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Distribution of Diacylglycerylhomoserines, Phospholipids and Fatty Acids in Thirteen Moss Species from Southwestern Siberia

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Abstract—The total lipids extracted from 13 moss species belonging to nine families collected of south-western Siberia were examined for their fatty acids by capillary GC–MS. The total lipids from *Sphagnum nemoreum*, *S. squarrosum* and *Helodium blandowii* yielded 2.25, 3.02 and 3.70% (of total fatty acids) as acetylenic acids, respectively. Some unusual acetylenic acids were found, i.e. 8a,11,14–20:3 and 6a,9,12,15–18:4. High levels of 16:1 fatty acid were found. Very long-chain fatty acids (C24–C26) were determined. The quantities of total, neutral, polar and glycolipids were estimated. Quantitative determination of polar lipid not containing phosphorus as diacylglyceryltrimethylhomoserine (DGTS) as performed; this varied from 13.3 to 38.3% of total polar lipids.

Introduction

Bryophytes are an interesting group of lower plants attracting the attention of chemists/bryologists due to the broad diversity of biologically-active compounds they contain, including those of lipid nature (Dembitsky, 1993; Whittemore, 1991; Zinsmeister and Mues, 1990). The most abundant fatty acids of the bryophytes are also common to most other organisms. Typical for many bryophytes, however, is a high content of acetylenic (Dembitsky *et al.*, 1993b,c; Dembitsky and Rezanka, 1994; Jamieson, 1975; Jamieson and Reid, 1976a; Kohn *et al.*, 1987a,b), arachidonic and eicosapentaenoic acids (Anderson *et al.*, 1974; Gellerman *et al.*, 1972, 1975; Hansen and Rossi, 1990; Hartmann *et al.*, 1986), compounds which are not found very abundantly in the rest of the plant kingdom.

The betaine lipids constitute a new group of polar lipids, which used to be classified into polar and glycolipids before the discovery of diacylglyceryltrimethylhomoserine (DGTS) and diacylglycerylhydroxymethyl-β-alanine (DGTA). Betaine lipids are widely detected in lower plants, mostly in cryptogamic green plants (Dembitsky, 1993; Eichenberger, 1993; Sato, 1992), in some microalgae (Brown and Elovson, 1974; Eichenberger, 1982; Evans *et al.*, 1982; Smith and Harwood, 1983), marine green macrophytes (Dembitsky and Rozentsvet, 1989; Khotimchenko *et al.*, 1990), ferns (Sato and Furuya, 1983, 1984a,b), fungi (Vaskovsky *et al.*, 1991; Yamada and Nozawa, 1979) and lichens (Dembitsky *et al.*, 1993a, 1994).

Our previous studies on lipids from mosses (Dembitsky *et al.*, 1993b,c; Dembitsky and Rezanka, 1994) and those of other authors (Eichenberger, 1993; Gellerman *et al.*, 1972; Jamieson and Reid, 1976a; Hansen and Rossi, 1990; Hartmann *et al.*, 1986; Kohn *et al.*, 1987a,b; Zinsmeister and Mues, 1990) have shown that bryophytes are plants with a very interesting lipid chemistry. The present paper reports an analysis of polar lipids and fatty acids from moss species sampled in the southwest of Siberia.

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Materials and Methods

All mosses were sampled in August 1992, in the Primorsky nature reserve near Lake Baikal (20–50 m above lake level). Freshly collected moss species were thoroughly cleansed of extraneous matter, and only clean mosses tissues were used for the extraction.

The extraction of lipids, their analyses and quantification, and the identification of individual phospholipid classes were carried out as described elsewhere (Dembitsky *et al.*, 1993b,c). DGTS was determined as described earlier (Kabara and Chen, 1976). A total of three to five parallel determinations were taken for each sample of phospholipids and DGTS using the qualitative determination methods described by Dembitsky *et al.* (1993a,c).

Fatty acids were prepared and analysed as trimethylsilyloxazolines by capillary GC–MS as previously described (the data in Tables 3–5 being obtained from three experiments) (Dembitsky *et al.*, 1993b,c). The identification of acetylenic acids was achieved using the method of Dembitsky *et al.* (1993b).

Results

The results obtained for quantitative estimation of lipids in the 13 moss species are given in Table 1. Total lipids vary from 10.4 in *Sph. squarrosum* to 91.0 mg g^{-1} dry wt. in *Atr. haussknechtii.* Neutral lipids were the most abundant lipid fraction (36.6–63.6%). Glycolipids make up more than 30% of total lipids in nine moss species and polar lipids varied from 8.3 to 30.6%.

Among the polar lipid classes only six phospholipids were found: phosphatidylcholine (PC), phosphatidylethanolamine (PE), phosphatidylglycerol (PG), phosphatidylserine (PS), phosphatidylinositol (PI), X and one lipid not containing phosphorus, DGTS. All the examined species showed the presence of DGTS when subjected to two-dimensional thin-layer chromatography. The results of the polar lipid fraction analyses are shown in Table 2. DGTS is major lipid in eight species and it varied from 13.3% in *Pl. medium* to 38.3% in *Sph. nemoreum.* PC is the major lipid in five species, which varied from 7.5% in *Sph. squarrosum* to 57.5% in *Cl. dendroides.*

GC–MS analysis of total lipids from mosses showed the domination of palmitic acid (7.92–13.75%), followed by stearic acid (3.68–6.32%) in all species (Table 3). The total percentage of saturated fatty acids ranged from 18.46 *Bryum pseudotriquetrum* to 29.07% in *Climacium dendroides.* All moss species contained *iso-* (from 0.85–1.50%),

TABLE 1. LIPID COMPOSITION OF SOME MOSS SPECIES

Family, Genus, Species	TL	NL	GL	PL
Amblystegiaceae				
Hygrohypnum ochraceum (Turn. ex Wils.) Loeske	14.9	42.5	36.1	21.4
Aulacomniaceae				
Aulacomnium palustre (Hedw.) Schwaegr.	17.6	52.2	30.5	17.3
Bartramiaceae				
Philonotis fontana (Hedw.) Brid.	26.9	36.6	32.8	30.6
Bryaceae				
Bryum pseudotriquetrum (Hedw.) Gaertn. *et al.*	65.7	58.4	18.7	22.9
Bryum sp. Hewd.	14.6	57.7	29.1	13.2
Climaciaceae				
Climacium dendroides (Hedw.) Wed. et Mohr.	25.2	41.4	31.0	27.6
Helodiaceae				
Helodium blandowii (Web. et Mohr) Warnst.	55.4	53.0	36.0	11.0
Mniaceae				
Pseudobryum cinclidiodes (Hueb.) T.Kop.	32.1	56.2	34.7	10.1
Plagiomnium medium (Bruch et Sohimp. in B.S.G) T. Kop	58.2	57.4	31.9	10.7
Polytrichaceae				
Atrichum haussknechtii Jur. et Milde	91.0	63.6	19.4	16.0
Polytrichum juniperinum Hedw.	28.8	44.9	35.3	19.8
Sphagnaceae				
Sphagnum nemoreum Socop.	30.8	54.9	33.8	11.3
Sphagnum squarrosum Crome	10.4	62.6	29.1	8.3

TL, total lipids, mg g^{-1} dry wt.; NL, GL and PL are given as percentages of TLs.

TABLE 2. DGTS AND PHOSPHOLIPID COMPOSITION OF SOME MOSSES

Family, Genus, Species	DGTS	PC	PE	PG	PI	PS	X
Amblystegiaceae							
Hygrohypnum ochraceum	28.2	23.3	16.4	15.4	5.0	6.9	4.8
Aulacomniaceae							
Aulacomnium palustre	14.7	42.2	17.8	14.8	4.4	6.1	—
Bartramiaceae							
Philonotis fontana	24.5	9.3	27.1	21.8	7.1	10.2	—
Bryaceae							
Bryum pseudotriquetrum	22.3	8.7	24.8	16.1	8.2	10.4	9.5
Bryum sp.	29.1	9.0	23.1	16.4	7.5	11.8	3.1
Climaciaceae							
Climacium dendroides	14.2	57.5	9.8	8.6	3.4	3.6	2.9
Helodiaceae							
Helodium blandowii	15.0	22.8	17.7	23.6	7.1	8.1	5.6
Mniaceae							
Pseudobryum cinclidiodes	16.8	11.8	17.2	29.1	12.5	12.6	—
Plagiomnium medium	13.3	30.6	12.1	23.7	10.6	9.9	—
Polytrichaceae							
Atrichum haussknechtii	19.8	31.7	11.9	12.2	8.3	8.8	7.3
Polytrichum juniperinum	26.4	18.1	15.0	16.1	6.6	8.8	9.0
Sphagnaceae							
Sphagnum nemoreum	38.3	9.2	16.2	21.9	7.5	6.9	—
Sphagnum squarrosum	33.4	7.5	21.8	23.1	5.4	8.8	—

anteiso- (0.62–0.84%) and *branched* (both pristanic and phytanic acids, 0.16–0.43%) compounds.

The monoenoic fatty acids were the third most prevalent fatty acid group after the polyenoic and saturated acids and ranged from 26.66 to 39.58%. The three acetylenic acids were identified among monoenes i.e. 6a–18:1, 9a–18:1, and 12a–18:1 in three mosses only: *Helodium blandowii* (1.14%), *Sphagnum nemoreum* (1.96%) and *S. squarrosum* (2.59%) (Table 4). Three fatty acids were the most abundant monoenes in all the moss species examined: 18:1 (n-9) (13.20–17.48%), 16:1 (n-9) (2.90–9.84%) and 16:1 (n-7) (1.62–4.65%).

Seven acetylenic acids were identified among the polyenoic FAs (Table 5); these were 6a,9–18:2, 9a,12–18:2, 9,12a–18:2, 6a,9,12–18:3, 8a,11,14–20:3, 6a,9,12,15–18:4 and 5a,8,11,14–20:4. The range of polyenes (38.74–54.88%) was greater than the monoenes and/or saturated acids (Tables 1 and 2). The most abundant polyenes were 18:3(n-3), 18:3(n-6), 18:2(n-6), 20:4(n-6) and 22:3(n-6).

Discussion

DGTS has been reported in some bryophytes, including moss species (Dembitsky *et al.*, 1993a, 1994; Sato, 1992). Sato and Furuya (1984a) have studied the distribution of DGTS in non-vascular green plants and found this betaine lipid in two liverworts, *Bazzania yoshinagama, Marchantia paleacea* and three mosses, *Dicranum scoparium, Polytrichum formosum* and *Pleurozium schreberi.* DGTS varied from 7 to 36 nmol mg^{-1} total lipids. Recently, Dembitsky *et al.* (1993c) and Eichenberger (1993) have reported DGTS in four mosses. Data on the distribution of DGTS and other polar lipids classes in mosses have not yet been obtained.

The betaine lipids DGTS and DGTA represent a prominent group of polar lipids and were detected in most species of cryptogamic plants (Eichenberger, 1993; Sato, 1992). Based on data mainly obtained by Sato and Furuya (1984a), DGTS has not been detected in seed plants (both angiosperms and gymnosperms) as yet. It is interesting that the organisms that accumulate high levels of DGTS contain no very low levels of

TABLE 3. SATURATED FATTY ACIDS OF SOME MOSS SPECIES

FAs	*Hy.o.*	*Au.p.*	*Ph.f.*	*Br.p.*	*Br.s.*	*Cl.d.*	*He.b.*	*Ps.c.*	*Pl.m.*	*At.h.*	*Po.j.*	*Sp.n.*	*Sp.s.*
n-12:0	0.81	0.80	1.08	0.62	0.82	1.08	1.04	0.81	0.82	0.61	0.72	0.72	0.63
n-13:0	0.11	0.10	0.23	0.05	0.11	0.23	0.22	0.11	0.11	0.18	0.06	0.06	0.13
n-14:0	0.17	0.52	0.26	0.12	0.17	0.26	0.25	0.47	0.17	0.27	0.15	0.15	0.32
n-15:0	0.64	0.60	0.78	0.54	0.64	0.78	0.75	0.61	0.64	0.61	0.61	0.61	0.42
n-16:0	7.92	12.29	13.74	9.24	8.04	13.75	13.24	9.07	8.02	10.07	10.66	10.65	10.25
n-17:0	0.71	0.67	0.89	0.56	0.72	0.89	0.86	0.71	0.72	0.71	0.67	0.67	0.47
n-18:0	3.68	6.68	6.31	3.07	3.74	6.32	6.08	3.95	3.73	4.91	5.30	5.29	6.05
n-19:0	0.25	0.17	0.30	0.23	0.26	0.30	0.29	0.27	0.26	0.17	0.13	0.13	0.60
n-20:0	0.44	0.67	0.85	0.33	0.45	0.85	0.82	0.48	0.45	0.48	0.46	0.46	0.87
n-21:0	0.77	0.28	0.33	0.59	0.78	0.33	0.32	0.38	0.78	0.30	0.32	0.32	0.55
n-22:0	1.02	0.18	—	0.13	1.03	—	—	0.25	1.03	0.95	1.24	1.24	0.96
n-23:0	0.24	0.32	0.28	0.41	0.25	0.28	0.27	0.25	0.25	0.25	0.38	0.37	0.48
n-24:0	0.17	0.19	0.40	0.12	0.17	0.40	0.39	0.38	0.17	0.18	0.12	0.12	0.32
n-25:0	0.36	0.35	0.51	0.29	0.37	0.51	0.49	0.34	0.37	0.34	0.35	0.34	0.76
n-26:0	0.56	0.52	0.56	0.50	0.57	0.56	0.54	0.55	0.57	0.50	0.60	0.60	0.52
i-12:0	0.11	0.10	0.23	0.05	0.11	0.23	0.22	0.11	0.11	0.11	0.06	0.06	0.13
i-13:0	0.17	0.16	0.26	0.12	0.17	0.26	0.25	0.16	0.17	0.16	0.15	0.15	0.32
i-14:0	0.46	0.47	0.54	0.39	0.47	0.54	0.52	0.47	0.47	0.47	0.45	0.45	0.43
i-15:0	0.15	0.14	0.26	0.11	0.15	0.26	0.25	0.15	0.15	0.15	0.12	0.12	0.19
i-16:0	0.04	0.07	0.02	0.05	0.04	0.02	0.02	0.13	0.04	0.13	0.06	0.06	0.13
i-17:0	0.12	0.21	0.16	0.13	0.12	0.16	0.15	0.22	0.12	0.18	0.20	0.20	0.30
ai-13:0	0.15	0.15	0.17	0.14	0.15	0.17	0.16	0.15	0.15	0.15	0.16	0.16	0.27
ai-15:0	0.40	0.38	0.47	0.34	0.41	0.47	0.45	0.38	0.41	0.38	0.40	0.40	0.39
ai-17:0	0.03	0.07	0.05	0.03	0.03	0.05	0.05	0.08	0.03	0.08	0.06	0.06	0.08
ai-19:0	0.11	0.09	0.15	0.11	0.11	0.15	0.14	0.15	0.11	0.05	0.05	0.05	0.09
Pristanic	0.02	0.04	0.03	0.05	0.02	0.03	0.03	0.05	0.02	0.05	0.05	0.05	0.13
Phytanic	0.14	0.25	0.19	0.14	0.14	0.19	0.18	0.24	0.14	0.24	0.20	0.20	0.30
Total saturated	19.75	26.47	29.05	18.46	20.04	29.07	27.98	20.92	20.01	22.68	23.73	23.70	26.09
normal	17.85	24.34	26.53	16.80	18.12	26.55	25.56	18.63	18.09	20.53	21.83	21.73	23.33
iso-	1.05	1.15	1.47	0.85	1.06	1.47	1.41	1.24	1.06	1.20	0.98	1.04	1.50
anteiso	0.69	0.69	0.84	0.62	0.70	0.84	0.80	0.76	0.70	0.66	0.67	0.67	0.83
branched	0.16	0.29	0.21	0.19	0.16	0.21	0.21	0.29	0.16	0.29	0.25	0.25	0.43

Abbreviations: *Hy.o.*, *Hygrohypnum ochraceum*; *Au.p.*, *Aulacomnium palustre*; *Ph.f.*, *Philonotis fontana*; *Br.p.*, *Bryum pseudotriquetrum*; *Br.s.*, *Bryum* sp.; *Cl.d.*, *Climacium dendroides*; *He.b.*, *Helodium blandowii*; *Ps.c.*, *Pseudobryum cinclidioides*; *Pl.m.*, *Plagiomnium medium*; *At.h.*, *Atrichum hassknechtii*; *Po.j.*, *Polytrichum juniperum*; *Sp.n.*, *Sphagnum nemoreum*; *Sp.s.*, *Sphagnum squarrosum*.

PC. This reciprocity between DGTS and PC can be interpreted that DGTS has been progressively replaced by PC during the process of evolution of green plants. The apparent reciprocity of the abundance of DGTS and PC among different species in lower plants and algae as described recently (Eichenberger, 1993; Sato, 1992), suggests that DGTS and PC are similar in their chemical and physical properties and are approximately interchangeable with each other in their roles within the cell.

Fatty acid compositions of some moss species are further characterized by the presence of acetylenic acids which are, as far as is known, restricted to the triglycerides (Kohn *et al.*, 1987a; Karunen *et al.*, 1988).

Some compounds that had been identified to date are: 6a,9–18:2 from *Riccia fluitans* (Kohn *et al.*, 1987b) and *Fontinalis antipyretica* (Jamieson and Reid, 1976b), and 6a–18:1, 9a–18:1, 12a–18:1, 6a,9,12–18:3, 6a,9,12,15–18:4, 8a,11,14–20:3, 5a,8,11,14–20:4 from other mosses (Dembitsky, 1993; Dembitsky *et al.*, 1993c). We found that the moss species yielded much smaller percentages of acetylenic acids (from 0 to 3.7%).

Several mosses such as *Bryum bicolor*, *Hylocomium splendens*, *Mnium cuspidatum*, *Mnium medium*, *Plagiothecium laetum* and *Pleurozium schreberi* contain 20:4 and 20:5 acids as their major fatty acids (Al-Hasan *et al.*, 1989; Gellerman *et al.*, 1975; Karunen, 1982). Hansen and Rossi (1990) studied 25 moss species for the

TABLE 4. MONOENOIC FATTY ACIDS OF SOME MOSS SPECIES

	Hy.o.	*Au.p.*	*Ph.f.*	*Br.p.*	*Br.s.*	*Cl.d.*	*He.b.*	*Ps.c.*	*Pl.m.*	*At.h.*	*Po.j.*	*Sp.n.*	*Sp.s.*
12:1(n-5)	0.46	0.47	0.54	0.39	0.47	0.54	0.52	0.47	0.47	0.47	0.45	0.45	0.43
13:1(n-5)	0.81	0.80	1.08	0.62	0.82	1.08	1.04	0.81	0.82	0.71	0.72	0.72	0.63
14:1(n-5)	0.15	0.15	0.17	0.14	0.15	0.17	0.16	0.15	0.15	0.15	0.16	0.16	0.27
15:1(n-9)	0.61	0.57	0.67	0.51	0.61	0.67	0.65	0.60	0.61	0.50	0.60	0.60	0.54
15:1(n-7)	0.14	0.13	0.08	0.15	0.14	0.08	0.08	0.15	0.14	0.16	0.17	0.17	0.29
16:1(n-9)	3.52	6.26	5.69	2.90	3.57	5.70	5.49	9.84	3.57	7.74	6.11	6.10	7.60
16:1(n-7)	4.58	2.50	2.72	1.62	4.65	2.72	2.62	4.02	4.64	3.62	3.28	3.27	4.26
t-16:1(n-13)	0.12	0.14	0.09	0.12	0.12	0.09	0.09	0.13	0.12	0.13	0.05	0.05	0.32
i-17:1(n-9)	0.28	0.30	0.36	0.23	0.29	0.36	0.35	0.33	0.29	0.38	0.30	0.30	0.60
ai-17:1(n-9)	0.11	0.32	0.26	0.11	0.11	0.26	0.25	0.34	0.11	0.30	0.26	0.26	0.29
17:1(n-9)	0.63	0.60	0.60	0.56	0.63	0.60	0.58	0.62	0.63	0.60	0.65	0.65	0.57
17:1(n-7)	0.36	0.35	0.37	0.32	0.37	0.37	0.36	0.36	0.37	0.36	0.38	0.37	0.54
18:1(n-11)	0.86	1.47	1.22	0.73	0.87	1.22	1.18	0.95	0.87	0.98	1.47	1.47	1.62
18:1(n-9)	13.33	17.48	13.69	15.57	13.53	13.70	134.20	14.55	13.51	14.95	15.70	15.67	14.54
18:1(n-7)	0.72	1.02	0.83	0.69	0.73	0.83	0.80	1.10	0.73	1.20	1.04	1.03	1.21
6a-18:1	—	—	—	—	—	—	0.13	—	—	—	—	0.71	0.89
9a-18:1	—	—	—	—	—	—	0.63	—	—	—	—	0.64	0.76
12a-18:1	—	—	—	—	—	—	0.38	—	—	—	—	0.61	0.94
19:1(n-8)	0.22	0.25	0.23	0.23	0.23	0.23	0.22	0.21	0.22	0.21	0.19	0.19	0.40
20:1(n-11)	0.25	0.46	0.40	0.23	0.26	0.40	0.39	0.24	0.26	0.34	0.32	0.32	0.50
20:1(n-9)	0.17	0.17	0.25	0.12	0.17	0.25	0.24	0.18	0.17	0.14	0.12	0.12	0.22
21:1(n-8)	0.17	0.19	0.39	0.12	0.17	0.39	0.38	0.38	0.17	0.18	0.12	0.12	0.12
22:1(n-11)	0.84	0.17	0.39	0.51	0.85	0.39	0.38	0.22	0.85	0.62	0.77	0.77	0.64
22:1(n-9)	0.15	0.34	0.53	0.08	0.15	0.53	0.51	0.57	0.15	0.27	0.24	0.24	0.21
24:1(n-11)	0.09	0.12	0.18	0.07	0.09	0.18	0.17	0.18	0.09	0.18	0.12	0.12	0.18
24:1(n-9)	0.12	0.06	0.19	0.05	0.12	0.19	0.18	0.13	0.12	0.13	0.06	0.06	0.13
25:1(n-9)	0.14	0.13	0.08	0.15	0.14	0.08	0.08	0.15	0.14	0.15	0.17	0.17	0.29
26:1(n-11)	0.25	0.18	0.08	0.21	0.26	0.08	0.08	0.19	0.26	0.29	0.25	0.25	0.35
26:1(n-9)	0.17	0.16	0.11	0.13	0.17	0.11	0.11	0.15	0.17	0.15	0.14	0.14	0.24
Total monoenoic	29.25	34.79	31.20	26.66	29.67	31.22	32.42	37.02	29.63	34.91	33.84	35.73	39.58

See Table 3 for abbreviations.

presence of 20:4 and 20:5 acids. Six species belonging to the families Brachytheciaceae and Hypnaceae contained the highest levels of these polyunsaturated acids (from 23 to 47%). The moss species examined in the present study yielded 20:4 (both isomers) from 1.68 in *Philonotis fontana* to 6.32% in *Bryum pseudotriquetrum* (Table 5).

Anderson *et al.* (1974), Karunen (1982) and Sewon (1992) have used the distribution of fatty acids as a criterion for the classification of bryophytes. These authors made the conclusion that there are variations in fatty acid composition within moss and liverwort families, the differences in levels of certain acids between suborders and orders are greater. An obvious marker was the occurrence or non-occurrence of certain fatty acids, for example, acetylenic and some polyunsaturated acids.

The Bryophyta species analyzed hitherto have shown a great variation in the proportions of C16 plus C18 (i.e. angiosperm-type) polyunsaturated acids on the one hand and the C20 (algae-type) polyunsaturated fatty acids on the other hand (Dembitsky, 1993; Karunen, 1982). The fatty acid pattern with a high proportion of 16:3(n-3) plus 18:3(n-3) in Bryophyta resembles the composition of angiosperms, and thus it can be considerered as an indication of a high evolutionary level. On the other hand a high proportion of the algal-type fatty acids, 20:4(n-6) plus 20:5(n-3) is an indication of early evolution. According to Sewon (1992) who studied fatty acid composition of 55 species of Bryophyta beloning to 13 orders and suborders the proportion of C20 fatty acids in monogalactosyldiacylglycerols (MGDG) was lowest in

TABLE 5. POLYENOIC FATTY ACIDS OF SOME MOSS SPECIES

	Hy.o.	*Au.p.*	*Ph.f.*	*Br.p.*	*Br.s.*	*Cl.d.*	*He.b.*	*Ps.c.*	*Pl.m.*	*At.h.*	*Po.j.*	*Sp.n.*	*Sp.s.*
14:2(n-5)	0.25	0.23	0.31	0.20	0.26	0.31	0.30	0.25	0.26	0.25	0.24	0.24	0.34
16:2(n-4)	0.37	0.34	0.19	0.39	0.38	0.19	0.18	0.37	0.38	0.30	0.38	0.37	0.31
18:2(n-6)	8.48	8.96	9.83	7.69	8.61	9.84	9.47	11.15	8.59	10.25	9.94	8.84	7.21
18:2(n-3)	0.68	0.84	0.50	0.70	0.69	0.50	0.48	0.91	0.68	0.92	1.01	1.01	1.00
6a,9–18:2	0.14	—	—	—	—	—	0.80	—	—	—	—	0.08	0.11
9,12a–18:2	0.55	—	—	0.04	0.05	—	0.78	—	0.05	—	—	—	—
9a,12–18:2	0.04	—	—	0.05	0.04	—	—	—	0.04	—	0.03	0.03	0.06
20:2(n-6)	0.43	0.52	0.27	0.43	0.44	0.27	0.26	0.62	0.44	0.60	0.42	0.42	0.35
22:2(n-6)	0.02	0.65	3.27	3.83	0.02	3.27	3.15	0.45	0.02	0.35	0.11	0.11	0.09
16:3(n-6)	0.53	0.51	0.30	0.56	0.54	0.30	0.29	0.54	0.54	0.51	0.51	0.51	0.40
16:3(n-3)	0.48	0.45	0.25	0.87	0.49	0.25	0.24	0.48	0.49	0.43	0.47	0.47	0.33
6a,9,12-18:3	0.15	—	—	—	—	—	—	—	0.10	—	—	0.07	0.09
18:3(n-6)	10.04	1.38	5.78	9.80	10.20	5.79	5.57	4.02	10.18	4.42	1.26	1.26	1.12
18:3(n-3)	13.09	10.10	10.87	13.46	13.24	10.88	10.48	10.17	13.31	12.07	10.89	10.92	9.11
8a,11,14-20:3	0.04	—	—	0.05	0.04	—	—	—	0.04	—	0.02	0.02	0.05
20:3(n-9)	0.27	0.81	0.24	0.28	0.28	0.24	0.23	0.72	0.28	0.42	0.57	0.57	0.44
20:3(n-6)	0.39	0.43	0.21	0.41	0.40	0.21	0.20	0.31	0.40	0.31	0.35	0.34	0.25
20:3(n-3)	0.04	0.16	0.18	0.07	0.04	0.18	0.17	0.27	0.04	0.28	0.07	0.07	0.09
22:3(n-6)	2.26	3.12	1.82	1.57	2.29	1.83	1.76	3.00	2.29	2.90	2.23	2.03	2.01
22:3(n-3)	0.56	0.93	0.33	0.33	0.57	0.33	0.32	0.59	0.57	0.50	0.57	0.57	0.64
24:3(n-3)	0.14	0.27	0.11	0.15	0.14	0.11	0.11	0.39	0.14	0.30	0.32	0.32	0.42
16:4(n-3)	0.95	0.93	0.56	0.97	0.96	0.56	0.54	0.95	0.96	0.99	0.67	0.67	0.53
6a,9,12,15–18:4	0.69	—	0.07	—	0.04	—	0.98	—	0.08	—	0.09	0.09	0.12
18:4(n-3)	2.78	1.60	1.39	2.87	2.80	1.39	1.34	1.56	2.82	1.52	1.24	1.24	1.02
5a,8,11,14–20:4	—	—	—	0.04	0.07	—	—	—	—	—	—	—	—
20:4(n-6)	1.96	5.07	1.49	6.27	1.99	1.48	1.43	4.32	1.98	5.02	3.45	3.14	2.31
20:4(n-3)	0.67	0.16	0.19	0.05	0.68	0.19	0.18	0.30	0.67	0.67	0.30	0.67	0.52
22:4(n-3)	1.96	0.51	1.48	1.62	1.99	1.48	1.43	0.31	1.98	0.31	3.45	3.21	2.40
20:5(n-3)	3.04	0.27	0.11	2.18	3.04	0.11	0.11	0.38	3.03	0.72	3.47	3.30	3.01
Total polyenoic	51.00	38.74	39.75	54.88	50.29	39.71	40.80	42.06	50.36	44.17	42.43	40.57	34.33
Total acetylenic	1.61	—	—	0.18	0.24	—	3.70	—	0.31	—	0.14	2.25	3.02

See Table 3 for abbreviations.

the liverworts, and increased in the following order: Liverworts>Sphagnales>Polytrichales>Bryales. Therefore, the fatty acid pattern of MGDG cannot just be considered to display an intermediate between algae and higher plants. Bryophytes seem to have an evolutionary pattern of their own for MGDG fatty acids from lower to higher levels of C20 polyenoic fatty acids as found with algae.

The present study clearly showed that DGTS was widely distributed among bryophytes. The analytical data for lipids, polar lipids, phospholipids and fatty acids from the 13 moss species reported in this study demonstrate the need to further investigate a greater number of bryophyte species from several families in order to elucidate the distribution trends existing for polar lipids and acetylenic acids. The investigation of the phylogenetic distribution of betaine lipids, mainly DGTS, is still in progress. Although most of the major complex polar lipids in bryophytes are now identified, there are still a number of chemically unidentified lipids in mosses and liverworts, e.g. one unidentified lipid was found in some moss species in this study.

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