

New Species and New Records of Offshore Members of the Rhodymeniales (Rhodophyta) in the Northern Gulf of Mexico

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Recent collecting cruises in the northern Gulf of Mexico have revealed a surprisingly diverse deepwater flora dominated by members of the Rhodymeniales (Rhodophyta). In this article, we describe four species new to science as inferred from morphological and comparative chloroplast-encoded *rbcL* sequence analysis: *Botryocladia ballantina* sp. nov., *Gloiocladia pelicana* sp. nov., *Gloiocladia tenuissima* sp. nov., and *Leptofaucha earleae* sp. nov. The new species were collected by dredging from 40- to 90-m depth offshore Louisiana or by SCUBA at 25- to 35-m depth from hard banks in the NW and NE Gulf of Mexico. Several species of Rhodymeniales are newly recorded for the Gulf of Mexico.

The Gulf of Mexico is characterized by a relatively shallow but well-developed continental shelf with an extensive system of generally deep hard banks of varying origin and composition (Rezak et al., 1985; Gore, 1992). These banks vary in the degree and type of structural expression, the nature of the substratum that underlies the banks, and the bank composition. Whereas banks of the southern Gulf (below Matagorda Bay, Texas) were typically formed on relict carbonate reefs, upper NW mid- and outer shelf banks originated on unique tectonically created salt diapirs, molded from Louann evaporite deposits below the sea floor during the Jurassic period, and they are rich in oil deposits (Rezak et al., 1985).

The outer shelf West (27°52'N 93°48'W) and East (27°54'N 93°36'W) Banks of the Flower Gardens Banks National Marine Sanctuary (NW Gulf, offshore Texas) together with the Florida Middle Ground (NE Gulf, offshore Florida, 28°33'N 84°16'W) represent separate biogeographic extremes in the northward distribution of tropical Atlantic coral reefs or communities dominated by corals. Mid-shelf NW Gulf banks such as Stetson (offshore Texas; 28°10'N 94°38'W) or Sonnier (offshore Louisiana; 28°20'N 92°27'W) are reported to support less diverse communities, with minor reef-building activity and a dominant *Millepora*-sponge zone (Rezak et al., 1985).

Taylor (1955) characterized the flora in the northern part of the Gulf of Mexico as an impoverished tropical Caribbean flora rather than a replacement by a temperate flora and considered coastal habitats ranging from Galveston, TX, to Alabama “botanically barren or at least monotonous” (Taylor, 1960), in great part because of the high turbidity caused by

effluents from the Mississippi, lack of hard substratum in the nearshore intertidal zones, and seasonal fluctuation in salinity and temperature.

In the NE Gulf, offshore seaweed collections from depths up to 73 m were made during the historic “Hourglass” expedition in the 1960s by Dawes and Van Breedveld (1969) in central west Florida. Dredged collections from the Florida Middle Ground, located on the outer edge of the continental shelf approximately 160 km WNW of Tampa, FL, were also included in Humm and Earle Taylor (1961). The Florida Middle Ground is characterized by discontinuous limestone outcroppings covered with shell, rock, and living and dead corals, with relief of 2–10 m at depths of 25–60 m. Cheney and Dyer (1974) listed 84 species of green, brown, and red seaweeds, and Hopkins et al. (1977) subsequently added 40 new records for the area, increasing the number of macroalgal species to 103; the seaweed flora was characterized as having distinct tropical affinities and undergoing a seasonal pattern of abundance and species diversity, both of which were maximal in the summer (Cheney and Dyer, 1974). Deepwater collections conducted in the NW Gulf (Eiseman and Blair, 1982) and east Florida (Hanisak and Blair, 1988) and off the NW Atlantic continental shelf in the Carolinas (Searles and Schneider, 1980; Searles, 1984a; Schneider and Searles, 1991) revealed a greater tropical affinity of the deepwater flora compared with the algae inhabiting the nearshore shallow-water habitats (e.g., Kapraun, 1974, for Louisiana algae).

One of the least known and poorly categorized groups of organisms inhabiting the deepwater communities in the NW Gulf of Mexico

hard banks are the benthic macroalgae, which are critical, productive, and sometimes dominant biotic components of these communities (e.g., Earle, 1972; Eiseman and Blair, 1982; Gavio et al., 2005). Over the past years, we participated in a series of SCUBA-collecting cruises (25- to 33-m depth) in the northern Gulf that were sponsored by the Flower Garden Banks National Marine Sanctuary, National Oceanic and Atmospheric Administration (NOAA), NOAA's National Undersea Research Center (NURC), Mineral Management Service, and the NOAA Sustainable Seas Expedition. Two midshelf NW Gulf hard banks, Stetson Banks and Sonnier Banks are historically viewed to be largely devoid of algae (Rezak et al., 1985, 1990); however, recent SCUBA collections off these hard banks point to a rich and diverse macroalgal flora (Fredericq et al., 2000). Similarly, new algal records based on recent SCUBA collections from the Flower Garden Banks Marine National Sanctuary (included in Famà et al., 2002; Lin and Fredericq, 2003; Gavio et al., submitted) continue to increase the number of species listed by Rezak et al. (1985). The algae collected from these shallow hard banks are typically small, cryptic, and intermixed, forming small turf or extensive mats. Most of these turfs are <1 cm in height and subject to heavy herbivore pressure. The ecological significance and biological uniqueness of these communities have been recognized nationally with the inclusion of several of these banks in the National Marine Sanctuary Program (East and West Banks of the Flower Gardens, Stetson Bank, Florida Middle Ground).

In addition, Department of Energy (DOE)-sponsored dredging cruises were conducted offshore Louisiana and Texas using the *R/V Pelican*, a University National Oceanographic Laboratory System (UNOLS) fleet oceanographic research vessel belonging to the Louisiana Universities Marine Consortium (LUMCON). Dredge collections 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. The dredged macroalgae are typically freestanding, leafy and large (up to 20 cm), epilithic on loose bedrock or on rhodoliths dominated by crustose coralline red algae. New records of dredged seaweeds offshore Louisiana have been incorporated in various taxonomic and phylogenetic treatments (e.g., Lin and Fredericq, 2003; Gurgel and Fredericq, 2004; Gurgel et al., 2004).

On the basis of our recent offshore collections from the northern Gulf of Mexico, in this study we describe and illustrate four new species of Rhodymeniales, assess their phylogenetic position in a molecular framework, and extend the distribution range of selected members of other Rhodymeniales.

MATERIALS AND METHODS

Morphological analysis.—Specimens used were either fixed in 5% formalin-seawater, pressed as herbarium sheets, or were silica gel dried, and deposited in the Algal Herbarium of the University of Louisiana at Lafayette (LAF). Holotypes mounted on herbarium paper are deposited in the National Herbarium, Smithsonian Institution (US). Herbaria abbreviations follow Holmgren et al. (1990). Hand sections through vegetative and reproductive structures were prepared using a stainless steel razor blade. Cross and longitudinal sections were stained with aniline blue (Tsuda and Abbott, 1984). Photographs of the sections were taken on an Olympus BX60 Compound Photomicroscope (Olympus, Melville, NY) with a Polaroid DMC 1e digital camera (Polaroid Inc., Cambridge, MA). Habits of specimens were scanned using a Microtek Scanmaker III (Microtek, Redonda Beach, CA) or photographed with a Nikon Coolpix 4500 digital camera (Nikon Inc., Melville, NY) attached to a Zeiss Semi-C Stereomicroscope (Carl Zeiss Inc., Thornwood, NY). Digital images were edited and assembled in plates using Photoshop v.6.0. The name of the illustrated taxa that are included in the *rbcl* tree are preceded by an *.

Molecular analyses.—Algal samples for molecular analyses were desiccated in the field in silica gel and deposited at the University of Louisiana at Lafayette and stored at -20 C. Collection information used in this study is listed in Table 1 and includes specimen locality, date, collector's name, percentage of *rbcl* sequenced, and GenBank accession numbers. Four species of Cryptonemiaceae (*Grateloupia filicina*, *G. turuturu*, *Cryptonemia borealis*, and *C. luxurians*) were used as the outgroup. Deoxyribonucleic acid (DNA) samples were prepared using the Dneasy Plant Minikit (QIAGEN, Valencia, CA) or were submitted to a CTAB-Cesium Chloride DNA procedure (Freshwater and Ruenes, 1994). Plastid-encoded *rbcl* was selected to infer a phylogeny for the Rhodymeniales. Protocols for DNA extraction, gene amplification, and cycle sequencing are as in Gavio and Fredericq (2002). Poly-

TABLE 1. List of species used in *rbdL* analysis with collection information. *Denotes sequences downloaded from GenBank.

Species	Location	Collector, collection date	Portion of <i>rbdL</i> sequenced and GenBank accession number
<i>Botryocladia ballantina</i> sp. nov	Dredged, 66-m depth, offshore Louisiana, U.S.A., 28°03.451'N 92°27.345'W	S. Fredericq, B. Gavio, C.F. Gurgel and J. Lopez-Bautista, 26 May 2000	40-1467 (97%)
<i>Botryocladia monica</i> Schmetter	E. Flower Garden Bank, Flower Garden Banks, National Marine Sanctuary, Texas, U.S.A., ~30 m	B. Gavio and B. Wysox, 29 Feb. 2000	32-1467 (98%) (AY168658)
<i>Botryocladia occidentalis</i> (Børgesen) Kylin	Dredged, 66 m, offshore Louisiana, U.S.A., 28°03.451'N 92°27.345'W	S. Fredericq, B. Gavio, C.F. Gurgel and J. Lopez-Bautista, 27 May 2000	43-866, 917-1467 (94%) (AY168659)
<i>Botryocladia occidentalis</i> (Børgesen) Kylin	Dredged, 50-55 m, offshore Louisiana, U.S.A., 28°06.470'N 90°55.359'W	S. Fredericq, J. Lopez-Bautista and E. Rita, 30 Jun 2001	43-1467 (97%) (AY168660)
<i>Botryocladia occidentalis</i> (Børgesen) Kylin	Florida Middle Grounds, Florida, U.S.A., 28°33.064'N 89°16.468'W, ~25 m	B. Gavio and B. Wysox, 12 Aug 2000	43-747 1020-1467 (79%) (AY168661)
<i>Botryocladia pyriformis</i> (Børgesen) Kylin	Dredged, 58 m, offshore Louisiana, U.S.A., 28°06.480'N 90°55.361'W	S. Fredericq, B. Gavio, C.F. Gurgel and J. Lopez-Bautista, 27 May 2000	606-1381 (53%) (AY168664)
<i>Botryocladia shanshii</i> Dawson	Long Bay Point, Isla Colon, Panama, at 12-15 m, on rocks	B. Wysox, 19 Oct 1999	9-1467 (99%) (AY168662)
<i>Botryocladia uvarionides</i> Dawson	Drift, Ocean Beach, San Diego, California, U.S.A.	B. Gavio and B. Wysox, 15 Jul 2000	33-1467 (98%) (AY168663)
<i>Botryocladia</i> sp.	Dredged, 50-55 m, offshore Louisiana, U.S.A., 27°53.384'N 93°18.359'W	S. Fredericq, B. Gavio, C.F. Gurgel and J. Lopez-Bautista, 25 May 2000	607-1467 (59%)
<i>Champia compressa</i> Harvey	Epiphytic on <i>Jania</i> sp., Florida Middle Grounds, Florida, U.S.A. 28°33.064'N 89°16.468'W	B. Gavio and B. Wysox, 10 Aug 2000	34-1467 (98%)
<i>Champia humbricalis</i> (L.) Desvaux	Kommeijie, Western Cape, S. Africa	S. Fredericq, 28 Jan 2001	41-1467 (97%)
<i>Champia parvula</i> (C. Ag.) Harvey	Epiphyte on <i>Thalassia</i> , Content Keyes, Florida Keyes, Florida, U.S.A.	T. Frankovitch, 19 Jul 2001	50-736, 1033-1467 (76%)
<i>Champia</i> cf. <i>salicornioides</i> Harvey	Epiphytic on <i>Botryocladia occidentalis</i> , Florida Middle Grounds, Florida, U.S.A. 28°33.064'N 89°16.468'W	B. Gavio and B. Wysox, 10 Jul 2000	34-1467 (98%)
<i>Champia</i> cf. <i>salicornioides</i>	Dredged at 55 m, offshore Louisiana, U.S.A. 27°56.785'N 92°00.645'W	S. Fredericq, B. Gavio, C.F. Gurgel and J. Lopez-Bautista, 27 May 2000	40-1467 (97%)
<i>Chrysmenia halymenioides</i> Harvey	Dredged at 58 m, offshore Louisiana, U.S.A., 28°06.480'N 90°55.361'W	S. Fredericq, B. Gavio, C.F. Gurgel and J. Lopez-Bautista, 27 May 2000	903-1467 (39%)
<i>Chrysmenia halymenioides</i>	Dredged at 65 m, offshore Louisiana, U.S.A., 28°06.066'N 91°02.481'W	S. Fredericq, J. Lopez-Bautista and E. Rita, 7 Jan 2001	674-1467 (54%)
<i>Chrysmenia halymenioides</i>	Dredged at 65 m, offshore Louisiana, U.S.A., 28°05.640'N 91°0.960'W	S. Fredericq, B. Gavio, C.F. Gurgel and J. Lopez-Bautista, 27 May 2000	607-1467 (59%)

TABLE 1. Continued.

Species	Location	Collector, collection date	Portion of rhd. sequenced and Genbank accession number
<i>Chrysonymia 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%)
<i>Chrysonymia</i> sp.	Rocher du Diamant, Martinique	S. Fredericq, M. and D. Littler, B. Brooks, 14 Jun 1995	645-1467 (56%)
<i>Coelarthrum cliffonii</i> (Harvey) Kylin	Dredged, 58 m, offshore Louisiana, U.S.A., 28°06.480'N 90°55.361'W	S. Fredericq, B. Gavio, C.F. Gurgel and J. Lopez-Bautista, 27 May 2000	110-611, 720-1430 (83%)
<i>Cryptonemia borealis</i> Kylin	Cobble, Hein Bank, Washington, U.S.A.	S. Lindstrom, 9 Aug 1993	41-1467 (97%)
<i>Cryptonemia luxurians</i> (C. Ag.) J. Agardh	Praia Rasa, Rio de Janeiro, Brazil	C.F. Gurgel, 12 Dec 1998	52-1467 (96%)
<i>Fauchea laciniata</i> J. Agardh	Ketchikan, Alaska, U.S.A.	S. Lindstrom, 2 July 2000	40-1467 (97%)
<i>Fauchea pygmaea</i> Kylin	Botanical Beach, Vancouver Island, BC, Canada	M. Wynne, 12 July 1995	68-1467 (95%)
<i>Fryxella gardneri</i> (Setchell) Kylin	Moss Beach, California, U.S.A.	S. Fredericq, 17 July 1996	84-1467 (94%)
<i>Gastroclonium subarticulatum</i> (Turner) Küzing	Pigeon Pt, San Mateo Co., California, U.S.A.	M.H. Hommersand, 21 June 1992	121-599, 640-1467 (89%) (U04178)
<i>Gelidiopsis</i> sp.	Deep Sponge Reef, KwaZulu Natal, S. Africa, 30 m	S. Fredericq, 11 Feb. 2001	40-1467 (97%)
<i>Gelidiopsis</i> sp.	La Calerita, Baja Santa Paz, BCS, Mexico	S. Fredericq, 27 Oct. 1999	42-1467 (97%)
<i>Gloiocladia iyoensis</i> (Okamura) R. Norris	<i>Kalymenia</i> flats, off Main Wall, Jervis Bay, New South Wales, Australia	A. Millar and D. Harden, 24 Oct. 1995	9-1467 (99%)
<i>Gloiocladia pelicana</i> sp. nov.	Dredged, 58-60 m offshore Louisiana, U.S.A., 28°05.561'N 91°02.205'W	S. Fredericq, B. Gavio, C.F. Gurgel and J. Lopez-Bautista, 27 May 2000	63-1467 (96%)
<i>Gloiocladia pelicana</i> sp. nov.	Dredged, 65-66 m offshore Louisiana, U.S.A., 28°05.640'N 91°0.960'W	S. Fredericq, B. Gavio, C.F. Gurgel and J. Lopez-Bautista, 27 May 2000	39-1467 (97%)
<i>Gloiocladia saccata</i> (J. Ag.) R.E. Norris	N. Island, Wellington Harbour, New Zealand	W. Nelson, 10 Mar 1996	84-773 (47%)
<i>Gloiocladia tenuissima</i> sp. nov.	Dredged, 58-60 m, offshore Louisiana, U.S.A., 28°05.561'N 91°02.205'W	S. Fredericq, B. Gavio, C.F. Gurgel and J. Lopez-Bautista, 2 May 2000	39-1467 (97%)
<i>Grateloupia filicina</i> (Lam.) C. Ag.*	Livorno, Italy	Kawaguchi <i>et al.</i> (2001)	107-1365 (86%) (AB055472)
<i>Grateloupia turuturu</i> Yamada	Murooran, Hokkaido, Japan	S. Fredericq, 6 Sep. 1993	9-1467 (99%)
<i>Haliobrysis micans</i> (Schm. and Hauptf.) Huvé and Huvé	Long-Shia Long, Hsiao Liuchi I., Taiwan, 3 m	S. Fredericq and S.M. Lin, 23 July 1993	84-1397 (90%)
<i>Hymenocladopsis crustigena</i> Moc	Pta Peñon, Bahía Fildes, King George I., South Shetland Islands, Antarctic Peninsula, 9 Feb. 1994	S. Fredericq and J. Rodriguez, 9 Feb. 1994	205-671, 718-1256 (69%) (U21640)
<i>Leptofaunchea raritase</i> sp. nov.	Dredged, 66 m, offshore Louisiana, U.S.A., 28°03.451'N 92°27.345'W	S. Fredericq, B. Gavio, C.F. Gurgel and J. Lopez-Bautista, 26 May 2000	31-1424 (95%)

TABLE 1. Continued.

Species	Location	Collector, collection date	Portion of <i>rbL</i> sequenced and GenBank accession number
<i>Lomentaria catenata</i> Harvey	Tokawa, Choshi, Japan	S. Fredericq and M. Yoshizaki, 2 Sep. 1993	125-1309 (81%) (U21642)
<i>Lomentaria habodlatensis</i> Yendo	Kermelehen (Plouezoch), Brittany, France	J. Cabioch, 12 June 1994	132-1467 (91%)
<i>Lomentaria habodlatensis</i>	Berkeley Pier, Contra Costa Co, California, U.S.A.	M.H. Hommersand, 23 Dec. 1992	133-1467 (91%) (U04180)
<i>Rhodymenia pseudopalpata</i> (Lamouroux) Silva	Intertidal, Port Aransas jetty, Texas, U.S.A.	C.F. Gurgel, 17 May 1998	9-1467 (99%) (AY168656)
<i>Rhodymenia pseudopalpata</i> (Lamouroux) Silva	Wrightsville Beach, New Hanover Co., NC, U.S.A.	D.W. Freshwater, June 1991	30-974, 1024-1467, (95%) (U04184)
<i>Rhodymenia skottsbergii</i> Dawson	La Boca Navidad, C. Chile	S. Fredericq and M.E. Ramirez, 17 June 1995	9-1467 (99%)
<i>Spartingia pertusa</i> (Post. and Rupr.) Saunders, Strachan and Kraft	Intertidal, bedrock, outside Sunshine Cove, near Juneau, Alaska, U.S.A.	S. Lindstrom, 26 April 1998	9-1363 (92%)

merase chain reaction (PCR) and sequencing primers used in this study were *FrbL* start, F7, F57, F577, F853, F993, R753, R1150, R1381, and *RrbS* start as listed in Gavio and Fredericq (2002). For some specimens, PCR amplification was not successful with the primer combinations; in this case, new primer combinations were adopted, such as F64-R753, F645-R1381 (see Lin et al., 2001).

The sequence data were compiled and aligned with Sequencher (Gene Codes Corp., Ann Arbor, MI) and exported for phylogenetic analysis in PAUP and MacClade (D. R. Maddison and W. P. Maddison, 2000). All phylogenetic analyses were performed with PAUP* v.4.0 beta 10 (Swofford, 2002). Phylogenetic trees were generated by maximum likelihood (ML) and maximum parsimony (MP) methods. The *rbL* alignment initially included 1,467 sites, but because information was missing for the 5' ends of many sequences, the first 60 sites were excluded from all phylogenetic analyses.

Parameters used in the ML analysis were obtained using the software Modeltest v.3.0 (Posada and Crandall, 1998) to compare different models of DNA substitutions in a hierarchical hypothesis-testing framework to select a base-substitution model that best fit the sequence data. The optimal ML model found was a GTR + I + G evolutionary model (General Time Reversible model + Invariable sites + Gamma distribution). The parameters were as follows: assumed nucleotide frequencies A = 0.3167; C = 0.1245; G = 0.1915; T = 0.3673; substitution rate matrix with A-C substitutions = 1.0366, A-G = 7.3541, A-T = 2.5225, C-G = 1.5142, C-T = 18.6354, G-T = 1.0000; proportion of sites assumed to be invariable = 0.5263; rates for variable sites assumed to follow a gamma distribution with shape parameter = 1.1020. Maximum Parsimony trees were inferred from heuristic searches of 5,000 replications of random sequence addition, using only the phylogenetically informative characters, unordered, under the Fitch criterion of equal weights for all substitutions (Fitch, 1971), Tree Bisection Reconnection, saving multiple trees but holding five trees at each step. Support for the nodes of the MP trees was assessed by bootstrap analysis (Felsenstein, 1985) on the dataset using 5,000 replicates, as implemented in PAUP*. Consistency (CI) and retention (RI) indices (Kluge and Farris, 1989) were calculated excluding uninformative characters. Bootstrap proportion values are abbreviated as BP.

RESULTS

List of species

Rhodymeniaceae Harvey, 1849:75*Asteromenia* Huisman and Millar, 1996:138*Asteromenia peltata* (W. R. Taylor) Huisman and Millar, 1996:139

Figures 1–2

Basionym: *Fauchea peltata* W. R. Taylor, 1942:139.Homotypic synonyms: *Weberella peltata* (W. R. Taylor) C. W. Schneider, 1975:133–134; *Halichrysis peltata* (W. R. Taylor) P. Huvé et H. Huvé, 1977:106; Wynne, 1986:2245, Schneider and Searles, 1991:345, figs. 406, 407.

Type locality: Tortuga Island, Venezuela.

Distribution: Recorded from Houtman Abrolhos, Western Australia, Norfolk Island, Taiwan (Huisman and Millar, 1996), Maldives (Silva et al., 1996), Iran (Nizzamuddin and Gessner, 1970), North Carolina, Bermuda, Cuba (Schneider, 1975), Venezuela, Brazil, Jamaica (Taylor, 1960), NE Gulf of Mexico (Cheney and Dyer, 1974).

Specimens examined: Offshore Louisiana, 50- to 65-m depth, 27°49.388'N 92°55.438'W (LAF-26-5-00-6-1; coll. S. Fredericq and B. Gavio, 26 May 2000); 27°58.020'N 91°39.718'W (LAF-27-5-00-7-3; coll. S. Fredericq and B. Gavio, 27 May 2000). Sterile specimens, growing on coral rubble and rocks.

Remarks: This species has been recorded as *F. peltata* from the East Flower Garden banks, from 33- to 50-m depth (Rezak et al., 1985). This is the first illustration of the species for the Gulf of Mexico.***Botryocladia*** Kylin, 1931:17****Botryocladia monoica*** Schnetter, 1978:13, figs. 1–7

Figures 3–4

Type locality: Punta Betin, Santa Marta, Atlantic Colombia.

Distribution: Atlantic Colombia, NW Gulf of Mexico (Gavio and Fredericq, 2003).

Specimens examined: East Flower Garden Bank, Flower Garden National Marine Sanctuary, on coral rubble, ~30-m depth, LAF-29-2-00-1-10, LAF-29-2-002-5. Rare, inconspicuous,

most likely present only during the winter months. Found only in Feb., bearing mature cystocarps.

Remarks: This species is the smallest described species of *Botryocladia*. In 1945 (p. 254), Taylor described *B. tenuissima*, from the Galapagos Islands, Ecuador. The two species share a small-sized habit and morphological attributes such as vesicles with an incomplete cortex and one-layered medulla. Additional illustrations of *B. tenuissima* from Hawaii by Abbott (1999, fig. 63C, D) clearly indicate that this species is distinct from *B. monoica* in having a creeping, stoloniferous habit with branched axes. Our specimen from the Gulf matches the description of *B. monoica* in having a single, short, erect axis bearing one to two spherical vesicles. Whereas Schnetter (1978) reported the presence of occasional gland cells in *B. monoica*, they were not observed in the Gulf specimens. In all other characters, our specimens fit the description of *B. monoica*.****Botryocladia pyriformis*** (Børgesen) Kylin, 1931:18

Figures 5–6

Basionym: *Chrysymenia pyriformis* Børgesen, 1910:187, figs. 8, 9

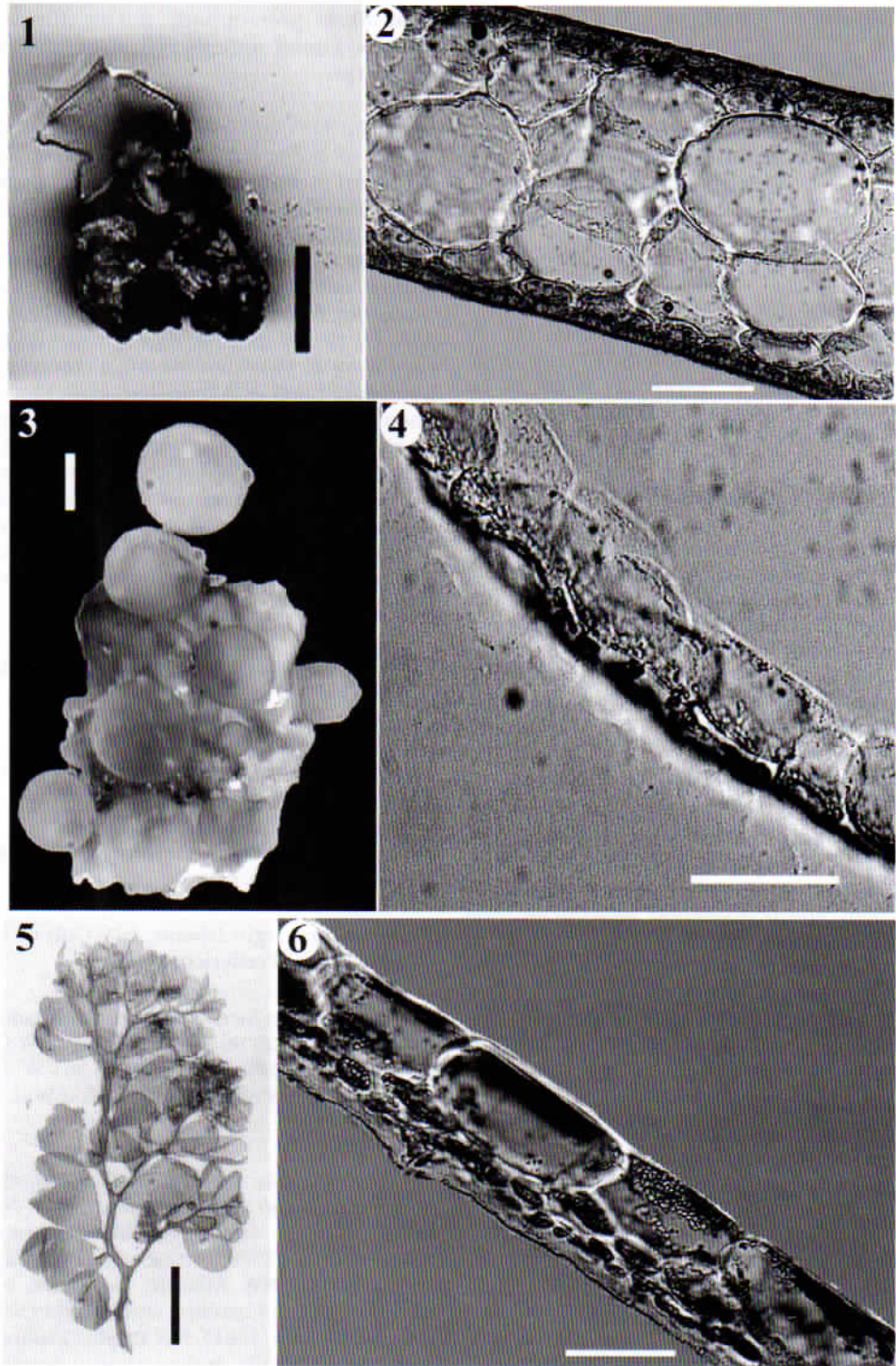
Type locality: Offshore St. John, Virgin Islands, 30- to 32-m depth.

Distribution: Virgin Islands; NW Gulf of Mexico (Gavio and Fredericq, 2003).

Specimens examined: Offshore Louisiana, 40- to 70-m depth, 28°06.480'N 90°55.361'W (LAF-27-5-00-10-7); 28°06.480'N 90°55.361'W (LAF-27-5-00-11-6); 28°05.640'N 91°00.960'W (LAF-8-1-02-1-6).

Doubtful records: Florida, Brazil, Bermuda, Jamaica (see Gavio and Fredericq, 2003). NE Atlantic: Canary Islands (Gil-Rodriguez and Afonso-Carillo, 1980; Price et al., 1986; Haroun et al., 2002). NW Atlantic: Bermuda, North Carolina, South Carolina, and Florida (Schneider and Searles, 1991). SW Pacific: Philippines (Silva et al., 1987). Indian Ocean: Seychelles, Réunion (Silva et al., 1996). Gulf of Mexico (Gavio and Fredericq, 2003).

Remarks: Taylor (1928) reported this species (as *Chrysymenia pyriformis*) from the Dry Tortugas, FL. However, his description and draw-



Figs. 1, 2. *Asteromenia peltata*. 1. Habit of sterile specimen. Bar = 1 cm. 2. Cross section through blade. Bar = 40 μ m. Figs. 3-4. *Botryocladia monoica*. 3. Habit of cystocarpic specimen. Bar = 1 mm. 4. Cross section through vesicle. Bar = 50 μ m. Figs. 5-6. *Botryocladia pyriformis*. 5. Habit of sterile specimen. Cross section through vesicle. Bar = 50 μ m.

ings (plate 23, fig. 17) refer to a separate taxon, *B. caraibica* (Gavio and Fredericq, 2003).

**Botryocladia ballantina* sp. nov.

Figures 7–15

Holotype: #Algol. Coll. US 204326 (Fig. 9), dredged offshore Louisiana, 60- to 70-m depth, between 28°03.451'N 92°27.345'W and 28°03.65'N 92°27.28'W, attached to rubble, 26 May 2000, coll. S. Fredericq et al. (LAF-26-5-00-46).

Isotypes: LAF-26-5-00-46.

Distribution: Offshore Louisiana.

Additional specimens studied: Dredged offshore Louisiana, 60- to 70-m depth, 28°06.066'N 91°02.481'W, attached to rubble, 1 July 2001.

Habitat: Deepwater, 50- to 80-m depth, attached to hard substratum.

Diagnosis: Plantae 10–15 mm altae; erecti axes cylindrici 0.5 mm diameter, 1.5–2 mm longi, e discis basalibus enascentes. Unoquoque axe 1 ramum vesiculatum ferente. Axis constitutus externo strato parvis cellulis subsphaericis, internum stratum a magnibus cellulis medullaris cum parvis cellulis inter eas. Vesiculae maturae 9–15 mm longae, 8–12 mm latae, obovatae-sphaericae. Paries vesicularum (80) 100–120 (140) μm crassa, a 2-tribus stratis cellularum constituta; externum stratum parvis cellulis subsphaericis, sparse dispositis 4–16 μm diam.; internum stratum polyhaedricis cellulis, 30–90 μm diam. Intermedium stratum irregularem e polyhaedricis cellulis. Tetrasporangia ovata, cruciate divisa, 16–25 \times 25–30 μm apud cellulas corticales dispersa. Gametophyta dioecia: spermatangia non visa. Cystocarpia matura, usque ad 520 μm diametro, ostiolo, in vesiculae cavitatem et e vesiculae superficie aequaliter projecta.

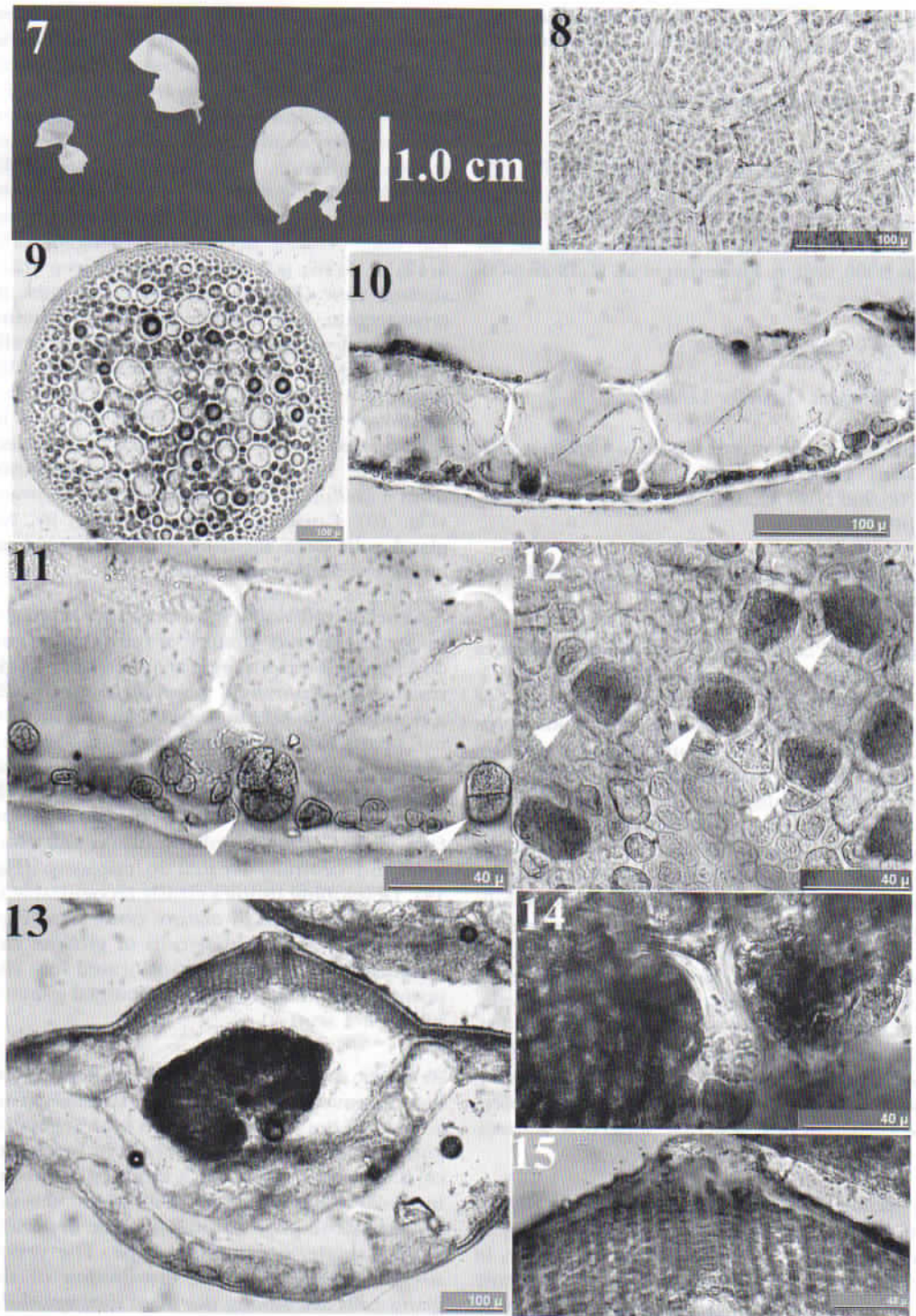
Etymology: The species epithet honors Dr. David Ballantine, Professor of Marine Botany at the University of Puerto Rico at Mayagüez, in recognition of his numerous taxonomic contributions to the genus *Botryocladia* in the western Atlantic.

Description: Thalli 10–15 mm high. Axis single, 0.5 mm in diameter, 1.5–2 mm long, arising from a small basal disc. Thalli univesiculate (Fig. 7) or possessing an additional minute ves-

icle developing laterally to the mature bladder. Erect axis consisting of a narrow peripheral zone of one to two layers of small subspherical cells, and a central area composed of larger, roundish colorless medullary cells interspersed with smaller colored cells (Fig. 9). Vesicles spherical-obovate, 9–15 mm long and 8–12 mm wide. Vesicle walls 80–140 μm thick, consisting of two to three cell layers comprising the outer cortex of roundish-elongate cells 4(12) \times 5(16) μm in diameter as seen from surface view (Fig. 8) and 2–10 μm thick in cross section. Intermediate cell layer discontinuous and composed of polygonal cells (20)30(45) μm in diameter; inner layer consisting of a single continuous layer of polygonal medullary cells, 30(80) \times 36(90) μm seen in surface view and 30–90 μm thick in cross section (Fig. 10). Occasionally, a protuberance from a medullary cell is formed thallus inward (Fig. 10). Cortication complete (Fig. 9). No gland cells were seen, even after staining an entire vesicle in aniline blue.

Crucially divided tetrasporangia scattered in cortical layer. A mixture of fully mature and developing tetrasporangia are present in single vesicle. Tetrasporangia generally ovate, 16–25 μm wide by 35–30 μm long (Figs. 11, 12). Sexual plants dioecious. Cystocarps scattered irregularly on vesicle walls. In cross section, mature cystocarps measure 390–520 μm (Figs. 13, 14), reaching up to 1 mm in diameter in surface view. Carposporophytic fusion cell elongate and centrally located in cystocarp (Fig. 14). Developing ostioles clearly recognizable in center of pericarps of mature cystocarps (Figs. 13, 15). All gonimoblast cells of globose carposporophyte becoming transformed into carposporangia (Fig. 13). Spermatangial gametophytes not seen.

Remarks: *Botryocladia ballantina* sp. nov. resembles *B. ganesanii* Aponte-Diaz (1988:44) from Venezuela but differs from it in both vegetative and reproductive features. Thalli in specimens of *B. ganesanii* consist of a ramified axis bearing 7–20 vesicles, whereas thalli of the new taxon always comprise a solitary vesicle departing from a single, nonramified stipe. The vesicle size and shape and the distribution of the gland cells are among the main distinguishing characters at the species level in *Botryocladia* (Aponte-Diaz, 1988; Ballantine, 1985, 1996; Brodie and Guiry, 1988; Ballantine and Aponte, 2002). Fully grown vesicles of *B. ballantina* are smaller than those of *B. ganesanii* and lack gland cells even after staining the entire thallus



Figs. 7–15. *Botryocladia ballantina* sp. nov. 7. Habit of holotype specimen. 8. Surface view of vesicle wall showing complete cortication. 9. Cross section through stipe showing cortical layer and large medullary cells interspersed among smaller cells. 10. Cross section through two to three cell-layered vesicle wall. 11. Cross section through vesicle wall with tetrasporangia (arrowheads). 12. Surface view of vesicle wall with tetrasporangia (arrowheads). 13. Cross section through mature cystocarp. 14. Close-up of fusion cell at base of carposporophyte bearing carposporangia. 15. Ostiolar region in pericarp.

in aniline blue; in contrast, gland cells are common in groups of 6–12 in *B. ganesanii*. Furthermore, *B. ganesanii* is monoecious, whereas the Gulf species is dioecious.

Taylor (1960) and Schneider and Searles (1991) reported deepwater specimens of *Botryocladia* bearing large, subsolitary bladders (2–4 cm diameter). They referred to this taxon as a deepwater form of *B. pyriformis*. Additional morphological and molecular analyses comparing *B. ballantina* and this entity should be addressed to determine their taxonomic status. The new finding brings to 11 the number of species of *Botryocladia* recorded for the tropical and subtropical western Atlantic (Gavio and Fredericq, 2003).

**Botryocladia* sp.

Specimens examined: 27°53.384'N 93°18.359'W (LAF-25-5-00-2-1), 50- to 54-m depth.

Remarks: An unidentified species of *Botryocladia* was found offshore Louisiana. The material was scarce and unfortunately completely used up for the molecular study. The habit is unknown because the little material analyzed was all fragmented in pieces less than 2 mm². From the *rbcL* sequence data, the taxon belongs in *Botryocladia*, has incomplete cortication, and rather abundant gland cells in groups of 2–8.

Chrysomenia J. Agardh, 1842:105

**Chrysomenia enteromorpha* Harvey, 1853:
187–188, Pl. E.
Figures 16–18

Type locality: Key West, Florida.

Distribution: Indian Ocean: Bangladesh, Seychelles (Silva et al., 1996). NE Atlantic: Canary Islands (Price et al., 1986; Haroun et al., 2002). W Atlantic: Bermuda, North Carolina, South Carolina, Georgia, Florida (Schneider and Searles, 1991), Caribbean (Taylor, 1960; Littler and Littler, 2002). SE Atlantic: Ghana (Price et al., 1986; Lawson and John, 1987). NW Gulf: Flower Garden Banks, Outer Shelf Banks (Rezak et al., 1985).

Specimens examined: Offshore Louisiana, 50- to 70-m depth: 27°56.789'N 92°00.789'W (LAF-27-5-00-7-1); 28°06.480'N 90°55.361'W (LAF-27-5-00-10-7); 28°06.480'N 90°55.361'W (LAF-27-5-00-15-2); 27°58.180'N 92°01.908'W (LAF-6-30-01-2-4); 27°56.358'N 92°00.540'W (LAF-7-1-01-

3-3); 28°05.106'N 90°58.606'W (LAF-7-1-01-8-2). Abundant.

Remarks: This is the first illustration of this species for the N Gulf of Mexico.

**Chrysomenia halymenioides* Harvey, 1853:188,
pl. XX.A.
Figures 19–20

Type locality: Key West, Florida ("thrown up from deep water").

Distribution: North Carolina, Bermuda (Schneider and Searles, 1991).

Specimens examined: Offshore Louisiana, 55- to 60-m depth, 28°06.480'N 90°55.361'W (LAF-27-5-00-13-2); 28°06.480'N 90°55.361'W (LAF-27-5-00-10-2); 27°56.358'N 92°00.540'W (LAF-R139).

Remarks: This species was reported from the East Flower Garden Bank by Eiseman and Blair (1982) and Rezak et al. (1985). This is the first illustration of this species for the N Gulf of Mexico.

Coelarthrum Børgesen 1910:192

**Coelarthrum cliftonii* (Harvey) Kylin, 1931:15
Figures 21–22

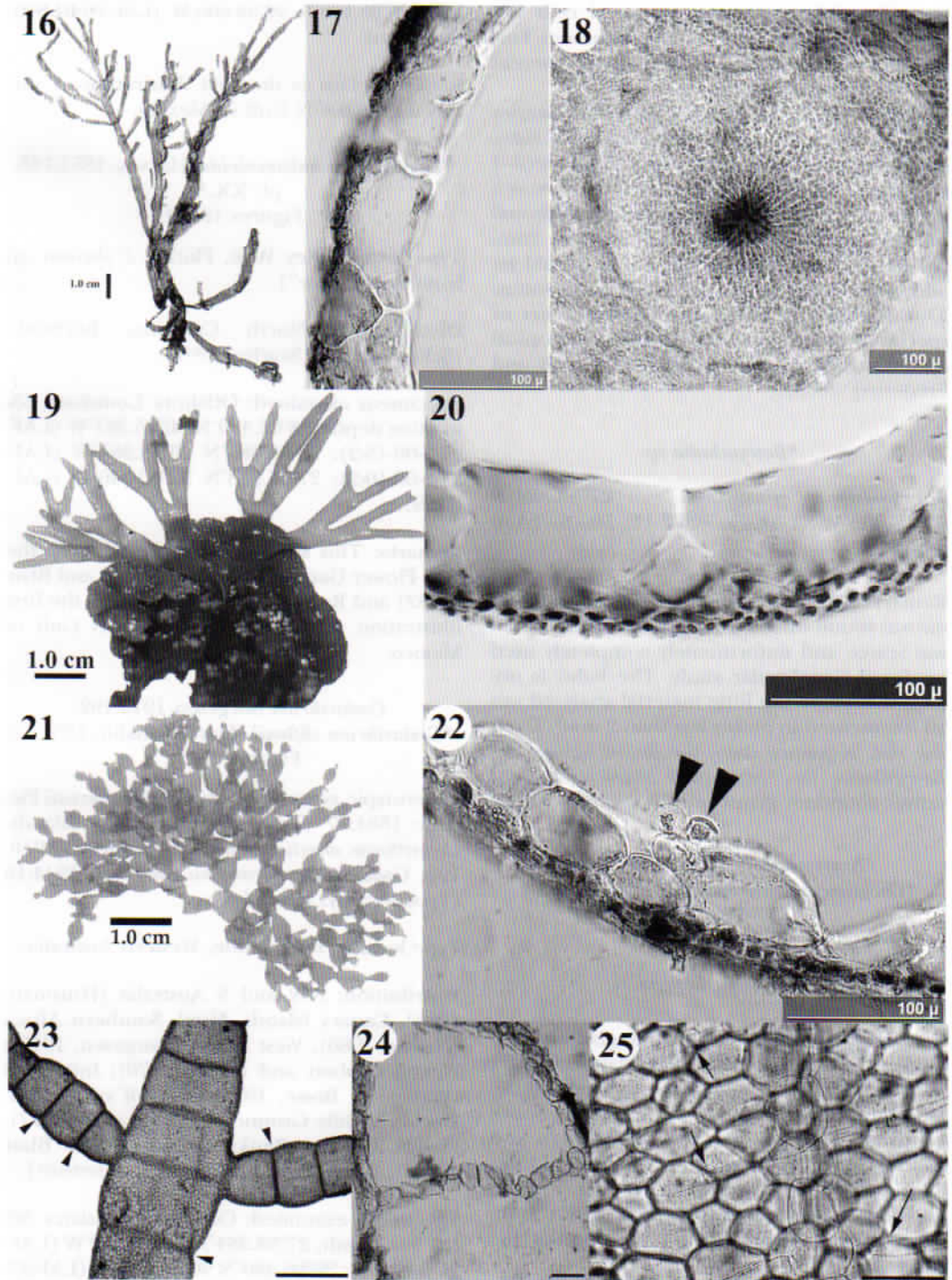
Heterotypic synonyms: *Chylocladia albertesii* Piccone 1884:37 (Type locality: Canary Islands, *Coelarthrum albertesii* (Piccone) Børgesen 1910:192, *Coelarthrum mortensenii* Børgesen 1944:19 (Type locality: Mauritius).

Type locality: Freemantle, Western Australia.

Distribution: NW and S Australia (Huisman, 1996), Canary Islands, Natal, Southern Africa (Norris, 1986); West Indies (Børgesen, 1910); Hawaii (Abbott and Littler, 1970); Indonesia (Weber-van Bosse, 1928). N Gulf of Mexico: Florida Middle Ground (Hopkins et al., 1977), Flower Garden Banks [Eiseman and Blair (1982), Rezak et al. (1985) (as *C. albertesii*)].

Specimens examined: Offshore Louisiana, 50- to 70-m depth, 27°53.384'N 93°18.359'W (LAF-25-5-00-2-2); 28°06.480'N 90°55.361'W (LAF-27-5-00-11-1); 28°06.480'N 90°55.361'W (LAF-27-5-00-12-4); 28°06.480'N 90°55.361'W (LAF-27-5-00-15-5); 28°05.106'N 90°58.606'W (LAF-7-1-01-7-2; LAF-7-1-01-8-3). Common.

Remarks: Huisman (1996) considered the type of the genus *C. albertesii* from the Canary Is-



Figs. 16–18. *Chrysymenia enteromorpha*. 16. Habit of cystocarpic specimen. 17. Cross section through thallus showing two-cell-layered wall. 18. Surface view of mature cystocarp with visible ostiole. Figs. 19–20. *Chrysymenia halymenioides*. 19. Habit of sterile specimen growing on *Peyssonnelia* sp. 20. Cross section of wall. Figs. 21–22. *Coelarthrum cliftonii*. 21. Habit of sterile specimen. 22. Cross section through wall showing gland cells (arrowheads). Figs. 23–25. *Champia compressa*. 23. Habit of specimen showing evident constrictions at diaphragms (arrowheads). 24. Longitudinal section showing diaphragm composed of 12–13 cells. 25. Surface view showing longitudinal filaments bearing gland cells (arrows).

lands to be conspecific with the earlier Australian taxon *C. cliftonii*.

Champiaceae Kützing, 1843:438–439

Champia Desvaux, 1809:245

**Champia compressa* Harvey, 1838:402
Figures 23–25

Type locality: Muizenberg, False Bay, Cape Province, South Africa.

Distribution: Atlantic Colombia, South Africa, Malaysia, Australia, Indian Ocean (Millar, 1990).

Specimens examined: Florida Middle Ground, 20- to 30-m depth, 28°33.064'N 89°16.468'W (LAF-8-10-00-3-6).

Remarks: Whereas Grunow (Silva et al., 1996) considers *C. compressa* and *Champia vieillardii* Kützing (1866:14; no type locality given) to be conspecific, Dawson (1954) regards these two species as different entities. Wynne (1986, 1998) is of the opinion that reports of *C. compressa* from the Caribbean are *C. vieillardii*. Both taxa are superficially similar and have been confused in the past. Millar (1990) shares Dawson's opinion and gives a detailed description of the differences between these two taxa. According to Millar, *C. compressa* is less flattened than *C. vieillardii*, the diaphragm is 10–18 cells across (compared with three to four cells in *C. vieillardii*), and the constrictions are associated with the diaphragm (in *C. vieillardii* they are not). Masuda et al. (2001), in their study of the Malaysian seaweeds, support Millar's observations and add as a distinguishing character the production of slender branches in *C. vieillardii*, that are lacking in *C. compressa*. In the Gulf specimen, the constrictions are associated with the diaphragm (Fig. 23), and the thallus is not flat. The diaphragm is 11- to 13-cells wide (Fig. 24); longitudinal filaments departing from the center of the thallus and bearing numerous roundish gland cells (Fig. 25) are clearly visible. All these characters are consistent with the description of *C. compressa*.

This is the first record of this species for the Gulf of Mexico.

Champia minuscula Joly et Ugadim in Joly, Cordeiro, Yamaguishi and Ugadim, 1966:164.

Type locality: Brazil: Guarujá, São Paulo State.

Distribution: Brazil.

Specimens examined: East Flower Garden Banks Marine Sanctuary (LAF-29-2-00-1).

Remarks: This is the first record of this taxon for the Gulf of Mexico.

**Champia* cf. *salicornioides* Harvey, 1853:76

The material examined was unfortunately fragmented, so it was not possible to determine the branching pattern of the thallus. Segments are consistent with the description of *C. salicornioides* Harvey as well as the size, shape, and arrangement of the cells. This taxon is genetically distinct from both *C. parvula* (Ag.) Harvey and *C. compressa* Harvey.

Type locality: Key West, Florida.

Distribution: NE Atlantic: Canary Islands (Harron et al., 2002). SE Atlantic: Senegal, Ghana (Price et al., 1986; Lawson and Price, 1987). SW Pacific: Philippines (Silva et al., 1987), Vietnam (Pham-Hoang, 1969), Indonesia (Silva et al., 1996). Indian Ocean: Maldives, Seychelles (Silva et al., 1996). Caribbean: general (D. S. Littler and M. M. Littler, 2002), Atlantic Florida, Bahamas, Antilles, Southern Caribbean (Taylor, 1960).

Specimens examined: Florida Middle Ground, 25-m depth, 28°33.064'N 89°16.468'W (LAF-8-10-00-1-2); Offshore Louisiana, 50- to 55-m depth, 27°56.785'N 92°00.645'W.

Faucheaceae Strachan, Saunders and Kraft in Saunders et al., 1999:36

Gloiocladia J. Agardh, 1842:87

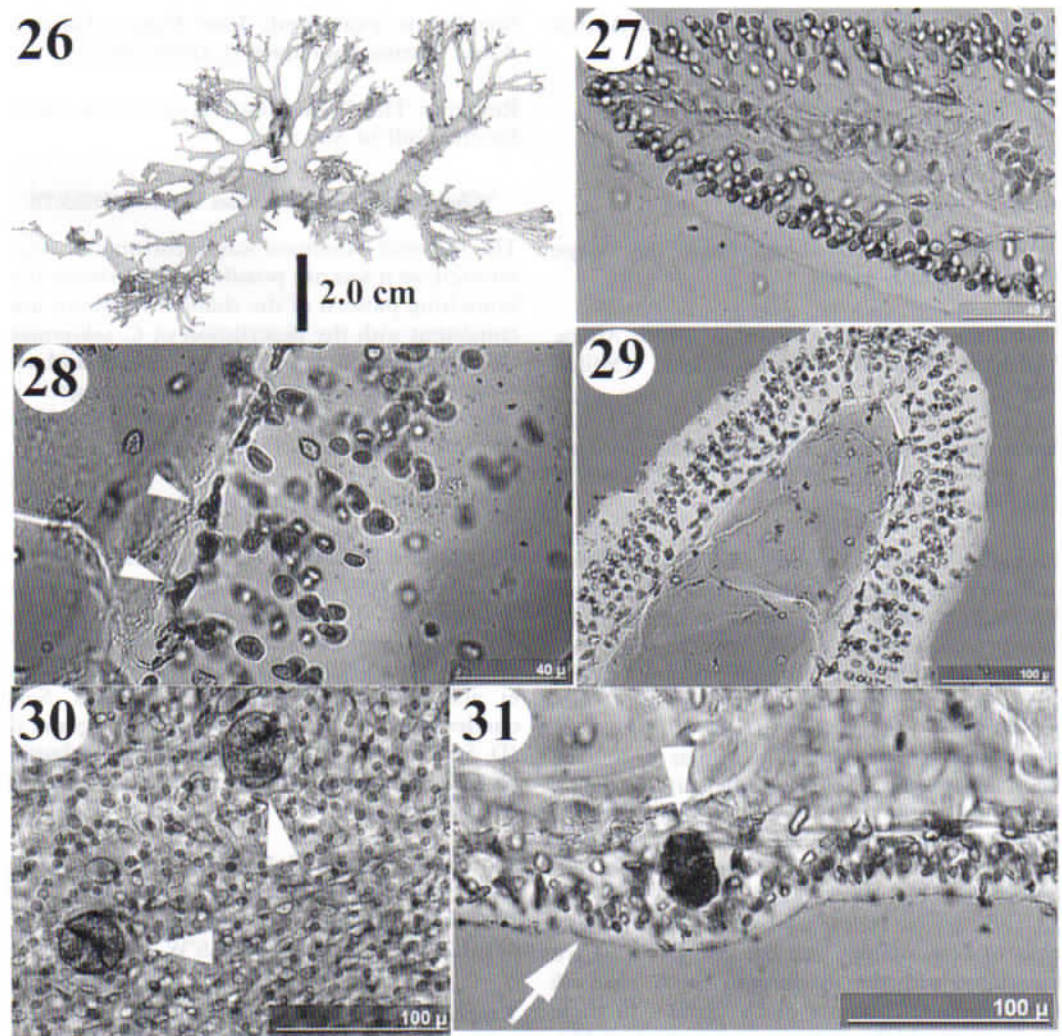
**Gloiocladia pelicana* sp. nov.
Figures 26–31

Holotype: LAF-27-5-00-10-11 (To be deposited in Algal Coll. US) (Fig. 21), dredged Offshore Louisiana, 58- to 60-m depth, 28°05.561'N 91°02.205'W, attached to rubble, 2 May 2000.

Distribution: Offshore Louisiana.

Additional specimen studied: Dredged offshore Louisiana, 60- to 70-m depth, 28°05.640'N 91°0.960'W (LAF-27-5-00-10-13).

Diagnosis: Plantae 6–12 cm altae, affixae per parvum hapteron. Ramificationes irregulares vel pseudodichotomae, rami ad 10–15 mm lati. Cortex externa 6–7 stratis parvarum cellularum sphaericarum (3)4–6(9,6) μm . Cortex interna e magnis cellulis elongatis; medulla



Figs. 26–31. *Gloiocladia pelicana* sp. nov. 26. Habit of holotype specimen. 27. Longitudinal section through uniaxial thallus showing anticlinal arrangement of cortical cells. 28. Cross section showing cortex with periclinally flattened subcortical cells (arrowheads). 29. Cross section through thallus showing the monostromatic medulla, and cortex. 30. Surface view with tetrasporangia (arrowheads). 31. Cross section with tetrasporangium (arrowhead). Note the slight bulging of cortex (arrow) where the tetrasporangium is located.

uno strato magnarum cellularum elongatarum, $135\text{--}220 \times 200\text{--}245 \mu\text{m}$. Tetrasporangia cruciata, sphaerica, $(23)27\text{--}35(43) \mu\text{m}$. Pagina thalli elevata est ubi tetrasporangia.

Etymology: The species epithet is named for the *R/V Pelican*, the UNOLS research vessel of LUMCON equipped for box dredging that made possible the collection of this new species.

Description: Thalli uniaxial, 2–14 cm tall, prostrate, gelatinous, broadly linear and complan-

ate with small marginal proliferations, attached to rubble by an inconspicuous holdfast. Thalli irregularly to pseudodichotomously branched up to three to four orders of branching, with the widest portion reaching 10–15 mm (Fig. 26) and gradually narrowing upward. Ultimate tips rounded and subdichotomous at a 45° angle. Outer cortex composed of widely spaced anticlinal dichotomous filaments, each comprising five to seven subglobose cells $(3)4\text{--}6(9.6) \mu\text{m}$ (Figs. 27–29). Inner cortex composed of single layer of stretched, axially elongated cells (Fig. 28) cut off secondarily from

the lowermost cortical cells that extend laterally toward apical region and connecting to neighboring cells by secondary pit connection. Entire cortex embedded in gelatinous matrix (Figs. 28, 29). Medulla composed of single layer of large, elongate, colorless cells, 135–220 × 200–245 μm (Figs. 27, 29). Tetrasporangia cruciately divided, roundish, (23)27–35(43) μm (Figs. 30, 31) embedded in cortex, scattered over blade. Thallus surface slightly raised where tetrasporangia are situated (Fig. 31). Sexual female and male gametophytes were not observed.

Remarks: This taxon superficially resembles the erect *Gloiocladia japonica* (Okamura) Yoshida (1997:163); however, the latter has a medulla that is several cell layers across and produces narrow rhizoidal filaments connecting lower cortical and medullary cells (see Kajimura, 1986). In the absence of cystocarpic material, this species is placed in the *Fauchea*ceae, genus *Gloiocladia* on the basis of vegetative anatomy. It shares with *Gloioderma blomquistii* (Searles in Schneider and Searles) R. E. Norris (as *G. blomquistii*) described from the continental shelf offshore North Carolina a unistratose medulla of large cells. On the basis of the smaller size of mature cystocarpic specimens, absence of a lacinate habit, a less expanded blade, squarish medullary cells, and ellipsoid tetrasporangia, *G. blomquistii* is a different species.

Currently, the characters used to differentiate the genera *Gloiocladia*, *Gloioderma*, and *Fauchea* are unclear (Irvine and Guiry, 1980; Guiry and Irvine, 1981). *Fauchea* Montagne and Bory (in Montagne 1846:64) is characterized on the basis of tetrasporangial nemathecia and scattered tetrasporangia in *Gloiocladia* and *Gloioderma*. Using this definition, the Gulf taxon is not a *Fauchea* species; it also differs from *Fauchopsis* Kylin (1931:9) because it lacks rhizoids surrounding the medullary cells (e.g., Womersley, 1996) and from *Webervanbossea* De Toni f. (1936:5) because the thallus is not segmented and lacks constrictions (Huisman, 1995). The genus *Gloiocladia* presently includes taxa formerly referred to as *Gloioderma* J. Agardh (1851:243). The genera have been separated by the mode of tetrasporangial division (tetrahedral in *Gloiocladia* versus cruciate in *Gloioderma*) and the shape of the cystocarp (coronate in *Gloioderma*). Irvine and Guiry (1986) questioned the distinctness between the two genera after finding cruciate tetrasporangia and coronate cystocarps in the type of *Gloiocladia*, *G.*

furcata (C. Ag) from the Mediterranean. Subsequently, Norris (1991) formally proposed the merger of *Gloioderma* in *Gloiocladia*.

Irvine and Guiry (1980) compared material of *Fauchea repens* with the illustration by Sparling (1957) of *Gloioderma saccatum* (J. Ag) Kylin and found that there was little difference between the subcortical network in both taxa. They agreed that the raised nemathecial sori found in *F. repens* may provide a more satisfactory basis to separate the two genera.

**Gloiocladia tenuissima* sp. nov.

Figures 32–40

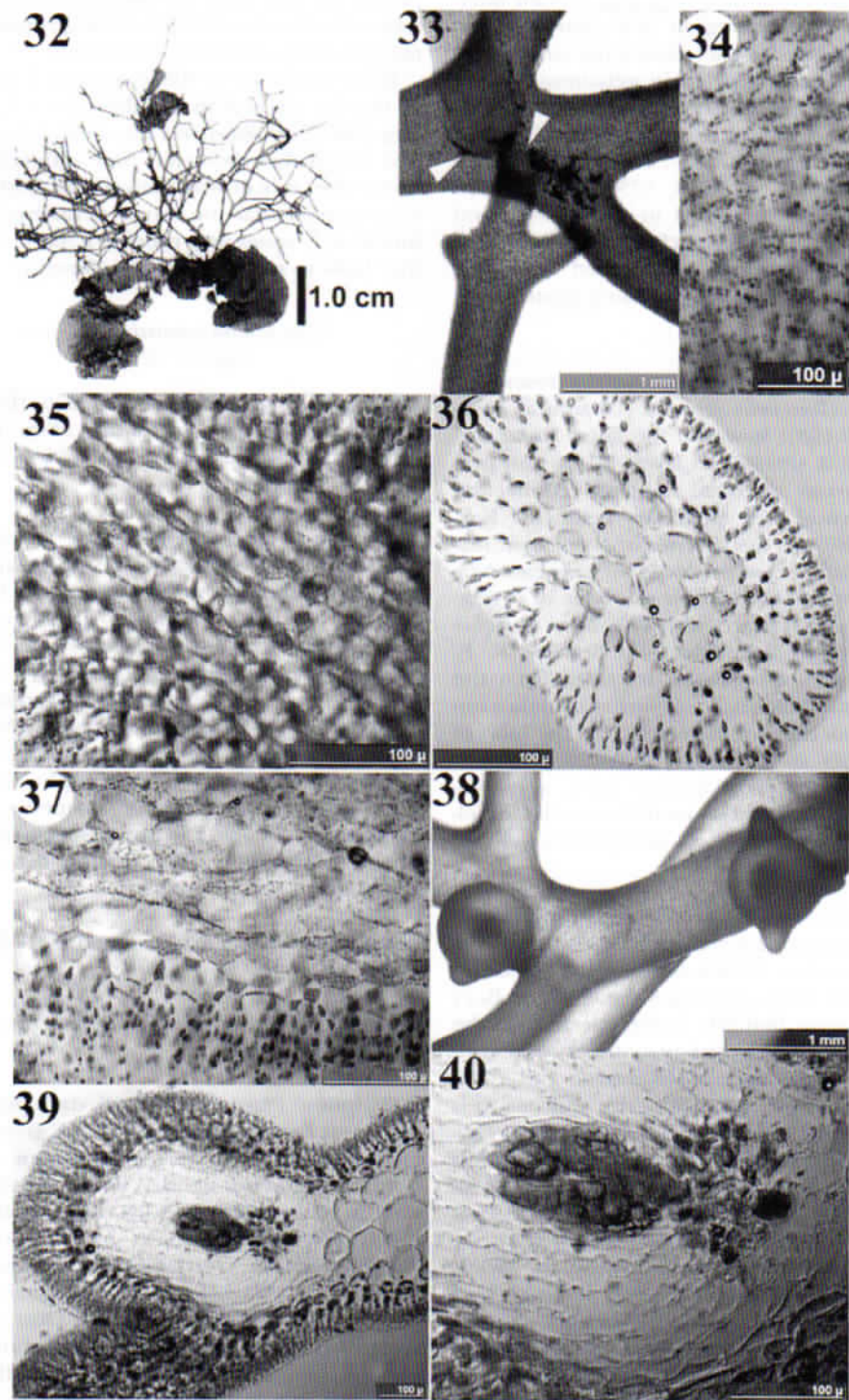
Holotype: #Algol. Coll. US-209076 (Fig. 33) dredged offshore Louisiana, 58-m depth, 28°05.561'N 91°02.205'W, attached to rubble (LAF-27-5-00-10-5).

Diagnosis: Plantae 3–4 cm altae, roseae, epiphyticae super *Peyssonnelia*, aut super parvis petris. Hapteron minimum, rami graciles, 0.2–0.5 mm lati maximo. Ramificatio irregularis, opposita, frequens. Rami anastomosantes. Cortex exteriore parvis cellulis elongatis, 3–6 × 8–13 μm . Stratum corticale interiore polygonalis cellulis, 8–14 × 16–22 μm , anostomosantibus parallelis ad paginam. Medulla constituta 2–3 stratis magnarum cellularum sphaerarum (22)35–40 × (35)45–60 μm diametro. Cystocarp marginali 535–720 μm diametro, cum vel sine 1–3 cornibus. Tela arachnoidea. Tetrasporangia et spermatangia non visa.

Additional specimens examined: LAF-26-5-00-4-13.

Etymology: The species epithet refers to its very slender habit.

Description: Plants 3–4 cm tall, dark pink, epiphytic on *Peyssonnelia* or saxicolous, growing attached to rubble by an inconspicuous discoid holdfast. Branches slender, terete, 0.2–0.5 mm wide in their widest portions (Fig. 32). Branching is irregularly alternate, and the branches are wider at fork. Overlapping branch portions tend to fuse with one another and anastomose mostly in a single plane (Fig. 33). Outer cortex composed of widely spaced anticlinal dichotomous filaments, each comprising small, elongate cells, 3–6 × 8–13 μm (Fig. 34). Inner cortex composed of larger, irregular cells 8–14 × 16–22 μm that cut off elongate secondary cells extending laterally (Fig. 37) toward apical region, run parallel to medullary filaments as seen in longitudinal section, and connect to



Figs. 32–40. *Gloiocladia tenuissima* sp. nov. 32. Habit of holotype specimen. 33. Surface view with overlapping branches anastomosing (arrows). 34. Surface view of thallus. 35. Longitudinal section through young branch showing regular pattern of elongate medullary cells connected to neighboring cells by means of slender secondary cells, and cortex. 36. Cross section through main branch showing multistratose medulla. 37. Longitudinal section through main branch showing subcortical cells laterally cutting off secondary cells.

neighboring cells by secondary pit connections. Medulla multistratose, comprising four to five colorless cells across (22)35–40 × (35)45–60 μm (Figs. 35–37). Entire thallus interior embedded within a gelatinous matrix. In young branchlets, the medullary cells are narrow, run longitudinally in the direction of thallus growth, and each produce fine tubular cells laterally and obliquely that connect with secondary pit connections to neighboring medullary cells (Fig. 35). In cross section, medullary cells of mature branches are obovate (Fig. 36).

Cystocarps, 535–720 μm in diameter, are globose and inserted at margin, mostly near branching forks (Fig. 38), with or without one to three hornlike projections. A prominent dome-shaped nutritive network develops at the base of the young carposporophyte (Figs. 39, 40). A *tela arachnoidea* occupies the larger portion of the elongate carposporophyte when young (Figs. 39, 40) and persists in older stages. All gonimoblasts become transformed into carposporangia. Tetrasporophytes and male gametophytes were not seen.

Remarks: The new taxon superficially resembles *G. furcata* (C. Ag.) J. Agardh (1842:87) the type species of the genus described from the Mediterranean; however, the Gulf taxon has a more sharply demarcated pericarp and a less elongate carposporophytic fusion cell than does *G. furcata* (see fig. 34 D-F in Womersley, 1996, p. 88).

Incertae Sedis

Leptofaucha Kylin, 1931:9

**Leptofaucha earleae* sp. nov.

Figures 41–48

Holotype: LAF-26-5-00-1-1 (To be deposited in Algol.Coll.US) (Fig. 41), offshore Louisiana, 55- to 65-m depth, 28°03.451'N 92°27.345'W.

Diagnosis: Plantae 2–3 cm altae, 6 cm latae, cum ramificationibus irregularis. Hapteron not observatum. Axis 5–6 ramosus dichotomus, cum apicibus obtusis. Rami anomostosantes. Thallus 100–130 μm crassus, cum uno strato corticale e parvis ellipticis cellulis, 4–9 (13) μm altis 4–5 (8) μm latis. Medulla e uno strato

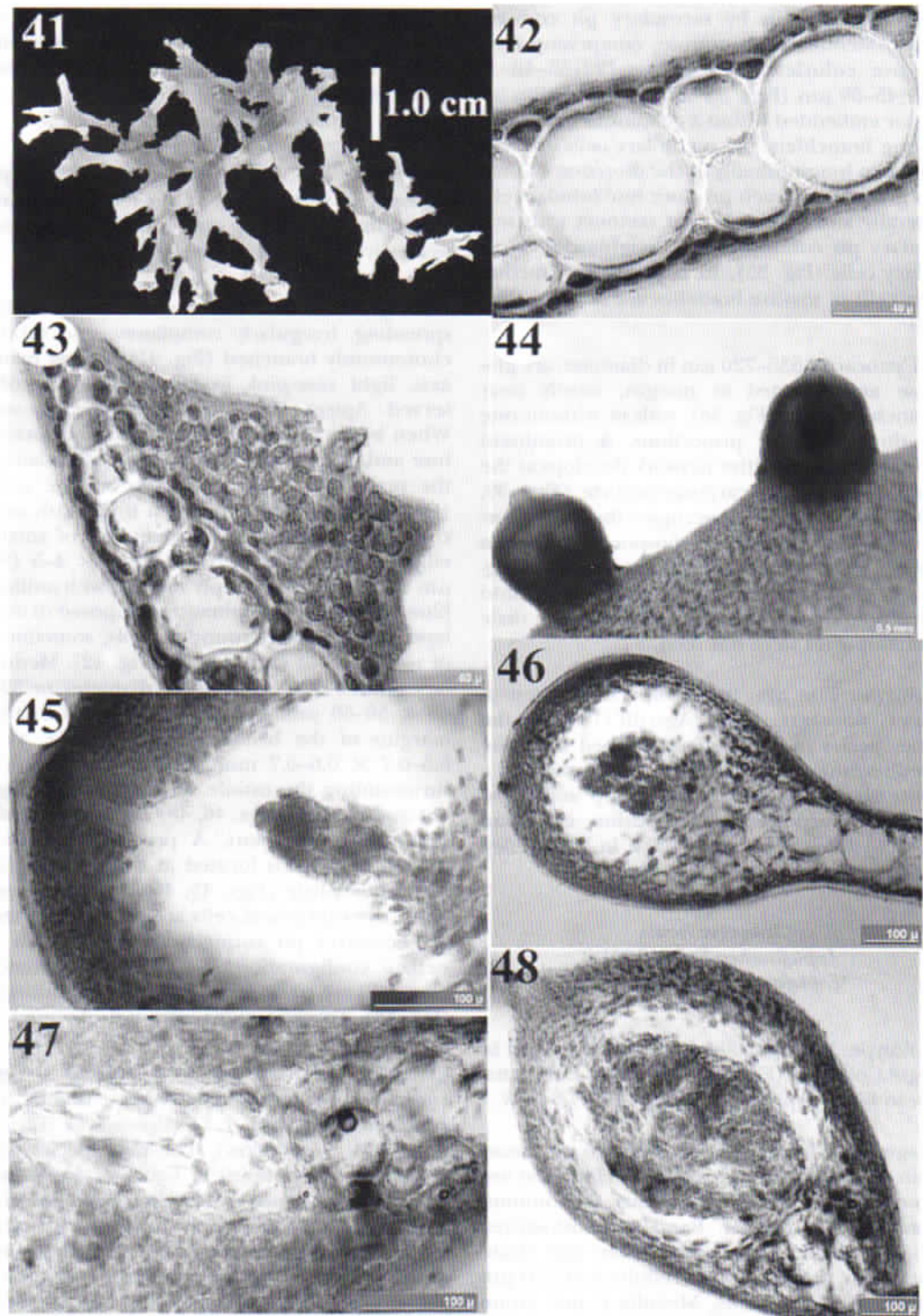
magnarum cellularum elongatarum 90–100 × 85–90 μm, aliquando e duo stratis parviorum cellularum 30–40 × 50–60 μm. Cystocarpia ad margines, 0.6–0.7 × 0.6–0.7 mm. Tela arachnoidea. Tetrasporangia non visa.

Etymology: The species epithet honors Dr. Sylvia Earle in recognition of her numerous contributions enhancing our knowledge of seaweed diversity in the Gulf of Mexico.

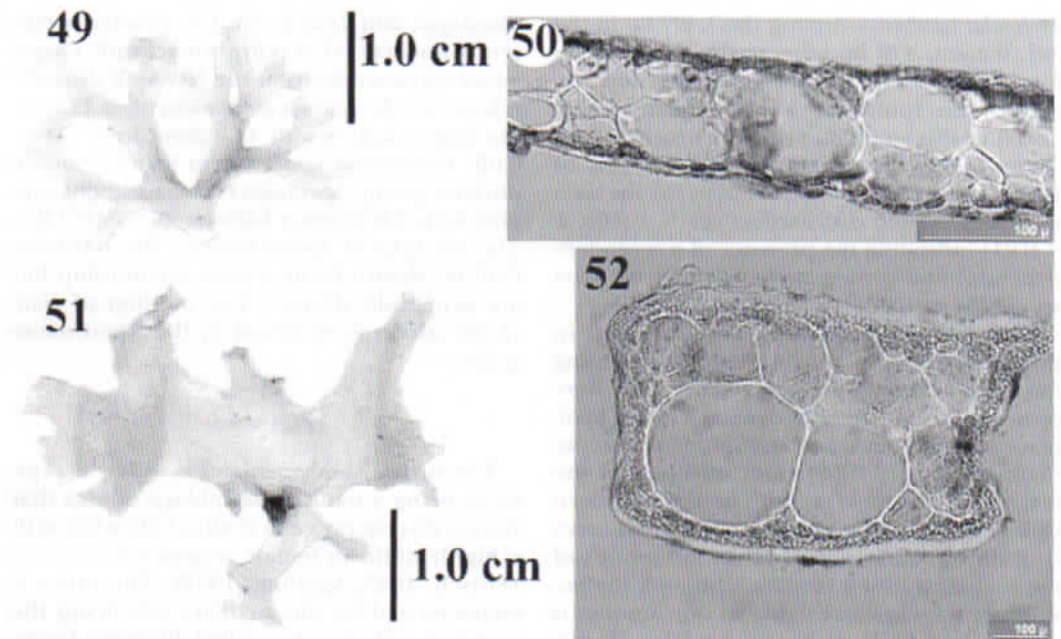
Description: Plants 2–3 cm tall, 6 cm wide, spreading, irregularly complanate and subdichotomously branched (Fig. 41) lacking main axis, light rose-pink in color. Stipe not observed. Apices of terminal branches obtuse. When blade portions overlap, they may locally fuse and anastomose in one plane, stimulating the proliferation of contiguous surface cells (Fig. 43). Thallus 100–130 μm thick, with one continuous cortical layer composed of small, elliptical cells, 4–9 (13) μm long, × 4–5 (8) μm thick (Fig. 42), deeply staining with aniline blue. Medulla predominantly composed of one layer of very large, roundish cells, sometimes of two layers of smaller cells (Fig. 42). Medullary cells 90–100 × 85–90 μm diameter, or 30–40 × 50–60 μm. Cystocarps restricted to the margins of the blades, numerous (Fig. 44), 0.6–0.7 × 0.6–0.7 mm, with a protuberance surmounting the ostiole. In both young (Fig. 45) and mature (Figs. 46, 48) cystocarps, a *tela arachnoidea* is absent. A prominent dome-shaped network is located at the base of the carposporophyte (Figs. 45, 46). In grazed sections, the subcortical cells are each connected by secondary pit connections resulting in a stellate configuration (Fig. 47). All gonimoblast cells are transformed into carposporangia (Fig. 48). Tetrasporangia were not observed.

Remarks: There are other two species of *Leptofaucha* recorded for the western Atlantic, *L. brasiliensis* Joly and *L. rhodymenioides* Taylor (1942:114) (see below). The new species differs from *L. brasiliensis* in habit. *L. brasiliensis* bears several ligulate axes, the branches are more or less dichotomous with constricted nodes and subspatulate terminal blades, and branches do not overlap or anastomose in one plane. *Leptofaucha rhodymenioides* has a dichot-

←
that connect to neighboring cells forming a network. 38. Surface view showing one- to three-horned cystocarps. 39. Cross section through young cystocarp showing a *tela arachnoidea* and darkly staining dome-shaped nutritive network at base of young carposporophyte. 40. Close-up of Fig. 39.



Figs. 41–48. *Leptofaucheia earleae* sp. nov. 41. Habit of holotype specimen. 42. Cross section through thallus showing monostromatic cortex and one to two layers of medullary cells. 43. Cross section through thallus showing stimulation of proliferating cortical cells as a result of anastomosing overlapping blade portions. 44. Surface view showing two cystocarps with protruding ostiole. 45. Cross section through young cystocarp showing prominent nutritive network at base of elongate carposporophyte, and lack of a *tela arachnoidea*. 46. Cross section through more mature cystocarp. 47. Grazed section below pericarp surface showing sub-cortical cells connected into a stellate configuration. 48. Cross section through mature cystocarp.



Figs. 49–50. *Leptofaucha rhodymenioides*. 49. Habit of sterile specimen. 50. Cross section through thallus showing monostromatic cortex and one to three medullary cell layers. Figs. 51–52. *Agardhinula browneae*. 51. Habit of sterile specimen. 52. Cross section through thallus.

omous branching pattern and a medulla composed of two to three cell layers, in contrast to the unistratose medullary layer of large cells, or of two layers of smaller cells but never three layers.

Leptofaucha rhodymenioides Taylor, 1942:114
Figures 49–50

Type locality: Aruba Island, Netherlands Antilles, deepwater.

Distribution: Netherlands Antilles (Taylor, 1960).

Specimens examined: Dredged offshore Louisiana, 95- to 155-m depth, 27°53.561'N 91°21.532'W (LAF-27-5-00-9-3).

Remarks: The unistratose cortex of this sterile specimen indicates it clearly belongs in *Leptofaucha*. This species was recorded from the Flower Garden Banks by Rezak et al. (1985). This is the first illustration of this species for the Gulf of Mexico.

Agardhinula browneae (J. Agardh) De Toni,
1897:64
Figures 51–52

Basionym: *Callophyllis browneae* J. Agardh, 1885: 36

Type locality: North Carolina or Florida (Taylor, 1928).

Distribution: North Carolina, South Carolina (Schneider and Searles, 1991), Florida (Taylor, 1960; D. S. Littler and M. M. Littler, 2002), and Lesser Antilles (D. S. Littler and M. M. Littler, 2002).

Specimen examined: Offshore Louisiana.

Remarks: The Gulf specimen is more broadly palmate than the specimen from offshore North Carolina illustrated by Schneider and Searles (1991). The medulla is similar to that of *Asteromenia* (as *Halichrysis*) with smaller cells regularly interspersed among the larger cells (Taylor, 1960). Additional material is needed for further study.

This is the first report of the monotypic genus in the northern Gulf of Mexico.

Molecular analysis.—Among the 1,407 bp in the *rbdL* dataset, 479 bp were phylogenetically informative (34%). No insertion or deletion mutations were found in the *rbdL* sequences produced in this study, allowing for unambiguous alignment of all sequences. Tree lengths of 100,000 randomly generated trees for the data set had a skewed distribution ($g1 = -0.68$, $P < 0.01$) indicating the presence of nonrandom structures and phylogenetic signal in the data set (Hillis and Huelsenbeck, 1992).

Forty-five *rbdL* sequences were included in this study, for a total of 41 taxa representing the four currently accepted families of Rhodymeniales, i.e., the Rhodymeniaceae, Champiaceae, Faucheaceae, and Lomentariaceae (Saunders et al., 1999), with members of the first three families present in the northern Gulf of Mexico. The MP (Fig. 53) and ML trees (not shown) each recovered the monophyly of the four established families, although the position of the families relative to one another is not resolved. Two *incertae sedis* are the *Fryeella/Hymenocladopsis* clade and *Leptofauchea*. The phylogenetic placement of these taxa is not resolved.

The MP produced 1,126 equally most parsimonious trees (MPT) of 2,316 steps, $CI = 0.3143$, $RI = 0.5887$, with one of the MPT shown in Fig. 52. The MP (Fig. 53) and ML (not shown) phylogenies differed from each other in the position of *Fryeella* and *Hymenocladopsis*, a strongly supported clade but allied without bootstrap support to either the Faucheaceae (MP) or the Champiaceae (ML). The Rhodymeniaceae is moderately supported in the MP tree ($BP = 72$), the Champiaceae is strongly supported ($BP = 99$), the Faucheaceae forms a monophyletic clade without support, and the Lomentariaceae is highly supported ($BP = 96$).

The Lomentariaceae comprises *Lomentaria* and *Gelidiopsis*. *Leptofauchea earleae* is basal to the Lomentariaceae with moderate support ($BP = 68$). The Faucheaceae is represented by *Fauchea* and *Gloiocladia*. The NW Gulf *Gloiocladia pelicana* clusters weakly with the two NE Pacific *Fauchea* species. The family also consists of *G. tenuissima* from the NW Gulf that is sister to *G. iyoensis* of E Australia. *Gloiocladia saccata* from New Zealand is also included in this assemblage. The topological relationship among the species is equivocal. The Champiaceae is represented by *Champia* and *Gastroclonium*. *Champia lumbricalis* from South Africa is basal to the three northern Gulf *Champia* species. The Rhodymeniaceae is represented by *Rhodymenia*, *Botryocladia*, *Chrysomenia*, *Coelarthrum*,

Sparlingia, and *Halychrysis*. *Chrysomenia* as currently understood is polyphyletic, with *Chrysomenia halymenioides* from the NW Gulf distantly related to *Chrysomenia procumbens* from Taiwan; the latter clusters with *C. cliftonii* from the N Gulf. *Rhodymenia sensu stricto* forms a monophyletic group. *Sparlingia* clusters without support with *Chrysomenia halymenioides* (MP, ML). The six taxa of *Botryocladia* in the northern Gulf of Mexico form a close relationship but are genetically distinct. The position of *Halychrysis micans* is equivocal in the Rhodymeniaceae.

DISCUSSION

The order Rhodymeniales is widely accepted as being a natural assemblage of taxa that show a diverse range in thallus habits but with a highly uniform female reproductive system (Fritsch, 1945; Sparling, 1957). The order is characterized by the auxiliary cell being the terminal cell of a two-celled filament borne on the supporting cell of a three- to four-celled carpogonial branch in a procarpic arrangement. The transfer of the diploid nucleus from the fertilized carpogonium to the auxiliary cell is mediated by a connecting cell (Sparling, 1957). The order, as originally proposed by Schmitz (1889), included a heterogeneous assemblage of genera with six families. With the subsequent removal of the Delesseriaceae, Rhodomelaceae, and Ceramiaceae from the Rhodymeniales and their transfer to a new order Ceramiales (Oltmanns, 1904) and the removal of the Sphaerococcaceae and its transfer to the new order Sphaerococcales (Sjöstedt, 1926), the Rhodymeniaceae was the only family left in the Rhodymeniales. Schmitz (1889) earlier had divided the Rhodymeniaceae into the *Gloiocladia* and *Rhodymenia*, on the basis of presence or absence of, respectively, a *tela arachnoidea*, a distinctive network of cobweblike filaments surrounding mature carposporophytes in cystocarps of the species under study.

Bliding (1928) considered presence or absence of a *tela arachnoidea* artificial and split from the Rhodymeniaceae Harvey an additional family, the Champiaceae. The main taxonomic character separating these two families, still accepted today, is that in the Champiaceae, most or part of the thallus is hollow and longitudinal filaments border the thallus cavity; in contrast, members of the Rhodymeniaceae are either solid or hollow in construction, but if hollow, they always lack longitudinal filaments. Kylin (1931) acknowledged

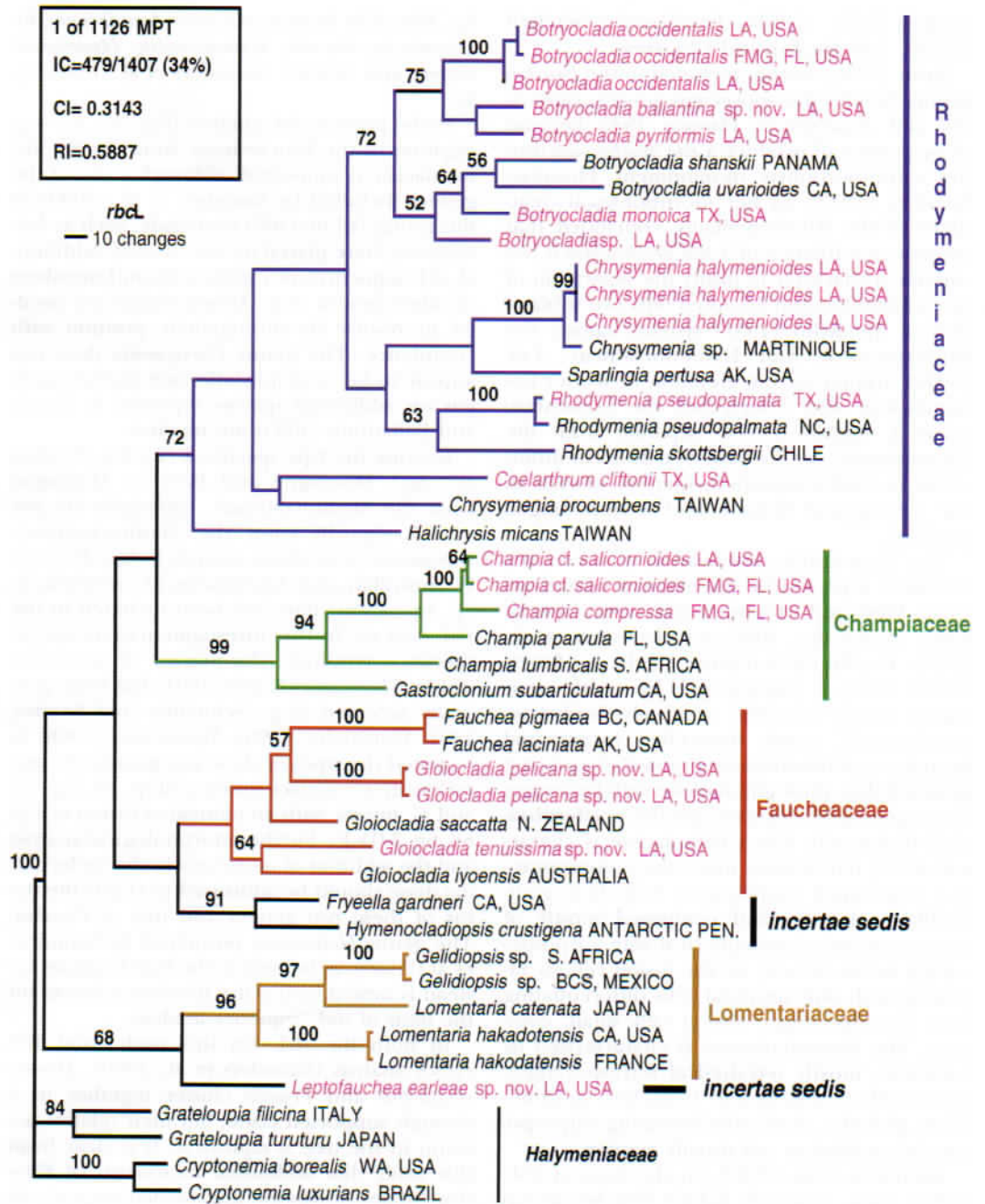


Fig. 53. One of 1,126 equally parsimonious *rbdL* trees. In pink are the taxa from the Northern Gulf of Mexico. The four currently recognized families of Rhodymeniales are highlighted in different colors. Bootstrap proportion values >50% are shown at the nodes.

Schmitz's (1889) findings of the taxonomic significance of a *tela arachnoidea* and subsequently subdivided the Rhodymeniaceae into the Faucheae and Rhodymeniaceae, the Faucheae being equivalent to Schmitz's Gloiocladieae (Sparling, 1957). The elusive Australian and New

Zealand genus *Hymenocladia* J. Agardh (1852) was placed in a third subfamily, the Hymenocladieae, on the basis of tetrahedral tetrasporangia and absence of a *tela arachnoidea*. Kylin (1931) grouped with *Fauchea* the genera *Binderia* (now *Webervanbossea* J. De Toni 1936), *Fau-*

cheopsis Kylin (1931), *Faucheocolax* Setchell (1923), *Leptofaucha*, and *Gloioderma*.

Kylin (1956) further included in the *Faucha* group, besides the above-cited genera, *Gloiocladia* and *Sciadophycus* Dawson 1945 because these genera all produce a *tela arachnoidea* during carposporophyte development. However, Sparling (1957), in her morphological treatment of the Rhodymeniales, concluded that presence or absence of a *tela arachnoidea* is too variable a character to justify the separation of two subfamilies and accepted only two subfamilies of the Kylin (1931) system, namely the Rhodymenieae and Hymenocladieae. Lee (1978) argued for the elevation of Kylin's Lomentariaceae and resurrected the Lomentariaceae J. Agardh (1876) separate from the Champiaceae, on the basis of consistent differences in thallus septation, number of cells in the carpogonial branch, and tetrasporangial position.

The three-family classification until recently has been accepted by the majority of authors (e.g., West and Hommersand, 1981; Norris, 1987; Womersley, 1996; see Saunders et al., 1999). The Rhodymeniaceae, the largest family in the order, is characterized by mostly intercalary (rarely terminal) cruciately divided tetrasporangia; mostly four-celled carpogonial branches; gonimoblasts composed of compact gonimolobes, most gonimolobe cells becoming carposporangia; elongate, slender postfertilization fusion cell. The Champiaceae is characterized by tetrahedral, intercalary tetrasporangia; four-celled carpogonial branches; gonimoblasts globular and composed mostly of carposporangia, hemispherical with carposporangia borne directly on the fusion cell, or radiating with only terminal cells differentiating into carposporangia; fusion cell small, compact. The Lomentariaceae is characterized by terminal, mostly tetrahedral tetrasporangia; three-celled carpogonial branches; gonimoblasts globular, most cells becoming carposporangia; and fusion cell usually massive.

Saunders et al. (1999) on the basis of SSU rDNA data, removed Kylin's *Faucha* group from the Rhodymeniaceae to a new family, the Faucheaceae, on the basis of thalli with either solid, pseudoparenchymatous, or hollow medulla; a small-celled, thin, deep, and anticlinal cortex; terminal, cruciately divided tetrasporangia; three-celled carpogonial branches; gonimoblasts globular with most cells becoming carposporangia, and narrow fusion cells. They included in this family all the genera Kylin had incorporated in his *Faucha* group, plus *Cenacrum*, *Halichrysis*, *Gloiodermatopsis*, and *Gloioco-*

lax. Placed in *incertae sedis* were *Agardhinula*, *Erythrymenia*, *Fryeella*, *Hymenocladia*, *Hymenocladidiopsis*, and *Minium* (Saunders et al., 1999, fig. 1).

In the present *rbcl* analysis (Fig. 53), the segregation of the Faucheaceae from the Rhodymeniaceae is supported, although some of the genera included by Saunders et al. (1999) in this group fall in a different clade, such as *Leptofaucha*, here placed in *incertae sedis*. Additional *rbcl* sequences of *Leptofaucha* and members of other genera (e.g., *Hymenocladia*) are needed to resolve its phylogenetic position with confidence. The genus *Chrysymenia* does not appear to be monophyletic, and further analysis on additional species reported in Norris and Ballantine (1995) are needed.

Because the type species of *Faucha* (*F. repens* (C. Ag.) Montagne and Bory in Montagne from the Mediterranean), *Gloiocladia* (*G. furcata* J. Agardh from the Mediterranean), *Gloioderma* (*Gloioderma australe* J. Agardh from W. Australia), and *Leptofaucha* (*L. nitophylloides* (J. Ag.) Kylin) have not been included in the *rbcl* data set, further investigation of these type species is required. The merger of *Gloioderma* within *Gloiocladia* (Norris, 1991) has been generally accepted (e.g., Schneider and Searles, 1991; Womersley, 1996). Womersley (1996) illustrated the types of these two genera (*G. australe* with a compact fusion cell, p. 98, fig. 39, and *G. furcata*, with an elongated fusion cell p. 88, fig. 34D-F). Further morphological analysis and the addition of more taxa in the molecular database should be addressed to clarify the status of these two genera and that of *Faucha*. The genus *Halichrysis*, postulated by Saunders et al. (1999) to belong in the Faucheaceae, instead is nested within the Rhodymeniaceae on the basis of *rbcl* sequence analysis.

In both the *rbcl* (in this study) and 18S rDNA analysis (Saunders et al., 1999), *Hymenocladidiopsis* and *Fryeella* cluster together in a strongly supported clade, but their relative position in the tree is equivocal. It is clear from this study that additional treatments of Rhodymeniales worldwide are needed urgently to fully understand the evolutionary histories and phylogenetic relationships of the various groups.

Biogeographic patterns can be determined by the abundance of species assemblages rather than presence and absence or percent endemism (Adey and Steneck, 2001). With regard to the assemblage of Rhodymeniales offshore the northern Gulf of Mexico, the great number of species belonging to the Rhodymeniales may shed light on their distribution

histories and establishment in the Gulf. The biogeography of the benthic algae from the Gulf of Mexico cannot be separated from that of Atlantic Ocean. A large component of the northern Atlantic red algal flora has special affinities with the algae of the Indo-West Pacific, especially the temperate algae of the Southeastern Pacific, with often the most primitive elements generally conserved in the northern Atlantic (Hommersand, 1990). Hommersand (1990) argued that taxa belonging to this floristic assemblage evolved along a gradient extending from western Europe to Australia, and he later postulated (Hommersand, 2005) that for a phylogenetic line to be identified as a component of a Tethyan flora, it should contain elements in the Indian Ocean, western Europe, and the Mediterranean Sea, with related taxa also commonly occurring in the western Atlantic Ocean and Caribbean Sea and in certain tropical and warm-temperate regions along North and South America; in some instances, there may be a disjunct distribution, with species in Europe and warm-temperate Pacific North America that are presently absent in the western Atlantic Ocean. The *Faucheaceae* is very likely a family having a disjunct Tethyan distribution between the eastern Atlantic and the eastern Pacific Oceans: the sister species of the two new species occur in the Austral Indo-west Pacific and NE Atlantic with extended distribution in the western Atlantic, Gulf of Mexico, and eastern Pacific Oceans (see *AlgaeBase*, Guiry and Nic Dhonncha, 2002 for the distribution of taxa.) *Faucheia* is represented in the NE Pacific (e.g., Hawkes and Scagel, 1986). On the Atlantic North Carolina shelf, three species of *Gloiocladia* were recently described [*G. atlantica* (Searles) R.E. Norris, *G. blomquistii* (Searles) R.E. Norris and *G. rubrispora* (Searles) R.E. Norris] (Searles, 1972, 1984b; Searles in Schneider and Searles, 1975). The type species of *Gloiocladia*, *G. furcata* is from the Mediterranean; *G. australe* is present in Australia (Womersley, 1996), *G. iyoensis* inhabits the waters of southern Japan, Hawaii, French Polynesia, E. Australia, and Natal-South Africa (Norris, 1991), and *G. japonica* is found in southern Japan (Yoshida, 1997). The extant presence of species of *Gloiocladia* in the tropical western Atlantic (Caribbean) and Indo-West Pacific Oceans suggests an adaptation to the environment of the modern tropics, as has been reported for the Solieriaceae (Hommersand, 1990; Hommersand and Fredericq, 2003; Fredericq et al., 1999). *RbdL* sequence data documented a Tethyan distribution for the Solieriaceae with representatives in the Indo-West

Pacific, Atlantic, and eastern Pacific Oceans (Fredericq et al., 1999).

A different biogeographic scenario could explain the extant distribution of *Coelarthrum*, *Asteromenia*, and *Halichrysis* in the northern Gulf of Mexico. *Coelarthrum* and *Asteromenia* contain a single, widely distributed tropical species, and *Halichrysis* (*Weberella*) currently includes five tropical species. A major pathway from Australia to the east coast of South Africa via the North Indian Ocean and from there to the Atlantic Ocean (Hommersand, 1990; Hommersand and Fredericq, 2003) and into the northern Gulf of Mexico could explain the distribution of representative species of these genera in the Gulf. The inclusion of additional *rbdL* sequences of taxa from the Gulf of Mexico and of representative algae worldwide, coupled with detailed taxonomic studies of the generatypes, will further clarify the evolutionary history and establishment of the Rhodymeniales in the Gulf of Mexico.

CONCLUSIONS

The algal species collected by means of SCUBA from SCUBA-diving depths at 25- to 35-m depth of offshore hard banks (~25- to 30-m depth) in the northern Gulf of Mexico are typically small, cryptic, and intermixed, forming small turfs or extensive mats. In contrast, macroalgae dredged offshore from 40- to 90-m depth are free standing, leafy, and large (up to 20 cm), with many newly reported for the region and some new to science. Contrary to the generally accepted notion that the northern Gulf of Mexico is poor in macroalgal diversity compared with the rich flora of the Caribbean, the deep banks of the northern Gulf harbor a remarkably diverse and species-rich benthic flora, especially comprising members of the Rhodymeniales.

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