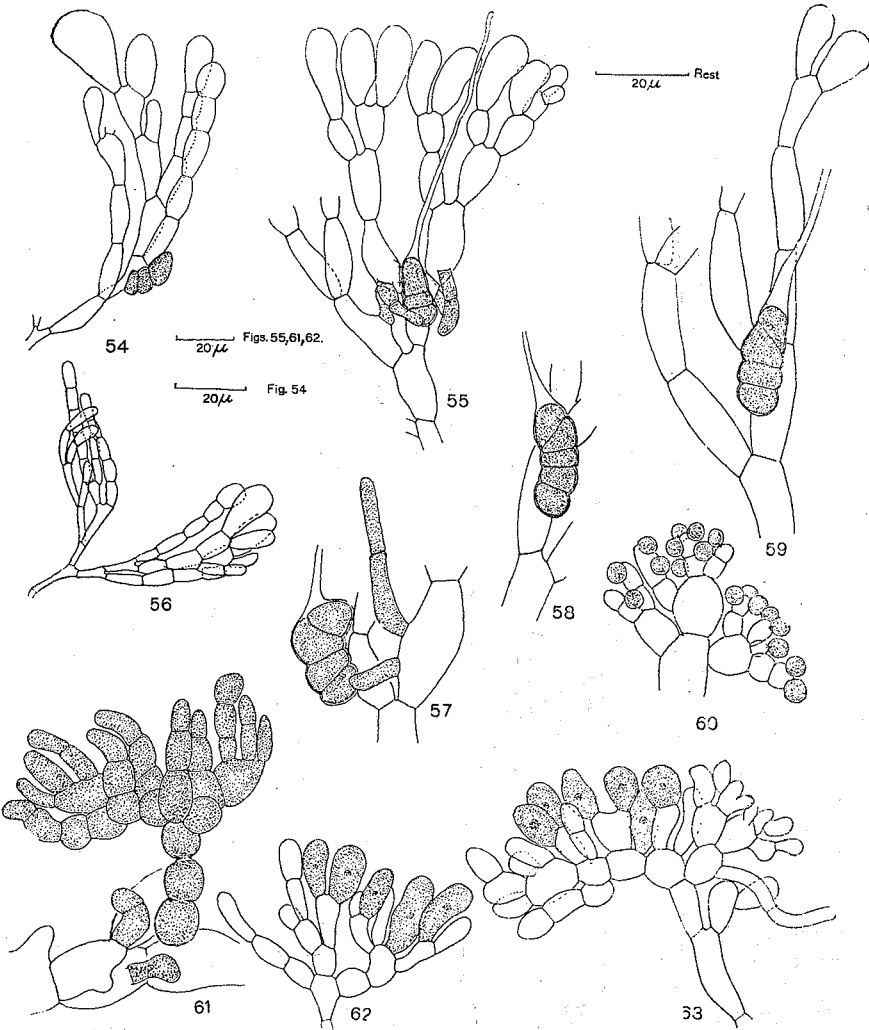
reason to doubt Levring's specific identification of New Zealand material. Till a reinvestigation proves the presence of longitudinal division, it may be accepted that obliquely transverse division is the normal one in *H. australis*.



TEXT-FIGS. 38-53. *Helminthocladia papenfussii*. Figs. 38, 39, 41, 43-49, 52. Post-fertilization changes in the carpegonium and the initiation of the involucral filaments. Fig. 40. Assimilatory branches. Fig. 42. Formation of the carpegonial branch. Fig. 50. Cystocarpic branches with carpospores. Fig. 51. Young cystocarp with fusion cell. Fig. 53. Carpegonial branch.

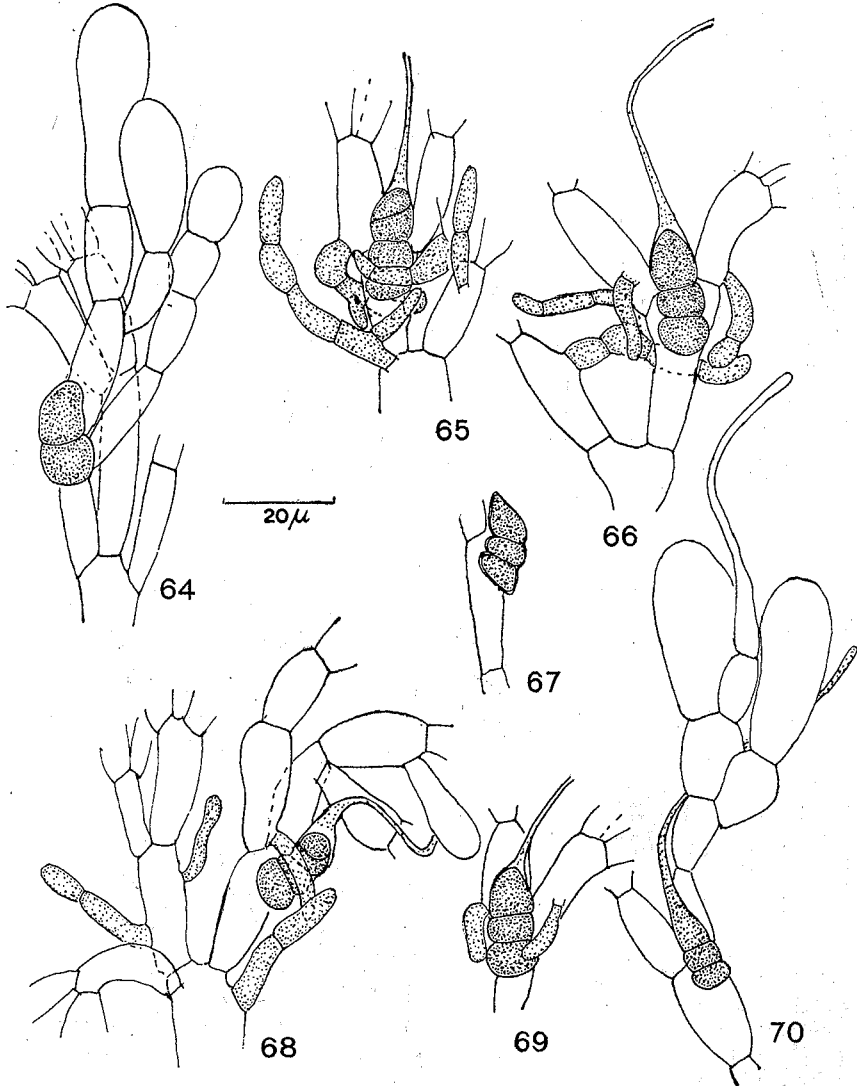
Levring (1953) seeks to exclude Okamura's (1923, p. 21) report of *H. australis* from Japan. According to him it does not appear to be identical with Australian and New Zealand plants. The very typical large end cells of the assimilatory filaments are considerably smaller

in the Japanese form. In other details they seem to be similar to the Australian and New Zealand plants. The present author has found the dimensions of the end cells highly variable and hence there is not sufficient ground for excluding the Japanese *H. australis*. The plane of division of the fertilized carpogonium is not known in the Japanese material.



TEXT-FIGS. 54-63. *Helminthocladia australis* from Stewart Island. Fig. 56. Young assimilatory branches. Fig. 54. Formation of the carpogonial branch. Fig. 60. Antheridia. Figs. 55, 57-59. Post-fertilization changes in the carpogonium and the formation of involucre filaments. Fig. 61. Developing cystocarp with fusion cell. Figs. 62, 63. Cystocarpic branches with carpospores.

The above study of the New Zealand material has further shown that the Indian material is not similar to *H. australis*. The writer does not find any justification for separating the Indian form from *H. calvadosii*. It is now identified as *H. calvadosii*. On account of the slight difference in the post-fertilization stages it is kept as f. *indica*. A



TEXT-FIGS. 64-70. *Helminthocladia australis* from Campbell Island. Figs. 64, 67. Formation of carpegonial branches. Figs. 65, 66, 68 and 69. Post-fertilization changes in the carpegonium and the formation of involucral filaments. Fig. 70. Carpegonial branch.

reinvestigation of *H. calvadosii* from Europe is very necessary to check up the details of post-fertilization stages given by Rosenvinge (1907) and Kylin (1930) especially on the development of the involucreal filaments.

*H. calvadosii* f. *indica*.—Similar to the type. First division of the fertilized carpogonium longitudinal.

Similis typicæ speciei; divisio prima carpogonii fertilissati longitudinalis.

*Typus lectus*.—Okha in statu Bombay, in India.

#### CONCLUSION

The genus *Helminthocladia* has at the present day eight species: (1) *H. calvadosii*, (2) *H. australis*, (3) *H. papenfussii*, (4) *H. hudsoni*, (5) *H. yendoana*, (6) *H. gracilis*, (7) *H. californica* and (8) *H. densa*. Of these the first three have already been discussed. The fourth has been fully investigated (Feldmann, 1939). The first division of the fertilized carpogonium is oblique very like in *H. calvadosii*. There is a fusion cell and the involucreal filaments are not developed. *H. hudsoni* is very distinct from the rest of the species by the formation of carpotetraspores instead of carpospores.

*Helminthocladia californica* Kylin was first described as *H. australis* f. *californica*. It is a dioecious plant, and the cystocarps are provided with a prominent involucre. The nature of the first division of the fertilized carpogonium is not known. This species awaits detailed study.

Very little is known of the post-fertilization stages in *H. gracile* Gardner (1924), and *H. yendoana* Narita. Recently Levring (1953) studied *H. densa*. His comments on this species are quoted below:

“I have collected a few specimens, which agree perfectly with the species Harvey has placed under this name in his exsiccata. Schmitz has referred the species to *Helminthocladia*. My own study of the anatomy and fruit development has also shown that it is a true representative of the genus.”

“The thallus is about 10–20 cm. high, repeatedly dichotomously branched with numerous side branches, cylindrical, gelatinous in older parts 1–2 mm. thick. Slender. Colour brownish or yellowish red, also when dried. The carpogonial branches are three-celled. They are developed as accessory branches from a cell in the middle part of the assimilatory filaments. The young carpogonial branches are developed just below the top of the branches. After fertilisation the carpogonium is at first divided into two cells. From the upper one of these are developed a number of branches bearing the carpospores. No fusion between the supporting cell, carpogonial branch cells or gonimoblast cells has been observed. The gonimoblast is not surrounded by sterile filaments. The development of the gonimoblast thus agrees very well with the type of *H. calvadosii* described by Kylin 1930 (p. 6).”

"I have also seen authentic material of *Nemalion insigne*, which was supposed by Harvey himself to be a synonym of this species. I can only agree with him in this opinion. According to Harvey tetrasporangia are formed in the terminal cells of the peripheral branches. Since I have not been able to find this, neither in Harvey's nor in my own specimens, Harvey's remark is probably due to a mistake."

From the above it appears that *H. densa* differs from the other *Helminthocladia* spp., in many important respects: (1) The characteristic end-cells of the assimilatory branches seem to be lacking (see his Fig. 25 F) and (2) the post-fertilization stages are more like those of *Helminthora*. In all the species of *Helminthocladia* so far fully studied, whatever be the plane of division, both the resultant cells partake in the formation of gonimoblast filaments (see Papenfuss, 1947, p. 432). In *Helminthocladia densa* according to Levring, the case is just like in *Helminthora*, i.e., only the upper cell takes part in the formation of gonimoblast filaments. Until further re-examination proves otherwise, *H. densa* should be transferred to *Helminthora* as *Helminthora densa* (Harv.) comb. nov.

The case of *H. densa* naturally leads on to a consideration of the distinction between *Helminthocladia* and *Helminthora*. Till Kylin's discovery of *Helminthocladia papenfussii*, it could have been said that longitudinal division of the fertilized carpogonium is characteristic of *Helminthocladia*. Other characters such as the nature of the medulla and the presence or absence of involucrel filaments are of not much use. Now that involucrel filaments definitely exist in *Helminthocladia* (e.g., *H. californica*) and that both longitudinal and transverse divisions of the fertilized carpogonium are known, search for a reliable character must be made elsewhere. The characteristic large, pyriform end-cells of the assimilatory filaments with a stellate chromatophore placed in the end position are not seen in *Helminthora*. Papenfuss (1947, p. 432) draws a fine distinction between the two genera based on the development of the gonimoblast from the products of the fertilized carpogonium. In *Helminthocladia* both the daughter cells take part, while in *Helminthora* only the upper of the two daughter cells takes part in the formation of gonimoblast filaments. In the writer's opinion these two characters are sufficiently stable characters and the genus *Helminthocladia* should be defined by these characters.

#### SUMMARY

*Helminthocladia* spp. collected from India and New Zealand are described and the structure and the development of the cystocarp is discussed.

The Indian plant, hitherto identified as *H. australis*, is now identified as *H. calvadosii* f. *indica* as in the Indian plants the fertilized carpogonium undergoes longitudinal division.

The New Zealand forms of *H. australis* are described in great detail and the variation in habit and the uniformity in the post-fertilization

stages are described. The fertilized carpogonium divides by a transversely oblique wall.

In both the Indian and New Zealand forms the two daughter cells of the fertilized carpogonium partake in gonimoblast formation. Involucral filaments are formed, though meagrely, from the cells above and below the supporting cell.

A comparison is made with the other species of *Helminthocladia*.

It is suggested that *Helminthocladia densa* be transferred to *Helminthora*.

Two features, viz., (1) the presence of large pyriform peripheral cells of the assimilatory branches and (2) the two daughter cells formed by the division of the fertilized carpogonium partaking in gonimoblast formation, are chosen as the essential characteristic features of the *Helminthocladia*.

#### ACKNOWLEDGEMENTS

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## EXPLANATION OF PLATES XV AND XVI

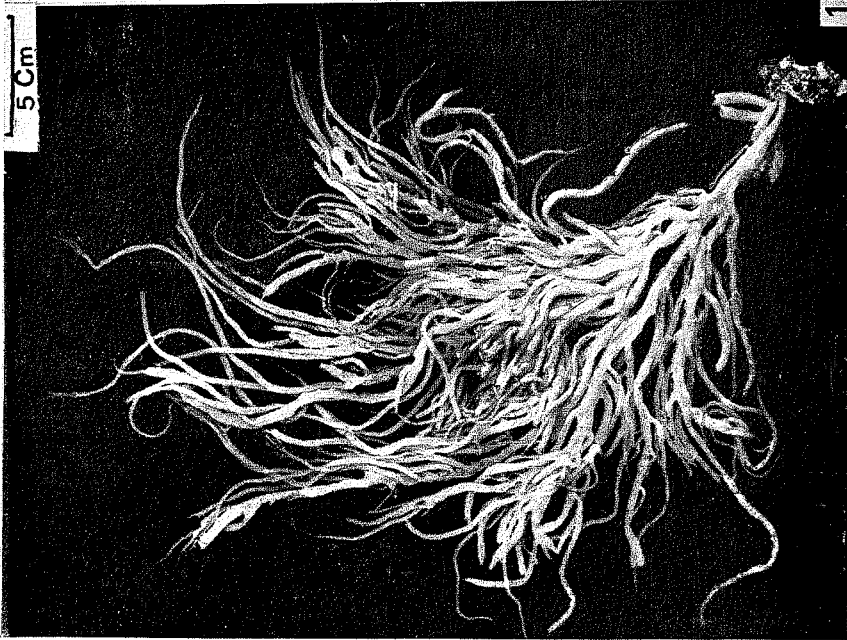
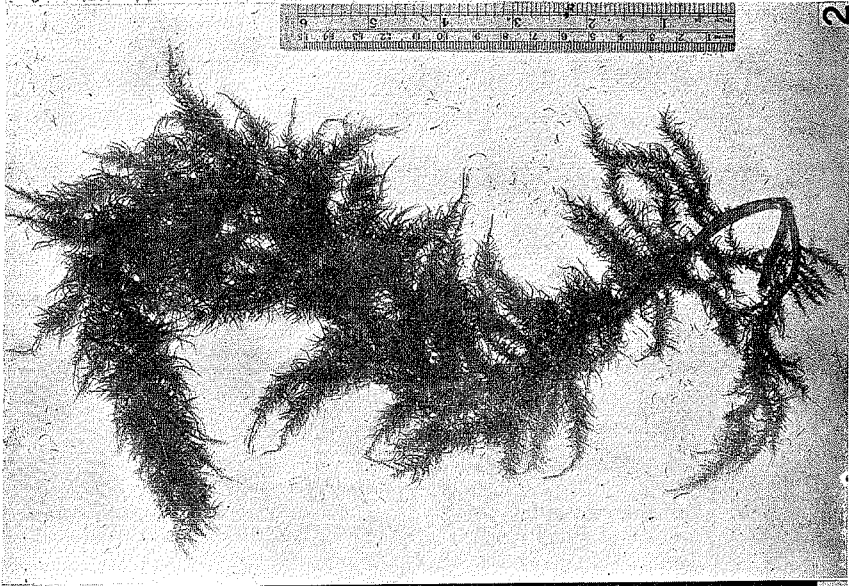
## PLATE XV

- FIG. 1. *Helminthocladia* from India. Habit of a female plant. 2/5 natural size.
- FIG. 2. *Helminthocladia australis* f. *ramosissima* from Stewart Island. A female plant.

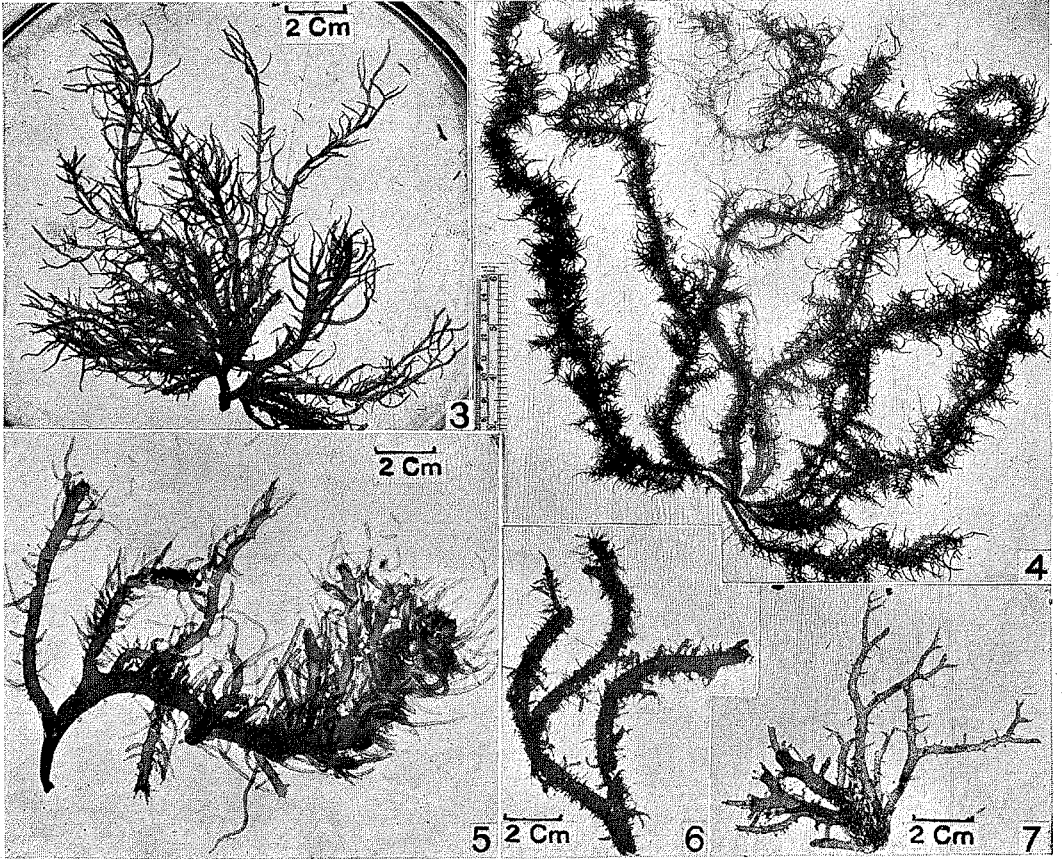
## PLATE XVI

- FIG. 3. *Helminthocladia* from Red Beach, New Zealand. A female plant.
- FIG. 4. *Helminthocladia australis* f. *ramosissima* from Stewart Island. A female plant.
- FIG. 5. *Helminthocladia* from Campbell Island. Female plant.
- FIG. 6. *Helminthocladia* from Narrow Neck near Auckland, New Zealand. A portion of the plant showing proliferation.
- FIG. 7. *Helminthocladia* from St. Leonard's Beach. Habit of a male plant.





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