

NOTE

LOW MOLECULAR WEIGHT CARBOHYDRATES OF THE
BANGIOPHYCIDAE (RHODOPHYTA)¹

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In the order Porphyridiales there are three clades based on molecular evidence. These show parallels with the low molecular weight carbohydrate (LMWCs) in different genera. Clade Porphyridiales 1 includes *Dixoniella*, *Glaucosphaera*, *Rhodella*, and one undescribed genus (3987) that all contain mannitol. Clade Porphyridiales 2 comprises taxa of the Stytonematales *Rhodorus* and *Stylonema* species and contains digeneaside and sorbitol, whereas *Chroodactylon* has only sorbitol. In clade Porphyridiales 3 *Flintiella*, *Porphyridium*, and the undescribed genus (3797) all possess only floridoside. In the Erythropeltiales *Rhodochaete* contains floridoside and digeneaside, *Erythrotrichia* species contain only floridoside, *Sahlingia subintegra* has floridoside and traces of D-floridoside, and *Smithora* has L-isofloridoside plus floridoside. In the Compsopogonales *Boldia* and *Compsopogon* have only floridoside. Within these genera as presently circumscribed, the LMWCs appear to be a reliable character to supplement the usual cytological characters.

Key index words: Bangiophycidae; chemotaxonomy; digeneaside; dulcitol; floridoside; mannitol; sorbitol

Abbreviation: LMWC, low molecular weight carbohydrate

Various carbohydrates have been used for many years as distinctive biochemical characters in various algal groups (Lobban and Harrison 1994, Graham and Wilcox 1999). In our previous publication (Karsten et al. 1999) we presented qualitative and quantitative data on the low molecular weight carbohydrates (LMWCs) of 22 different species of the red algal subclass Bangiophycidae. Several interesting differences and similarities were evident in the LMWCs among the representatives of the Porphyridiales, Compsopogonales, and Erythropeltiales. The Bangiales (*Porphyra* and *Bangia*) all showed a uniform pattern of floridoside, D-isofloridoside, and L-isofloridoside. Extensive DNA molecular phylogeny research has been carried out recently, and this has clarified the placement of many genera and species in distinct clades of the Bangiophycidae (Hara et al. 2000, Zuccarello et al. 2000, Müller et al. 2001). Here we provide further information on additional isolates of the Bangiophycidae genera and species.

The algal materials used for analyses are listed in Table 1. Most isolates were grown using culture methods similar to those used in the previous research (Karsten et al. 1999). However, *Glaucosphaera* was cultured in Peat Medium (960 mL Milli-Q water [Millipore, Billerica, MA, USA], 20 mL peat extract, 10 mL 30 psu seawater, 10 mL modified Provasoli's medium [West and McBride 1999] all combined and steam-sterilized for 1 h). Peat extract was prepared by heating (90° C) 15 g commercial peat in 500 mL Milli-Q water for 1 h. This was filtered with Whatman No. 1 paper (Whatman, Spring Mill, UK) to yield a clear dark brown liquid that was presterilized and stored at

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TABLE 1. Sources of specimens analyzed.

Order and species	Habitat or culture	Culture no.	Locality and date of collection
Porphyridiales			
<i>Flintiella sanguinaria</i> Ott	Marine culture 30 psu	3629	UTEX 2060, F. Ott,
<i>Glaucosphaera vacuolata</i> Korshikov	Peat medium	3927	UTEX 1662
<i>Porphyridium</i> sp.	Marine culture 30 psu	3827	Mud sample, West Gate Bridge, Port Phillip Bay, Victoria, Australia, 11 ii 1998
<i>Porphyridium</i> sp.	Marine culture 30 psu	3904	On <i>Caloglossa lepieurii</i> , Tewantin, Queensland, Australia, 25 vii 1998
<i>Rhodella cyanea</i> Fresnel et Billard	Marine culture 30 psu	4072	Type culture, from Menton, Alpes Maritimes, France, August 1980, provided by J. Fresnel
<i>Rhodella cyanea</i>	Marine culture 30 psu	3988	Tobishima strain, Tobishima Island, Yamagata, Japan, 7 iv 1997
<i>Rhodella</i> sp.	Marine culture 30 psu	3990	Nagura 1 strain, Nagura River, Ishigaki Island, Okinawa, Japan, date unknown
<i>Rhodella</i> sp.	Marine culture 30 psu	3989	Gamou T4 strain, Gamou Tideland, Miyagi, Japan, 24 iii 1997
Undescribed genus	Marine culture 30 psu	3797	Yacura I., Cuvu Bay, Viti Levu, Fiji, 6 vi 1997
Undescribed genus	Marine culture 30 psu	3987	A. Yokoyama
Stylonematales			
<i>Chroodactylon ornatum</i> (C. Agardh) Basson	Marine culture 30 psu	3862	On <i>Murrayella pericladus</i> , Olango I., Cebu, The Philippines, 15 iv 1998
<i>Rhodosorus magnei</i> Fresnel et Billard	Marine culture 30 psu	4016	RHO 8, Magne, The French Antilles, Caribbean, date unknown
<i>Rhodosorus marinus</i> Geitler	Marine culture 30 psu	3607	UTEX 1723, on coral fragments, Coconut Island, Oahu, Hawaii, USA, iv 1960
<i>Rhodosorus marinus</i>	Marine culture 30 psu	4014	RHO 1, Fresnel, Lattaquié, Syria, date unknown
<i>Rhodosorus marinus</i>	Marine culture 30 psu	4015	RHO 1 bis, Fresnel, Calvi, Corsica, date unknown
<i>Rhodosorus marinus</i>	Marine culture 30 psu	4023	Gengaoakawa R. 212 strain, Gengaoakawa, Okinawa, Japan, date unknown
<i>Rhodosorus sordida</i>	Marine culture 30 psu	3628	UTEX 2616, from sandstone rock, Shelter Cave, Blanchard Spring State Park, near Mountain View, AR-USA, 25 × 1977; isolated by F.D. Ott
<i>Stylonema alsidii</i> (Zanardini) K. Drew	Marine culture 30 psu	3480	On Spermiothamnion, Williamstown, Victoria, Australia, 15 iii 1995
<i>Stylonema alsidii</i>	Marine culture 30 psu	3610	UTEX 1424, isolated by F.D. Ott, MO-110
<i>Stylonema alsidii</i>	Marine culture 30 psu	3784	UTEX, 1689, isolated by J. Ramus, Moss Beach, California, USA, as <i>Goniotrichopsis sublittoralis</i> , 1964.
<i>Stylonema alsidii</i>	Marine culture 30 psu	3789	UTEX 2204, on jetty, Port Aransas, Texas, USA, 27 vi 1979, Isolated by B. Baca
<i>Stylonema alsidii</i>	Marine culture 30 psu	4051	Brodie 140, on hydroid, Lizard, Cornwall, England, 31 vii 1994
<i>Stylonema alsidii</i>	Marine culture 30 psu	4052	Brodie 152, Lizard, Cornwall, England, 30 vii 1994
<i>Stylonema alsidii</i>	Marine culture 30 psu	4053	Brodie 155, on bryozoan, Bognor, Devon, England, ix 1994
<i>Stylonema alsidii</i>	Marine culture 30 psu	4055	Brodie 206, on hydroid, Sketch Pole Head, Pembrokeshire, England, 18 vi 1997
<i>Stylonema cornu-cervii</i> Reinsch	Marine culture 30 psu	3505	On <i>Padina</i> , Cooks Bay, Moorea, French Polynesia, 7 vii 1995
Compsopogonales			
<i>Boldia erythrosiphon</i> Herndon	Field		
<i>Compsopogon coeruleus</i> (Balbis) Mont	Marine culture 5 psu	3152	On <i>Bostrychia moritziana</i> , Rio Cariaco, Edo Sucre, Venezuela, 10 iv 1991
<i>Compsopogon coeruleus</i>	Marine culture 5 psu	3479	On rock, Framingham, Hopkins River, Victoria, Australia, 25 iii 1995
Erythropeletiales			
<i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh	Marine culture 30 psu	4050	Brodie 115, Blackhead, Co. Clare, Ireland, 20 viii 1993
<i>Erythrotrichia carnea</i>	Marine culture 30 psu	4054	Brodie 200, Langstone Harbour, Portsmouth, England, 26 vi 1997
<i>Erythrotrichia carnea</i>	Marine culture 30 psu	4056	Brodie 209, on <i>Osmundea pinnatifida</i> , Port Eryon, Gower, Wales, 5 viii 1997
<i>Erythrotrichia</i> sp.	Marine culture 30 psu	4057	Brodie 212, on <i>Ceramium</i> , Port Eryon, Gower, Wales, Britain, 5 viii 1997
<i>Erythrotrichia foliiformis</i> South et Adams	Marine culture 30 psu	4058	On <i>Sargassum</i> , Bare I., New South Wales, Australia, 29 vii 1998

continued

TABLE 1. (continued).

Order and species	Habitat or culture	Culture no.	Locality and date of collection
<i>Porphyropsis coccinea</i> (Areschoug) Rosenvinge	Marine culture 30 psu	4073	Brodie 243, North Porth Calmon, Lley Peninsula, Wales, 2viii 1998
<i>Rhodochaete parvula</i> Thuret	Marine culture 30 psu	3924	On <i>Palmophyllum</i> sp., Point Lonsdale, Victoria, Australia, 10 xi 2998
<i>Sahlvingia subintegra</i> (Rosenvinge) Kornmann	Marine culture 30 psu	4059	On <i>Gelidium ceramoides</i> , Tirohanga, Nugget Point, SE Otago, S. Island, NZ. 46°26'S, 169°47.5'E, collected 26.x.1999 by J.E. Broom, T.J. Farr, W.A. Nelson
<i>Smithora naiadum</i> (Anderson) Hollenberg	Field, intertidal		On <i>Phyllospadix</i> , Pigeon Point, Santa Cruz Co, California, USA, 20 xi 1998

4° C. Carbohydrate analytical methods (¹³C-NMR, GLC, HPLC) are also as indicated in Karsten et al. (1992a, 1999). The LMWC data are shown in Figure 2.

In the subclass Florideophycidae, two general groups of LMWC chemistry are evident (Kremer 1980). In most orders floridoside is found and in most Ceramiales digeneaside is present, although certain exceptions are known: 1) in the subfamily Bostrychioideae (Rhodomelaceae) with the genera *Bostrychia* and *Stictosiphonia* sorbitol and dulcitol are present but digeneaside is absent (Karsten et al. 1992a, 1995); 2) in *Laurencia* (Rhodomelaceae) floridoside is present but digeneaside absent (Barrow et al. 1995); and 3) in *Caloglossa* (Delesseriaceae) mannitol and digeneaside are present (Karsten et al. 1992b, 1994).

In the subclass Bangiophycidae the order Porphyridiales is comprised of a very heterogeneous taxonomic assemblage. Although the molecular phylogeny data of Hara et al. (2000) and Müller et al. (2001) do not show the same number of clades, both authors defined at least three separate clades in this order consisting of identical species. The LMWCs are also diverse, although they are generally consistent within genera and species (Karsten et al. 1999).

Clade L-1 (Hara et al. 2000) contains the acid hot spring genera *Cyanidium* and *Galdieria* but is now properly placed in the subclass Cyanidiophyceae. We have not analyzed these taxa.

Clade L-2 of Hara et al. (2000) (Porphyridiales 2 [Stylonematales] of Müller et al. [2001]) includes the filamentous genera *Bangiopsis*, *Chroodactylon*, and *Stylonema* and the unicellular genera *Rhodosorus* and *Rhodospira*. *Rhodospira sordida* (3628) is surprising because it contains only sorbitol and dulcitol. The only other red algae that contain both these compounds are *Bostrychia* and *Stictosiphonia* of the family Rhodomelaceae (subfamily Bostrychioideae), order Ceramiales (Karsten et al. 1992a, 1995). Because this is so strikingly unique to this isolate, we cultured the same isolate independently in two different laboratories under different conditions to verify the results. West grew the isolate at 22–26° C, 15–20 μmol photons·m⁻²·s⁻¹ cool white fluorescent lighting on a Brunswick model G2 rotary shaker (New Brunswick Scientific Co., Edison, NJ, USA) at about 70 rpm, 12:12-h light:dark photoperiod, in

Pyrex (no. 3250, Corning Inc., Acton, MA, USA) 500 mL storage dishes containing approximately 250 mL of modified Provasali medium (MPM/2, 10 mL enrichment per liter of seawater; West and McBride 1999). Yokoyama grew the isolate at 20° C, 20 μmol photons·m⁻²·s⁻¹ cool white fluorescent lighting, 12:12-h light:dark photoperiod, in a Pyrex 5-L flask containing approximately 1 L of modified ESM medium (Okachi et al. 1982) with 20 mL soil water per liter prepared with 10% seawater and 90% freshwater. Under both sets of conditions the only LMWCs detected in *R. sordida* were sorbitol and dulcitol.

Among the filamentous forms investigated here, *Chroodactylon ornatum* (3862) contains sorbitol as does *C. ornatum* (2903) (Karsten et al. 1999). However, *Stylonema alsidii* isolates (3610, 3789, 3784, 4051, 4052, 4053, and 4055) from diverse localities (Florida, California, Texas, and England) all contained digeneaside and sorbitol, which contrasts sharply with our previous data (Karsten et al. 1999) on *S. alsidii* (3480 from Victoria, Australia) and *S. cornu-cervi* (3505 from Moorea, French Polynesia), both of which contained floridoside, D-isofloridoside, digeneaside, and sorbitol. For this new investigation the reanalysis of the original air-dried sample of 3480 revealed only floridoside and digeneaside, whereas the reanalysis of 3505 sample revealed only digeneaside and sorbitol. Unfortunately, these two cultures were lost when a growth cabinet overheated in 1997. *Stylonema alsidii* 3480 may be reisolated from the localities around Williamstown, Victoria to determine if this is a unique population that is perhaps a different genus or if there was possibly an error in original sample preparation. The reanalysis of 3505 shows that it is consistent with all other *Stylonema* isolates, indicating that the first analysis showing the presence of floridoside and D-isofloridoside was probably in error. It may not be possible to reisolate a new strain from French Polynesia because of time and cost.

Rhodosorus marinus (3607, 4014, 4015, and 4023) from diverse localities in Florida (USA), Syria, France, and Japan as well as *R. magnei* (4016) from The French Antilles (Caribbean) all contained both digeneaside and sorbitol (Table 2). These data are identical to our previous results obtained with *R. marinus* (3608) from

TABLE 2. LMWC patterns of different members of the Bangiophycidae as detected by ¹³C-NMR spectroscopy.

Species	L-isofloridoside	Floridoside	Digeneaside	Mannitol	Sorbitol	Dulcitol	Total
Porphyridiales							
<i>Flintiella sanguinaria</i>	3629 n.t.	37.2 ± 9.8	n.t.	n.t.	n.t.	n.t.	37.2
<i>Glaucosphaera vacuolata</i>	3927 n.t.	n.t.	???	n.t.	n.t.	n.t.	
<i>Porphyridium</i> sp.	3827 n.t.	111.8 ± 5.2	n.t.	n.t.	n.t.	n.t.	111.8
<i>Porphyridium</i> sp.	3904 n.t.	94.6 ± 4.3	n.t.	n.t.	n.t.	n.t.	94.6
<i>Rhodella cyanea</i>	4072 n.t.	n.t.	n.t.	400.3 ± 30.1	n.t.	n.t.	400.3
<i>Rhodella cyanea</i>	3988 n.t.	n.t.	n.t.	86.9 ± 5.7	n.t.	n.t.	86.9
<i>Rhodella</i> sp.	3990 n.t.	n.t.	n.t.	286.4 ± 48.3	n.t.	n.t.	286.4
<i>Rhodella</i> sp.	3989 n.t.	n.t.	n.t.	194.6 ± 1.4	n.t.	n.t.	194.6
Undescribed genus	3987 n.t.	n.t.	n.t.	140.2 ± 40.7	n.t.	n.t.	140.2
Undescribed genus	3797 n.t.	280.9 ± 10.1	n.t.	n.t.	n.t.	n.t.	280.9
Stylonematales							
<i>Chroodactylon ornatum</i>	3862 n.t.	n.t.	n.t.	n.t.	53.3 ± 17.7	n.t.	53.3
<i>Rhodosorus magnei</i>	4016 n.t.	n.t.	178.5 ± 0.5	n.t.	48.8 ± 1.5	n.t.	66.6
<i>Rhodosorus marinus</i>	3607 n.t.	n.t.	235.3 ± 15.1	n.t.	88.6 ± 29.6	n.t.	323.9
<i>Rhodosorus marinus</i>	4014 n.t.	n.t.	109.7 ± 39.8	n.t.	91.7 ± 11.5	n.t.	201.4
<i>Rhodosorus marinus</i>	4015 n.t.	n.t.	131.1 ± 7.9	n.t.	52.1 ± 5.4	n.t.	183.2
<i>Rhodosorus marinus</i>	4023 n.t.	n.t.	73.3 ± 15.4	n.t.	82.7 ± 6.9	n.t.	156.0
<i>Rhodosorus sordida</i> JAW	3628 n.t.	n.t.	n.t.	n.t.	114.3 ± 17.9	25.4 ± 2.9	139.7
<i>Rhodosorus sordida</i> AY	3628 n.t.	n.t.	n.t.	n.t.	133.4 ± 29.7	82.9 ± 14.4	216.3
<i>Stylonema alsidii</i>	3480 n.t.	96.2 ± 0.2	46.4 ± 0.4	n.t.	n.t.	n.t.	142.6
<i>Stylonema alsidii</i>	3505 n.t.	n.t.	46.7 ± 2.1	n.t.	63.3 ± 2.4	n.t.	110.0
<i>Stylonema alsidii</i>	3610 n.t.	n.t.	16.3 ± 8.0	n.t.	154.3 ± 20.2	n.t.	170.6
<i>Stylonema alsidii</i>	3784 n.t.	n.t.	16.1 ± 3.5	n.t.	88.5 ± 34.0	n.t.	104.6
<i>Stylonema alsidii</i>	3789 n.t.	n.t.	44.3 ± 7.1	n.t.	147.2 ± 48.4	n.t.	191.5
<i>Stylonema alsidii</i>	4051 n.t.	n.t.	38.3 ± 24.7	n.t.	173.5 ± 14.4	n.t.	211.8
<i>Stylonema alsidii</i>	4052 n.t.	n.t.	70.7 ± 6.4	n.t.	187.4 ± 3.9	n.t.	258.1
<i>Stylonema alsidii</i>	4053 n.t.	n.t.	192.0	n.t.	29.6	n.t.	221.6
<i>Stylonema alsidii</i>	4055 n.t.	n.t.	77.4 ± 0.4	n.t.	193.6 ± 7.6	n.t.	271.0
<i>Stylonema cornu-cervi</i>	3505 n.t.	n.t.	46.7 ± 2.1	n.t.	63.3 ± 2.4	n.t.	110.0
Compsopogonales							
<i>Boldia erythrosiphon</i>	field n.t.	29.3 ± 1.8	n.t.	n.t.	n.t.	n.t.	29.3
<i>Compsopogon coeruleus</i>	3152 n.t.	174.0 ± 1.0	n.t.	n.t.	n.t.	n.t.	174.0
<i>Compsopogon coeruleus</i>	3479 n.t.	175.4 ± 5.7	n.t.	n.t.	n.t.	n.t.	175.4
Erythropeltoidales							
<i>Erythrotrichia carnea</i>	4050 n.t.	263.0 ± 7.5	n.t.	n.t.	n.t.	n.t.	263.0
<i>Erythrotrichia carnea</i>	4054 n.t.	273.6 ± 15.8	n.t.	n.t.	n.t.	n.t.	273.6
<i>Erythrotrichia carnea</i>	4056 n.t.	261.5 ± 17.2	n.t.	n.t.	n.t.	n.t.	261.5
<i>Erythrotrichia foliiformis</i>	4058 n.t.	111.0 ± 1.7	n.t.	n.t.	n.t.	n.t.	111.0
<i>Erythrotrichia</i> sp.	4057 n.t.	243.9 ± 22.3	n.t.	n.t.	n.t.	n.t.	243.9
<i>Porphyropsis coccinea</i>	4073-1 n.t.	190.4 ± 73.4	n.t.	n.t.	n.t.	n.t.	190.4
<i>Porphyropsis coccinea</i>	4073-2 n.t.	267.3 ± 15.4	n.t.	n.t.	n.t.	n.t.	267.3
<i>Rhodochaete parvula</i>	3924 n.t.	219.9 ± 13.1	56.0 ± 3.3	n.t.	n.t.	n.t.	275.9
<i>Sahlingia subintegra</i>	4059 n.t.	117.1 ± 22.8	n.t.	n.t.	n.t.	n.t.	117.1
<i>Smithoria naiadum</i>	field 156.6 ± 28.2	54.7 ± 28.2	n.t.	n.t.	n.t.	n.t.	211.3

The concentrations were determined with GC-LC or high-pressure LC and are expressed as $\mu\text{mol}\cdot\text{g}^{-1}$ dry weight. Results are given as mean \pm SD ($n = 4$). n.t., no trace.

Hawaii (USA) (Karsten et al. 1999). *Rhodosorus* also has one other distinctive character that separates it from all other unicellular red algal genera, that is, chloroplast rotation (Pickett-Heaps et al. 2001, Wilson et al. 2002). Based on Müller et al. (2001) we placed the above genera in the Stylonematales. Even though digeneaside is present in *Rhodosorus* and *Stylonema*, there is presently no molecular phylogenetic data indicating that the order Stylonematales is linked to the Ceramiales in which digeneaside is the primary LMWC (Lobban and Harrison 1994).

Clade L-3 of the Porphyridiales (Hara et al. 2000) (Porphyridiales 3 [Müller et al. 2001]) includes the colonial genus *Flintiella* and the unicellular genus *Porphyridium*. Karsten et al. (1999) showed that two isolates of *Porphyridium* contain floridoside only. In the present work floridoside was confirmed in two other

isolates of *Porphyridium* sp. (3827 and 3904) from Australia. This is also evident in the *Flintiella sanguinaria* isolate (3629, UTEX) and the undescribed genus (3797) from Fiji, both of which have only floridoside. Preliminary molecular phylogeny data for 3797 and the carbohydrate evidence supports its placement in this clade (Yokoyama and Hara, unpublished data).

The three genera *Rhodella*, *Glaucosphaera*, and *Dixonniella* as well as several unidentified taxa are placed in clade L-4 (Hara et al. 2000) (Müller et al. 2001 in Porphyridiales I). In our previous investigations (Karsten et al. 1999), *Rhodella maculata*, *R. violacea*, and *Dixonniella grisea* (including *Rhodella reticulata*) were shown to contain only mannitol. This same carbohydrate pattern is apparent in the results presented here (Table 2) for *Rhodella cyanea* (4072, the type culture of the species), *Rhodella cyanea* (3988 from Japan), *Rhodella*

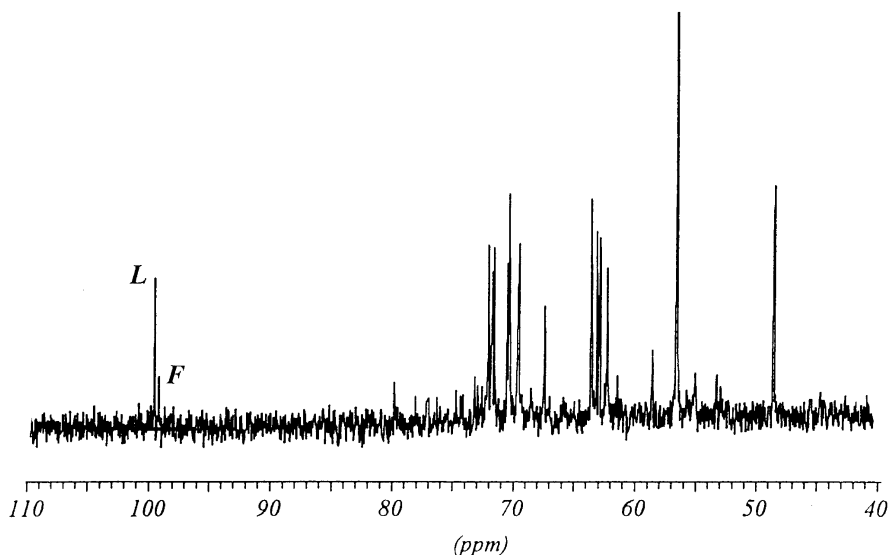


FIG. 1. ^{13}C -NMR spectrum of the 70% ethanol extract of *Smithora naiadum*. L and F refer to the anomeric C-1 atom of the glycosides L-isofloridoside and floridoside, respectively.

sp. (3989), and *Rhodella* sp. (3990) both from Japan as well as the undescribed genus 3987 from Japan.

The Erythropeltidales are also a rather heterogeneous group with respect to carbohydrate composition. For example, floridoside and L-isofloridoside are present in *Smithora naiadum* (Fig. 1). Using ^{13}C -NMR spectroscopy the glycosides L-isofloridoside and floridoside were distinguished easily by the respective NMR signal of the anomeric C-1 atom of the appropriate galactose at 99.3 and 98.9 ppm, which represents a good marker for each of both chemically closely related compounds. In contrast to *Smithora naiadum*, *Erythrotrichia carnea* (4050, 4054, and 4056 from Ireland, Wales, and England, respectively) and *Erythrotrichia* sp. (4057 from Wales) all contain only

floridoside as was reported previously (Karsten et al. 1999) for *E. carnea* (3338 from Western Australia). In our earlier study (Karsten et al. 1999) the LMWC composition of *Sahlugia (Erythrocladia) subintegra* differed in the two isolates: 3442 from South Carolina contained floridoside and D-isofloridoside, whereas 3515 from Australia contained only floridoside. *Sahlugia subintegra* 4059 from New Zealand contained only floridoside (Table 2). The filamentous stage (conchocelis phase?) and blade stage of *Porphyropsis coccinea* 4073 also contained only floridoside. *Rhodochaete parvula* was shown to belong in the Erythropeltidales (Zuccarello et al. 2000) and contains floridoside and digeneaside (Fig. 2). ^{13}C -NMR clearly shows signals at 99.4 and 98.9 ppm that are characteristic for

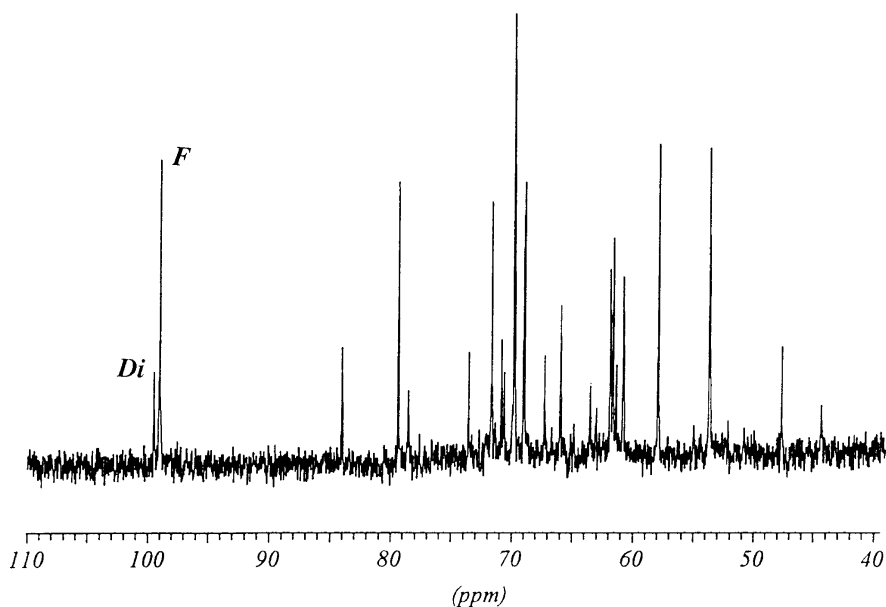


FIG. 2. ^{13}C -NMR spectrum of the 70% ethanol extract of *Rhodochaete parvula*. Di and F refer to the anomeric C-1 atom of the glycosides digeneaside and floridoside, respectively.

the anomeric C-1 atom of mannose in digeneaside and galactose in floridoside, respectively (Karsten et al. 1999). The occurrence of both heterosides is quite different from other genera in this order. The presence of digeneaside perhaps links *Rhodochaete* to the Stylonematales. Again, molecular phylogeny data show no link to the Ceramiales.

In the Compsopogonales we investigated two genera. *Compsopogon coeruleus* isolates (3152 and 3479) from freshwater localities in Australia and Venezuela contain only floridoside, which is identical to the results obtained with the estuarine isolate from Florida (USA) as we reported previously (Karsten et al. 1999). *Boldia erythrosiphon* from Tennessee (USA) also contains only floridoside (Table 2). This uniform pattern is quite different from the diversity evident in the Porphyridiales and Erythropeltidales.

Based on the present investigation and the previous study (Karsten et al. 1999), we now have compiled enough data on the LMWCs of the Bangiophycidae to show that clear patterns of composition are evident in most genera and species. The biochemical exceptions that require further investigation are the inconsistent LMWC patterns in *Stylonema* in the Porphyridiales and in *Sahlingia* in the Erythropeltidales. A phylogenetic tree based on small subunit rRNA supported the LMWC patterns outlined (Karsten et al. 1999). The data presented here confirm the earlier conclusions. The comparative synthetic pathways for the carbohydrates in the various taxa reported here are being elucidated (K. van den Daele and U. Karsten, personal communication). Zuccarello and West also have initiated extensive DNA molecular analyses of multiple isolates of many different genera and species of the Bangiophycidae from around Australia to provide a comprehensive comparison.

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