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The Relationship between *Gracilariopsis* and *Gracilaria* from Japan

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The genus *Gracilariopsis* was distinguished from *Gracilaria* by Dawson¹⁾ mainly on the basis of the absence of nutritive filaments** extending from the placenta toward the pericarp in the cystocarp. A second character used by Dawson concerns the size of the gonimoblast cells, which supposedly are small in *Gracilariopsis*, large in *Gracilaria*. Dawson's segregation was accepted by many authors, but Papenfuss²⁾ proposed that these two genera should be merged, the reasons being that the presence of nutritive filaments could not always be confirmed in British material of *Gracilaria verrucosa* (the type species of its genus) and that there was no fundamental difference in the size of the cells of the placenta in that species compared with *Gracilariopsis sjoestedtii* (the type species of its genus).

In the course of the writer's studies on gracilariaceous plants of Japan, he examined carefully the materials and found that the nutritive filaments varied considerably in number not only between species, but also in different cystocarps in the same species. Considering Papenfuss's results and the writer's observations, it seemed very difficult to draw a definite line between these two genera on the presence or absence of nutritive filaments. As a result, the writer tried to establish a possible relationship between *Gracilariopsis* and *Gracilaria* on the basis of the three types of male organs in Japanese plants which he had reported previously in detail.^{3,4,5)}

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

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

3) **Verrucosa type:** This type is represented by *Gracilaria verrucosa*. A

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** The term "nutritive filament" is tentatively used in the description of the cystocarp in this paper, in agreement with other authors (Dawson, 1949; Ohmi, 1958; Papenfuss, 1966, etc.), until the function of this filament becomes clear in further study.

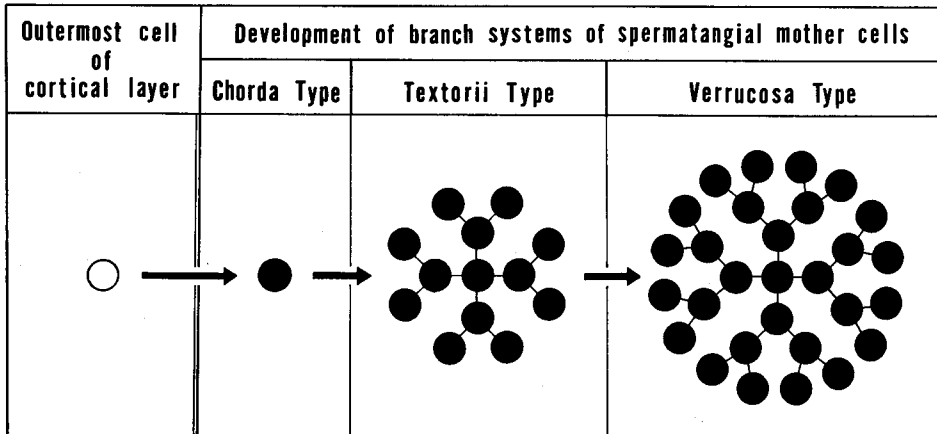


Fig. 1. Scheme showing possible phylogenetic line of advance among the three types of male organs.

spermatangial mother cell primordium is converted from an outermost cell of the cortical layer. Each mother cell primordium forms a branch system by dividing repeatedly. The vigorous growth of a branch system results in the formation of a deep, pot-shaped conceptacle and compresses the surrounding vegetative cells, causing them to become narrow and elongated. Spermatangia are produced by one or two divisions of each mother cell of the branch system, which finally covers the entire inner surface of the conceptacle. The conceptacles are not raised above the thallus surface.

The foregoing three types vary with respect to the degree of the conversion of the outermost cortical cells into spermatangial mother cells or mother cell primordia. In the Chorda type, all of the outermost cells may be converted into mother cells. In the other two types, on the other hand, there are some outermost cells that always remain sterile. The number of mother cell primordia per unit area is greater in the Textorii type than in the Verrucosa type and consequently the difference in the density of the conceptacles between these two types is apparent even in surface view. The fully mature conceptacles in the former are so crowded as to come in contact with one another and fuse in some cases. The conceptacles in the latter are distinctly separated by the outermost vegetative cells even at maturity.

In view of the formation of branch system of mother cells that covers the entire inner surface of a deep conceptacle, the Verrucosa type is considered to be the most efficient type with respect to spermatangial production. It seems likely that the Chorda type is the most primitive from the view point of phylogeny and the Verrucosa type the most advanced. The writer has looked in vain among Japanese materials for a bridge between the Chorda type (continuous superficial layer) and the other two types (conceptacles). It would appear, however, that *Gracilaria symmetrica* and *Gracilariopsis costaricensis*, which

Dawson¹⁾ described from Costa Rica as new species, are intermediate forms. In these species there is an anastomosis of small, circular, superficial sori separated by sterile cortical cells, but further detailed study of the developmental process would be necessary to clarify the situation.

After reviewing the literature and investigating the Japanese species of

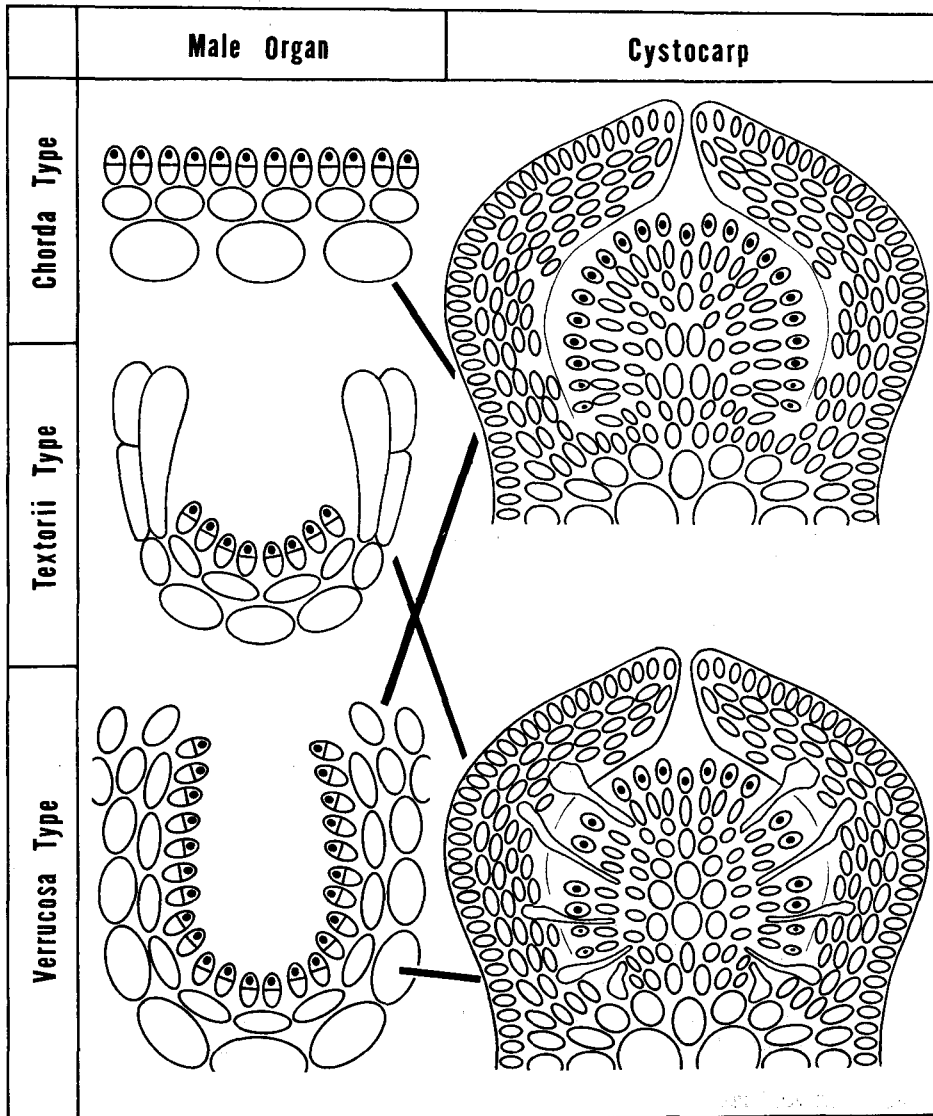


Fig. 2. Scheme showing the relationship between the three types of male organs and the structure of cystocarps.

Gracilaria, the writer suggests that a relationship may exist between the type of male organ and the presence or absence of nutritive filaments. Species belonging to the Chorda type always have cystocarps destitute of nutritive filaments, whereas the Textorii type appears exclusively in species having cystocarps provided with nutritive filaments. Though the Verrucosa type is almost the same as the Textorii type, Dawson^{1,6)} and Papenfuss²⁾ reported some species destitute of nutritive filaments in this type. Nutritive filaments are variable in number even in the same species depending on age and habitat, and are also found frequently in species usually assigned to the genus *Gracilariopsis* (Yamamoto, unpublished observations). The use of the nutritive filaments as a taxonomic character is thus seen to be unreliable. Each type of male organ, on the other hand, can be distinctly separated from each other in anatomy and arranged in a phylogenetic line. It thus seems more reasonable to consider the type of male organ as a fundamental character and the nutritive filament as a subsidiary element in the treatment of the systematics of this group of species. Papenfuss's proposal that the genus *Gracilariopsis* should be merged with the genus *Gracilaria* is therefore supported.

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

Subgenus *Gracilariella*

Spermatangia superficialia, dispersa continuo super paginam frondis.

Spermatangia superficial, scattered continuously over thallus surface.

Type species: *Gracilaria chorda* Holmes.

This subgenus includes only one Japanese species, *Gracilaria chorda* Holmes.

Subgenus *Textoriella*

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

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

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

This subgenus includes the following 8 species in Japan: *Gracilaria bursa-pastoris* (Gmel.) Silva, *G. gigas* Harvey, *G. blodgettii* Harvey, *G. denticulata* (Kuetz.) Weber van Bosse, *G. purpurascens* (Harv.) J. Agardh, *G. punctata* (Okam.) Yamada, *G. incurvata* Okamura and *G. textorii* (Sur.) De Toni.

Subgenus *Gracilaria*

Conceptacula spermatangiorum profunde olliformia, utrumque primordium

cellularum matricalium spermatangialium systema ramorum demum superficiem interioram totam conceptaculi obtectante formans, utraque cellula matricalis spermatangia procreans.

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

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

This subgenus includes the following 6 species in Japan: *Gracilaria verrucosa* (Huds.) Papenfuss (including material from Japan assigned to *G. rhodotricha* by Ohmi⁷⁾), *G. vermiculophylla* (Ohmi) Papenfuss, *G. arcuata* Zanardini, *G. edulis* (Gmel.) Silva, *G. sublittoralis* Yamada et Segawa and *G. coronopifolia* J. Agardh*.

The systematic position of the following species is not certain because male organs are not yet known: *G. crassa* Harvey, *G. salicornia* (C. Ag.) Dawson and *G. eucheumoides* Harvey.

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Summary

The relationship between *Gracilariopsis* and *Gracilaria* from Japan is assessed on the basis of the developmental process of the male organ as well as the existence of nutritive filaments in the cystocarp. Three types of male organs exist in the plants of Japan: Chorda type, Textorii type, and Verrucosa type.

The Chorda type is thought to be the most primitive, because all of the outermost cortical cells may be converted into spermatangial mother cells in a continuous superficial layer. The other two types appear advanced in that spermatangial branch systems and conceptacles are formed. The Textorii type differs from the Verrucosa type in having a larger number of mother cell primordia but forming a less extensive branch system. The relationship between the existence of nutritive filaments in a cystocarp and the three types of male organs is discussed. It is concluded that the genus *Gracilariopsis* should be merged with the genus *Gracilaria*, and three subgenera are proposed on the basis of the three types of male organs.

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* The male organ of this species is known but has not yet been discovered in Japanese material.

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