



***Gracilaria*, Subgenus *Textoriella* (Gracilariaceae, Rhodophyta) in the Gulf of Mexico and the Mexican Caribbean**

***Gracilaria*, subgénero *Textoriella* (Gracilariaceae, Rhodophyta) en el golfo de México y el Caribe mexicano**

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Abstract. Four species of *Gracilaria* (Gracilariaceae, Rhodophyta) with *textorii*-type spermatangial conceptacles (subgenus *Textoriella* Yamamoto) are recorded for the Gulf of Mexico and the Mexican Caribbean: *Gracilaria blodgettii*, *G. cervicornis*, *G. mammillaris*, and *G. tikvahiae*. The general distribution of the subgenus for Central America, both Pacific and Atlantic, displays a disjunct pattern explainable based on the geologic vicariant events that interrupted the connection between Pacific and Atlantic at the Isthmuses of Panama (closed 3.1-2.8 million years ago), and Tehuantepec (southern Mexico, closed 4-3.5 million years ago). *Gracilaria cuneata*/*G. crispata*, and *G. mammillaris* (*G. hayi*)/*G. veleroae* are 2 pairs of sibling species, or sister taxa, that diverged as a result of the final emergence of the Isthmus, and of the same age as the Central American Isthmus itself.

Key words: *Gracilaria*, *Textoriella*, floristics, biogeography.

Resumen. Se registran 4 especies de *Gracilaria* (Gracilariaceae, Rhodophyta) con conceptáculos espermangiales tipo *textorii*- (subgénero *Textoriella* Yamamoto) para el golfo de México y Caribe mexicano: *Gracilaria blodgettii*, *G. cervicornis*, *G. mammillaris* y *G. tikvahiae*. La distribución general del subgénero para Atlántico y Pacífico de Centroamérica despliega un patrón disyunto explicable por los eventos geológicos vicariantes que interrumpieron la conexión entre Pacífico y Atlántico en los istmos de Panamá (cerrado hace aprox. 3.1-2.8 millones de años) y Tehuantepec (sur de México, cerrado hace aprox. 4-3.5 millones de años). *Gracilaria cuneata*/*G. crispata* y *G. mammillaris* (= *G. hayi*)/*G. veleroae* corresponden a 2 pares de especies hermanas que divergieron como resultado de la emersión del istmo, y con aproximadamente la misma edad del istmo centroamericano.

Palabras clave: *Gracilaria*, *Textoriella*, florística, biogeografía.

Introduction

The genus *Gracilaria* Greville *sensu lato* (incl. *Gracilariopsis* E.Y. Dawson, and *Hydropuntia* Montagne, Gracilariaceae, Rhodophyta) are distinguished from other gracilarioid algae in the structure and organization of male cells or spermatia. There are 4 recognized general arrangements (Homi 1958; Yamamoto 1975, 1978; Liao and Hommersand, 2003): in superficial or epicortical sori; in cortical concave depressions, in deep cortical oval depressions, single or confluent, and in subcortical multi-cavernous conceptacles. Based on the differential distribution of these anatomical patterns within the genus *Gracilaria*, Yamamoto (1975) proposed the taxonomic

establishment of 3 subgenera. The first, *Gracilariella* Yamamoto, is characterized by superficial spermatangia distributed all over the algal surface. The type of this subgenus is *Gracilaria chorda* Holmes. The second subgenus is *Textoriella* Yamamoto, which is characterized by spermatangial conceptacles in shallow depressions, each primordium of spermatangial mother cell giving place to a branched system that covers the floor of conceptacle when mature, each spermatangial mother cell producing spermatia. The type of *Textoriella* is *Gracilaria textorii* Suringar De Toni. Finally, subgenus *Gracilaria* has spermatangia in deep oval conceptacles, with each primordium of spermatangial mother cells giving rise to a branched system that covers the inner surface of the whole conceptacle when mature; each spermatangial mother cell produces spermatia. The type of this subgenus is *Gracilaria*

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verrucosa (Hudson) Papenfuss. Recently, Tseng and Xia (1999) proposed a fourth subgenus, *Hydropuntia*, based on the occurrence of spermatangia in multi-cavernous conceptacles. The type of *Hydropuntia* is *Gracilaria edulis* (S. G. Gmelin) P. C. Silva.

The only available monograph of Gracilariaceae on the Mexican shores of the Gulf of Mexico and the Caribbean Sea is Taylor (1960). Because the family has experienced a great deal of taxonomic changes during the last 45 years, a monographic project that incorporates those changes is needed. As a part of that project, we present here our results on the subgenus *Textoriella*.

Materials and methods

Algal material was collected along the Mexican shores of the Gulf of Mexico (Tamaulipas, Veracruz, Tabasco, Campeche), and the Mexican Caribbean (Yucatán and Quintana Roo) throughout the past 10 years, preserved in 3-4% formalin/seawater solution, and housed as herbarium specimens at UAMIZ. We also studied herbarium material from AHFH, CIQRO, ENCB, FCME, MEXU, UAT, UC, UNL, and US. Small segments were cut into cross or longitudinal sections with a razor blade, stained with aniline blue, and mounted in 100% glycerine for anatomical observations. When specimens came from dry material, segments were rehydrated in a 1-2% aqueous solution of children's shampoo and warmed for 1-2 min in a microwave oven before sectioning. Schematic drawings of the 4 gracilariacean spermatangial types mentioned above were drawn with pen and ink on bright-white 90 g paper from a Leica™ DMLB compound microscope, and are presented below as figures 1-5. Maps were also drawn on bright-white 90 g paper, and composed with Adobe™ Photoshop™ CS2. Photographs were taken with a Nikon™ D60 digital camera equipped with a standard Nikon™ 35-55 mm Zoom lens.

Descriptions

Gracilaria blodgettii Harvey, 1853: 111 (Type loc.: Key West, Florida, USA).

Synonym: *Gracilaria cylindrica* Børgesen, 1920: 375-377, figs. 364 and 365 (Syntype locs.: Virgin Islands; north of America Hill, St. John, and between St. John and St. Thomas). Figs. 6 and 7.

Thallus erect, up to 14 cm tall, texture soft, substance rubbery, dark red to pinkish *in situ*, pale brown once fixed. Adherence to herbarium sheets good. Holdfast a disc, small. Branching irregular, in more than one plane,

second or alternate in some parts. Axis and branches terete, (1.2)1.6-1.7(1.9) mm diameter, constant in width, branches strongly constricted at the bases, frequently arched. Segments between forks variable in length. Apex rounded. Stipe large. Transition between medulla and cortex abrupt. Medulla with 7-10 cells, subspherical to polygonal (240)340-600(740) µm diameter. Cortex formed by (1-3)8-12(15) cellular layers. Cortical cells (6)10-15(20) µm large, 7-10(20) µm diameter, anticlinal. Spermatangia 30-45 µm high, 30-50(50) µm wide. Cystocarps hemispherical, apiculate and sessile, 550-880 µm high, 750-1000(1200) µm diameter. Carpospores in clusters. Gonimoblast columnar. Tetrasporangia ovate, 28-50 µm large, 26-35 µm diameter, distributed all over the thallus except on main axis, apical region and stipe, rounded by 2-4 cortical cells, pyriform, and longer than ordinary.

Selected specimens: Tamaulipas: ENCB 4977, Escolleras de Altamira, Ma. E. Sánchez R., 28.09.1983. Veracruz: ENCB 10461, Sobre Malecón, calle Colón, C. Mendoza et al., 17.06.1993. Campeche: ENCB 2955, Playas cercanas a Ciudad del Carmen, Rzedowski #30048, 23.12.1972; ENCB 2969, 69 km al N.E. de Isla Aguada, sobre la carretera a Champotón, Rzedowski #30098, 23.12.1972; MEXU 1340, La Laguna de Términos, en la desembocadura de Ciudad del Carmen, M.M. Ortega #1027, 00.05.1964. Quintana Roo: ENCB 6680, Isla Mujeres, C. Mendoza, 01.03.1985; ENCB 8793, Puerto Morelos, C. Mendoza, 13.06.1987; ENCB 6614 Playa Lancheros, Isla Mujeres, L.E. Mateo, 10.10.1983. Note: Synonym proposed by Norris and Fredericq (1990), and Fredericq and Norris (1992).

Gracilaria cervicornis (Turner) J. Agardh, 1852 [1851-1863]: 604.

= *Fucus cervicornis* Turner, 1808-1809: 131-132, pl. 121 (Type loc.: West Indies).

Synonym: *Gracilaria ferox*. J. Agardh, 1852 [1851-1863]: 592 (Lectotype loc.: Martinique, West Indies *fide* Oliveira et al., 1983:3003). Figs. 8 and 9.

Thallus erect, up to 10-25 cm tall, texture smooth, substance tough, brown red to yellowish green. Axes and branches complanate, 1-5 mm width. Branching dichotomous, in 2 planes, bases continuous (with no constrictions). Adherence to herbarium sheets regular to good. Margins with horn-like (*cervicornis*) branchlets. Segments between forks variable in length. Stipe very short or inconspicuous. Holdfast not distinct, disc-like. Apex, as margins, with horn-like processes or branchlets. Subcortex formed by 2 cellular layers, each 20-30 µm diameter, slightly pigmented. Transition is, however, abrupt. Cortex composed by 1-7 cellular layers, superficial or external

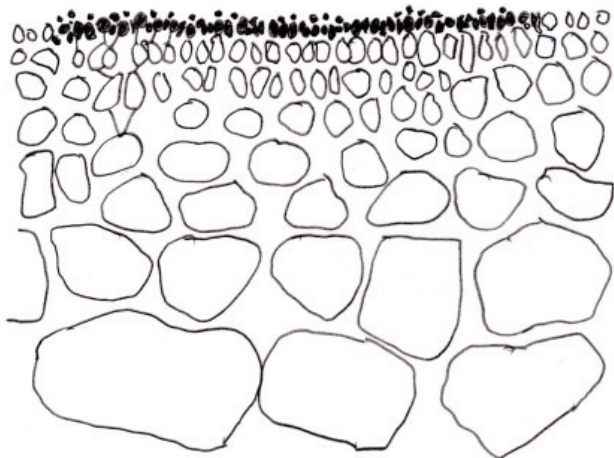


Figure 1. Schematic drawing of superficial or epicortical spermatangial sori (characteristic of genus *Gracilariopsis* E.Y. Dawson).

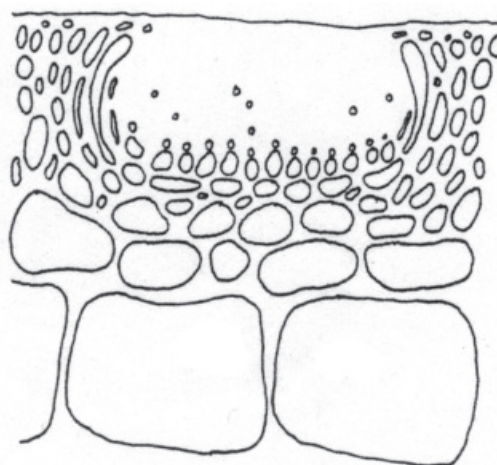


Figure 2. Schematic drawing of cortical concave spermatangial depressions (characteristic of the “Textoriella complex” of *Gracilaria* Greville).

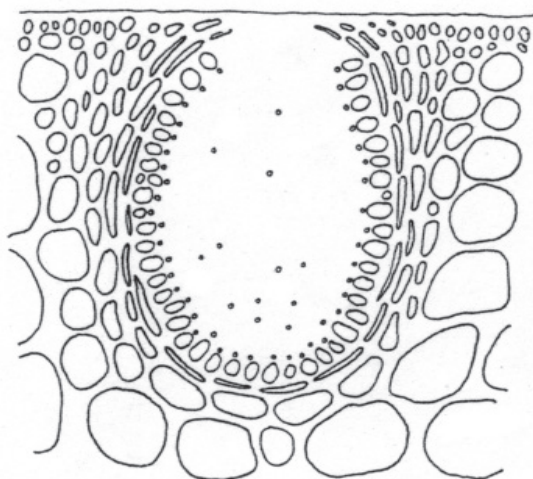


Figure 3. Schematic drawing of single deep cortical oval spermatangial depressions (characteristic of the “Verrucosa complex” of *Gracilaria* Greville; best morphological representative is *Gracilaria gracilis* (Stackhouse) Steentoft, Irvine et Farnham).



Figure 4. Schematic drawing of confluent deep cortical oval spermatangial depressions (characteristic of the “Verrucosa complex” of *Gracilaria* Greville; best morphological representatives are *Gracilaria damaecornis* J. Agardh, and *Hydropuntia* -*Gracilaria*?- *caudata* (J. Agardh) Gurgel et Fredericq).

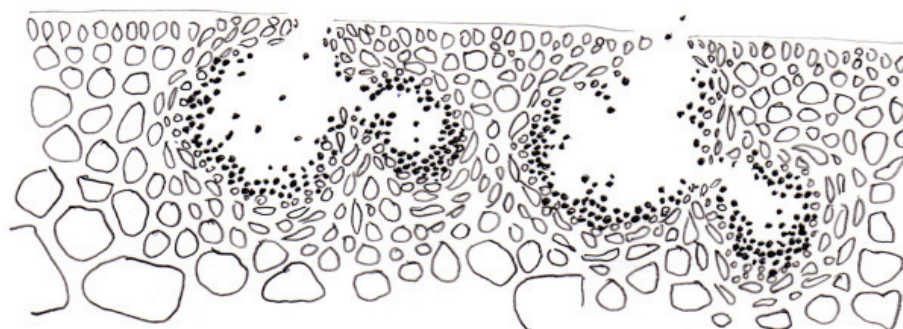


Figure 5. Schematic drawing of subcortical multi-cavernous spermatangial conceptacles (representative is genus *Hydropuntia* Montagne).

ones 6-10 μm diameter, very pigmented, anticlinal. Medullar cells hemispherical, 170-300 μm diameter, thick cell walls with no pigmentation, less than 10 layers from one surface to the other (in cross section). Spermatangia 40-60 μm width, 35-40 μm depth. Cystocarps hemispherical, 0.5-1.1 mm diameter, mostly on horn-like branchlets, base-constricted



Figure 6. Habit of *Gracilaria blodgettii* Harvey.



Figure 7. Mexican Atlantic distribution of *Gracilaria blodgettii* Harvey.



Figure 8. Habit of *Gracilaria cervicornis* (Turner) J. Agardh.

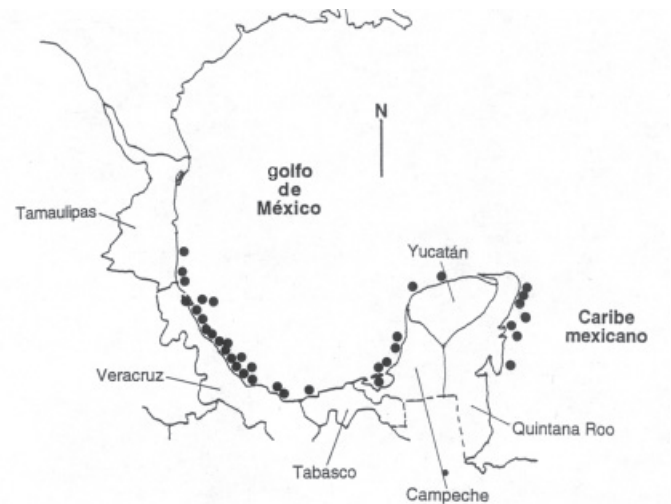


Figure 9. Mexican Atlantic distribution of *Gracilaria cervicornis* (Turner) J. Agardh.

and apiculate. Carpospores in clusters. Gonimoblast columnar. Nutritive tubular cells in contact with external pericarp. Tetrasporangia ovate, 30–40 μm large, 22–25 μm diameter, spread in wide groups (but not sori) below external cortical cells, specially on flattened branches at medium-superior thirds.

Selected specimens: Tamaulipas: ENCB 4785, Escolleras del río Pánuco, Ciudad Madero, Leg.: H. Alfaro García, 17.10.1982, Det.: J.M. López Bautista, Hab.: Sobre rocas a 2 m de profundidad. Veracruz: UAMIZ 487, Morro de La Mancha, K.M. Dreckmann, 02.12.1990; UAMIZ 752, Barra de Cazones, Laguna de Tamiahua, N. Hernández Soto M-26, 06.06.1994; US 34264 (Barcode: 00551339), Bajo Tuxpan, J.F. Longoria #102, 17.07.1965. Campeche: ENCB 4519, Lerma, L. Aguirre J., 28.12.73; MEXU 1123, Lagune de Terminos; dans l'embouchure de Paso Real, LTS 11, Rodolfo Cruz #1269, 00.09.65. Yucatán: ENCB 8773, Yucaltepén, L. Huerta, 02.06.1987. Quintana Roo: ENCB 6649, Playa Maya, Cozumel, C. Mendoza, 27.02.1985. Note: Synonymy proposed by Oliveira *et al.* (1983).

Gracilaria mammillaris (Montagne) M. Howe, 1918: 515

= *Rhodymenia mammillaris* Montagne, 1842: 252 (Type locality: Martinique). Figs. 10 and 11.

Thallus erect, (3)5–10(14) cm high, dark red, texture smooth, substance tough. Adherence to herbarium sheets minimal. Branching dichotomous, in 2 planes. Branches flattened, up to 1 cm width, no base-constricted. Margins free of proliferations or branchlets. Segments between forks constant in length up from the stipe. Apex rounded. Stipe



Figure 10. Habit of *Gracilaria mammillaris* (Montagne) M.A Howe.

short and stout. Holdfast not distinct, disc-like. Subcortex absent, hence, transition abrupt. Cortex formed by 1-3 cellular layers, external ones are slightly rectangular, 5-18 μm diameter, strongly pigmented, anticlinal. Medullary cells spherical to ovate, 50-150 μm diameter with no apparent pigmentation, less than 10 cellular layers from one surface to the other (in cross section). Spermatangia 18-20 μm depth, 40-45 μm width. Cystocarps hemispherical, 1.0-1.3 mm diameter, constricted and slightly to evidently apiculate. Carpospores in clusters, spherical to slightly pyriform, up to 30 μm large. Gonimoblast columnar. Nutritive tubular cells in contact with external pericarp. Tetrasporangia spherical to slightly ovate, 25-35 μm diameter, at external cortex, and rounded by enlarged cortical cells.

Selected specimens: Tamaulipas: ENCB 4071, Escolleras de Ciudad Madero, G. Galdi, 31.03.1978. Veracruz: ENCB 6644, Tuxpan, S. Pierdánt, 06.02.1986; UAMIZ 761, Mocambo-Boca del Río, N. Hernández Soto M2, 26.11.1994. Campeche: ENCB 4204 Ciudad del Carmen, A. Vargas #RHG 1543, 24.05.1965; US 36604 (Barcode: 00557649), Ciudad Del Carmen, Isla Carmen, A. Vargas #Rhg-1544, 24.05.1965; MEXU 1122, Lagune de Terminos; dans la lagune en face a Ensenada, LTS 12, Rodolfo Cruz #1026a, 00.04.1964. Quintana Roo: ENCB 6631, Muelle de Isla Mujeres, C. Mendoza, 13.09.1985; UAMIZ 762, Playa del Carmen, A. Senties G., 01.03.1994; US 14417, Xel-Ha, Quintana Roo, D.L. Ballantine #Dlb 1933, 12.04.1983.

Note: Schneider (1975), when comparing material of *Gracilaria mammillaris* from North Carolina (USA) with that of *G. veleroae*, collected by Dawson in the Gulf of California and housed in various herbaria, found no clear differences and proposed the heterotypic (or taxonomic)



Figure 11. Mexican Atlantic distribution of *Gracilaria mammillaris* (Montagne) M.A Howe.

synonymy of *G. veleroae* with *G. mammillaris*. Norris (1985) suggested that, because Schneider never saw the type material belonging to either of the 2 binomials, both taxa should remain as distinct. Recently, Gurgel *et al.* (2004: 178) described *Gracilaria hayi* and included in it *Gracilaria mammillaris sensu* Schneider (1975) and Schneider and Searles (1991) not *G. mammillaris*, thus reducing the problem to nonexistent.

Gracilaria tikvahiae McLachlan, 1979: 19, Fig. 1 (Type loc.: Barrachois Harbour, Colchester County, Nova Scotia, Canada).

Holotype: Hoja #6919 in the Marine Algal Herbarium, National Research Council of Canada, Halifax (NRCC, !, in McLachlan [1979:21, fig. 1]). Figs. 12 and 13.

Thallus erect, (7)9-15(30) cm tall, texture smooth, substance loose, color highly variable, olive brown, reddish, dark purple or even, yellowish green. Adherence to herbarium sheets minimal. Branching dichotomous to irregular. Axes complanate, bases not constricted. Apex rounded to acute. Stipe large and slender. Cortical cells 8-9 μm diameter, in 1-2 layers, anticlinal. Medullary cells variable in size, around 100-120 μm diameter, more than 10 layers from one surface to the other (cross section). Spermatangia 18-20 μm depth 25-30(40) μm width. Cystocarps prominent, hemispherical, distributed all over the branch surface, 500-520 μm diameter, slightly apiculate, constricted. Carpospores in clusters. Gonimoblast columnar. Nutritive tubular cells in contact with external pericarp. Tetrasporangia ovate, distributed over the branches, variable in size, 25-30 μm width, 25-40 μm large.

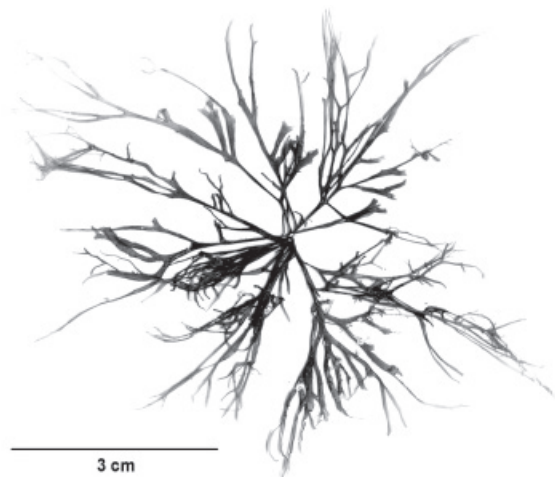


Figure 12. Habit of *Gracilaria tikvahiae* McLachlan.

Selected specimens: Tamaulipas: ENCB 5332, Punta Piedra, Municipio de San Fernando, J. Herrera, 20.09.1986. Veracruz: US 42509, Lagoon De Alvarado, G.B. Saunders #556, 31.01.1952. Campeche: MEXU 1056, Lagune de Terminos; dans la Lagune, en fase à Ensenada, LTS 12, Rodolfo Cruz #1026, 00.04.1964. Yucatán: US 45386 (Barcode: 00556795), Río San Miguel, Chicxulub, Puerto Progreso, M.A. Garza Hernandez #473, 12.03.67. Quintana Roo: ENCB 6678, Playa San Juan, Isla Cozumel, C. Mendoza, 04.06.1985.

Discussion

Phylogenetic relationships of subgenus Textoriella. Using 36 SSU rDNA sequences of Gracilariaceae from the tropical Atlantic and Pacific, Bellorin et al. (2002) found evidence that is relevant for subgenus *Textoriella*. For example, they found that the recognition of subgenera within *Gracilaria* based on spermatangial arrangement was not supported, and that most Pacific species with either “*textorii*” or “*verrucosa*” type spermatangia were deeply separated from Atlantic species (the exception being some sister taxa, as we will discuss below). Those Pacific taxa are *G. chilensis* Bird, McLachlan et Oliveira (central Chile), *G. pacifica* I.A. Abbott (California, subgenus *Gracilaria* Yamamoto), and *Gracilaria* “sp. Mexico” (California). Later, *Gracilaria* “sp. Mexico” proved to be *G. vermiculophylla* (Ohmi) Papenfuss (Bellorin et al., 2004). They also found that *G. isabellana* Gurgel, Fredericq et J.N. Norris (as *G. lacinulata* (Vahl) M. Howe; see Gurgel et al., 2004, and Wynne, 2005) from the Caribbean (Cumaná, Venezuela) and northern Brazil (Bahia), *G. foliifera* (Forsskål)



Figure 13. Mexican Atlantic distribution of *Gracilaria tikvahiae* McLachlan.

Børjesen var. *angustissima* (Harvey) W.R. Taylor from the Caribbean, and *G. tepocensis* (E.Y. Dawson) E.Y. Dawson from Santa Catarina, Brazil, are closely related to *G. tikvahiae* from Canada, thus forming what they called the “*tikvahiae*” lineage. In this lineage, the temperate and subtropical isolates *G. tikvahiae* and *G. tepocensis* were closely related. It is significant, by the way, that the molecular study of Bellorin et al. (2002), supported the early proposal that *G. foliifera* var. *angustissima* is a taxonomic synonym of *G. tikvahiae* (Wynne, 1998). For the southern Pacific, Bellorin et al. (2002) found that *G. chilensis* and *G. tenuistipitata* C.F. Chang et B.M. Xia grouped in a single clade, although with very low bootstrap support (65%-68%).

Instead of SSU, Gurgel and Fredericq (2004) used the chloroplast-encoded *rbc* gene from 67 specimens worldwide, and found that selected taxa from subgenus *Textoriella* (*G. textorii*, *G. cervicornis*, *G. curtissiae*, *G. tikvahiae*, *G. mammillaris*, and *G. chilensis*) appear as belonging to sister groups such as *verrucosa*-type-bearing species (which is expected), as well as with *Hydropuntia* taxa (which they treat as a different genus); for example, *G. tikvahiae* is in the same clade of *Gracilaria damaecornis*, a multi-cavernous type bearing species that should belong to subgenus *Hydropuntia sensu* Tseng et Xia (1999). It is clear that not all *textorii*-type bearing taxa share a common ancestor (this, however, does not contradict the fact that *G. cuneata*/*G. crispata*, and *G. mammillaris*/*G. veleroae* are 2 pairs of sister taxa in the Central American Isthmus. See below). According to Gurgel and Fredericq’s Fig. 1 (2004: 141), some of them even do share a common ancestor with *Hydropuntia*.

While authors like Tseng and Xia (1999), based on

anatomy, support a subgeneric scheme for genus *Gracilaria* (subgenera *Gracilariella*, *Textoriella*, *Gracilaria*, and *Hydropuntia*), other researchers (Gurgel and Fredericq, 2004; Gargiulo et al., 2006; Kim et al. 2008), based on molecular evidence, suggest the taxonomic independence of genus *Gracilariopsis*, *Gracilaria*, and *Hydropuntia* (but see Liao and Hommersand, 2003, for a morphological study that also supports this view). Although well aware that the representation of the *textorii*-type in 2 distinct clusters of *Gracilaria sensu stricto* (Gugel and Fredericq, 2004) apparently represents homoplasy, we will recognize at least the subgenera *Textoriella* and *Gracilaria*, which are respectively close to the *Bursa-pastoris* and *Gracilis* morphological groups of Liao and Hommersand (2003), until more studies on *textorii* and *verrucosa* spermatangial arrangements are done, especially in the western Atlantic where, as Gurgel and Fredericq (2004) pointed out, the number of species is underestimated.

Distribution. The general distribution of subgenus *Textoriella* in the Central America, both Pacific and Atlantic (Lists 1 and 2), displays a regional pattern explainable with reference to geologic vicariant events that interrupted the connection between the Pacific and Atlantic at the Isthmus of Panama (closed 3.1-2.8 million years ago. Coates and Obando, 1996), and the Isthmus of Tehuantepec (southern Mexico, closed 4-3.5 million years ago. See below). If we look at the notes for lists 1 and 2, we will see an apparently more general pattern that would reflect an early pantropical Tethyan distribution, from the early-middle Eocene (60-50 million years ago) to the closure of the Tethys sea, about the middle Miocene (15-12 million years ago. Tomlinson, 1986; Brown and Lomolino, 1998).

List 1. Subgenus *Textoriella* in the tropical-subtropical western Atlantic (Oliveira, 1984; Schneider and Searles, 1991; Ganesan, 1994; Gurgel et al., 2004; Wynne, 2005).

Gracilaria armata (C. Agardh) J. Agardh¹

G. blodgettii Harvey²

G. cervicornis (Turner) J. Agardh³

G. cuneata J.E. Areschoug⁴

G. curtissiae J. Agardh⁴

G. galeensis Gurgel, Fredericq et J. Norris

G. hayi Gurgel, Fredericq et J. Norris

G. intermedia J. Agardh subsp. *ganesana* Gurgel, Fredericq et J. Norris

G. isabellana Gurgel, Fredericq et J.N. Norris

G. mammillaris (Montagne) M. Howe

G. smithsonensis Gurgel, Fredericq et J. Norris

G. tepocensis (E.Y. Dawson) E.Y. Dawson

G. tikvahiae McLachlan⁵

Notes: ¹Also recorded for the Mediterranean Sea (Gargiulo et al., 1992), and the Indian Ocean (Silva et al., 1996), ²Also

recorded for Western Australia (Millar and Xia Bangmei, 1997), and the Indian Ocean (Silva et al., 1996). ³Also recorded for Canary Islands (Sosa et al., 1996), tropical West Africa (Lawson and John, 1982, as *G. ferox*), and the Indian Ocean (Silva et al., 1996). ⁴Not found in the subject area. ⁵Recorded as a commercial introduction for the Hawaiian Islands (Abbott, 1999).

List 2. Subgenus *Textoriella* in the tropical-subtropical eastern Pacific (Taylor, 1945; Dawson, 1949; Norris, 1985; Dreckmann, 2002).

Gracilaria cerrosiana W.R. Taylor

G. crispata Setchell et Gardner

G. pachydermatica Setchell et Gardner

G. parvispora I.A. Abbott¹

G. pinnata Setchell et Gardner²

G. ramisecunda E.Y. Dawson

G. subsecundata Setchell et Gardner³

G. tepocensis (E.Y. Dawson) E.Y. Dawson

G. textorii (Suringar) De Toni

G. turgida E.Y. Dawson

G. veleroae E.Y. Dawson⁴

Notes: ¹Hawaiian Islands (Abbott, 1999). ²Reported as endemic for Central, and ³Northern Gulf of California (Espinoza-Avalos, 1993). ⁴Also recorded for the Indian Ocean (Silva et al., 1996).

Taking into account the available distributional data, we found that there are 2 sibling pairs, or twin species (Collins, 1996), between the tropical eastern Pacific, and its western Atlantic counterpart: (1) *G. cuneata*/*G. crispata*, and (2) *G. mammillaris* (or *G. hayi*)/*G. veleroae*. Because these 2 pairs are very similar morphologically (Dreckmann, 2002. Also see note for *G. mammillaris* in this work), and the ranges of both are restricted to areas adjacent to the Central American Isthmus (they are not cosmopolitan), we take them as sister taxa that diverged as a result of the final emergence of the Isthmus, and to be of the same age as the Isthmus itself as the most parsimonious explanation for the pattern (Humphries and Parenti, 1999; Collins, 1996). Such patterns of morphologically similar sister taxa are common in most of the groups that have been studied in the area (Collins, 1996), including sea stars, sea urchins, brachyuran crabs, gastropods, bivalves, chitons, and polychaetes among others mentioned by Collins (1996). But also see Craw et al., 1999, for a worldwide review on vicariance).

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