

2005

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DOI: 10.18785/goms.2301.05

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Recommended Citation

Gavio, B., E. Hickerson and S. Fredericq. 2005. *Platoma chrysymenoides* sp. nov. (Schizymeniaceae), and *Sebdenia integra* sp. nov. (Sebdeniaceae), Two New Red Algal Species from the Northwestern Gulf of Mexico, with a Phylogenetic Assessment of the Cryptonemiales Complex (Rhodophyta). *Gulf of Mexico Science* 23 (1). Retrieved from <https://aquila.usm.edu/goms/vol23/iss1/5>

Platoma chrysymenioides sp. nov. (Schizymeniaceae), and *Sebdenia integra* sp. nov. (Sebdeniaceae), two New Red Algal Species from the Northwestern Gulf of Mexico, with a Phylogenetic Assessment of the Cryptonemiales Complex (Rhodophyta)

BRIGITTE GAVIO, EMMA HICKERSON, AND SUZANNE FREDERICQ

Recent collecting cruises conducted in the Northwestern Gulf of Mexico at 40- to 90-m depth revealed a diverse deepwater flora that is dominated by members of the Cryptonemiales complex. In this article, we describe two species new to science, *Platoma chrysymenioides* sp. nov. (Schizymeniaceae) and *Sebdenia integra* sp. nov. (Sebdeniaceae). Chloroplast-encoded *rbcl* sequence analyses corroborate morphological and nuclear small subunit ribosomal RNA gene data that the red algal orders Cryptonemiales and Rhodymeniales are closely related. The allied order Nemastomatales is strongly supported to include the Nemastomataceae and Schizymeniaceae, but the phylogenetic position of the Sebdeniaceae and Tsengiaceae remains equivocal. The Cryptonemiales, Rhodymeniales, Nemastomatales, Sebdeniaceae, and Tsengiaceae form a well-supported monophyletic assemblage—the Cryptonemiales complex—within the Rhodophyta.

We describe two red algal species new to science collected offshore Louisiana and Texas in the northwestern Gulf of Mexico basin, a region characterized by an extensive continental shelf with an average width of about 100 miles. Along this shelf, there are peculiar topographic features, such as salt domes or diapirs (offshore Louisiana). These formations harbor biotic communities that are still poorly known, as recent findings have highlighted (Fenner, 2001; Larsen and Heard, 2002; Ruiz-Carus et al., 2002). Published records documenting the offshore presence of deepwater macroalgae in the northwestern Gulf have been even more sparse and restricted to a few hard banks such as the Flower Garden Banks National Marine Sanctuary (e.g., Eiseeman and Blair, 1982; Rezak et al., 1985). Recent nondestructive Sonsub remotely operated vehicle (ROV)-facilitated collections of macroalgae were conducted in the West Flower Garden Bank National Marine Sanctuary on board the National Oceanic and Atmospheric Administration (NOAA) Ship *R/V Ronald H. Brown*, at depths between 50 and 68 m. In addition, dredge collections on board the *R/V Pelican*, a University National Oceanographic Laboratory System (UNOLS) fleet oceanographic research vessel belonging to the Louisiana Universities Marine Consortium, were made on unconsolidated rubble banks with box dredges or “scrapes” as previously used for the “Hourglass Cruises” (Joyce and Williams, 1969) at depths ranging from 40 to 90 m outside the Sanctuary. The macroalgae are

typically freestanding, leafy and large (up to 20 cm), epilithic on loose bedrock or on rhodoliths dominated by crustose coralline algae. Of particular interest, this unrecorded flora was dominated by gelatinous red algae encompassing the Cryptonemiales sensu lato, Rhodymeniales, and Nemastomatales. We describe in this article two new species from the Northwestern Gulf of Mexico, *Platoma chrysymenioides* sp. nov. (Schizymeniaceae) and *Sebdenia integra* sp. nov. (Sebdeniaceae).

MATERIALS AND METHODS

Silica gel-dried specimens, alcohol-preserved collections, and extracted DNA samples are deposited at the University of Louisiana at Lafayette and stored at -20°C . Deoxyribonucleic acid samples were prepared using the DNAeasy Plant Minikit (Qiagen, Valencia, CA) or were submitted to a CTAB-Cesium Chloride DNA procedure (Freshwater and Rueness, 1994). Plastid-encoded *rbcl* was selected to infer a phylogeny for red algae. Protocols for DNA extraction, gene amplification, and sequencing are as described in Gavio and Fredericq (2002, 2003). Polymerase chain reaction (*Frbcl*start-R753, F7-R753, F57-R753, F577-R1381, F645-R1381, F993-*Rrbcl*Start) and sequencing primers (*Frbcl*start, F7, F57, F577, F753, F993, R376, R753, R1105, R1381, *Rrbcl*Start) used in this study are listed in Gavio and Fredericq (2002, 2003). Species identification was based on the original descriptions, critical analysis of the literature, and the type method (Silva, 1952).

Partial and complete *rbcl* sequences were produced for a total of 78 specimens (Table 1), comprising representatives of the four families of Rhodymeniales (Rhodymeniaceae, Champiaceae, Lomentariaceae, Faucheaceae), the three families in the Cryptonemiales (Sebdeniaceae, Halymeniaceae, Tsengiaceae), the Nemastomatales (Schizymeniaceae, Nemastomataceae), as well as representatives of Gelidiales, Ceramiales, Gracilariales, Plocamiales, Corallinales, and six families routinely placed in the Gigartinales *sensu lato*. A sequence of *Ahnfeltia plicata* (Ahnfeltiales) was used as the outgroup on the basis of phylogenetic hypotheses derived from earlier global analyses of the Florideophycideae as a whole (Fredericq et al., 1996). GenBank accession numbers, species identification and authors, information concerning origin, data, and collector are listed in Table 1.

The generated *rbcl* sequence data were compiled and aligned with Sequencher (Gene Codes Corp., Ann Arbor, MI) and MacClade 4.0 (D. R. Maddison and W. P. Maddison, 2000) and exported for phylogenetic analysis. Because some sequence data were incomplete at the 5' terminus of the coding region in many taxa, the analyzed data set was restricted to the last 1,407 base pairs (bp) of the 1,467-bp *rbcl*.

Phylogenetic analyses were conducted with Maximum Parsimony (MP) and Neighbor Joining (NJ) algorithms as implemented in PAUP* v.4.0 beta 10 (Swofford, 2002) and the Bayesian likelihood as implemented in MrBayes 1.11 (MB) (Hall, 2001; Huelsenbeck and Ronquist, 2001). Parsimony trees obtained under the Fitch criterion of equal weights for all substitutions (Fitch, 1971) were inferred from a heuristic search, excluding uninformative characters, consisting of 5,000 random sequence additions holding five trees at each step, MULTIPARS and Tree-Bisection-Reconnection algorithms. Consistency (CI) and retention (RI) indices were calculated (Kluge and Farris, 1989).

The optimal model of sequence evolution to fit the data alignment estimated by hierarchical likelihood ratio tests performed by Modeltest v.3.04 (Posada and Crandall, 1998) was the GTR + I + Γ (General Time Reversible model with invariable sites and gamma distribution). The parameters used were as follows: assumed nucleotide frequencies A = 0.4064, C = 0.0677, G = 0.1283, T = 0.3976; substitution rate matrix A-C substitutions = 4.3780, A-G = 8.4271, A-T = 1.9726, C-G = 8.9229, C-T = 47.2764, G-T = 1.0; proportion of sites as-

sumed to be invariable = 0.3990; and rates for variable sites assumed to follow a gamma distribution with shape parameter = 0.5316. These likelihood parameters were applied in the Bayesian analysis [Iset basefreq = (0.3475, 0.1202, 0.1556, 0.3767) nst = 6 revmat = (4.3780, 8.4271, 1.9726, 8.9229, 47.2764, 1.0) rates = invgamma; gamma = 0.5316].

For the Bayesian analysis, we ran four chains of the Markov chain Monte Carlo, sampling one tree every 100 generations for 1,050,000 generations starting with a random tree. Stationarity was reached at above generation 50,000. Thus the first 50,000 generations were the "burn in" of the chain, and inferences about the phylogeny were based on those trees sampled after generation 50,000. A 50% consensus tree (majority rule as implemented by PAUP*) was computed from the 100,000 trees saved after the "burn in" point. Reliability of the Bayesian consensus tree is given by the frequency at which each node appears among all saved trees after the "burn in" generation. This frequency corresponds to the posterior probability of the clades (Hall, 2001).

Neighbor Joining (Saito and Nei, 1987) was performed with a maximum likelihood distance correction set with the GTR substitution rate matrix parameters listed above, excluding variable sites and the gamma distribution. Neighbor Joining only recovered the most probable hypothesis similar to those given by the MP and Bayesian methods when simpler models of sequence evolution were applied (data not shown). Support for nodes was assessed by calculating bootstrap proportion (BP) values (Felsenstein, 1985) based on 5,000 resamplings (NJ) and 1,000 resamplings (MP).

Specimens studied for the morphological study including vouchers, were fixed and liquid-preserved in 8% formalin/seawater, and pressed on herbarium sheets and deposited in US Algal Collection and University of Louisiana Herbarium (LAF) (herbaria abbreviations follow Holmgren et al., 1990). Specimens 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). Transverse and longitudinal sections were handmade using stainless steel razor blades, and then stained in a 3% aniline blue solution (Tsuda and Abbott, 1985) for 10–15 min. The stained specimens were fixed with one drop of 3% acetic acid, rinsed with distilled water, and then were mounted in a 50% Karo[®] clear corn syrup/distilled water solution with phenol added as a preservative. Pho-

TABLE 1. List of species used in *rbdL* analysis with collection information and GenBank accession number (Co. = County; BCS = Baja California Sur; s.l. = locality unknown; s.d. = date unknown).

Species	Collection locality	Collection data	<i>RbdL</i> portion sequenced	GenBank Accession number
<i>Ahnfeltia plicata</i> (Hudson) Fries	Broadhaven, Pembrokeshire, Wales, U.K.	C. A. Maggs, 9 Feb. 1993	36-1467 (98%)	U04168
<i>Agardhiella subulata</i> (C. Agardh) Kraft & Wynne	Federal Basin, New Hanover Co., North Carolina, U.S.A.	D. W. Freshwater, March 1991	64-1467 (96%)	U04176
<i>Bonnemaisonia asparagoides</i> (Woodward) C. Agardh	Norway, s.l.	J. Rueness, s.d.	97-1467 (93%)	AF212188
<i>Bostrychia radicans</i> (Montagne) Montagne	St. Louis Bay, Mississippi, U.S.A.	C. F. D. Gurgel, 11 Feb. 1998	43-1467 (97%)	AF259497
<i>Botryocladia shanskii</i> Dawson	Long Bay Point, Isla Colón, Caribbean Panama	B. Wysor, 19 Oct. 1999	9-1467 (99%)	AY168662
<i>Callophyllis pinnata</i> Setchell & Swezy	Angelmo food market, Puerto Montt, Chile	S. Fredericq and M. E. Ramírez, 24 Feb. 1994	19-1467 (99%)	AY294397
<i>Carpopeltis maillardii</i> (Montagne et Millardet) Chiang	Magang, Taiwan	S. Fredericq and S. M. Lin, 11 March 1993	41-1467 (97%)	AY294400
<i>Caulacanthus ustulatus</i> (Turner) Kützing	Swakopmund, Namibia	M. H. Hommersand, 7 Nov. 1993	102-1467 (93%)	AF099687
<i>Ceramium diaphanum</i> (Lightfoot) Roth	North Carolina, U.S.A.	D. W. Freshwater, s.d.	65-1467 (96%)	U04020
<i>Ceratodictyon spongiosum</i> Zanardini	Haitzu ku, Hsiao Liu Shu I., Taiwan	S. Fredericq and S. M. Lin, 22 Aug. 1993	304-1467 (79%)	U21639
<i>Champia compressa</i> Harvey	Epiphytic on <i>Jania</i> sp., Florida Middle Ground, Florida, U.S.A. 28°33.064'N 89°16.468'W	B. Gavio and B. Wysor, 10 Aug. 2000	34-1467 (98%)	AY294358
<i>Chrysmenia procumbens</i> Weber van Bosse	Wan Li Dung, Kenting National Park, S. Taiwan	S. Fredericq and S. M. Lin, 25 Aug. 1993	352-1467 (76%)	AY294381
<i>Cordylecladia erecta</i> (Greville) J. Agardh	Black Head, Co., Clare, Ireland	C. A. Maggs, 20 Jan. 1992	148-378, 448-1172 (65%)	AY294399
<i>Corynomorpha clavata</i> (Harvey) J. Agardh	Key Largo, Florida, U.S.A.	D. W. Freshwater, 19 June 1994	46-1467 (97%)	AY294360
<i>Cryptonemia luxurians</i> (C. Ag.) J. Agardh	Praia Rasa, Rio de Janeiro, Brazil	C. F. D. Gurgel, 12 Dec. 1998	52-1467 (97%)	AF488813
<i>Delesseria sanguinea</i> (Hudson) Lamouroux	Newcastle, Co. Down, N. Ireland, U.K.	C. A. Maggs, 15 March 1999	23-1118, 1228-1467 (91%)	AF254182
<i>Delisea flaccida</i> (Suhr) Papenfuss	Shark's Cove, South Africa	M. H. Hommersand, s.d.	106-1467 (93%)	AF212187
<i>Dendrymenia skottsbergii</i> Dawson	La Boca Navidad, Chile	S. Fredericq, 17 Jan. 1995	9-1467 (99%)	AY294354
<i>Dicranema revolutum</i> (C. Ag.) J. Agardh	Port Mac Donnell, Australia	M. H. and F. Hommersand, 28 Aug. 1995	122-1467 (92%)	AY294379
<i>Dumontia contorta</i> (S. G. Gmelin) Ruprecht	Manomet Bluffs, Plymouth Co, Massachusetts, U.S.A.	M. H. Hommersand, 23 April 1993	38-1467 (97%)	AY294378
<i>Epymenia capensis</i> (J. Agardh) Papenfuss	Kommetjie, Cape Peninsula, South Africa	O. De Clerck, 24 Jan. 2001	35-1467 (98%)	AF385646

TABLE 1. Continued.

Species	Collection locality	Collection data	RbL portion sequenced	GenBank Accession number
<i>Faucheia laciniata</i> J. Agardh	Ketchikan, Alaska, U.S.A.	S. C. Lindstrom, 2 July 2000	40-1467 (97%)	AY294355
<i>Furcellaria lumbricalis</i> (Hudson) Lamouroux	Penmarch, Brittany, France	M. H. Hommersand, 21 Dec. 1992	91-1467 (94%)	AY294371
<i>Gastroclonium subarticulatum</i> (Turner) Kützing	Pigeon Point, San Mateo Co. California, U.S.A.	M. H. Hommersand, 21 June 1992	121-599, 640-1467 (89%)	AY294398
<i>Gelidium americanum</i> (Taylor) Santelices	Radio I., Carteret Co., North Carolina, U.S.A.	D. W. Freshwater, s.d.	1-1467 (100%)	L22459
<i>Gelidiopsis</i> sp.	La Calerita, Baja Santa Paz, BCS, Mexico	S. Fredericq, 27 Oct. 1999	42-1467 (97%)	AY294357
<i>Gigartina pistillata</i> (Gmelin) Stackhouse	Santec, Brittany, France	J. Cabioch, 6 April 1993	22-1467 (99%)	AY294375
<i>Gracilaria bursa-pastoris</i> (Gmelin) Silva	Anse de Caro, Brittany, France	Coll. J. Cabioch, 3 July 2000	100-1467 (93%)	AY049375
<i>Gracilariopsis lemneiformis</i> (Bory de St. Vincent) Dawson, Acleto & Foldvik	Yacilla, Paita, Piura, Peru	C. Acleto and R. Zuninga 3 March 1994	35-1467 (98%)	AY049415
<i>Grateloupia dichotoma</i> J. Agardh	Ubatuba, Brava Beach, São Paulo State, Brazil	S. M. Guimarães, 26 May 2001	41-1467 (97%)	AF488824
<i>Grateloupia livida</i> (Harvey) Yamada	Muroran, Hokkaido, Japan	S. Fredericq, 6 April 1993	40-1467 (97%)	AF488815
<i>Grateloupia ramosissima</i> Okamura	Ho Ping Island, Keelung, North Taiwan	S. Fredericq and S. M. Lin, 12 Aug. 1993	40-1467 (97%)	AF488810
<i>Grateloupia</i> sp.	Isla Culebra, Pacific Panama	B. Wysor, 16 April 1999	41-1467 (97%)	AY294382
<i>Grateloupia turuturu</i> Yamada	Muroran, Hokkaido, Japan	S. Fredericq, 6 Sep. 1993	9-1467 (99%)	AF488820
<i>Halymenia floridana</i> J. Agardh	Parati Beach, Anchieta, Espiritu Santu, Brazil	S. M. Guimarães and M. Fujii, 17 Sep. 2001	63-1467 (96%)	AY294361
<i>Heterosiphonia plumosa</i> (Ellis) Batters	Penmarch, Brittany, France	M. H. Hommersand, 20 June 1993	104-1467 (93%)	AF259494
<i>Kallymenia reniformis</i> (Turner) J. Agardh	Pighuet, Brittany, France	J. Cabioch, 22 June 1993	133-1467 (91%)	AY294377
<i>Lomentaria hakodatensis</i> Yendo	Kermelehen (Plouezoch), Brittany, France	J. Cabioch, 12 June 1994	132-1467 (91%)	AY294380
<i>Mychodea hamata</i> Harvey	Port MacDonnell, Australia	M. H. Hommersand, 14 July 1995	97-1467 (93%)	AF212191
<i>Nemastoma canariensis</i> (Kützing) Montagne (sample 1)	Canary Islands, s.l.	R. Haroun, s.d.	106-1467 (93%)	AY294369
<i>Nemastoma canariensis</i> (sample 2)	Canary Islands, s.l.	R. Haroun, s.d.	37-1467 (98%)	AY294370
<i>Nizymenia australis</i> Sonder	Warnambool, South Australia	M. H. Hommersand, 13 June 1995	37-1467 (97%)	AF212192
<i>Pachymenia carnosa</i> (J. Agardh) J. Agardh	Kommetjie, Cape Peninsula, South Africa	O. De Clerck, 9 Nov. 1999	41-1467 (97%)	AF385640
<i>Phacelocarpus tortuosus</i> Endlicher & Diesing	Shark's Bay, The Kowie, Port Alfred, Cape Prov., S. Africa	M. H. Hommersand, 19 June 1993	9-1467 (99%)	AY294372
<i>Phyllophora crispa</i> (Hudson) Dixon	Spidall, Co. Galway, Ireland	M. D. Guiry, 7 March 1993	47-1467 (97%)	U02990
<i>Platoma cyclocolpa</i> (Montagne) Schmitz	Faje Grande, Azores	W. F. Farnham, 2 Aug. 1995	358-1467 (76%)	AY294384

TABLE 1. Continued.

Species	Collection locality	Collection data	<i>RbdL</i> portion sequenced	GenBank Accession number
<i>Platoma cyclocolpa</i>	Canary Islands, s.l.	Y. de Jong, s.d.	127-1467 (91%)	AY294385
<i>Platoma chrysymenioides</i> Gavio & Fredericq (sample 1)	Dredged offshore Louisiana, U.S.A. (66-m depth), 28°03.451'N 92°27.345'W	S. Fredericq, B. Gavio, C. F. Gurgel and J. Lopez-Bautista, 27 May 2000	31-1467 (98%)	AY294359
<i>Platoma chrysymenioides</i> (sample 2)	Dredged offshore Louisiana, U.S.A. (60-m depth), 28°03.492'N 92°27.665'W	S. Fredericq, B. Gavio, C. F. Gurgel and J. Lopez-Bautista, 27 May 2000	10-1467 (99%)	AY294362
<i>Platoma</i> sp.	Taiwan s.l.		133-324, 352-1467 (89%)	AY294368
<i>Plocamium cartilagineum</i> (Linnaeus) Dixon	Spiddall, Co. Galway, Ireland	M. D. Guiry, 28 Feb. 1993	141-1467 (90%)	U21701
<i>Polyopes constrictus</i> (Turner) J. Agardh	Kommetjie, Cape Peninsula, South Africa	Coll. R. Anderson and J. Bolton, 31 Jan. 2001	31-1467 (94%)	AF385642
<i>Portieria hornemannii</i> (Lyngbye) Silva	Magang Harbor, NE Taiwan	S. Fredericq and S. M. Lin, 11 Aug. 1993	84-1467 (94%)	AF212185
<i>Predaea feldmannii</i> Børgesen	Long Bay Point, Isla Colon, Caribbean Panama	B. Wysor 17 Oct. 1999	9-1467 (99%)	AY294366
<i>Predaea feldmannii</i>	Puerto Rico, s.l.	D. Ballantine, s.d.	93-1467 (94%)	AY294383
<i>Predaea pusilla</i> (Berthold) Feldmann	Dredged offshore Louisiana, U.S.A. (66-m depth), 28°03.451'N 92°27.345'W	S. Fredericq, B. Gavio, C. F. Gurgel and J. Lopez-Bautista, 27 May 2000	48-1467 (97%)	AY294367
<i>Pseudolithophyllum muricatum</i> (Foslie) Steneck & Paine	Botanical beach, Vancouver, Canada	P. Gabrielson, 8 June 1994	105-1467 (93%)	AY294373
<i>Pterocladia lucida</i> (Brown ex Turner) J. Agardh	Owhiro Bay, South Wellington, New Zealand	W. Nelson, s.d.	58-1476 (96%)	U01048
<i>Rhodogorgon carriebowensis</i> Norris & Bucher	St. Ann's Bay, Jamaica	C. Pueschel, s.d.	49-1467 (97%)	U04183
<i>Rhodophyllis divaricata</i> (Stackhouse) Papaenfuss	Cranatex, Brittany, France	J. Cabioch, 22 June 1993	114-1467 (92%)	AF385658
<i>Rhodymenia pseudopalmata</i> (Lamouroux) Silva	Intertidal, Port Aransas jetty, Texas, U.S.A.	C. F. Gurgel, 17 May 1998	9-1467 (99%)	AY168656
<i>Sarcodia montagneana</i> (Hooker f. et Harvey) J. Agardh	Taipa, New Zealand	W. Nelson, 2 Dec. 1993	43-1467 (97%)	AY294374
<i>Schizymenia dubyi</i> (Chauvin ex Duby) J. Agardh	Piguet, Brittany, France	J. Cabioch, s.d.	119-437, 625-1467 (79%)	AY294389
<i>Schizymenia dubyi</i>	Jodogahama, Miyako, Iwate-ken, Japan	M. H. Hommersand and M. Yoshizaki, 10 July 1994	10-1467 (99%)	AY294388

TABLE 1. Continued.

Species	Collection locality	Collection data	RbL portion sequenced	GenBank Accession number
<i>Schizymenia obovata</i> (J. Agardh) J. Agardh	Swakopmund, Namibia	M. H. Hommersand, 6 July 1993	13-1467 (99%)	AY294401
<i>Schizymenia pacifica</i> (Kyllin) Kylin	Vancouver, British Columbia, Canada (drift)	S. C. Lindstrom, 15 April 1994	141-1467 (90%)	AY294394
<i>Schizymenia pacifica</i>	Kanaha Bay, W. Juan Island, Washington, U.S.A.	M. J. Wynne, 26 July 1995	8-1467 (99%)	AY294393
<i>Schizymenia</i> sp. 1	Oshoro, Japan	S. Fredericq, 5 Sep. 1995	9-1467 (99%)	AY294390
<i>Schizymenia</i> sp. 2	Japan, s.l.	S. Fredericq, s.d.	43-1467 (97%)	AY294391
<i>Schizymenia</i> sp. 3	Taiping Cape, Shandong province, Chi- na	M. H. Hommersand, s.d.	9-1467 (99%)	AY294392
<i>Sebdenia monardiana</i> (Montagne) Berthold	Lachea I., Catania, Italy	G. Furnari and M. Cormaci, Oct. 1994	32-1467 (98%)	AY294395
<i>Sebdenia integra</i> Gavio & Fredericq	Dredged offshore Louisiana, U.S.A., 66 m, 28°03.451'N 92°27.345'W	S. Fredericq, B. Gavio, F. C. D. Gurgel and J. Lopez-Bautista, 26 May 2000	33-1467 (98%)	AY294363
<i>Solieria filiformis</i> (Kützing) Gabrielson	Isla Culebra, Balboa, Pacific Panama	B. Wysor, 4 April 1999	41-1467 (97%)	AY294356
<i>Sphaerococcus coronopifolius</i> Stackhouse	Finavarra, Co. Clare, Ireland	M. D. Guiry, 7 Feb. 1993	26-1467 (98%)	AY294376
<i>Titanophora incrustans</i> (J. Ag.) Børgesen	Offshore Louisiana, U.S.A., 58 m, 28°06.470'N 90°55.359'W	S. Fredericq, J. Lopez-Bautista and F. Rita, 30 June 2001	9-1467 (99%)	AY294365
<i>Titanophora pikeana</i> (Dickie) J. Feldmann	Deep Sponge Reef, Sodwana Bay, Kwazu- lu-Natal, S. Africa	S. Fredericq and O. DeClerck, 11 Feb. 2001	41-1467 (97%)	AY294364
<i>Titanophora weberae</i> . Børgesen	Wang Hai Xiang, N. Taiwan	S. Fredericq and S. M. Lin, 7 Aug. 1994	388-575, 640- 1467 (69%)	AY294387
<i>Tsengia lanceolata</i> J. Agardh	Kommetje, Western Cape, S. Africa	S. Fredericq, 28 Jan. 2001	40-1467 (97%)	AY294386

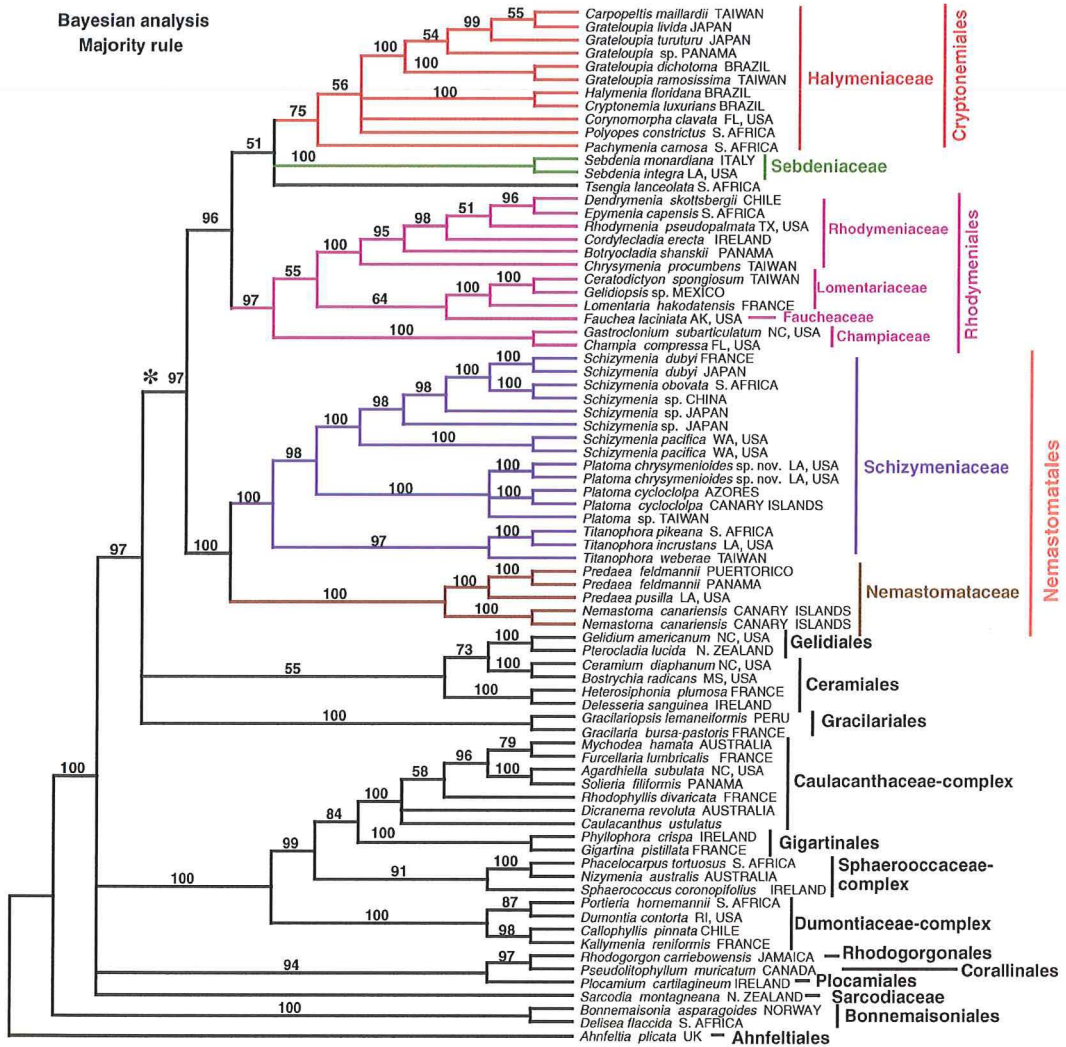


Fig. 1. Bayesian tree for *rbcL* sequences showing the close relationship (*) among the Cryptonemiales, Rhodymeniales, Sebdeniaceae, and Nemastomatales, using Ahnfeltiales as the outgroup in a global phylogeny of florideophycean red algae. Majority rule bootstrap support is shown above the nodes. Branch lengths are proportional to the amount of sequence change.

tomicographs were taken with a Polaroid DMC 1e digital camera (Polaroid Inc., Cambridge, MA) attached to an Olympus BX60 (Olympus, Melville, NY). Images were edited and assembled into plates using *Photoshop* v.5.0 (Adobe Systems Inc., San Jose, CA).

RESULTS

No insertions or deletion mutations were found in the *rbcL* sequences, which permitted the unambiguous alignment of all sequences. Tree lengths of 100,000 randomly generated trees had a skewed distribution ($g1 = -0.411$, $P < 0.01$), indicating the presence of nonran-

dom structure (Hillis and Huelsenbeck, 1992; Hillis et al., 1993). Among the 1,307 bp in the dataset, 697 are identical, and 710 vary, of which 615 are phylogenetically informative. Sequences of 78 samples representing 72 species were included in the phylogenetic analyses (Figs. 1, 2), with *Ahnfeltia plicata* as the outgroup. The MB (Fig. 1) and MP (Fig. 2) analyses produced similar topologies, with the exception of the position of the Gelidiales and the unsupported position of the Sebdeniaceae. The NJ tree topology (not shown) is similar to the MP tree.

In all analyses, the Cryptonemiales, Rhodymeniales, and the Nemastomatales comprise

three major clades and are each other's closest taxa relative to other families and orders of Red Algae. In the MB analysis (Fig. 1), the Sebdeniaceae and Tsengiaceae are weakly nested within the Cryptonemiales; their inclusion in the Cryptonemiales decreases bootstrap support for the order (BP = 51 vs BP = 75) whereas their exclusion increases the support of a monophyletic Cryptonemiales to BP = 75. The order Rhodymeniales is strongly supported (BP = 97) and forms a sister clade to the Cryptonemiales (BP = 96). The Schizymeniaceae and Nemastomataceae are fully supported sister taxa (BP = 100), and in turn form a sister clade to the Cryptonemiales–Rhodymeniales complex. The Gigartinales sensu stricto, comprising the Gigartinae and Phyllophoraceae, are distantly related; similarly, families placed in the Gigartinales sensu lato (Areschougaceae, Mychodeaceae, Furcellariaceae, Rhodophyllidaceae, Dicranemataceae, Caulacanthaceae, Phacelocarpaceae, Nizymeniaceae, Sphaerococcaceae, Dumontiaceae, Kallymeniaceae) comprise separate clades, all distant from the Schizymeniaceae–Nemastomataceae complex.

In the MP (Fig. 2) and NJ (not shown) analyses, the Nemastomatales clade is well supported (BP = 85, BP = 97, respectively) and sister to the Rhodymeniales. The Sebdeniaceae clusters with the Rhodymeniales but without bootstrap support. The Halymeniaceae is sister to the Nemastomatales–Rhodymeniales assemblage but without bootstrap support.

In all analyses, the Corynomorphaceae, represented by *Corynomorpha clavata*, consistently is nested within the Halymeniaceae. The monophyly of the Tsengiaceae, represented by *Tsengia lanceolata*, is weakly supported in a Cryptonemiales that includes the Halymeniaceae and Sebdeniaceae in the Bayesian analysis and in the Halymeniaceae in the MP analysis.

Platoma chrysymenioides Gavio, Hickerson et Fredericq sp. nov.

Latin diagnosis: Thallus leviter mucosus, 10–20 cm altus et latus, subcylindraceus, lobatus, stipite brevi. Hapteron discoideum. Cortex systematum ramorum discretorum pseudodichotomorum trichotomorum formatus. Medulla filamentorum laxorum longitudinalium intricatorumque. Thalli sexuales dioecii. Rami carposogoniales tricellulares, in cellulis interioribus corticalibus portati, cellulis contiguibus fusce tinctis. Cellula carposogoniales post fecundationem efferens extensiones bilateriter distal-

esque conjugentes cellulis subsidiariis. Cellulae subsidiariae diploidicae efferentes filamenta connectiva. Cellulae auxiliares in cellulis sustentibus similiter superpositae. Carposporophyticus subsphaericus in cortice, cellulis totis carposporangia ferentibus. Porus absens. Spermatangia ab cellulis extimis corticalibus abscissa. Tetrasporangi ignota.

Holotype: A cystocarpic specimen from Fish Haven, 65- to 66-m depth, 28°05.64'N 91°00.960'W, coll. D. L. Felder, 1 Aug. 2002, deposited at US (US 208900). Attached to a rhodolith.

Isotypes: Two vegetative specimens, 66-m depth, 28°03.451'N 92°27.345'W, coll. S. Fredericq, B. Gavio, C. F. Gurgel, and J. Lopez-Bautista, 27 May 2000 (27-5-00-10-1); 60-m depth, 28°03.492'N 92°27.665'W, S. Fredericq, B. Gavio, C. F. Gurgel, and J. Lopez-Bautista, 27 May 2000 (27-5-00-11-1). Deposited at LAF.

Additional material: Female specimen, 50-m depth, 27 Sep. 2003 (27-9-03-1-3), 27°51.916'N 93°51.822'W, ROV dive 39, S. Fredericq and E. Hickerson.

Etymology: This species is named for its superficial resemblance in habit and texture to irregular dichotomously branched members of *Chrysymenia* (Rhodymeniales).

Habit and vegetative structures: Thalli up to 20 cm tall, bright pink, erect, mucilaginous, cleft into several marginal subcylindrical to irregularly elongate lobes (Fig. 3). A small discoid holdfast bears a denuded stipe that is narrow below but fans out distally (Fig. 3). Carposporophytes formed at the surface of the elongate lobes are readily apparent with the naked eye (Fig. 4). Growth is multi-axial, with the thallus consisting of an open network of loose masses of interwoven filaments (Figs. 6, 7) that easily tear apart upon squashing of the coverslip. Medullary filaments are filiform, unbranched, uniseriate, laxly interconnected, and distally bear regularly spaced, predominantly pseudodichotomous but also trichotomous cortical branch systems that fan out thallus outward (Figs. 6, 7, 10). Secondary pit connections are absent throughout. Every one to two cells, each intercalary cortical cell distally bears a pseudodichotomous or trichotomous branch system, for a total up to four to six orders of branching. Surface cells have blunt apices (Figs. 6, 7). Pseudodichotomies result from longitudinal concavoconvex

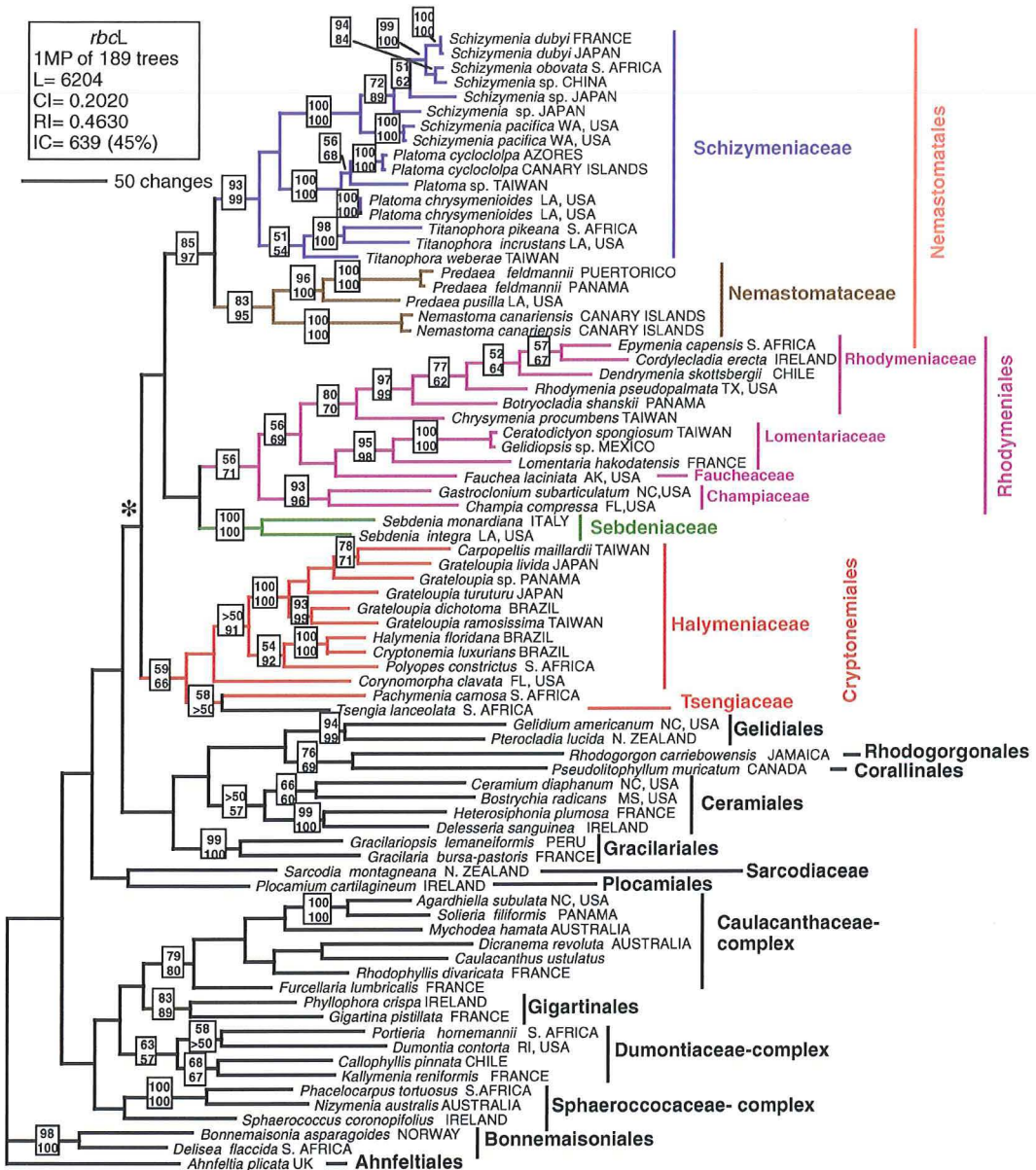
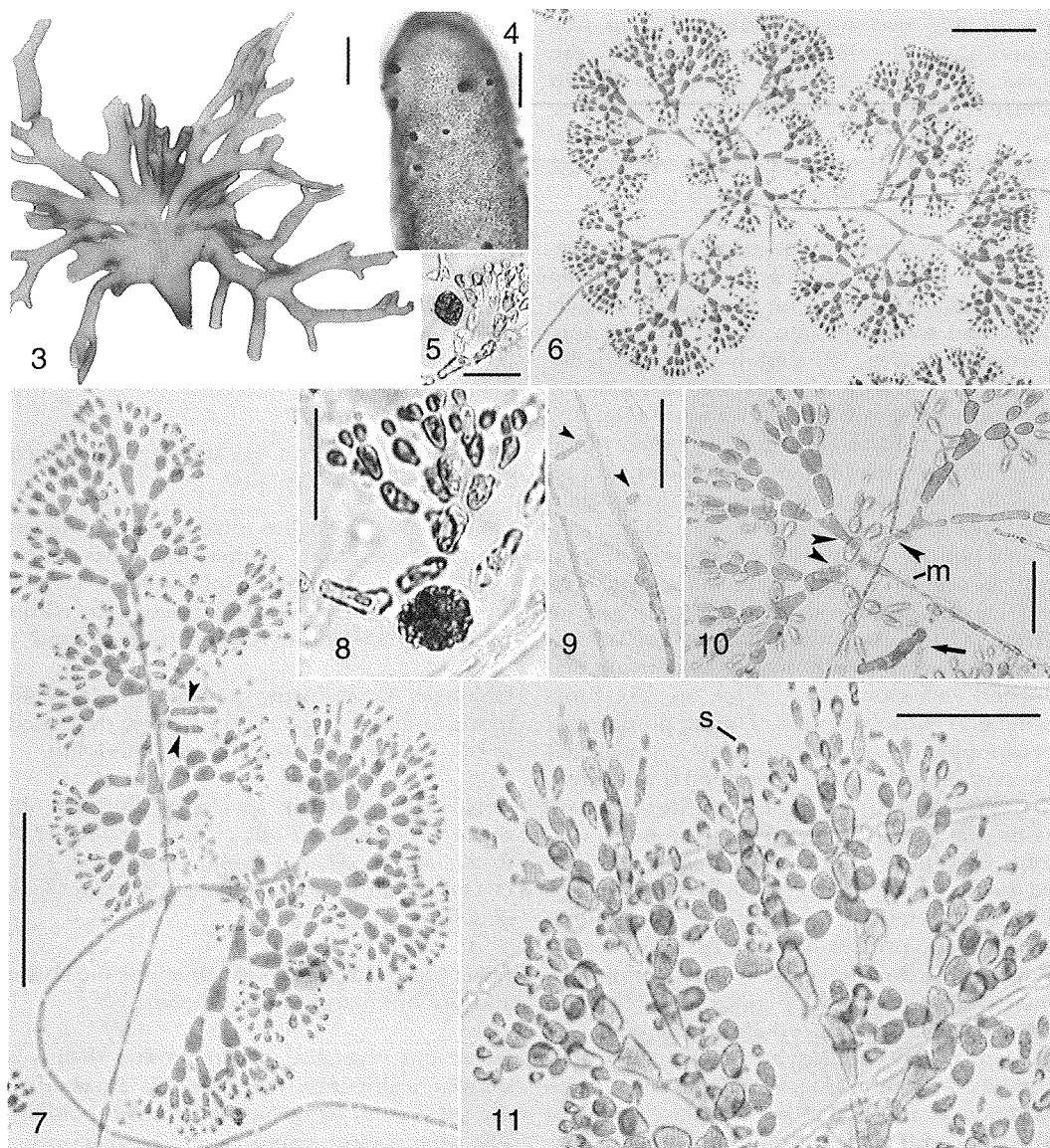


Fig. 2. One of 189 equally most parsimonious trees for *rbcL*. Tree length = 6,204, CI = 0.20, RI = 0.46, Informative characters = 639/1,407 (45%). Bootstrap proportion values >50% for MP (top, 1,000 replicates) and NJ (bottom, 5,000 replicates) are shown at the nodes. Branch lengths are proportional to the amount of sequence change.

divisions of terminal cortical cells. Additional cortical cells are produced upon septation (Fig. 7, arrowhead) of extensions budding laterally from intercalary cells. Whereas innermost cortical cells are subcylindrical with the basal part narrower than the distal end, outermost cortical cells are ovoid. Intercalary cortical cells are each typically linked to two or three cells above and one cell below, thus

bearing respectively a pseudodichotomy or trichotomy at each consecutive order of branching (Fig. 7).

Medullary cells are elongate-rectangular (Fig. 9) and cut off narrow rhizoidal cells laterally, which continue to septate (Fig. 7, arrowheads) and increase the number of medullary filaments. These secondarily formed rhizoidal



Figs. 3–11. *Platoma chrysmenioides* sp. nov. Habit and vegetative structure. 3. Habit of cystocarpic holotype. Bar = 1 cm. 4. Close-up of terminal branch in Figure 3 showing carposporophytes. Bar = 0.5 mm. Figs. 5–11. Squash preparations. 5. Gland cell intercalary in outer cortical cell file. Bar = 20 μ m. 6. Loose masses of filaments showing regular pseudodichotomous branching of cortical filaments and medulla composed of unbranched filiform rhizoidal filaments. Bar = 100 μ m. 7. Secondarily formed cortical cell file initials (arrowheads) cut off from intercalary cells subtending pseudodichotomy. Note occasional trichotomous branching in outer cortical cell files. Bar = 100 μ m. 8. Gland cell intercalary in cortical cell file. Bar = 20 μ m. 9. Rhizoidal branch initials (arrowheads) cut off from medullary cells. Bar = 40 μ m. 10. Medullary cell (m) subtending cortical trichotomy (arrowheads) and rhizoidal filament primordium (arrow). Bar = 40 μ m. 11. Spermatangia (arrowhead) cut off singly from outer cortical cells. Bar = 50 μ m.

initials are distinguished from the laterally formed cortical branch initials by growing thallus inward and by becoming more elongate. X-shaped cells are infrequent and are formed when an intercalary cortical cell linked to a pseudodichotomous branch above and a med-

ullary cell below cut off a rhizoidal cell that continues growing thallus inward (Fig. 7). Any medullary cell may also bear cortical trichotomies (Fig. 10, arrowheads) and cut off a rhizoidal filament primordium (Fig. 10, arrow).

Intercalary cortical cells of outer cortical fil-

aments may occasionally transform into subspherical gland cells (Figs. 5, 8). Typically, the cortical cells linked distally to the gland cells remain uniseriate and unbranched (Fig. 8) or have ceased to grow (Fig. 5). Gametophytes are apparently dioecious, with ovoid spermatangia cut off by outermost cortical cells (Fig. 11).

Pre- and early-postfertilization structures: Intercalary cortical cells bearing a pseudodichotomous branch system on both sides at their distal end transform into darkly staining supporting cells (Fig. 12) slightly bulging distally. Consecutive irregular-transverse divisions by the supporting cell thallus outward (Fig. 13) result in a conical carpogonial branch initial (Fig. 13), a developing two-celled carpogonial branch (Fig. 14), and a mature three-celled carpogonial branch (Figs. 15, 16). The carpogonial branch consists of a hemispherical basal cell, an oval hypogynous cell, and a distal conical carpogonium with a straight trichogyne (Figs. 15, 16). Adjacent basal cortical cells in branch systems borne on the supporting cell expand and stain darkly (Figs. 15, 16), functioning as subsidiary cells. The supporting cell occasionally bears trichotomous cortical cell clusters (Fig. 16). After presumed fertilization, the carpogonium produces two lateral extensions that fuse at midlevel with the two lowermost subsidiary cells, each bilaterally connected to the supporting cell (Figs. 17, 18). The fate of the fertilization nucleus was not followed. Upon presumed diploidization, the subsidiary cells initiate cellular connecting filament primordia at their lower end (Figs. 17, 18) that continue to septate into connecting filaments. The trichogyne persists after presumed fertilization (Fig. 18). Unfertilized, non-functional carpogonial branches are common and are distinguished from functional ones by the frequent expansion and bulging of adjacent cells and their subsequent septation (Figs. 19, 20).

Postfertilization structures: Auxiliary cells are intercalary cortical cells bearing two- to three-branch systems, and each produces a single gonimoblast initial (Figs. 21, 23) thallus outward. As the connecting filament contacts the auxiliary cell, which expands in size, the cortical cells linked to the auxiliary cell elongate (Fig. 21). The incoming connecting filament segment fuses basally with auxiliary cell depositing a derivative of the fertilization nucleus, and the outgoing connecting filament continues its course (Fig. 22). Auxiliary cells are homologous in position to the supporting cell of

the carpogonial branch, expanding in size and becoming subspherical. A subglobular carposporophyte is cut distally from the auxiliary cell and is centrally located among the elongate cortical filaments linked to the auxiliary cell. All gonimoblast cells transform into subspherical to ovoid carposporangia (Figs. 22–24). A pore or ostiole above the carposporophyte is absent, and the elongate cortical cells connected to the auxiliary cell loosely surround the gonimoblasts (Fig. 24).

Distribution: Only known from offshore Louisiana and Texas.

Sebdenia integra Gavio, Hickerson et Fredericq sp. nov.

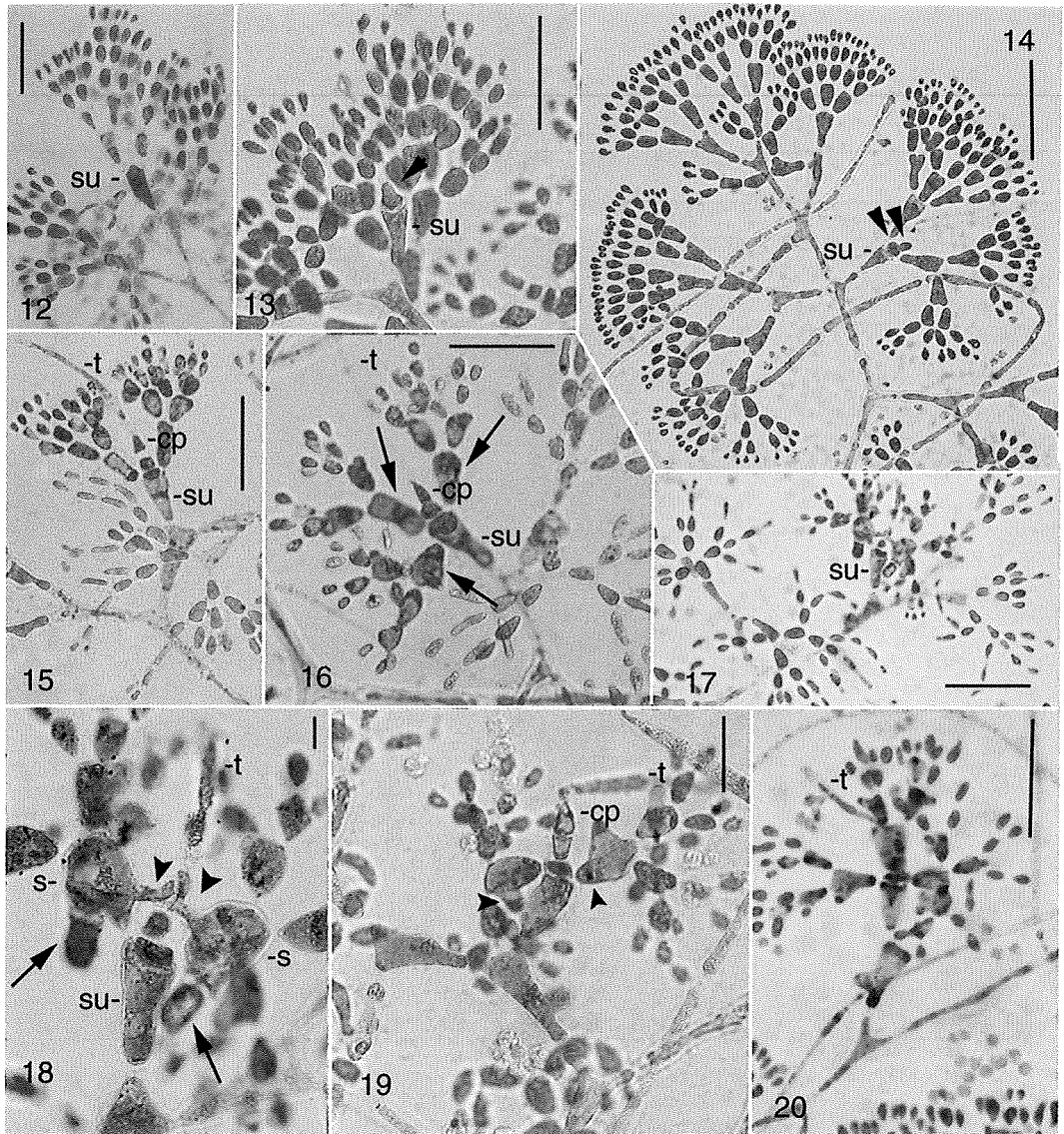
Latin diagnosis: Thallus subsphaericus, integer, complanatus. Stipes compactus, brevis, cellulosis. Lamina interna cellulis stellatis, lacunis intercellulosis parte centrali, numerosis cellulis conjunctis. Structurae reproductivae ignotae.

Holotype: A cystocarpic specimen dredged offshore Louisiana, coll. D. L. Felder, deposited at US, US 208900. Attached to a rhodolith.

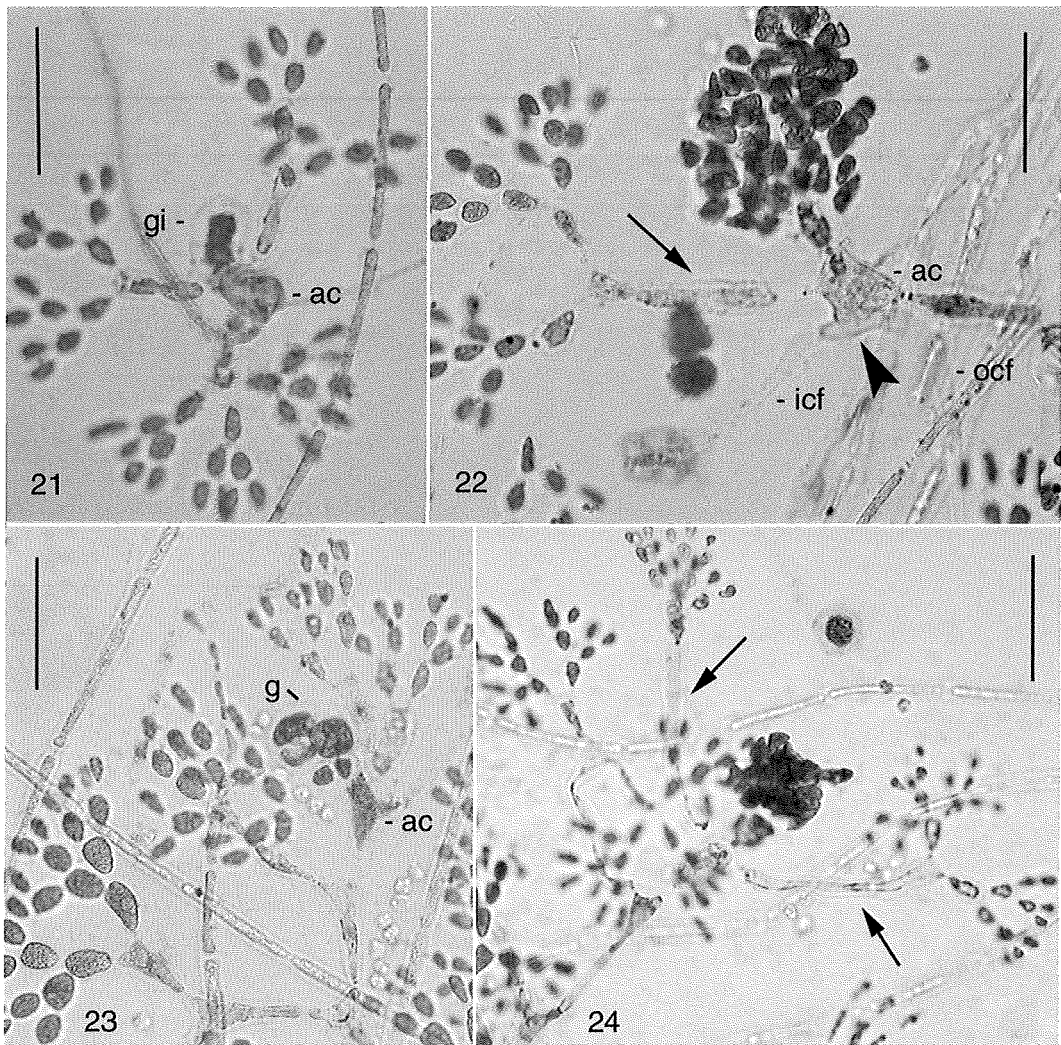
Isotype: A vegetative specimen dredged offshore Louisiana, 66 m, 28°03.451'N 92°27.345'W, coll. B. Gavio, S. Fredericq, F. C. D. Gurgel, and J. Lopez-Bautista, 26 May 2000, deposited at LAF.

Etymology: This species is named for the entire and smooth margin of the thallus.

Habit and vegetative structure: The thallus is subspherical, entire, flat, (Fig. 25) attached to the substratum by means of a discoid holdfast. The stipe is short, compact, and cellular, with a central medulla consisting of four to five layers of cells and one to two layers of flattened outer cortical cells (Fig. 26). The outermost cortical cells are markedly smaller than the innermost cells and growth is multiaxial throughout. Above the stipe, primary growth in the blade has stopped, and the production of copious mucilaginous material in the central zone results in the separation of the innermost cells and the production of large intercellular spaces (Figs. 27, 28). Centrally located cells accommodate for this expansion by stretching parts of their cytoplasm laterally with the result that they become stellate (Fig. 28) and by producing filiform cells bearing terminal conjuncture cells (Fig. 29) that reach across and fuse to cells on the opposite side establishing numerous secondary pit con-



Figs. 12–20. *Platoma chrysymenioides* sp. nov. Pre- and early postfertilization structures. 12. Darkly staining supporting cell (su). Bar = 40 μm . 13. Supporting cell (su) and carpogonial branch initial (arrowhead). Bar = 40 μm . 14. Two-celled carpogonial branch (arrowheads) borne on intercalary supporting cell (su). Note regular pseudodichotomous construction of cortical cell files. Bar = 50 μm . 15. Three-celled carpogonial branch borne on supporting cell (su), with terminal carpogonium (cp), and trichogyne (t). Bar = 40 μm . 16. Three-celled carpogonial branch with terminal carpogonium (cp) and trichogyne (t) borne on supporting cell (su) linked to three cortical branch systems (arrows). Bar = 20 μm . 17. Early postfertilization events, with connecting filament initiation, see Figure 18. Bar = 50 μm . 18. Magnification of Figure 17 showing presumed diploidization with fusion extension (arrowheads) of carpogonium to lowermost subsidiary cell (s) connected on each side of supporting cell and connecting filament primordium (arrows) from diploidized subsidiary cells. Note the persisting trichogyne (t) and lower cells of the carpogonial branch borne on the supporting cell (su). Bar = 4.5 μm . 19. Unfertilized nonfunctional carpogonial branch with terminal carpogonium (cp) and trichogyne (t). Note production of bulges from subsidiary cells (arrowheads), which become irregular in outline. Bar = 20 μm . 20. Unfertilized nonfunctional carpogonial branch with trichogyne (t) and adjacent cortical cells that become irregular in outline. Bar = 100 μm .



Figs. 21–24. *Platoma chrysmenioides* sp. nov. Postfertilization structures. 21. Auxiliary cell (ac) connected to three cortical cell files, with distal gonimoblast initial (gi). Bar = 40 μ m. 22. Auxiliary cell (ac) bearing subspherical cluster of gonimoblast cells, incoming (icf) forming segment (arrowhead) fused to auxiliary cell basally, and outgoing (ocf) connecting filament. Note that the cortical cells connected to the auxiliary cell have elongated (arrow). Bar = 40 μ m. 23. Auxiliary cell (ac) bearing gonimoblasts (g). Bar = 40 μ m. 24. Mature carposporophyte; note elongate cortical cells (arrows) weakly enveloping carposporophyte. Bar = 50 μ m.

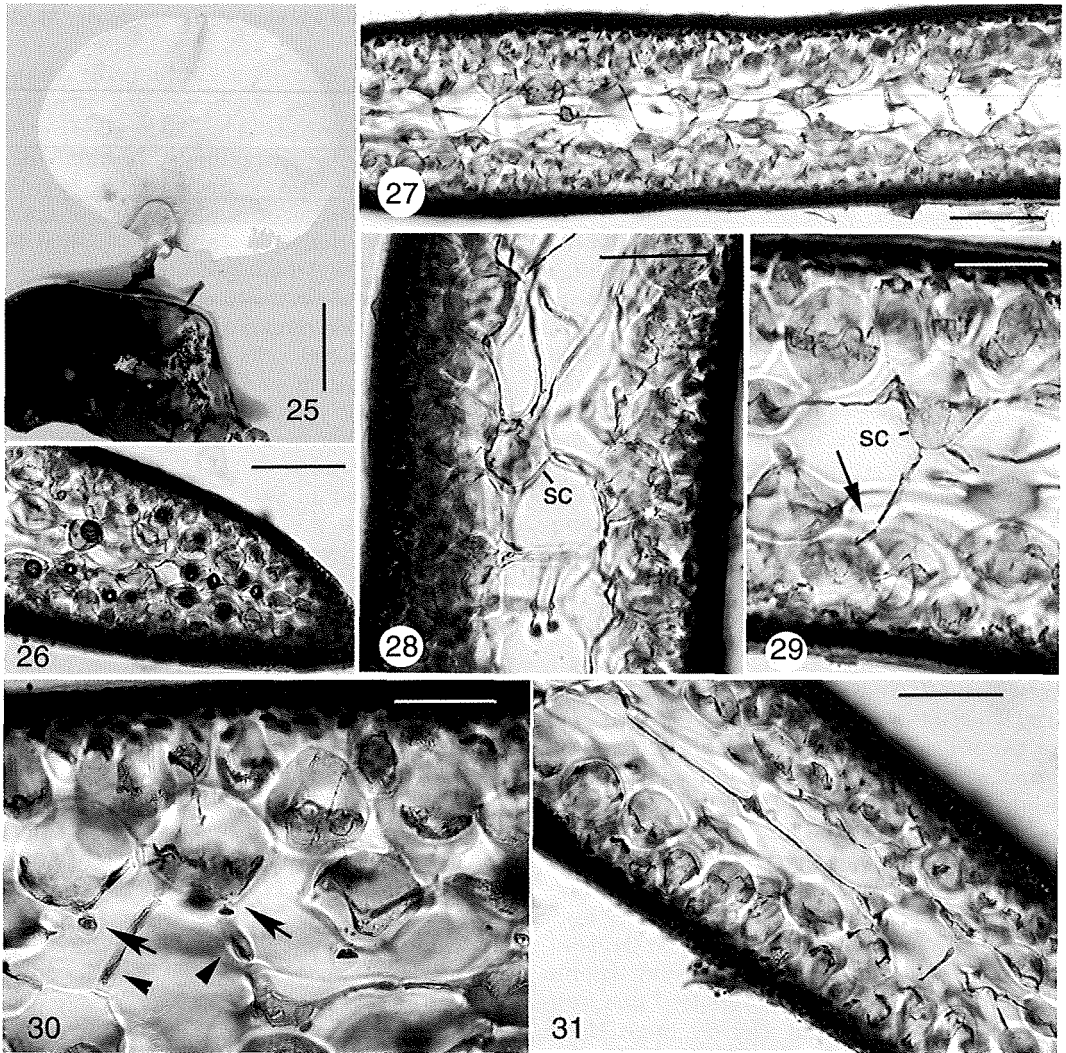
nections (Fig. 30). The result is a mixture of elongate medullary cells, stellate cells, subspherical cells interspersed with large intercellular spaces (Fig. 31). Reproductive structures were not found.

Distribution: Only known from offshore Louisiana.

DISCUSSION

The nonprocarpic family Nemastomataceae currently includes four genera with a hetero-

morphic life history (Masuda and Guiry, 1995), *Nemastoma* J. Agardh (1842), *Predaea* G. De Toni (1936), *Adelophycus* Kraft in Womersley and Kraft (1994 = *Adelophyton* Kraft 1975) and *Itonoa* (Masuda and Guiry, 1995). Representative taxa of the first two genera were used in the study. *Nemastoma* includes about eight species that are mucilaginous and more or less cartilaginous (Guiry and Nic Dhonncha, 2002). *Predaea* comprises about 18 soft-gelatinous species (Kajimura, 1995; Conde et al., 1998; Ballantine et al., 2002; Saunders and



Figs. 25–31. *Sebdenia integra* sp. nov. 25. Holotype, vegetative. Bar = 1 cm. Figs. 26–30. Cross sections. 26. Portion of stipe showing cellular medulla. Bar = 100 μ m. 27. Cellular cortex with stellate cells, filiform medullary cells reaching across opposite side and large intercellular spaces. Bar = 100 μ m. 28. Close-up of stellate cell (sc) and large intercellular spaces. Bar = 40 μ m. 29. Stellate cell (sc) having cut off filiform rhizoidal medullary cell bearing terminal conjuncture cell (arrow). Bar = 40 μ m. 30. Filiform medullary cell (arrowheads) and conjuncture cells (arrows). Bar = 40 μ m. 31. Longitudinal section showing filiform medullary filament, cellular cortex and large, centrally located intercellular spaces. Bar = 100 μ m.

Kraft 2002; Schils and Coppejans, 2002). The procarpic and isomorphic Tsengiaceae (Saunders and Kraft, 2002) is monotypic, with *Tsengia* K. C. Fan and Y. P. Fan (1962; Maggs, 1997) encompassing seven species (Womersley and Kraft, 1994; Guiry and Nic Dhonncha, 2002). *Tsengia lanceolata* was selected in the analysis to represent the family.

Nemastoma and *Predaea* in the Nemastomataceae inhabit predominantly tropical to subtropical waters worldwide (e.g., Huisman, 1999). The two genera share a female repro-

ductive apparatus composed of simple, straight carpogonial branches that are laterally inserted on intercalary cells of cortical filaments. The carpogonial branches are never associated with darkly staining, protein-rich nutritive cells, and single connecting filaments develop directly from the fertilized carpogonium. Gonimoblasts arise either directly from the auxiliary cell, typically an intercalary cell in a cortical filament, or from a portion of the connecting filament close to its point of contact with the auxiliary cell (e.g., Masuda and Guiry, 1995).

We contend that most species placed in *Nemastoma* (for example *N. confusum* Kraft and John, 1976) may in fact be species of *Predaea*, because the original drawings by Berthold (1884) of the type *N. dichotomum* from the Bay of Naples depict auxiliary cells encompassing one to two swollen cells toward the ends of filaments; however, such rhizoidal auxiliary filaments were the basis for the recognition of the monotypic *Adelophycus* (as *Adelophyton*) Kraft, a genus which thus may have to be merged with *Nemastoma*.

The distinguishing feature of *Predaea* is that small-celled nutritive filaments flanking the auxiliary cell are produced before fertilization in clusters; these are absent in *Nemastoma*. Species of *Predaea* are routinely distinguished by the number and shape of the nutritive cells (Millar and Guiry, 1989; Kajimura, 1995), ranging from elaborate grape-like clusters to being reduced to a single cell (e.g., in *P. goffiana*, Ballantine et al., 2002, fig. 9). Typically, the nutritive cells expand after an auxiliary cell has been contacted by a connecting filament. Ultrastructural studies (Siotas and Wetherbee, 1982) established that pit plugs between cells of the nutritive filaments break down and disappear at the time of gonimoblast formation, whereas the nuclei and cytoplasm remain intact (see Hommersand and Fredericq, 1990).

In the tropical Western Atlantic, four species of *Predaea* are currently acknowledged (Wynne, 1998): *P. feldmannii* Børgesen, *P. weldii* Kraft and Abbott, *P. masonii* (S and G.) G. De Toni, and *P. goffiana* Ballantine, Ruiz and Aponte (2002). Bula Meyer (1992) reported that western Atlantic records of *Platoma tenuis* Howe and Taylor should be referred to as *Predaea tenuis*; however, Kajimura (1995) indicated that the combination was not properly made and questioned Bula Meyer's identification. On the basis of Kajimura's (1987, 1995), Verlaque's (1990), Vergés et al. (2004) and Kraft's (1984) monographic treatments of *Predaea*, and on the recent description of a new diminutive species of Puerto Rico, *P. goffiana* (Ballantine et al., 2002), we refer the newly reported Gulf of Mexico specimens of *Predaea* that were collected from offshore Louisiana as *Predaea pusilla* (Berthold) Feldmann, awaiting fertile Gulf of Mexico specimens for additional study and examination of the Mediterranean species. Photographs of *Predaea pusilla* from Corsica (Verlaque, 1990, fig. 21) agree in all available aspects to the Gulf vouchers in their pseudodichotomous habit, small height, submoniliform cortical cells, and regularity of filamentous construction. This is the first record of *P. pus-*

illa in the Gulf of Mexico and outside the Mediterranean.

Species of *Nemastoma* are principally distinguished on the basis of whether the carpogonial branch supporting cells and auxiliary cells are intercalary in adventitious rhizoidal filaments, as in the type *N. dichotomum* J. Agardh (Berthold, 1884), or in ordinary cortical fascicles, as in *N. canariense* (Kützting) J. Agardh (Børgesen, 1929; Athanasiadis, 1988).

In their article on *Itonoa marginifera*, Masuda and Guiry (1995) remark that the frequent occurrence of lateral cells or branches on the carpogonial branch of *Itonoa* may be characteristic for that genus; however, carpogonial branches in some species of *Predaea* may (e.g., *P. goffiana* Ballantine et al., 2002, figs. 5–7; *P. kraftiana* Millar and Guiry, 1989, figs. 3, 4) or may not bear lateral initials on the hypogenous or basal cell. These laterals resemble ordinary vegetative cells and never stain darkly. It has become evident that the generic distinction within the Nemastomataceae is quite blurred, and in all likelihood, species currently placed in *Nemastoma* may just be species of *Predaea* lacking auxiliary nutritive cells. The inclusion of the type species, *N. dichotomum*, is needed to clarify the generic boundaries in the family.

The Schizymeniaceae was proposed to accommodate *Platoma* Schousboe ex Schmitz (1894) and *Schizymenia* J. Agardh (1851) and perhaps *Titanophora* (J. Ag.) Feldmann (1942) (Masuda and Guiry, 1994). There are slight variations on a single theme in the early reproductive development in the type of each genus, i.e., *Schizymenia dubyi* (Ardré, 1980), *Platoma cyclocolpa* (Masuda and Guiry, 1994), and *Titanophora pikeana* (Feldmann, 1942; Børgesen, 1949), in which the carpogonial branch is always associated with protein-rich nutritive cells. The fertilized carpogonium typically fuses directly with one of the darkly staining nutritive cells associated with the carpogonial branch; the fusion process then progresses to the other nutritive cells and from that fusion product one or more connecting filaments are cut off. The connecting filament grows toward and contacts an intercalary auxiliary cell, which cuts off a gonimoblast initial outward. Cortical cells surrounding auxiliary cells develop into an involucre surrounding the carposporophyte, and the carposporangia are released through a gap in the cortical fascicles (e.g., Itono and Tsuda, 1980; Bucher and Norris, 1992; Masuda and Guiry, 1994; Saunders and Kraft, 2002).

Seven species of the calcium carbonate-encrusted genus *Titanophora* have been described

from tropical waters (e.g., Mshigeni and Papefuss, 1980; Bucher and Norris, 1992). Large intercalary gland cells are typical for the genus. Specimens of *T. incrustans* were collected from offshore Louisiana but most were sterile.

Nine species of *Platoma* have been described from tropical waters since the genus was established by Schmitz (1894) based on *P. cyclocolpa* from the Bay of Naples. Specimens belonging to *Platoma* were collected from offshore Louisiana, but the species did not conform to any of the species descriptions by Norris and Bucher (1977), Womersley and Kraft (1994), Kajimura (1997), Kraft and Abbott (1997), Athanasiadis (2000), and Schils and Coppejans (2002). This is the first report of the genus for the northern Gulf of Mexico. *Platoma chrysymenioides* is most closely related to *P. izumomense* from southern Japan (Kajimura, 1997) in which the fertilized carpogonium does not divide but fuses with one or both subsidiary cells or a cortical cell distal to the one of the latter.

Nutritive elaborations are thus seemingly at the level of the auxiliary cell in the Nemastomataceae and at the level of the carpogonium in the Schizymeniaceae; both taxa are characterized by septate filaments that terminate at an intercalary auxiliary cell or may continue to diploidize additional auxiliary cells. In the Schizymeniaceae (i.e., *Titanophora*, *Platoma*, *Schizymenia*), existing cortical cells flanking the auxiliary cell typically stretch and elongate secondarily, weakly enveloping the carposporophyte developing from the generative auxiliary cell, a situation not occurring in the Nemastomataceae (i.e., *Predaea*, *Nemastoma*).

A prominent vegetative auxiliary cell characterizes the monotypic Sebdeniaceae (e.g., Sjöstedt, 1926; Hansen, 1989; Schneider and Wynne, 1991; Saunders and Kraft, 1996). There currently are about 15 species of *Sebdenia* described worldwide (E. Soler-Onís, pers. comm.). The terete to subcylindrical, dichotomously branched species *Sebdenia flabellata* (J. Agardh) Parkinson recorded from the Caribbean and North Carolina (Schneider and Searles, 1991) has also been dredged from offshore Louisiana (collections at LAF). In addition, dredged specimens belonging to an undescribed species of *Sebdenia* from offshore Louisiana comprised small sterile blades. We provisionally name the new taxon *S. integra* sp. nov. on the basis of its entire blade but await fertile specimens and a critical examination of additional flat, entire species worldwide for comparison; Soler-Onís et al. (1996) have not found thalli resembling the Louisiana taxon in

the Canary Islands. The commonly reported "gland-like cells" reported for the genus (e.g., Feldmann, 1942; Balakrishnan, 1961; Norris and Bucher, 1977; Norris and Aken, 1985; Hansen, 1989) may in fact be large conjunctive cells cut off from lower cortical and medullary cells as indicated for the new Louisiana species. *Sebdenia rubra* Taylor (1945) described from the tropical eastern Pacific (Ecuador), and currently placed in synonymy with *S. dawsonii* (see Hansen, 1989) from California is small (only 10 cm tall), flattened, unbranched and nonproliferous, and of all the described species superficially most resembles the new Louisiana species in habit.

The Halymeniaceae has been placed in the Halymeniales together with the monogeneric family Sebdeniaceae on the basis of molecular sequences of the nuclear small subunit ribosomal RNA gene (SSU rDNA) (Saunders and Kraft, 1996). In our analysis, this taxonomic move is not supported because the Sebdeniaceae clusters alternatively with the Halymeniaceae or the order Rhodymeniales with no bootstrap support. This result needs to be taken with caution because of the small sample size available for the family. However, in the original article by Saunders and Kraft (1996), only one sequence of *Sebdenia* was used to determine the order Halymeniales. *Sebdenia* Berthold (1882) was originally placed in the Halymeniaceae (respectively as Cryptonemiaceae and Grateloupiaceae) by both Berthold (1882) and Howe (1914); Schmitz and Hauptfleisch (1897) considered the genus a member of the Rhodymeniaceae, and Sjöstedt (1926) included *Sebdenia* in the Nemastomataceae. Kylin (1932) created the family Sebdeniaceae and included it in the Gigartinales because of the position of the generative auxiliary cell, which is intercalary in a normal cortical filament; he also considered the Sebdeniaceae as closely related to the Nemastomataceae. The close relationship between the Sebdeniaceae, Cryptonemiales, Tsengiaceae, and Nemastomatales corroborates phylogenetic studies inferred from nuclear SSU rDNA data (Saunders et al., 2004). In all taxa, the connecting filaments appear branched, multinucleate, and segmented.

The procarpic Rhodymeniales is distinguished on the basis that the auxiliary cell is the terminal cell of a two-celled filament borne on the supporting cell of the carpogonial branch (e.g., Sparling, 1957). Although the Cryptonemiales as an order was characterized by Kylin (1956) on the basis of an accessory auxiliary cell, Fredericq et al. (1993) reported that the initial of the auxiliary cell in a species

of *Grateloupia* (Halymeniaceae) (misidentified as *Chondriella* Levring 1941 from the Juan Fernandez Islands), in actuality is a normal vegetative cell that also cuts off ampullary filaments.

The female reproductive features that unite a monophyletic assemblage of Sebdeniaceae, Nemastomatales, Rhodymeniales, and Cryptonemiales are found at the level of gonimoblast initiation. In all taxa, the auxiliary cell cuts off a single gonimoblast initial thallus outward in which all gonimoblasts continue dividing in a compact, globose cluster of cells and become transformed in carposporangia; there are no interactions nor are there fusions established between intercalary or terminal gonimoblast and vegetative cells. The carposporophyte is surrounded by untransformed or vegetative nutritive cells (Nemastomataceae), involucrel filaments (Schizymeniaceae), ampullary carpogonial and auxiliary branch systems (Cryptonemiales), or by a cellular pericarp with an ostiole (Sebdeniaceae and Rhodymeniales). Nonampullary carpogonial branches are also found in *Norrissia*, *Isabbottia*, and *Zymurgia*, genera placed in the Halymeniaceae (Balakrishnan, 1986; Lewis and Kraft, 1992). Norris (1989) had already proposed that the "ampullae," which carry the carpogonia and auxiliary cells in separate adventitious systems in the Halymeniaceae (see Chiang, 1970) evolved from similar appearing structures in the "Titanophoraceae" Norris (ined.).

In light of the recent debates about the appropriateness of the name Halymeniales instead of Cryptonemiales, the authors agree with Silva (2002) and reinstate the name Cryptonemiales (Schmidt) Kylin (see also Silva and Johansen, 1986) to accommodate the Halymeniaceae (including the Corynomorphaceae) and Tsengiaceae. The Corynomorphaceae Balakrishnan is here viewed as not deserving of separate family rank. The phylogenetic position of the Sebdeniaceae is ambiguous and needs further investigation. However, in view of the close relationship of this monogeneric family to the Cryptonemiales–Rhodymeniales complex, the Sebdeniaceae may prove to belong in its own order. This large complex of red algae could then be grouped in a monophyletic superassemblage comprising the Cryptonemiales, Rhodymeniales, Nemastomatales, and Sebdeniaceae on the basis of morphological and molecular evidence.

ACKNOWLEDGMENTS

This research was supported by a J. Bennett Johnston Foundation Grant, a Physiological So-

ciety of America Grant-in Aid-of-Research to BG, NOAA's National Undersea Research Center grant NA96RU-026, and National Science Foundation grant DEB0315995 to SF, and NOAA's Office of Ocean Exploration grant to EH. We wish to thank all collectors listed in Table 1. We also thank M. H. Hommersand, J. Norris, E. Soler-Onís, S. Lindstrom, and Dan Nicolson for their helpful suggestions.

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