

Taxonomic criteria in the genus *Gracilaria* Grev. (Rhodophyta): An experience with the western Atlantic species

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Introduction

The majority of *Gracilaria* species from the warm waters of the American Atlantic can be identified with reference to Taylor (1960). However, examination of extensive collections leads to unconvincing naming of specimens. This situation is not peculiar to the warm Atlantic but also to other areas having already received monographic treatment of *Gracilaria* (e.g., Bodard 1966; May 1948; Umamaheswara Rao 1972). In a better situation regarding *Gracilaria* taxonomy are Baja California, Mexico (Dawson 1949), Japan (Ohmi 1958; Yamamoto 1978), and China (Chang & Xia 1976). Even so, the existence in these areas of taxa with very broad disjunct distributions is still a matter of concern that justifies further studies.

In an attempt to monograph the genus in the western Atlantic (Oliveira, *et al* 1983) we were faced with several difficulties, indicating the necessity of assessing the usefulness of the traditional as well as some new criteria to separate the infrageneric taxa. This paper summarizes my personal view on the taxonomy of this genus based on the study of the western Atlantic material.

Distribution

Recent reports on the occurrence of *Gracilaria* in the western Atlantic place the distribution limits at about 47°N (Chapman, *et al*, 1977) and 45°S (Mayer 1981), with each limit reached by only one species, although former papers refer to a larger number of species and a broader southern limit (cf. Papenfuss 1964). While recognizing that it is still premature to map the species distribution in view of the numerous taxonomic problems, the general trend shown in Fig. 1 and Table 1 should not change very much, as the genus has its center of dispersal in the warmer waters of the region.

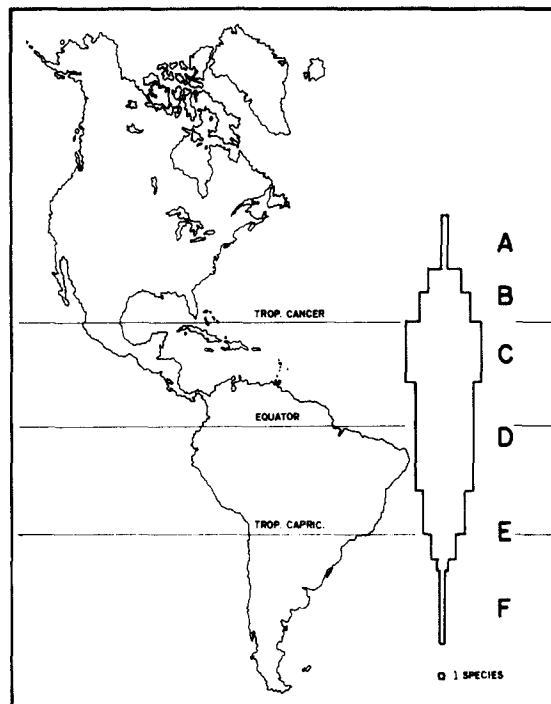


Fig. 1. Distribution of *Gracilaria* species in the American Atlantic based on data from Taylor (1960), Oliveira (1977), McLachlan (1979) and Mayer (1981). The species present in each zone are shown in Table 1.

Taxonomic criteria

Gross morphology. The macroscopic morphology, manifested as size and thallus architecture, was the basis for the first species distinction, and included the morphology of the basal and apical portions of the lateral branches, color, texture and adherence to herbarium paper. Although strongly criticized as unreliable (May 1948) these criteria are still extensively used in modern works (Yamamoto 1978) in combination with anatomical and reproductive characters. In this context, and if used within a limited geographical area and based on an adequate

Table 1. Distribution of the western Atlantic species as referred to by Taylor (1960), Oliveira (1977), McLachlan (1979) and Mayer (1981) along the zones shown in Figure 1.

Species	Zone	Species	Zone
<i>G. andersonii</i>	E	<i>G. domingensis</i>	C-E
<i>G. armata</i>	B-E	<i>G. ferox</i>	B-E
<i>G. blodgettii</i>	B-D	<i>G. foliifera</i>	B-E
<i>G. compressa</i>	B-D	<i>G. mammillaris</i>	B-E
<i>G. cearensis</i>	D	<i>G. ornata</i>	C-D
<i>G. cervicornis</i>	B-E	<i>G. sjoestedtii</i>	B-E
<i>G. crassissima</i>	B-C	<i>G. tepocensis</i>	E
<i>G. cuneata</i>	C-D	<i>G. tikvahiae</i>	A
<i>G. curtissiae</i>	C-D	<i>G. venezuelensis</i>	C
<i>G. cylindrica</i>	C-D	<i>G. verrucosa</i>	B-E
<i>G. damaecornis</i>	B-C	<i>G. usneoides</i>	C
<i>G. debilis</i>	B-D	<i>Gracilaria</i> sp.	F

sample, they can be very useful and in most occasions enough for a first identification hypothesis. Recently we found a curious distribution of an unknown calcium deposit on an unidentified species of *Gracilaria* from Brasil (Fig. 2; Oliveira & McLachlan, unpubl.), that could also be used as a diagnostic character.

Anatomy. The structure of the thallus as seen in cross section has been used in the taxonomy of *Gracilaria* since J. Agardh (1876). He established the categories Micro-, Macro-, Platy- and Plectocystideae (Agardh 1901), based on the transitional pattern of cell size and shape between the cortex and the medulla. The importance of these group-

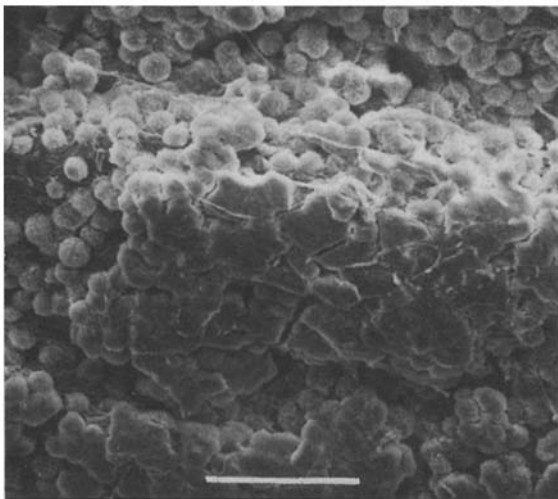


Fig. 2. SEM of calcium deposit on thallus surface of *Gracilaria* sp. from Itamatata (PE), Brasil. Bar = 100 μ m (Oliveira & McLachlan, unpublished).

ings have been stressed by some authors (e.g., May 1948) and neglected by others (Taylor 1960); however, they are helpful in distinguishing terete species, especially when typical micro- and macrocystidiate structures are recognized. The presence of small cells of various sizes among the typically large medullary cells is an attribute of some species such as *G. crassissima* Crouan & Crouan ex. J. Ag. and the '*G. debilis* complex' (Oliveira, Bird & McLachlan, unpublished), and although very conspicuous have not been reported thus far in these species. The number of cortical layers, here understood as a succession of outer cells of approximately the same size, is an additional character if used to compare branches of similar stages of development. The more quantitative and elegant approach of Yamamoto (1978) to this problem did not give rewarding results so as to justify its use on the western Atlantic species.

The thickness of the medullary cell walls can be utilized as a taxonomic criterion, but only in extreme cases as we noticed some variation in specimens of the same population depending on the way the material was treated, the preservation, resoaking and mounting medium used. The frequency of hair scars on herbarium material varies from plant to plant and along the same thallus; hair cells are very similar in most species, but their size and shape are distinctive in the *G. debilis* complex. The existence of small protoplasm-rich cells among the large medullary cells, as first referred to in *G. cervicornis* (Turn.) J. Ag. and *G. domingensis* Sonder ex Kütz., pro syn. (Oliveira, *et al* 1983) is certainly helpful as another diagnostic character.

Reproduction. Descriptions of the size, shape and distribution of the cystocarps are as old as the genus itself. Their structure, including the presence of the connecting tubes ('absorbing filaments') between the pericarp and the gonimoblast, was correctly described and beautifully illustrated by Thuret & Bornet in 1868. Significant progress in studies of the ontogeny of the *Gracilaria* cystocarp was attained only much later by Sjöstedt (1926) who recognized and clearly presented differences in the structure of the gonimoblasts. Those differences were emphasized by Dawson (1949), who erected the genus *Gracilariopsis*, subsequently synonymized with *Gracilaria* by Papenfuss (1966), although this has not been accepted unanimously (Umamaheswara Rao 1972). The literature is controversial

about the importance of the size and content of the gonimoblastic cells in the taxonomy of the genus (Papenfuss 1966; Edelman, *et al* 1978). In the western Atlantic species, the frequency of the connecting tubes can vary among cystocarps of a single specimen; however, their presence versus absence, if carefully screened in this case, is still a useful character to distinguish species.

The structure of the pericarp as a diagnostic character was especially stressed by Bodard (1966) and Chang & Xia (1976), but was questioned by Yamamoto (1978). We noticed that the pericarp structure varies with the cystocarp maturity, and that usually three distinctive cell types are recognized in most species: the two or three outer (radially elongated), the several median (radially flattened) and the two or three innermost (roundish) layers of cells, probably reflecting different mechanical pressure during the cystocarp ontogeny. In some cases, the existence of extensive cell fusions and peculiar sclereid-like cells (Oliveira, *et al* 1983) as well as the regular production of vegetative branches from the pericarp (Fig. 3) can be used as diagnostic features. The carpogonial branches and postfertilization development seen in several western Atlantic species seems to be fairly uniform in the genus, supporting published accounts (Sjöstedt 1926; Yamamoto 1978).

The different patterns of spermatangial grouping were described as early as 1868 by Thuret, who recognized three basic types. However, their importance as a specific character was rediscovered much later by Dawson (1949), followed by Chang & Xia

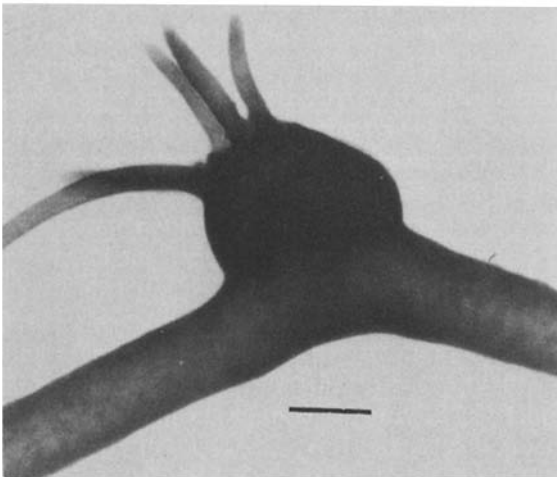


Fig. 3. Cystocarp of *Gracilaria* sp. from Itanhaem (SP), Brasil, showing young branches arising from the pericarp. Bar = 1 mm.

(1976), and especially emphasized by Yamamoto (1978) who used this feature to distinguish subgenera. The spermatangial grouping so far seems to be constant within populations and can be easily recognized, despite the occurrence of transitional types in a few species. As the type of spermatangial grouping was usually not described earlier and as they cannot always be found in the type collections, they should be sought in additional material from the type locality whenever possible.

The grouping of tetrasporangia has limited value as a specific character. The degree of modification of the cortical cells on tetrasporic plants, although used by some authors, is not a reliable character since it varies in the material studied as a consequence of the stage of maturation and closeness of sporangia. The same applies, with very few exceptions, to the sizes of the tetrasporangia, for it is difficult to assess their degree of maturation.

Recent approaches. So far, only a few species of *Gracilaria* have had their chromosome number determined (cf. Bird & McLachlan 1982), and since the chromosome number is identical in all but one species, this feature may have only limited value. The same can be said about the few chemotaxonomical approaches to the genus, although some species could be separated on the basis of gel strength and sulfate content (Hong, *et al* 1969). Other attempts to 'fingerprint' the species on the basis of chemical substances such as carotenoids (Brown & McLachlan 1982), sterols and fatty acids (J. Wright, pers. commun. 1979), proved unsuccessful.

The life history in the group, as expected, shows no basic deviation from the '*Polysiphonia*-type' in the species studies so far (Oliveira & Plastino 1984) except for the known mixed reproductive phases in some species.

Conclusions

Considering the economic importance of *Gracilaria* in the western Atlantic as well as elsewhere, it is imperative to have a workable system of species recognition. Obviously the purpose of this system should be clearly established a priori: will it (a) consider mostly the industrial perspective, (b) attempt a phenetic, or (c) a phylogenetic classification? Alternative (a) can be approached by screen-

ing the populations for strains showing desired agar quality, followed by their maintenance in culture for further improvement. If the purpose is the one stated in (b), its stability demands a study of all the type specimens and history of the epithets, including supplementation of the original collections, whenever possible, with material from the type locality in order to secure tetrasporic, male and cystocarpic plants. The objectives of (c) will be attained through cladistics, including experimental taxonomy. Although the three systems will mutually profit from progress in the others, they can always maintain a considerable degree of independence.

My experience with the American Atlantic species indicates that the first priority is that of obtaining a realistic, utilitarian and stable phenetic system that would provide testable hypotheses for a phylogenetic approach. This will be attained only through an extensive and critical analysis of the morphology and anatomy of all the reproductive phases, based on sample sizes large enough to comprise a significant amount of the existing variability in the populations. At this state of our knowledge there seems to be little hope for the more recent and sophisticated techniques of plant analysis including information from allozymes and DNA hybridization. Numerical analysis is a powerful technique and certainly will be useful in some specific situations when we manage to gain a better understanding of the criteria to be utilized.

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