Gracilariopsis silvana sp. nov., G. hommersandii sp. nov., and G. cata-luziana sp. nov., Three New Species of Gracilariaceae (Gracilariales, Rhodophyta) from the Western Atlantic

Gracilariopsis silvana sp. nov., G. hommersandii sp. nov., and G. cata-luziana sp. nov., Tres especies nuevas de Gracilariaceae (Gracilariales, Rhodophyta) para el Atlántico Occidental

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ABSTRACT

Species of Gracilariopsis are typically characterized as slender, elongate, cylindrical fronds with varying degrees of branching that exhibit less habit diversity than species of Gracilaria. Of the thirteen currently known species of Gracilariopsis worldwide, ten have been described from the Pacific Ocean and the Gulf of California, and three from the Atlantic Ocean and the Caribbean Sea. Sequence analysis of chloroplast-encoded rbcl provides sufficient phylogenetic signal for species level resolution in Gracilariopsis, and for assessing the intrageneric evolutionary relationships. Results showed the identification of previously described species and the delineation of three new western Atlantic species: Gp. silvana sp. nov. from Venezuela, is the first of the genus to be characterized by flattened, strap-shaped thalli that are sparingly or profusely, subdichotomously or irregularly pinnately branched up to 4(6) orders; Gp. hommersandii sp. nov. from Panama and Venezuela, is a cylindrical, stringy unbranched to branched species, that sometimes bear short, uncinate branchlets, formed mostly apically or along the axes, and often hooked-up to adjacent thalli; and, Gp. cata-luziana sp. nov. from Campeche Bay, Gulf of Mexico, is also cylindrical and stringy, but with very slender, delicate, and much elongated, loosely and profusely branched thalli, up to 40 cm tall, that have a medulla of few, large cells. Parsimony analysis inferred from rbcl sequences of 22 taxa worldwide supports the distinctness of these new species. This study indicates species diversity in Gracilariopsis, now with sixteen species worldwide, including six in the Atlantic Ocean, has been underestimated, and the diagnosis of the genus must be expanded to include flattened species.

Key words: Gracilariopsis, Gracilariales, new species, rbcl, phylogeny, Western Atlantic.

RESUMEN

Las especies de Gracilariopsis están caracterizadas típicamente por frondas delgadas, elongadas y cilíndricas con grados diversos de ramificación, que exhiben una diversidad menor de hábitos que las especies de Gracilaria. De las trece especies actualmente reconocidas de Gracilariopsis a nivel mundial, diez han sido descritas para el Océano Pacífico y Golfo de California y tres para el Atlántico y Mar Caribe. El análisis de secuencias de nucleótidos del gen codificante rbcl, en cloroplasto, brindan información filogenética suficiente, a nivel de especie, para inferir las relaciones evolutivas intragenéricas en Gracilariopsis. Los resultados mostraron la identificación de especies
descritas previamente y la delineación de especies nuevas para el Atlántico occidental. *Gp. silvana* sp. nov. de Venezuela, es la primera dentro del género caracterizada por talos aplanados y acintados, ramificados subdicotómicamente o de manera pinada irregular. La ramificación puede ser profusa o esparsa hasta 4 (6) órdenes; *Gp. hommersandii* sp. nov. de Panamá y Venezuela posee talos cilíndricos, fibrosos, ramificados o no, algunas veces con ramitas cortas uncinadas que se desarrollan apicalmente o a lo largo de los ejes y que con frecuencia se aferzan a otros talos cercanos y *Gp. cata-luziana* sp. nov. proveniente de la Bahía de Campeche, Golfo de México, también cilíndrica y fibrosa pero con talos muy delicados, delgados y alargados, ramificados profusamente o escasamente de hasta 40 cm de longitud, con una médula de pocas células grandes. Un análisis de parsimonia, a partir de secuencias del gen *rbcL* de 22 taxas mundiales respalda la distinción de estas tres especies nuevas. El presente estudio indica que la diversidad específica en *Gracilariopsis*, ahora con 16 especies en todo el mundo, incluyendo seis para el Atlántico, ha sido subestimada y que la diagnóstico del género debe ser ampliada para incorporar a especies aplanadas.

**Palabras clave:** Gracilariopsis, Gracilariaeae, especies nuevas, *rbcL*, filogenia, Atlántico occidental.

**INTRODUCTION**

Members of the red algal genus *Gracilariopsis* Dawson (1949:40) (Gracilariaeae Nägeli 1847:240; Gracilariales Fredericq et Hølmeranders 1989a:225) are typically characterized as slender, elongate cylindrical fronds with varying degree of branching, and a range of habit types considered to be less diverse than those of *Gracilaria* Greville nom. cons. (1830:iv,121). This thallus uniformity, coupled with a lack of obvious discriminating macro-features, complicates species identification. *Gracilariopsis* (=*Gp.*) was separated from members of *Gracilaria* (=*G.*) primarily on reproductive differences in the internal anatomy of the cystocarp.

The genus *Gracilariopsis* [generic type: *Gracilariopsis sjoestedti* (Kylin) Dawson 1949:40] is characterized by the absence of 'nutritive filaments' (=tubular nutritive cells), connecting the gonimoblasts to the pericarp, a broad-based gonimoblast of small cells, and by the superficial arrangement of spermatangia. In contrast, *Gracilaria* [generic type: *G. compressa* (C. Agardh) Greville 1830:iv, typ. cons.] possesses 'nutritive filaments' and spermatangia arranged in pits. The presumed generic type for years was *Gracilaria verrucosa* (Hudson) Papenfuss (1950:195; *Fucus verrucosus* Hudson 1762:470) from southern England.

Later Papenfuss (1967) in studying material he identified as 'G. verrucosa' reported tubular nutritive cells present in some specimens and absent in others, and considered the two genera indistinct, placing *Gracilariopsis* in synonymy with *Gracilaria*.

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1*Gracilariopsis sjoestedti* [basionym: *Gracilaria sjoestedti* Kylin 1930:55; type locality: "biologischen Station" (=Hopkins Marine Station of Stanford University), Agazzi (=west beach of Mussel Point, Pacific Grove, California) is now considered to be a taxonomic synonym of *Gp. andersonii* (Grunow) Dawson 1949:43 [basionym: *Corynecladia andersonii* Grunow in Piccone 1886:92] (Gurigel et al. 2003).


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Detailed morphological studies of *Gracilariopsis sjoestedti* (Kylin) Dawson (=*Gp. lemaneiformis* sensu Abbott 1983; non *Gp. lemaneiformis* [Bory] Dawson, Acetil et Foldvik 1964) from California by Fredericq and Hølmeranders (1989a,b) resulted in their resurrecting *Gracilariopsis*. While noting the generic characters used by Dawson (1949) for *Gracilariopsis*, i.e., the absence of multinucleate tubular nutritive cells in the cystocarp and the superficial arrangement of the spermatangia, Fredericq and Hølmeranders (1989a,b, 1990) also emphasized another feature: that the gonimoblast cells become linked to gametophytic cells of the cystocarp floor by means of secondary pit connections through gonimoblast conjunctor cells. Several genetic studies have corroborated the taxonomic validity of *Gracilariopsis* (e.g., Goff and Coleman 1988, Kapraun 1993, Kapraun et al. 1993, Goff et al. 1994, Bellorín et al. 2002, Gurigel et al. 2003). While many taxonomists recognize *Gracilariopsis* as distinct from *Gracilaria* (e.g., Ohmí 1958; Yamamoto 1975; Fredericq and Hølmeranders 1990; Womersley 1996, Silva et al. 1996), others have treated them as one, i.e., *Gracilaria* (e.g., Gargiulo et al. 1992; Abbott 1995, 1999; Terada & Ohno 2000).

Gurigel et al. (2003) recently provided a molecular phylogenetic study inferred from maximum parsimony and maximum likelihood analyses of chloroplast-encoded *rbcL* sequences, along with nomenclatural and taxonomic changes, based on twenty-two specimens of *Gracilariopsis* encompassing ten of the currently recognized species worldwide (7 from the Pacific; 3 from the Atlantic), and three out-group species. Of these studied taxa (Gurigel et al. 2003) six were recognized to be undescribed species, but a formal description was not provided.

Ten species of *Gracilariopsis* have been described from the Pacific Ocean (Table 2): *Gp. andersonii* (Kylin) Dawson (1949), [the correct name for the generic type *Gp. sjoestedti* Kylin 1930, see Gurigel et al. 2003 for nomenclatural note from central, California]; *Gp. chorda* (Holmes) Ohmí (1958) from Japan; *Gp. costaricensis* Dawson (1949) from Costa Rica; *Gp. heteroclada* (Zhang et Xia) Zhang et Xia in Abbott et al. (1991) from the Philippines; *Gp.
lameaneiformis (Bory) Dawson, Acleto et Foldvik (1961) from Peru; Gp. megaspora Dawson (1949; Norris 1985) from Sonora, Gulf of California; Gp. ngami Pham-Hoang (1969) and Gp. phantesiensis Pham-Hoang (1969) both from Vietnam (Nguyen 1992); Gp. panamensis (W. Taylor) Dawson (1949) from Panama; and Gp. rhodotricha Dawson (1949) from Pacific Mexico and Vietnam (Dawson 1954; Nguyen 1992). Sequence analyses of rbcL revealed two other unidentified Pacific taxa of Gracilariopsis (Gurgel et al. 2003; herein): Gp. sp. 1 (Table 1) from southern Australia and the Gulf of California; and Gp. sp. 3 (Table 1) from China and Japan.

Fewer species have been described for the Atlantic Ocean (Table 2). Dawson (1953) first reported a Gracilariopsis from the southern Caribbean and considered it close to but distinct from "Gp. spoedestini." Gracilariopsis tenuifrons (Bird et Oliveira) Fredericq et Hoomersand (1989a) is a species originally described from Maceió, Brazil (Bird et Oliveira 1986, as 'Gracilaria tenuifrons'). Fredericq and Hoomersand (1989a) first identified another Gracilariopsis from the eastern Atlantic, a species later recognized as Gp. longissima (Gemlin) Steentoft, Irvine et Farnham (1995) from Kent, southern England. More recently a new western Atlantic species, Gp. carolinensis Liao et Hoomersand in Gurgel et al. (2003), was described from North Carolina. An economically important species, Gp. 2 (Table 1), of the local agar industry of western South Africa and Namibia (Stegenga et al. 2002, as 'Gp. lameaneiformis'; Wakiba et al. 2001, as 'Gp. sp.'), was based on rbcL sequence analyses (Gurgel et al. 2003; herein), to also be an unknown taxon.

Our comparative studies of three unknown Atlantic species (Table 1; Gurgel et al. 2003: as 'Gp. sp.' from Venezuela, 'Gp. aff. panamensis' from Caribbean Panama and Venezuela; and 'Gp. sp.' from the Gulf of Mexico) revealed them to be distinct from any currently known species of Gracilariaeae (e.g., Taylor 1960, Wynne 1986), nor did they match with photographs of type specimens (PCI, NYI or BM) of Schramm and Mazé (1865, 1866). Therefore we herein describe them as new species, based largely on the analysis of chloroplast encoded rbcL sequences, and broaden the description of the genus to include a flat species.

**MATERIAL AND METHODS**

**Morphology.** Voucher specimens were fixed and stored in 5% Formalin/seawater, and/or pressed and air-dried on herbarium sheets and deposited in LAF, Alg. Coll. US and UC (herbarium abbreviations follow Holmrgen et al. 1990). Specimens were photographed on a Zeiss Stemi 2000-C dissecting scope (Carl Zeiss Inc., Thornwood, NY, USA) attached to a Minolta 35mm camera (Minolta Corporation USA, Ramsey, NJ, USA). Some were scanned into the computer either as 'wet' (liquid-preserved) specimens, or directly from a herbarium sheet using a Microtek ScanMaker III scanner (Microtek International, Hsinchu, Taiwan). Cross-sections for morphological studies were hand-made using stainless steel razor blades, and then stained in a 3% aniline blue solution (Tsuda and Abbott 1985) for 10-15 minutes. The stain was fixed with 1 drop of 3% acetic acid, rinsed with distilled water and then mounted in a 50% Karo® corn syrup/distilled water solution with phenol added as a preservative. Photomicrographs were taken with a Polaroid DMC 1 digital camera (Polaroid, Inc., Cambridge, MA, USA) attached to an Olympus BX60 (Olympus, Melville, NY, USA). Images were edited and assembled in plates using Photoshop v.5.0 (Adobe Systems Inc., San Jose, CA, USA).

**Molecular Phylogeny.** Silica gel-dried specimens and extracted DNA samples were deposited in the Seaweed Laboratory at the University of Louisiana at Lafayette, and stored at -20°C. DNA samples were prepared using the DNAeasy Plant Mini Kit (QIAGEN, Valencia, CA, USA), or were submitted to a CTAB-Cesium Chloride DNA procedure (Freshwater and Rueness 1994). Plastid-encoded rbcL was selected to infer a phylogeny for Gracilariopsis. PCR and sequencing primers used in this study were FrbcL start, F7, F57, F492, F577, F753, F993, R753, R1381 and RhrbcS start as listed in Freshwater and Rueness (1994) and Hoomersand et al. (1994). Protocols for gene amplification, automated sequencing and alignment are identical to those given in Lin et al. (2001) and Gurgel et al. (2003).

Partial rbcL sequences were produced from 22 recently collected samples of Gracilariopsis. Collection information (Table 1) includes specimen locality, date and collector's name, percentage of rbcL gene sequenced, and GenBank accession numbers (see also Gurgel et al. 2003). Melineathia obtusata (Labilliardière) J. Agardh and Curdia coriacea (Hooker et Harvey) J. Agardh from New Zealand, and C. crassa Millar from southern Australia were chosen as outgroup taxa based on their close phylogenetic relationship with the ingroup in global searches of the Gracilariaeae (data not shown).

Phylogenetic analysis was performed with PAUP* v.4.0 beta 10 (Swofford 2002) for Macintosh using maximum parsimony (MP). Because the first 40 base pairs (bp) were missing in many sequences, the phylogenetic analysis was restricted to the last 1427/1467 bp of rbcL. Maximum parsimony trees were inferred from: 1) heuristic searches of 5000 replications of random sequence addition (Fitch 1971) using, unordered, only the phylogenetically informative characters, under the Fitch criterion of equal weights for all substitutions; 2) Tree Bisection- Reconnection (TBR), saving multiple trees (MULTTREES) but holding 20 trees at each step; and, 3) STEEPEST DESCENT. Support for all nodes (bp) for all trees was assessed by bootstrap analysis (Felsenstein 1985) on the data set using 3000 replicates and "as is" sequence addition, as implemented in PAUP*. 

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<table>
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<th>Entity</th>
<th>Collection data</th>
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<td>Curdita coriacea (Hook. &amp; Harv.) J. Agardh</td>
<td>Doubtless Bay, New Zealand, coll. W. Nelson, 1 xii 1993</td>
<td>AY049425, 66.5%</td>
<td>Gurgel et al. 2003</td>
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<td>Curdita crassa Millar</td>
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<td>Gurgel et al. 2003</td>
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<td>2 miles West of Anton Lizardo, Veracruz area, Gulf of Mexico; coll. C.F.D. Gurgel; 10 ii 1999</td>
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<td>AY049421, 85%</td>
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Table 2. Recognized Species of *Gracilariosis* Dawson.

   *Gracilaria sjoestedtii* Kylin 1930:55. 
   *Gracilaria sjoestedtii* (Kylin) Dawson 1949: 40.
3. *Gracilariosis cata-huiana* Gurgel, Fredericq et J. Norris sp. nov. (herein)
7. *Gracilariosis hommersandii* Gurgel, Fredericq et J. Norris sp. nov. (herein)
   Basionym: *Gigartina lemaneiformis* Bory 1828:151, as *lemaneiformis*.
   Synonyms: *Cordycecladia lemaneiformis* (Bory) Howe 1914:128, as *lemaneiformis*.
   Basionym: *Fucus longissimus* Gmelin 1788:134.
15. *Gracilariosis silvana* Gurgel, Fredericq et J. Norris, sp. nov. (herein)

RESULTS

**Gracilariosis silvana** Gurgel, Fredericq et J. Norris, sp. nov. (Figs. 1-16)

Holotype. #US Alg. Coll. -204316 (Fig. 1). Venezuela: Playa Barranquilla, Estado Falcón, 14 vii 1999, coll. C. F. D. Gurgel, J. E. Conde and C. Carmona, # FG-37. Isotypes: LAF; UC.


Etymology: This species is named in honor of Dr. Paul C. Silva (Herbarium, University of California at Berkeley) on the occasion of his 80th birthday, and to celebrate his groundbreaking contributions to the taxonomy and nomenclature of the algae. In choosing the epithet, "silvana", we follow Stern (1973:294) who noted Lindley (1832) had suggested that when the epithet is to compliment the person it should be rendered in the adjective form.


Description: *Thalli* flattened throughout, strap-shaped (Figs. 1-5), sometimes slightly undulated (Figs. 1, 3), 14-16 (-20) cm tall, 1-3 cm wide, (275-) 488 (-600) μm thick, red, pinkish red, sometimes with yellow regions. Young plants usually solitary and thin, arising from small, rounded holdfasts (Figs. 3, 5-6). Older *thalli* thick, cartilaginous, borne on wart-like irregular holdfasts formed from the coalescence of neighboring holdfasts (Figs. 1, 7) from which new juvenile uprights (Fig. 7) may arise. Main axes sparingly (Fig. 1) or profusely (Fig. 5) subdichotomously or irregularly branched for up to 4 (-6) orders; branches gradually decreasing in width distally (Fig. 5). Lateral branches not constrained at base, curved upward, irregularly pinnate, mostly arising from thallus margin (Figs. 1-5), damaged tips, and the mid-region of main axes (Figs. 1-2). Apices variable, acute to roughly blunt. Gradual transition in cell size between a medulla composed of 5-6 (-9) layers of large, laterally compressed, thin-walled central cells (250-) 330 (-400) μm by (60-) 105 (-140) μm (Figs. 9-10), to an outer cortex composed of 1-3 layers of isodiametric cells, 7.5-10 μm diameter (Fig. 11). Cortical gland cells present, rounded in surface view.

Cystocarps hemispherical (Fig. 8), scattered on lower and upper surfaces of main axes, 1-2mm diameter and slightly constrained at base where protruding from thallus (Figs. 12-13), with a centrally located, occasionally rostrate ostiole (Fig. 12). Carposporangia organized in tightly packed branched filges. Pericarp composed of 12-14 cell layers, 150-165 μm thick, pericarp cells (Fig. 14) distally squarish becoming star-shaped to rounded below to accommodate the cystocarp expansion. Cystocarps wide-based (Figs. 12-13); gonimoblasts at maturity completely filling cystocarp cavity and composed of small, regular thin-walled cells, 3-5 μm diameter. Carposporangial cell not pronounced. Transition zone at base of cystocarp (within lower carposporophytic region), composed of elongated cells corresponding to former subcortical cells that expanded upon schizogenous formation of cystocarp cavity directly distally to these cells; terminal gonimoblast conjunct cells subsequently fusing downward onto these enlarged cells.
to form secondary pit connections. As the cystocarp expands laterally, degenerating carpogonial branches may become incorporated and are seen as darkly staining multinucleate cells (Figs 15, 16). Sporogamous and tetrasporangial specimens not seen.

**Gracilaropsis hommersandi**i Gurgel, Fredericq et J. Norris, sp. nov. (Figs. 17-23, 26-30)

Holotype. #US Alg. Coll. -204312 (Fig. 19). Republic of Panama: cystocarpic thallus, on rock in shallow water, 0.75 m depth, Fort Randolph, Colon City, Bahia Limon, Provincia Colon, (Caribbean Panama), 26 iii 1999, coll. B. Wyssor, #BW-00197. Isotypes: LAF.


**Figures 1-8. Gracilaropsis silviana Gurgel, Fredericq et J. Norris sp. nov. 1: HOLOTYPE (#US Alg. Col. -204316). 1-4: Range of habit variation in Venezuela specimens from Playa Barranquilla; and, 5: from La Vela de CoRo. 6: Characteristic round holdfast of a solitary specimen. 7: Detail of coalesced holdfasts bearing multiple thalli and a juvenile upright (arrow head). 8: Surface view of cystocarps. Scales: Figs 1-4: ruler =4cm; 5: ruler =5cm; 6: bar =750mm; 7: bar =500μm; 8: bar =2.25mm.**

**Figures 9-16. Gracilaropsis silviana Gurgel, Fredericq et J. Norris sp. nov. 9-10: Transverse section of thallus. 11: Detail of cortex and outer medulla. 12-13: Transverse section of a mature, broad-based cystocarp slightly constricted at base, with central ostiole in pericarp and gonimoblasts completely filling cystocarp cavity. 14: Detail of a pericarp. 15-16: Cystocarp base showing elongated cells and incorporation of degenerating carpogonial branch cells. Scales: Figs. 9, 14-15: bar =100 μm; 10, 12-13: bar =500μm; 11: bar =20 μm; 16: bar =40 μm.**


Etymology: This species, 'hommersandi', is named in honor of Dr. Max H. Hommersand (University of North Carolina at Chapel Hill) whose contributions to algal systematics, including the Gracilariales have greatly enhanced our knowledge of the red algae.

Latin diagnosis: Thalli flavi, saepe subrosei basi, interdum pallidivirides, erecti aut prostrati, 20-45 cm long., cartilaginei, graciles laevigatique, exorientes haptero discoidoe. Plures thalli plerumque fasciuciati simul eodem haptero inconspicuo. Thalli plerumque ramosi non profuse, saepe solum compositis axium linearium rectorum ramis. Apices acuminati, uncinati vel compositi 1-4 unciformior um ramorum, 0.5-0.8 cm long, deorsum extensorum formatorum antea fractorum apicum crescentium. Interdum superfiae partes axium spiratae circum alios axes contiguos. Ramuli minuti retroanastomosantes axem formantes regiones locales circulares annuliformes.
Description: Thalli 20-45 cm long, 1.0-2.3 mm diameter, terete, stringy, slender, cartilaginous, smooth, sparingly (Figs. 17-18) to profusely (Fig. 19) branched. One to several yellowish thalli (Fig. 19), sometimes pale-green or often pinkish at the base, arise above a small, discoid holdfast (Figs. 17-18). Thalli > 30 cm often composed solely of straight linear axes with branching towards the base limited to a few sparse, branches. Apices either acuminate (Fig. 17), or uncinate (Figs. 20-21), comprised of one-to-four hook-like branchlets, 0.5-0.8 cm long, spreading downward. Uncinate branchlets originating on axes below tend to coil around both adjacent axes (Fig. 22) or around their own axis, forming localized ring-like regions (Fig. 18) arrow. Medulla 6-7 cell layers, of large vacuolate, thick-walled, roundish cells, (175-) 244 (-284) μm by (125-) 165 (-225) μm (Figs. 26, 28, 30). Transition between medulla and sub cortex abrupt; sub cortex composed of evenly spaced, slightly anticlinally elongated cells, (6.0) 8.8 (-10) μm by (3.8-) 5.0 (-7.5) μm, with innermost sub cortical cells the largest and thick-walled (Fig. 28). Outermost cortical cells of distal most 3-6 cell layers radially elongated, (5.0) 7.5-8.8 (-10) μm by 3.8-5.0 μm.

Cystocarps hemispherical, protruding (Fig. 23), scattered along axes, slightly constricted at base, 0.8-0.9 mm tall, 0.9-1.0 mm wide. Pericarps (Fig. 27) of mature cystocarps composed of 9-10 cell layers, 125 μm to 240 μm diameter; composed of evenly spaced, rounded-ellipsoidal cells, 6.25-8.75 μm by 7.5-11.25 μm, with cell walls 3.75-8.75 μm thick. Central gonimoblasts composed of tightly packed files of evenly-sized, roundish cells filling the cystocarp cavity (Figs. 26-27, 29). Carposporial fusion cell not pronounced. Inner pericarp cells at base of cystocarp cavity (Fig. 27), 31.25-43.75 μm by 18.75 μm diameter. Sporangial and tetrasporangial specimens not seen.

*Gracilariopsis cata-luziana* Gurgel, Fredericq & J. Norris, *sp. nov.* (Figs. 31-36)

Holotype. #US Alg. Coll. -204314 (Fig. 31), México: protected sandy beach near lagoon (19°03.31' N; 96°00.44' W), 2 miles west of Anton Lizardo (close to Veracruz), Estado Veracruz, Campeche Bay, Gulf of Mexico, coll. C. F. D. Gurgel, # FG-204, 10 ii 1999. Isotypes: LAF

Etymology: The adjectival ending, -ana, is chosen (Stern 1973:294; Lindley 1832) for "cata-luziana", named in honor of Professors Catalina Mendoza and Luz Elena Mateo-Cid (Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México D.F.), who have greatly enhanced our floristic knowledge of the marine algae of México. Following Art. 60.9 of the ICBN (Greuter et al. 2000), we use the hyphen to indicate that the given names of these two phycologists, Catalina and Luz, are formed independently.


Description: Habit bushy, up to 25 (-36) cm long, with clumps up to 6 cm broad, composed of several distinct thalli mostly entangled to each other (Fig. 31). Individual main axes wiry, thin, delicate in texture, terete to slightly compressed, mostly 25-30 (-36) cm long by (373-) 447 (-555) μm thick. Main axes laterally bearing elongate, mostly alternate, linear, simple side branches, slightly constricted at the base, may produce an order of very thin branch initials (Fig. 31). Two lateral branches may originate from same insertion point (Fig.

as seen in transverse section. A single-celled medulla is the result of collapsing cell walls of contiguous medullary cells. A two-celled inner medulla comprises slightly compressed cells, 125 μm by 200 μm (Fig. 34). When composed of 3-4 cells, inner medullary cells measure 66.5 μm by 135 μm. The subcortex is composed of (13.75-) 14.2 (1-21.25) μm by (12.5-) 13.75 (1-15) μm, radially or anticlinally compressed cells, rich in floridean starch. Cystocarpic, spermatangial and tetrasporangial specimens not seen.

**DISCUSSION AND TAXONOMIC CONCLUSION**

The distinctness of the new western Atlantic members *Gracilariopsis silvana*, *Gp. hommersandii* and *Gp. cata-luziana* at the species level is corroborated by the rbCL analysis (Fig. 37; Table 1 & Gurgel et al. 2003: as 'Gp. sp.'; 'Gp. aff. panamensis', and 'Gp. sp.'.). Molecular results show *Gp. heteroclada* from the Philippines as the most basal species in the data set followed by *Gp. silvana* and *Gp. hommersandii* and an as yet undescribed species (Gp. sp. 3) from Japan and China. Despite the absence of bootstrap support values at the deeper nodes in the *Gracilariopsis* tree, these four species always grouped basally in the phylogenetic analyses.

The four haplotypes of *Gp. hommersandii* confirm the phenotypic variation in overall habit shape displayed by members of this species in the Caribbean, ranging from pseudodichotomously branched thalli typical of Caribbean Panama (Fig. 19) to unbranched or sparsely branched specimens collected in Venezuela (Figs. 17-18). The range of genetic variation present among the *Gp. hommersandii* haplotypes, is minimal at 0-0.07% sequence divergence (P distance), confirming that specimens with such divergent habit in fact belong to the same species.

The eastern Pacific *Gp. lemaeiformis* from Peru, *Gp. costaricensis* from Costa Rica, and the recently described western Atlantic *Gp. carolinensis* (Gurgel et al. 2003) form a well-supported clade (bp = 91) sharing similar cystocarp features. Gurgel et al. (2003) also showed that *Gp. carolinensis* is morphologically and genetically more closely related to *Gp. lemaeiformis* than it is to *Gp. andersonii*. *Gracilariopsis andersonii* stands alone in the *Gracilariopsis* phylogram.

*Gracilariopsis cata-luziana* is a sister taxon to *Gp. tenuifrons*, and both species form a well-supported clade (bp = 95) (Fig. 37). *Gracilariopsis* sp. 2 from Namibia corresponds to an undescribed species.

The most derived and well supported clade (bp = 92) is composed of *Gp. longissima* and *Gp. sp. 1. Gracilariopsis* sp. 1, collected from Lake Butler, is apparently an invasive species in southern Australia (=Womersley 1996: 29-31, figs. 8A-F, as 'Gp. lemaeiformis'), and is shown to be the same entity as specimens from the Baja California Norte coast of the Gulf of California (=Pacheco-Ruiz et al. 1999, as 'Gp. lemaeiformis') (Fig. 37; Table 1). Two entities that may be separate taxa have both been
misidentified as *Gp. longissima* in Europe; one species is from the Mediterranean, and the other is in the northeastern Atlantic.

Based solely on external habit, the distinction between *Gracilariopsis silvana* and flat species of *Gracilaria* from the Caribbean and Gulf of Mexico may not be readily apparent, especially when dealing with small, immature or non-reproductive specimens. Specimens of *Gp. silvana* that lack the characteristic abundance of marginally inserted branches on their strap-shaped thalli may superficially resemble specimens of *Gracilaria curtissiae* J. Agardh (1885: 5); type locality: Florida, lectotype LDI). *G. cuneata* Areschoug (1854: 351; type locality: vicinity of Pernambuco, Brasil; syntypes SI), or misidentified specimens from Venezuela (Rodriguez de Rios 1986, as *G. textori*). However, fully grown specimens of *Gp. silvana* are easily distinguished from *G. curtissiae* by possessing narrower and thinner blades that may bear abundant and irregular pinnate branches curved slightly upwards. On the other hand, *G. curtissiae* usually has thicker (0.5-1.0 mm) blades, sometimes with distinct di- to tripartite (palmate) branches radially distributed along the margin. The medullary region of *G. curtissiae* is composed of fewer (3-4 cell layers across) but larger, less compressed central cells, and a sharp medullary-cortex transition. Cortical gland cells were never seen in *Gp. silvana*, but they are conspicuous in *Gp. curtissiae*. *Gracilariopsis silvana* represents the first report of a truly flat-foliose species of *Gracilariopsis*.

*Gracilariopsis hommersandi* is most likely a common member of Caribbean sandy beach habitats of the upper subtidal. Usually, several distinct thalli grow closely together forming isolated clusters of entangled, long, cylindrical axes. Occasionally, a few short, hook-like branchlets are formed near the apices, probably the result of regenerated grazed, damaged or fragmented tips, and in the mid portion of the axis, where they hook up to adjacent thalli, keeping the entire cluster together. Such uncinate branchlets were also observed in an isotype specimen of *Gp. chorda* (BMI; Enoura, Japan, coll. Prof. Saiga #6, March 1894). Specimens of *Gp. hommersandi* from exposed shores in Venezuela (e.g., La Encrucijada) are thicker and seldom branched, whereas those from calm, protected bays and seagrass beds of *Thalassia testudinum* (e.g., Francisky Is., Los Roques Archipelago) are thinner, more delicate, sometimes more branched and beset with more distal uncinate branchlets.

Unbranched specimens of *Gp. hommersandi* collected at the islands of Los Roques Archipelago may superficially resemble *Gp. panamensis* (W. Taylor) Dawson (see: *G. panamensis* Taylor 1945:231, pl. 76, figs. 1-4) from Pacific Panama, with a recorded range from Costa Rica to the Galápagos Islands. *Gracilariopsis hommersandi* may be a sister species to *Gp. panamensis*, and the rise of the Panamanian Isthmus 3.1-3.6 million years ago (Vermeij and Rosenberg 1993, Haug and Tiedemann 1998) would probably be the vicariant event responsible for their isolation and subsequent speciation. Examination of *Gracilariopsis panamensis* (isotypes: UCI; US Alg. Coll. -56496) shows it differs from *Gp. hommersandi* in being longer, up to 165 cm long, lacking the hook-like branchlets, and in possessing a more narrow-based cystocarp in which the gonimoblasts extend farther vertically, and have a pericarp more antically elongated cells (Figs 24, 25). Dawson's (1953) report of a southern Caribbean species of *Gracilariopsis* might also be *Gp. hommersandi*.

*Gracilariopsis cata-luziana* is described from specimens collected from a single locality in Campeche Bay, southern Gulf of Mexico, and may be endemic to that region. Clusters of specimens are attached to coarse sand by small rounded holdfasts. Among the newly described western Atlantic species of *Gracilariopsis*, *Gp. cata-luziana* is morphologically and genetically the closest to *Gp. tenuifrons* (Bird et Oliveira) Fredericq et Hommersand (see: *Gracilaria tenuifrons* Bird and Oliveira 1966; figs. 2-3). Both species possess exceedingly slender, delicate,
stringy thalli, grow to about 40 cm tall, and are loosely and profusely branched. Entangled axes are common, and ultimate branches are short and filiform. Both species are typical of protected bays and turbid waters, sometimes inhabited areas subjected to eutrophication, and occurring in shallow waters about one meter depth where they readily colonize loose debris and other substrata, often with their basal portions buried in fine sediment. *Gracilaria* *cata-luziana* is readily distinguished from *Gp. tenuifrons* in being more delicate, with main axes that are brittle when wet and easily break up when dried.

Population studies on certain species of marine organisms in the southern Gulf of Mexico reveal some degree of uniqueness when compared to populations of the same species from other areas, and that southern Gulf region seems to promote the isolation needed for speciation to take place (Reed and Avise 1990). The geographic structure of the Gulf of Mexico, especially its southern embayment configuration (e.g., Campeche Bay) may be similarly acting as the vicariant event that has isolated Caribbean and Gulf of Mexico populations into two ancestrally related species, *Gp. tenuifrons* and *Gp. cata-luziana*.

Results also found three other undescribed species (Table 1): *Gp. 2* from Namibia; *Gp. 3* from Japan and China; and *Gp. 1*, which is reportedly an invasive species in southern Australia (Womersley 1996, as 'Gp. lemaneiformis') and is also found in the Gulf of California (Pacheco-Ruiz et al. 1999, as 'Gp. lemaneiformis'). These taxa await additional data for final taxonomic diagnosis. All are characterized by being terete, sterile, stringy, and by thriving in protected shallow embayments with thalli commonly drifting close to the shore. Because of their high biomass in Namibia (Stegenga et al. 1997, as 'Gp. lemaneiformis') and in the Gulf of California, Mexico (Pacheco-Ruiz et al. 1999, as 'Gp. lemaneiformis') these species have been used in their local agro industries.

This study has shown that *rbcl* gene sequence analysis provides sufficient phylogenetic signal for species level resolution in the genus *Gracilaria* for the identification and delineation of new and previously described species, and for assessing the evolutionary relationships within the genus. The lack of distinct vegetative and reproductive characters and the high degree of morphological similarity among many species of *Gracilaria* may be the reason that genetically distinct species were not previously recognized on the basis of their morphology alone.

Prior to this study, there were only three species of *Gracilaria* described for the Atlantic Ocean, namely *Gp. longissima* (Stentoft et al. 1995) from the eastern Atlantic, and *Gp. tenuifrons* (Federicq and Hommersand 1989b) and *Gp. carolinensis* (Gurgel et al. 2003) from the western Atlantic. Our results reveal that species diversity of *Gracilaria* now with at least six species in the Atlantic Ocean and sixteen species recognized worldwide (Table 2), has been underestimated. The genus is also expanded to include flattened species.

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