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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 *rbc*L 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 *rbc*L 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*, Gracilariaceae, new species, *rbc*L, 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 *rbc*L, 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 esparcida 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 aferran 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 *rbc*L, de 22 taxa 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 al Atlántico, ha sido subestimada y que la diagnosis del género debe ser ampliada para incorporar a especies aplanadas.

Palabras clave: *Gracilariopsis*, Gracilariaceae, especies nuevas, *rbc*L, filogenia, Atlántico occidental.

INTRODUCTION

Members of the red algal genus *Gracilariopsis* Dawson (1949:40) (Gracilariaceae Nägeli 1847:240; Gracilariales Fredericq et Hommersand 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:liv,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 sjoestedii* (Kylin) Dawson 1949:40[4]] 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:liv, *typ. cons.*[5]] 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*.

Detailed morphological studies of *Gracilariopsis sjoestedtii* (Kylin) Dawson [=*Gp. lemaneiformis sensu* Abbott 1983; non *Gp. lemaneiformis* (Bory) Dawson, Acelto et Foldvik 1964] from California by Fredericq and Hommersand (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 Hommersand (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, Bellorin *et al.* 2002, Gurgel *et al.* 2003). While many taxonomists recognize *Gracilariopsis* as distinct from *Gracilaria* (*e.g.*, Ohmi 1958; Yamamoto 1975; Fredericq and Hommersand 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).

Gurgel *et al.* (2003) recently provided a molecular phylogenetic study inferred from maximum parsimony and maximum likelihood analyses of chloroplast-encoded *rbc*L 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 (Gurgel *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 generitype *Gp. sjoestedtii* Kylin 1930, see Gurgel *et al.* 2003 for nomenclatural note from central, California]; *Gp. chorda* (Holmes) Ohmi (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.*

[4] *Gracilariopsis sjoestedtii* [basionym: *Gracilaria sjoestedtii* 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: *Cordylecladia andersonii* Grunow in Piccone 1886:62] (Gurgel *et al.* 2003).

[5] Conserved generic type, *Gracilaria compressa* (C. Agardh) Greville 1830:liv [basionym: *Sphaerococcus compressus* C. Agardh 1822:308; type locality: Cádiz, Spain] (see: Steentoft *et al.* 1991; Silva 1994:263; Silva *et al.* 1996:917-918); is a taxonomic synonym of *G. bursa-pastoris* (Gmelin) Silva 1952:265 [basionym: *Fucus bursa-pastoris* Gmelin 1768:121] (Silva *et al.* 1996:157).

lemaneiformis (Bory) Dawson, Acleto et Foldvik (1961) from Peru; *Gp. megaspora* Dawson (1949; Norris 1985) from Sonora, Gulf of California; *Gp. nganii* Pham-Hoàng (1969) and *Gp. phantietensis* Pham-Hoàng (1969) both from Viêtnam (Nguyen 1992); *Gp. panamensis* (W. Taylor) Dawson (1949) from Panama; and *Gp. rhodotricha* Dawson (1949) from Pacific Mexico and Viêtnam (Dawson 1954; Nguyen 1992). Sequence analyses of *rbc*L 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. sjoestedtii." Gracilariopsis tenuifrons* (Bird et Oliveira) Fredericq et Hommersand (1989b) is a species originally described from Maceió, Brazil (Bird and Oliveira 1986, as *'Gracilaria tenuifrons'*). Fredericq and Hommersand (1989b) first identified another *Gracilariopsis* from the eastern Atlantic, a species later recognized as *Gp. longissima* (Gmelin) Steentoft, Irvine et Farnham (1995) from Kent, southern England. More recently a new western Atlantic species, *Gp. carolinensis* Liao et Hommersand 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. lemaneiformis;'* Wakibia *et al.* 2001, as '*Gp.* sp.'), was shown, based on *rbc*L 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 Gracilariaceae (*e.g.*, Taylor 1960, Wynne 1998), nor did they match with photographs of type specimens (PC!, NY! or BM!) of Schramm and Mazé (1865, 1866). Therefore we herein describe them as new species, based largely on the analysis of chloroplast encoded *rbc*L 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 Holmgren *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 Ie 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 –20ºC. DNA samples were prepared using the DNeasy Plant Mini Kit (QIAGEN, Valencia, CA, USA), or were submitted to a CTAB-Cesium Chloride DNA procedure (Freshwater and Rueness 1994). Plastid-encoded *rbc*L was selected to infer a phylogeny for *Gracilariopsis*. PCR and sequencing primers used in this study were *Frbc*L start, F7, F57, F492, F577, F753, F993, R753, R1381 and *Rrbc*S start as listed in Freshwater and Rueness (1994) and Hommersand *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 *rbc*L sequences were produced from 22 recently collected samples of *Gracilariopsis*. Collection information (Table 1) includes specimen locality, date and collector's name, percentage of *rbc*L gene sequenced, and GenBank accession numbers (see also Gurgel *et al.* 2003). *Melanthalia obtusata* (Labillardière) J. Agardh and *Curdiea 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 *Gracilariaceae* (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 *rbc*L. 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 (MULTREES) 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*.

Table 1. List of Algal Species Studied, with their Collection Information, and the *rbc*L GenBank Accession Numbers Followed by *rbc*L Fraction (in %) Sequenced.

Entity	Collection data	GenBank #	Source
Curdiea coriacea (Hook. et Harv.) J. Agardh	Doubtless Bay, New Zealand, coll. W. Nelson, 1 xii 1993	AY049425, 66.5%	Gurgel *et al.* 2003
Curdiea crassa Millar	Bongin Bongin Bay, North of Sydney, NSW Australia; coll. A. Millar & P. Richards; 18 ii 1994	AY049427, 98.1%	Gurgel *et al.* 2003
Gracilariopsis andersonii (Grunow) Dawson	Pigeon Point, San Mateo Co., California; coll. M.H. & F.H. Hommersand; 20 v 1992	AY049413, 94.2%	Gurgel *et al.* 2003
Gracilariopsis andersonii (Grunow) Dawson	Seal Rock, Lincoln Co., Oregon; coll. S. Fredericq; 15 v 1999	AY049414, 96.4%	Gurgel *et al.* 2003
Gracilariopsis cata-luziana Gurgel, Fredericq et J. Norris (herein)	2 miles West of Anton Lizardo, Veracruz area, Gulf of Mexico; coll. C.F.D. Gurgel; 10 ii 1999	AY049406, 80.2%	Gurgel *et al.* 2003 (as '*Gp.* sp. nov.')
Gracilariopsis costaricensis Dawson	South end, Playa Tamarindo, Nicoya Penninsula, Guanacaste, Costa Rica; coll. D.T. Talbot & D.W. Freshwater; 17 iii 1999	AY049423, 98.4%	Gurgel *et al.* 2003
Gracilariopsis carolinensis Liao et Hommersand in Gurgel et al., *ined.*	Kure Beach, Fort Fisher, NC; coll. D.W. Freshwater; 14 iv 1991	AY049412, 96.7%	Gurgel *et al.* 2003
Gracilariopsis heteroclada (Zhang et Xia) Zhang et Xia in Abbott, Zhang et Xia	Dapdap, Bulusan, Luzon, Philippines; coll. S.M. Lin, 22 iv 1998	AY049411, 91.1%	Gurgel *et al.* 2003
Gracilariopsis hommersandii Gurgel, Fredericq et J. Norris (herein)	Fort Randolph, Colón City, Panama; coll. B. Wysor; 26 iii 1998	AY049405, 97.1%	Gurgel *et al.* 2003 (as '*Gp.* aff. *panamensis*')
Gracilariopsis hommersandii Gurgel, Fredericq et J. Norris (herein)	La Encrucijada, Peninsula Paraguana Panama, Falcon State, Venezuela; coll. C.F.D. Gurgel, J.E. Conde & C. Carmona; 13 vii 1999	AY049407, 93.3%	Gurgel *et al.* 2003 (as '*Gp.* aff. *panamensis*')
Gracilariopsis hommersandii Gurgel, Fredericq et J. Norris (herein)	Los Francisky Is., Los Roques Archipelago, Venezuela; coll. C.F.D. Gurgel; 4 vii 1999; specimen # 1	AY049408, 98.4%	Gurgel *et al.* 2003 (as '*Gp.* aff. *panamensis*')
Gracilariopsis hommersandii Gurgel, Fredericq et J. Norris (herein)	Los Francisky Is., Los Roques Archipelago, Venezuela; coll. C.F.D. Gurgel; 4 vii 1999; specimen #2	AY049409, 98.4%	Gurgel *et al.* 2003 (as '*Gp.* aff. *panamensis*')
Gracilariopsis lemaneiformis (Bory) Dawson, Acleto et Foldvik	Yacilla, Paita, Piura, Peru; coll. C. Acleto & R. Zuniga; 3 iii 1994	AY049415, 97.6%	Gurgel *et al.* 2003
Gracilariopsis longissima (Stackhouse) Irvine, Steentoft et Farnham	Venetian lagoon, Adriatic Sea, Italy; coll. K.S. Cole; 7 ix 1998	AF527881, 97.5%	Gurgel *et al.* 2003
Gracilariopsis longissima (Stackhouse) Irvine, Steentoft et Farnham	Cadiz, Spain; coll. J.R. Andria Gonzalez; s.d.	AY130244, 97.5%	Gurgel *et al.* 2003
Gracilariopsis longissima (Stackhouse) Irvine, Steentoft et Farnham	off Sandfoot Castle, Portland Harbour, Dorset, England; coll. W. Farnham & M. Steentoft; 30 viii 1992; leg. C. Bird	AY049420, 97.3%	Gurgel *et al.* 2003
Gracilariopsis silvana Gurgel, Fredericq et J. Norris (herein)	La Vela de Coro, Falcon State, Venezuela; coll. C.F.D. Gurgel; 14 vii 1999	AY049309, 96.7%	Gurgel *et al.* 2003 (as '*Gp.* sp. *nov.*')
Gracilariopsis tenuifrons (Bird et Oliveira) Fredericq et Hommersand	Ilet Caret, Guadeloupe, French West Indies; coll. A. Renoux; 2 xii 1993	AY049418, 97.8%	Gurgel *et al.* 2003
Gracilariopsis tenuifrons (Bird et Oliveira) Fredericq et Hommersand	Arya Peninsula, Sucre, Venezuela, coll. D.W. Freshwater; v 1990	AY049417, 82.4%	Gurgel *et al.* 2003
Gracilariopsis sp. 1	Bahía de Las Animas, Gulf of California, Mexico; aquaculture; leg. J. Zertuche-Gonzáles; vi 1998	AY049416, 41.1%	Gurgel *et al.*. 2003 (as *'Gp. lemaneiformis'*)
Gracilariopsis sp. 1	Lake Butler, Robe, So. Australia, Australia; coll. H.B.S. Womersley; 03 iii 1995	AY049422, 97.8%	Gurgel *et al.* 2003 (as *'Gp. lemaneiformis'*)
Gracilariopsis sp. 2	Swakopsmund, Namibia; coll. M.H. Hommersand; 06 vii 1993	AY049410, 98.2%	Gurgel *et al.* 2003 (as *'Gp. longissima'*)
Gracilariopsis sp. 3	Tosa Bay, Shikiku I., Japan; coll. M. Ohono, D.B. Largo & J. Rebello, leg. L. Liao; 11 ix 1992	AY049419, 97.8%	Gurgel *et al.*. 2003 (as *'Gp. lemaneiformis'*)
Gracilariopsis sp. 3	Qingdao, Shandong Prov., China; coll. M.H. Hommersand; 23 iv 1994	AY049421, 65%	Gurgel *et al.* 2003 (as *'Gp. lemaneiformis'*)
Melanthalia obtusata (Labillardière) J. Agardh	Warrnambool, Victoria, Australia; coll. M.H. Hommersand; 13 vii 1995	AY049431, 99%	Gurgel *et al.* 2003

Table 2. Recognized Species of *Gracilariopsis* Dawson.

1. *Gracilariopsis andersonii* (Grunow) Dawson 1949: 43.
   Basionym: *Cordylecladia andersonii* Grunow in Piccone 1886:62.
   Synonyms: *Gracilaria andersonii* (Grunow) Kylin 1941:21.
   Gracilaria sjoestedtii Kylin 1930:55.
   Gracilariopsis sjoestedtii (Kylin) Dawson 1949: 40.
2. *Gracilariopsis carolinensis* Liao et Hommersand in Gurgel *et al.* 2003: 163
3. *Gracilariopsis cata-luziana* Gurgel, Fredericq et J. Norris *sp. nov.* (herein)
4. *Gracilariopsis chorda* (Holmes) Ohmi 1958:50.
   Basionym: *Gracilaria chorda* Holmes 1896:253.
5. *Gracilariopsis costaricensis* Dawson 1949:46.
   Synonym: *Gracilaria costaricensis* (Dawson) Papenfuss 1967:100.
6. *Gracilariopsis heteroclada* (Zhang et Xia) Zhang et Xia *in* Abbott, Zhang et Xia 1991:22.
   Basionym: *Gracilaria heteroclada* Zhang et Xia 1988:132.
7. *Gracilariopsis hommersandii* Gurgel, Fredericq et J. Norris *sp. nov.* (herein)
8. *Gracilariopsis lemaneiformis* (Bory) Dawson, Acleto et Foldvik 1964:59.
   Basionym: *Gigartina lemaneiformis* Bory 1828:151, as *'lemanaeformis.'*
   Synonym: *Cordylecladia lemaneiformis* (Bory) Howe 1914:128, as *'lemanaeformis.'*
9. *Gracilariopsis longissima* (Gmelin) Steentoft, Irvine et Farnham 1995:117.
   Basionym: *Fucus longissimus* Gmelin 1768:134.
10. *Gracilariopsis megaspora* Dawson 1949: 45.
    Synonym: *Gracilaria megaspora* (Dawson) Papenfuss 1967:100.
11. *Gracilariopsis nganii* Pham-Hoàng 1969:179.
12. *Gracilariopsis panamensis* (W. Taylor) Dawson 1949: 44.
    Basionym: *Gracilaria panamensis* W. Taylor 1945:231.
13. *Gracilariopsis phantietensis* Pham-Hoàng 1969:180.
14. *Gracilariopsis rhodotricha* Dawson 1949:47.
    Synonym: *Gracilaria rhodotricha* (Dawson) Papenfuss 1967:100.
15. *Gracilariopsis silvana* Gurgel, Fredericq et J. Norris, *sp. nov.* (herein)
16. *Gracilariopsis tenuifrons* (Bird et Oliveira) Fredericq et Hommersand 1989b:240.
    Basionym: *Gracilaria tenuifrons* Bird et Oliveira 1986:314.

RESULTS

Gracilariopsis 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.

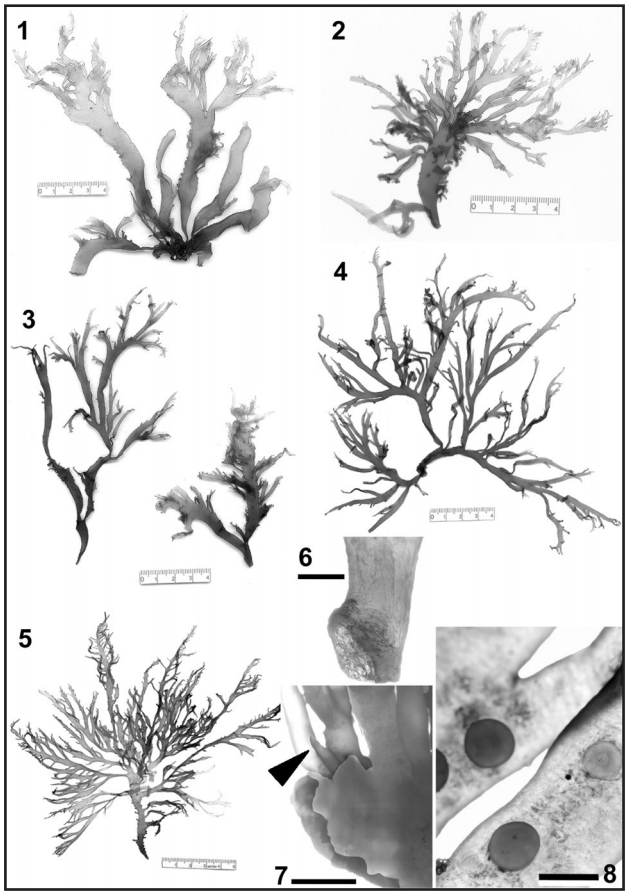
Paratype. Venezuela: La Vela de Coro, Estado Falcon, 13 vii 1999, coll. C. F. D. Gurgel, J. E. Conde and C. Carmona #FG-13 (#US Alg. Coll. -204317).

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 adjectival form.

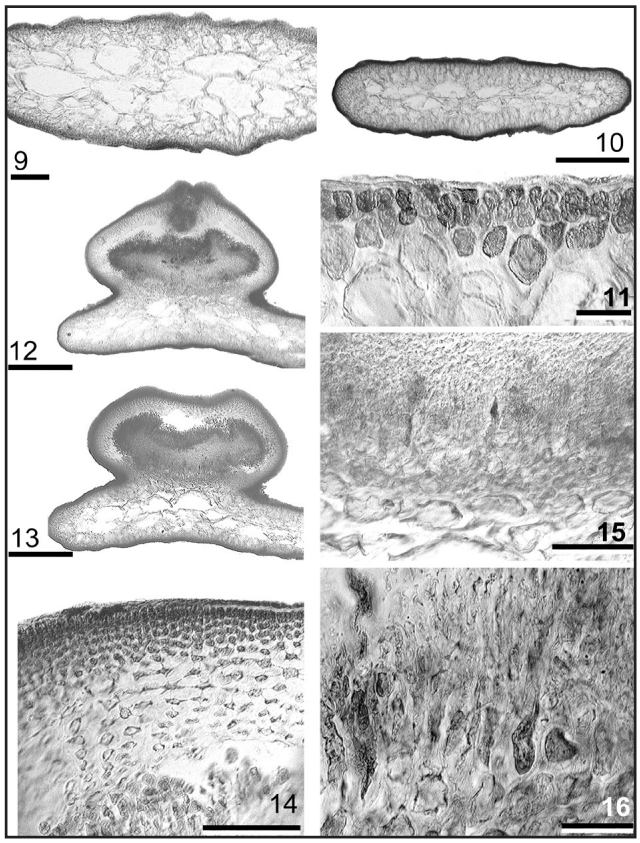
Latin diagnosis: *Thalli plerumque* 14-16 (-20) cm *alt.*, 1-3 cm. *lat. Thalli juniores plerumque solitarii tenues delicatique, vetustiores crassi cartilagineique uterque exorientes haptero parvo oributalato, interdum haptera anastomosantia. Thalli complanati omnino, interdum undulati. Axes principales ligulati, dichotomi, subdichotomi, polychotomi vel ramosi irregulariter. Ramificatio abunde, rami longi apicem versus. Rami numquam constricti basi, maximam partem orti margine, apicibus fractorum thallorum sed intersum mediregionibus laminae axium principalium.*

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 constricted at base, curved upward, irregularly pinnate, mostly arising from thallus margin (Figs. 1-5), damaged tips, and the midregion of main axes (Figs. 1-2). Apices variable, acute to roundly 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 constricted at base where protruding from thallus (Figs. 12-13), with a centrally located, occasionally rostrate ostiole (Fig. 12). Carposporangia organized in tightly packed branched files. 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 for 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. Carpogonial fusion 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 conjunctor cells subsequently fusing downward onto these enlarged cells



Figures 1-8. *Gracilariopsis silvana* Gurgel, Fredericq et J. Norris sp. nov.. 1: HOLOTYPE (#US Alg. Coll. -204316). 1-4: Range of habit variation in Venezuela specimens from Playa Barranquila; 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. *Gracilariopsis silvana* 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.

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). Spermatangial and tetrasporangial specimens not seen.

Gracilariopsis hommersandii 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, Colón City, Bahía Limon, Provincia Colón, (Caribbean Panama), 26 iii 1999, coll. B. Wysor, #BW-00197. Isotypes: LAF.

Paratypes. Venezuela: Los Roques Archipelago: Los Francisky Island, coll. C. F. D. Gurgel, # FG-02, # FG-05, 4 vii 1999; Madrisky Island, coll. C. F. D. Gurgel, # FG-06, 7 vi 1999; and, Crasky Island, coll. C. F. D. Gurgel, # FG-07, # FG-08, 7 vii 1999. Venezuela: La Encrucijada, Peninsula Paraguana, Estado Falcon, 13 vii 1999, coll. C. F. D. Gurgel, #FG-18 (#US Alg. Coll. 204313).

Etymology: This species, *"hommersandii"*, 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 discoideo. Plures thalli plerumque fasciculati simul eodem haptero inconspicuo. Thalli plerumque ramosi non profuse, saepe solum compositi axium linerarium rectorum ramis. Apices acuminati, uncinati vel compositi* 1-4 *unciformium ramulorum,* 0.5-0.8 cm *long, deorsum extensorum formatorum antea fractorum apicum crescentium. Interdum superae 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 subcortex abrupt; subcortex composed of evenly spaced, slightly anticlinally elongated cells, (6.0) 8.8 (-10) µm by (3.8-) 5.0 (-7.5) µm, with innermost subcortical 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). Carpogonial fusion cell not pronounced. Inner pericarp cells at base of cystocarp cavity (Fig. 27), 31.25-43.75 µm by 18.75 µm diameter. Spermatangial and tetrasporangial specimens not seen.

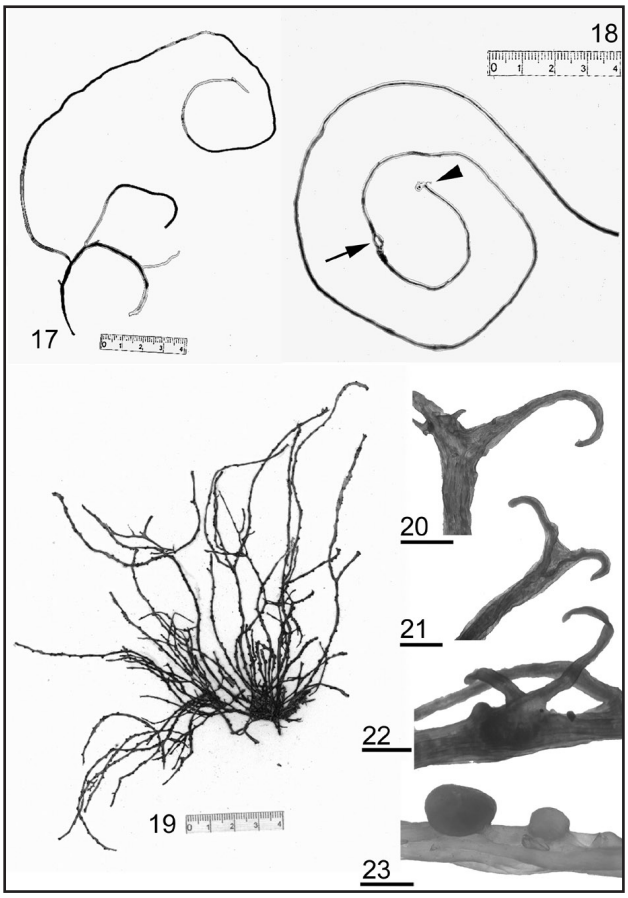
Gracilariopsis cata-luziana Gurgel, Fredericq et J. Norris, *sp. nov.* (Figs. 31-36)

Holotype. #US Alg. Coll. -204314 (Fig. 31). México: protected sandy beach near lagoon [19º 03.31' N; 96º 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

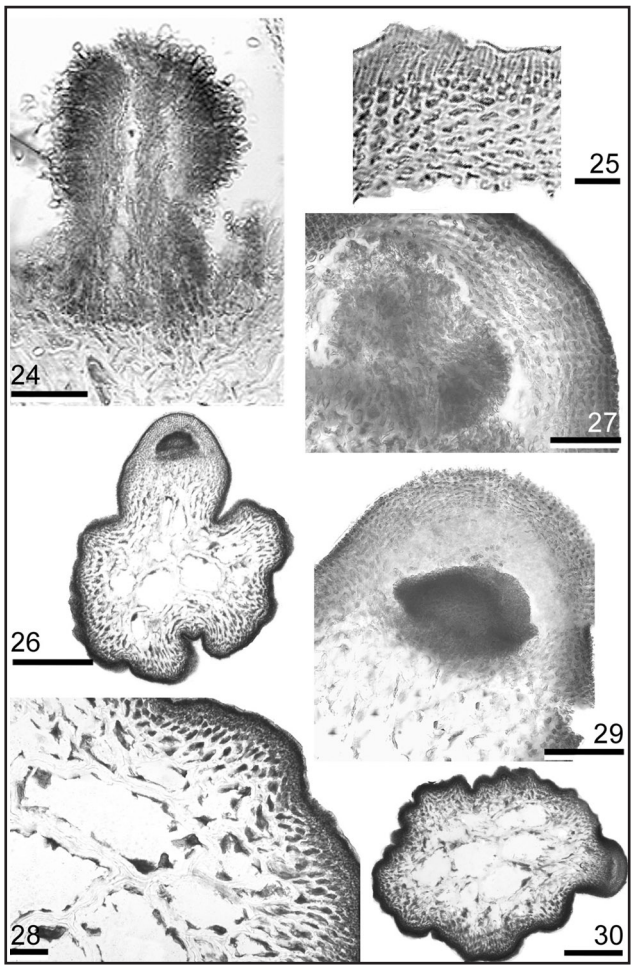
Etymology: The adjectival ending, *-ana*, is chosen (Stern 1973:294; Lindley 1832) for *"cata-luziana"*, named in honor of Professors Catalina Mendoza and Luz Elena Mateo-Cid (Escuela National de Ciencias Biológicas, Instituto Politécnico Nacional, México D.F.), who have greatly enhanced our floristic 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.

Latin diagnosis: *Thalli dumales compositi aliquot specimeninum intricatorum. Individua specimena gracilia,* 25 cm *long., usque ad* 6 cm *alt. Segregati axes principales cartilaginei, filo metallico similis, teretes ad paucicompressi, aliquot ramulis irregularibus ad subdichotomos, ramosis profuse. Ramificatio pro parte maxima alternata, irregularis, interdum duo ramis insertis in eadem regionem. Rami tenuissimi, lineares leviter constricti basi distributi omnino thallo descrescentes in apices acutatos.*

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.



Figures 17-23. *Gracilariopsis hommersandii* Gurgel, Fredericq et J. Norris *sp. nov.* 17-18: specimens from La Encrucijada, Venezuela. 17: Sparsely branched. 18: Unbranched specimen with apex bearing terminal uncinate branchlets (arrowhead) and anostomosed branchlet (arrow). 19: HOLOTYPE (Ft. Randolph, Caribbean coast of Panama; #US Alg. Coll. -204312), an irregularly branched specimen with protruding cystocarps. 20-21: Uncinate branchlets at apices of sparsely branched Venezuelan specimens. 22: Uncinate branchlets coiling around contiguous branches in the middle part of the thallus. 23: Surface view of cystocarps constricted at base. Scales: Figs. 17-19: ruler =4 cm; 20-21, 23: bar =1.0 mm; 22: bar =900µm.



Figures 24-25. *Gracilariopsis panamensis* (W. Taylor) Dawson (Isotype: UC). 24: Transverse section through cystocarp. 25: Detail of pericarp wall. Figs. 26-30: *Gracilariopsis hommersandii* Gurgel, Fredericq et J. Norris sp. nov. from La Encrucijada, Venezuela. 26: Transverse section through main axis bearing cystocarp, showing large, thick-walled innermost medullary cells. 27: Transverse section of cystocarp showing pericarp with anticlinal rows of cells and tightly organized gonimoblasts. 28: Detail of transition between the thick-walled medullary cells and cortex. 29: Transverse section of a cystocarp. 30: Transverse section through main axis bearing young cystocarp at right. Scales: Figs. 24, 26-28: bar =100µm; 25: bar =40µm; 29: bar =200µm; 30: bar =250µm.

35). Branch initials spine-like, distributed all over thallus at wide 45º-90º angles, tapering into acute tip, mostly of two sizes, 2.5 and 4.0 cm long. Hair cells rare. Cortical region composed of two distinct layers of pigmented cells. Cells of outer cortical layer typically refringent, of variable shape (Figs. 32-34, 36), but mostly rounded, (5.0) 7.5 (-8.5) µm by 4.5-5.0 µm, or spherical or squarish, (7.0) 10 (-12.5) µm by (6.5-) 7.5 (-10) µm. Subcortex composed of spherical to anticlinally elongated larger cells, (6.25-) 13 (-21.25) µm by (9.4-) 12 (-23.75) µm, rich in floridean starch. Transition zone between medulla and subcortex abrupt. Medulla composed of one central cell (Fig. 32), 250-330 µm diameter, or up to five large central vacuolate cells (Figs 33-34, 36) 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 (-21.25) µm by (12.5-) 13.75 (-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 *rbc*L 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.

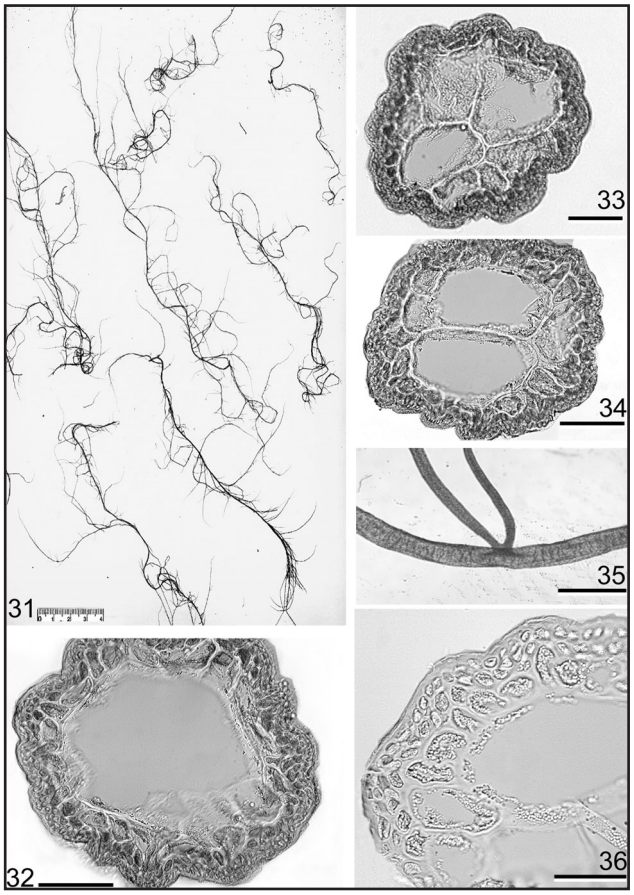
The eastern Pacific *Gp. lemaneiformis* from Peru, *Gp. costaricensis* from Costa Rica, and the recently described western Atlantic *Gp. carolinensis* (Gurgel *et al.* 2003) form a well-supported clade (bp = 91) sharing similar cystocarp features. Gurgel *et al.* (2003) also showed that *Gp. carolinensis* is morphologically and genetically more closely related to *Gp. lemaneiformis* 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. lemaneiformis'*), and is shown to be the same entity as specimens from the Baja California Norte coast of the Gulf of California (=Pacheco-Ruíz *et al.* 1999, as *'Gp. lemaneiformis'*) (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: 61; type locality: Florida, lectotype LD!), *G. cuneata* Areschoug (1854: 351; type locality: vicinity of Pernambuco, Brasil; syntypes S!), or misidentified specimens from Venezuela (Rodriguez de Rios 1986, as *'G. textorii'*). 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*.



Figures 31-36. *Gracilariopsis cata-luziana* Gurgel, Fredericq et J. Norris *sp. nov.* 31: HOLOTYPE (#USAlg. Coll. -204314). 32-34: Transverse sections through different portions of main axis showing varying number of very large, innermost medullary cells. 35: Two branchlets originating from single insertion point on main axis. 36: Detail showing transition between large-celled medulla and cortical zone bearing refringent cells. Scales: Fig. 31: ruler =4cm; 32-34: bar =100mm; 35: bar =1.0mm; 36: bar =40mm.

Gracilariopsis hommersandii 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* (BM!; Enoura, Japan, coll. Prof. Saida #6, March 1894). Specimens of *Gp. hommersandii* 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. hommersandii* 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 hommersandii* may be a sister species to *Gp. panamensis*, and the rise of the Panamean 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: UC!; #US Alg. Coll. -56496!) shows it differs from *Gp. hommersandii* 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 with more anticlinally elongated cells (Figs 24, 25). Dawson's (1953) report of a southern Caribbean species of *Gracilariopsis* might also be *Gp. hommersandii*.

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 1986: figs. 2-3). Both species possess exceedingly slender, delicate,

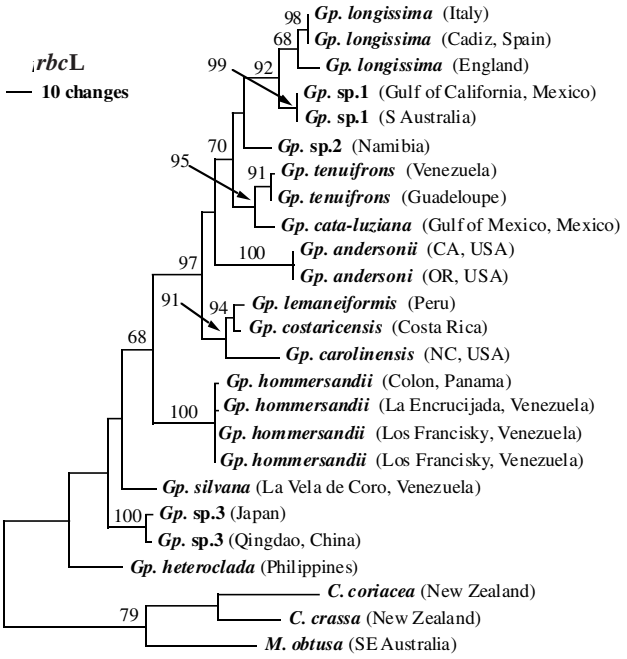


Figure 37. One of four maximum parsimony trees inferred from *rbc*L sequences of 22 samples of *Gracilariopsis* (Length =591, Consistency Index =0.58, Retention Index =0.68). Bootstrap proportions based on 3000 replicates are shown above the nodes. *Curdiea* and *Melanthalia* species were selected as outgroup taxa.

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 inhabiting 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. *Gracilariopsis 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-Ruíz *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 agar industries.

This study has shown that *rbc*L gene sequence analysis provides sufficient phylogenetic signal for species level resolution in the genus *Gracilariopsis*, 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 *Gracilariopsis* 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 *Gracilariopsis* described for the Atlantic Ocean, namely *Gp. longissima* (Steentoft *et al.* 1995) from the eastern Atlantic, and *Gp. tenuifrons* (Fredericq and Homnersand 1989b) and *Gp. carolinensis* (Gurgel *et al.* 2003) from the western Atlantic. Our results reveal that species diversity of *Gracilariopsis*, 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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