An evaluation of some vegetative features and some interesting problems in Japanese populations of *Gracilaria*

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Okamura was the first to study Japanese species of *Gracilaria*, and described 11 species between 1901 and 1936 (Okamura 1936). Yamada (1933, 1938, 1941) followed him and added three new species for Japan. Historically, species were identified mainly on the basis of external features, for example, branching mode, the grade of constriction at the bases of branches, and so on. Subsequently, Ohmi (1958) reviewed Japanese species, introducing Dawson's system (Dawson 1949) and assigning three species to *Gracilariopsis* and 13 species to *Gracilaria*.

Fifteen years ago, the study of Japanese *Gracilaria* remained as it had been completed by those three researchers. My research has focussed on the male reproductive organs (spermatangia) of each species and their development. Through these studies, I recognized the spermatangial distinctions as made by Thuret & Bornet (1878) and Dawson (1949, 1961) and applied them to Japanese *Gracilaria* which allowed a systematic arrangement based on this characteristic (Yamamoto 1975, 1978).

Table 1 shows the five spermatangial patterns which have been reported in species from all over the world. In Japanese species, only three of these patterns have been confirmed to date. I termed the three Japanese patterns Chorda-type, Textorii-type and Verrucosa-type, each after the earliest species in each group (Yamamoto 1975). Type 2 has been described by Dawson (1949) in *G. symmetrica* and *G. costaricensis*. This type is discontinuously superficial and seems to be slightly more advanced than the Chorda-type in view of the degree of the conversion of the outermost cortical cells into spermatangial mother-cell primordia. Consequently, I think it might be reasonable to place this type after the Chorda-type in a systematic line. However, it is still questionable whether this type should be independent from the others or merged with the Chorda-type. Type 5 was first discovered in *G. multifurcata* by Børgesen (1953). This type seems to be the most complicated and advanced. Since I have never examined the developmental process of this type, it is ranked next to Verrucosa-type tentatively. However, I must add that Chang & Xia (1963) have established a new genus *Polycavernosa* in Gracilariaceae on the basis of the combination of prostrate rhizome and type-5 spermatangial pattern.

Among Japanese species, it has not been possible to associate any features of the female reproductive organs that could be consistently tied to spermatangial characteristics and if such were found, generic segregation would have been contemplated. However, I did not find any difference in female reproductive organs. In the present overall classification of red algae, the male features are less impor-

Table 1. Spermatangial patterns in *Gracilaria*.

Type 1 →	Type 2 →	Type 3 →	Type 4 →	Type 5
continuously superficial	discontinuously superficial	shallow cavity	deep pot-like cavity	aggregation of Verrucosa type
Chorda type ↓	Symmetrica type ↓	Textor ii type ↓	Verrucosa type ↓	Henriquesiana type ↓
Subgenus Gracilariella	Subgenus ?	Subgenus Textoriella	Subgenus Gracilaria	Subgenus ? / Genus Polycavernosa

tant than those of the female, therefore too much emphasis on the male might make the relationship with other genera unbalanced.

There are 19 species of *Gracilaria* in Japan. Of those species, the male reproductive organs have been described in 15 species (Table 2). Male reproductive organs of four species have never been found and *G. eucheumoides* is one of those. Male plants as well as carposporic and tetrasporic are commonly collected for all species except the rare *G. sublittoralis* and *G. cuneifolia.*

Classification based only on reproductive organs is inconvenient in practice because, as is often pointed out, the reproductive organs are only one of the indicators in the practical identification of a species. Good all-around indicators are needed, which are visible regardless of whether the frond is young or old, in whole or in part. I have been trying to find some diagnostic differences in vegetative structure but have not found any which are wholly reliable. Nevertheless, certain vegetative features bear further examination, i.e., shape of fronds, their color, and their texture.

The most effective way to divide Japanese species into groups is based on whether fronds are cylindrical or flattened in cross-sectional view. This method was once used in the early years of the classification. As far as Japanese species are concerned, this classification is convenient and very useful with uniform results in Japan. However, May (1948) reported the fronds of *G. lichenoides* (now *G. edulis*) of Australia were usually cylindrical but sometimes flattened, and if her identification is correct, the value of this procedure for that species is diminished and indicates that it cannot be used universally. Nonetheless, this procedure may deserve more attention in other parts of the world.

Table 2 shows the cylindrical- and flattened-frond species with their spermatangial pattern as far as is known, and some vegetative features of each species. There is a tendency for cylindrical-frond species to be of the Verrucosa- or Chorda-type spermatangial arrangement. Of these cylindrical-type species, three of them, *G. verrucosa, G. vermiculophylla* and *G. chorda* are the most difficult to distinguish from each other on the basis of external form, but fortunately each of them has a distinctive color which rarely changes as a function of environmental conditions. For example, *G. chorda* is reddish, *G. verrucosa* is light or dark

Table 2. Main features and spermatangial patterns of Japanese *Gracilaria.*

Species	Features	Spermatangial pattern
Cylindrical		
G. chorda	reddish	Chorda-type
G. bursa-pastoris	soft, dichotomously branching	Textorii-type
G. gigas	cartilaginous	T
G. blodgettii	reddish, constricted at branch bases	T
G. verrucosa	light or dark brown	Verrucosa-type
G. vermiculophylla	blackish	V
G. arcuata	branches curved	V
G. edulis	rigidly cartilaginous	V
G. coronopifolia	branches anastomotic	?
G. salicornia	articulated	?
G. crassa	articulated	?
G. eucheumoides	compressed, prostrate	?
Flattened		
G. textorii	leathery, medullary cells less than 600 μm	Textorii-type
G. incurvata	soft, twisted	T
G. punctata	lobes obovate	T
G. denticulata	margins dentate, branches more than 3 mm wide	T
G. purpurascens	margins dentate, branches less than 3 mm wide	T
G. cuneifolia	membranous	T
G. sublittoralis	leathery, medullary cells more than 600 μm	Verrucosa-type

brown and *G. vermiculophylla* is blackish or blackish brown. Since these colors are very characteristic, even though these specimens are mingled it is relatively easy to identify each from the mixture. *Gracilaria blodgettii* is also similar to *G. chorda* in external form, but can be distinguished by its dark or purplish red color, and by the extremely constricted bases of branches. Although species other than the ones mentioned are similar in color, they each have their own characteristic external form. Using characteristics such as branching mode, constriction at the basal portion of branches and form of branches, it is not very difficult to separate them. In another example, *G. bursa-pastoris* and *G. gigas* look alike, but the texture of the fresh plants is different, i.e. *G. bursa-pastoris* is soft, and *G. gigas* is rather hard and cartilaginous.

In contrast, species of the flattened-frond type have color similar to each other, so the color is useless for distinguishing species. But flattened-frond species have very characteristic external form which makes them distinguishable from each other. The most difficult problem is with the forms of *G. textorii* which vary by geographic location. One local form of *G. textorii* is like *G. incurvata,* the other one is like *G. sublittoralis* and in addition, a local form often assumes a markedly different appearance from the norm. As *G. textorii* has a rather wide distribution range in foreign countries, I am interested in the variability of its external characteristics.

I have been evaluating differences in the vegetative structures, especially in the gradation of cell size from the outermost layer to the medulla. No definitive difference among species has been found except in *G. eucheumoides.* This species has a gradual transition, while all of the others have an abrupt one.

Table 3 shows a summary of indicators for distinguishing Japanese species. If spermatangial pattern is available, the combination of it and other criteria mentioned above makes the identification of species easier.

Japan is located between the subarctic and subtropical zones. Consequently, there is considerable difference in the water temperature between the northern and southern parts. In northern Japan, the water temperature varies from a maximum of 17 °C to a minimum of 0 °C. In southern Japan, it varies between 29 °C and 19 °C. The difference in water temperature between the districts seems to affect the distributional pattern of each species.

What is called *G. verrucosa* has the widest distribution and is the only species found throughout Japan. All of the other species have limited distributional ranges (Fig. 1). Generally speaking, more species are found in the warmer region than in the colder region. Some species such as *G. eucheumoides, G. blodgettii* and *G. denticulata* are confined to the southern part of Japan.

Japanese *Gracilaria* populations seem to be very closely related to Chinese populations, because there are 13 species in common between the two

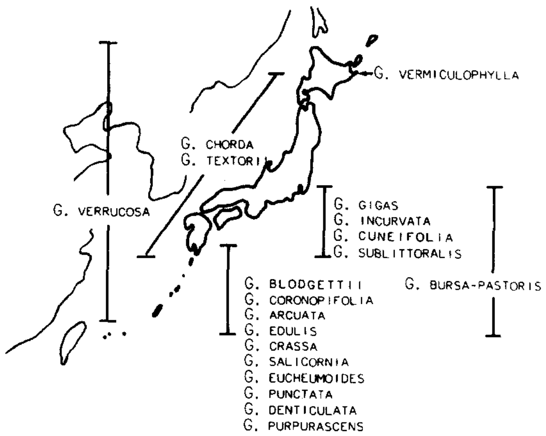

Fig. 1. Distributional range of Japanese species of *Gracilaria.*

Table 3. Indicators for distinguishing Japanese species of *Gracilaria.*

cylindrical →	color →	texture →	branching mode →	cell size in medulla
flattened	↑		form of branch	gradation of cell size, cortex to medulla
			condition of margin	
			constriction at branch base	
	spermatangial pattern			

floras. I think that Japanese *Gracilaria* must have originated from southeast Asian populations. Southern Japan is on the fringe of the distribution of those species which have the center of their distribution in southeast Asia. From this situation, I wonder whether the Japanese species are typical of those southeast Asian and Chinese populations. As it is generally known, the features of individuals far from the center of the distribution are liable to show variation from the typical form.

A problem exists with *G. verrucosa* which is the most common species in Japan. This species is of the Verrucosa-type of spermatangial pattern. I am not sure whether or not the spermatangial pattern is changeable with morphology, because I have seen a report (Kim 1970) which considers this species to have Textorii-type spermatangia (Ed. note: see paper of Bird & McLachlan, this volume). I feel that it is necessary to reexamine the specimens that have been identified as *G. verrucosa* throughout the world. There are probably many separate species included in the taxon known as *G. verrucosa.*

On the other hand, *G. chorda* was collected in Japan for the first time and later reported in China (Chang & Xia 1976). The distributional range of this species is rather wide. It occurs all around Japan except in the southernmost district. Towards the colder regions, however, the female and male reproductive organs become more uncommon, and in the coldest region, they have never been seen in spite of extensive investigations there. Reproduction is apparently accomplished only by tetraspores and new shoots from old fronds. The life cycle of this Japanese species does not include all of the normal stages at the northern extreme of its range in Japan, and shows only an imperfect life cycle there. In addition to life cycles, I am also interested in the relationship between *G. sjoestedtii* of the coast of China and the western coast of the United States, and *G. chorda* of Japan, as these species have the superficial type of spermatangial pattern in common, *G. chorda* being the only species in Japan having this type of pattern. *Gracilaria sjoestedtii* is the type species of *Gracilariopsis* which Dawson (1949) established on the basis of absence of 'nutritive filaments' in the cystocarp together with superficial spermatangia.

The interesting point of *G. vermiculophylla* is that its distributional range is confined to a single lagoon in the coldest-water region of Japan. One might expect that it would be very sensitive to the variation of environmental conditions, but unexpectedly it is very adaptable to other conditions. Experimentally, I have determined that this species is both euryhaline and eurythermal and that laboratory culture of the complete life cycle is easily accomplished. Another interesting point is that the 'nutritive filaments' of this species are as few as were once diagnostic of *Gracilariopsis,* in spite of the fact that it has the Verrucosa-type of spermatangial pattern.

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