NORDIC JOURNAL OF
BOTANY

Research

New finds of charophytes in Iceland with an update on the distribution of the charophyte flora

Thora Hrafnsdottir, Finnur Ingimarsson, Haraldur R. Ingvason, Stefán Már Stefánsson, Eva G. Þorvaldsdóttir, Hilmar J. Malmquist and Anders Langangen

T. Hrafnsdottir (https://orcid.org/0000-0003-3803-8621) ✉ (thora@nmsi.is), F. Ingimarsson, H. R. Ingvason, S. M. Stefánsson, Natural History Museum of Kópavogur, Hamraborg 6a, 200 Kópavogur, Iceland. – TH and H. J. Malmquist, Icelandic Museum of Natural History, Reykjavík, Iceland. – E. G. Þorvaldsdóttir, Reykjavík, Iceland. – A. Langangen, Oslo, Norway.

Nordic Journal of Botany
2019: e02111
doi: 10.1111/njb.02111

Subject Editor: Nina Lundholm
Editor-in-Chief: Torbjörn Tyler
Accepted 16 April 2019

Charophyte species new to the flora of Iceland are reported and an update on the distribution of the previously known species is given. Four species are new to Iceland; *Chara aspera* Willdenow, *Chara contraria* Braun ex Kützing, *Tolypella canadensis* Sawa and *Tolypella glomerata* (Desvaux) Leonhardi, while four species were previously known: *Chara globularis* Thuiller, *Chara virgata* Kützing, *Nitella flexilis* (L.) Agardh and *Nitella opaca* (Agardh ex Bruzelius) Agardh. The finding of the species new to Iceland add to the hitherto known worldwide distribution of those species, including a significant extension to the north.

Keywords: *Chara*, charophytes, Iceland, lakes, *Nitella*, *Tolypella*

Introduction

Until recently, the knowledge of the charophyte flora of Iceland was very limited, and charophytes have not been the focus of much research in Iceland. In the 1980s, the coverage and ecology of *Nitella opaca* in Lake Thingvallavatn was studied (Kairesalo et al. 1992) and it was recently re-evaluated (Natural History Museum of Kópavogur, unpubl.). Apart from sporadic reports of charophyte species from the 18th and 19th century (Hallgrímsson 1975), the first synopsis on charophytes in Iceland was published in 1972 based on material available in four Nordic herbaria (Langangen 1972). Three species were reported: *Nitella opaca* Agardh, *N. flexilis* (L.) Agardh and *Chara globularis* Thullier. In a recent checklist of Icelandic algae (Hallgrímsson 2007) four species are listed; the three above mentioned species and *Chara virgata* Kützing (Hallgrímsson 2007, p. 51, with reference to a letter from Anders Langangen in 2007).

However, Iceland is rich in freshwaters, most of which are oligotrophic (Karst-Riddoch et al. 2009, Jensdóttir Fjeld et al. 2016), providing habitats for aquatic organisms such as charophytes. The subarctic island (103 000 km^2) is located in the North Atlantic Ocean, characterised by a maritime climate with cool summers and mild winters (Einarsson 1984). Situated astride the geologically active Mid-Atlantic Ridge, the island is entirely built up of volcanic material, mainly basalt (Sæmundsson 1979). This causes Icelandic lakes to be generally high

© 2019 The Authors. This is an Open Access article
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

in pH, i.e. pH 7–9 (Karst-Riddoch et al. 2009, Jensdóttir Fjeld et al. 2016).

A recent survey on macrophytes in Icelandic lakes revealed new distribution sites for the previously known charophytes, as well as four species new to Iceland. The survey was conducted by the Natural History Museum of Kópavogur in 2012 and 2013 as a part of a large project implemented in accordance with the European habitat classification system (EUNIS) under the supervision of the Icelandic Institute of Natural History (Ottósson et al. 2016). The charophytes new for Iceland are: *Chara aspera* Willdenow, *Chara contraria* Braun ex Kützing, *Tolypella canadensis* Sawa and *Tolypella glomerata* (Desvaux) Leonhardi. An account of their findings is given in the present paper as well as an update on the distribution of the four previously known species.

Methods and material

The charophytes in the present study were sampled primarily in a survey of the macrophytes in 72 Icelandic lakes conducted from July to August 2012 and 2013 (Jensdóttir Fjeld et al. 2016). Macrophytes were surveyed with an aquascope and sampled by a rake or grapnel, and water depth and substrate type were recorded. In each lake, water temperature, pH, specific conductivity and secchi depth were measured and water samples were taken at 0.5 m depth for measurements of chlorophyll-a and nutrients (P-total, N-total). For further information on methods see Jensdóttir Fjeld et al. (2016).

Charophytes sampled for closer examination were mounted and dried in a plant-press for subsequent species identification in the laboratory. Specimens were identified under a stereoscope according to Blindow et al. (2007), Langangen (2007) and Bryant and Stewart (2002). Specimens of the new species for Iceland were identified by Anders Langangen.

In addition to the above sampling of charophytes, a number of unpublished records are presented for the first time in this paper. First, records which originate from two research projects; the Ecological Survey of Icelandic Lakes (ESIL) sampled in August during the years 1992–2002 (Malmquist et al. 2005) and the EU Euro-limpacs project sampled in July and August 2004 and 2005 (Jeppesen et al. 2010). Secondly, unpublished records based on preserved material in the herbaria at the Icelandic Institute of Natural History (ICEL and AMNH).

Results

Charophytes are widespread in Iceland according to the present compilation of records (Fig. 1). Charophytes have been found at 126 different localities in Iceland, whereof 102 new localities are presented in this paper (Supplementary material Appendix 1). Eight species occur in Iceland, whereof four species are new to the Icelandic flora, namely *Chara aspera* Willdenow, *Chara contraria* Braun ex Kützing, *Tolypella canadensis* Sawa and *Tolypella glomerata* (Desvaux) Leonhardi. Specimens of the four species are deposited in the

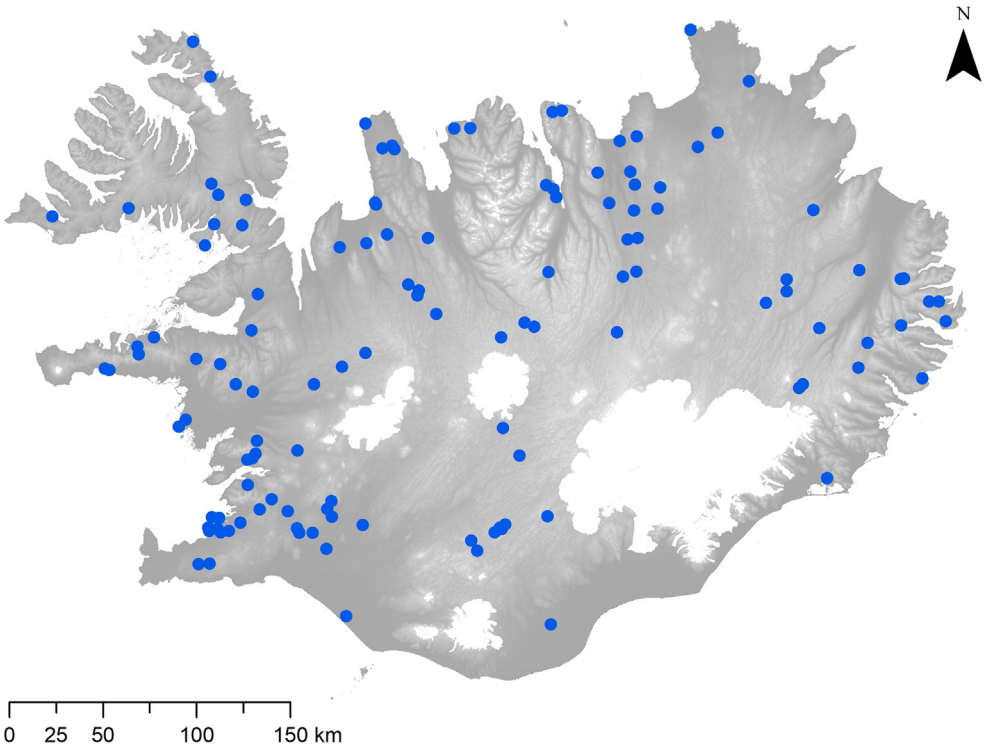


Figure 1. Distribution of charophytes in Iceland based on a total of 126 published and unpublished records. See also Supplementary material Appendix 1.

herbaria at the Icelandic Institute of Natural History (ICEL and AMNH). In the species account below new species for Iceland are denoted with an asterisk (*).

Chara aspera Willdenow * (Fig. 2a)

Short description of species. 5–10 cm long and commonly encrusted, grey in colour (Langangen 2007). Cortex triplostichous, isostichous to tylacanthous. Spine-cells solitary and up to as long as the stem diameter. Dioecious. Oogonia solitary and up to 0.8 mm long. Oospores black and up to 0.7 mm long. Antheridia red and up to 0.6 mm in diameter. White, round bulbils up to 1 mm in diameter are common. Known from both brackish water and freshwater (Langangen 2007).

Description of specimens from Iceland. 1–2 cm long and not encrusted. Triplostichous, tylacanthous cortex and with mostly short spine-cells. Sterile. White, ovoid bulbils up to 0.35 mm in diameter.

Occurrence in Iceland. One lake; Skúmsstaðavatn, 23.7.2012 (Fig. 3, Table 1).

Lake depth of species occurrences. Found at a single station, at 10 cm depth on sandy bottom.

Remarks. Lake Skúmsstaðavatn in the Southern lowlands is 3 km from the seashore where wave intensity is estimated to be moderate (Georgsdóttir et al. 2016) with low ridges at the boundary of shore and land shielded from the sea. The lake is shallow (max. depth 2 m) with more or less sandy bottom, and not considered brackish (Table 1) but might occasionally be affected by seaspray. Specific conductivity, chlorophyll-a and nutrients (P, N) measured were relatively high at the date of sampling compared to other Icelandic lakes (Karst-Riddoch et al. 2009).

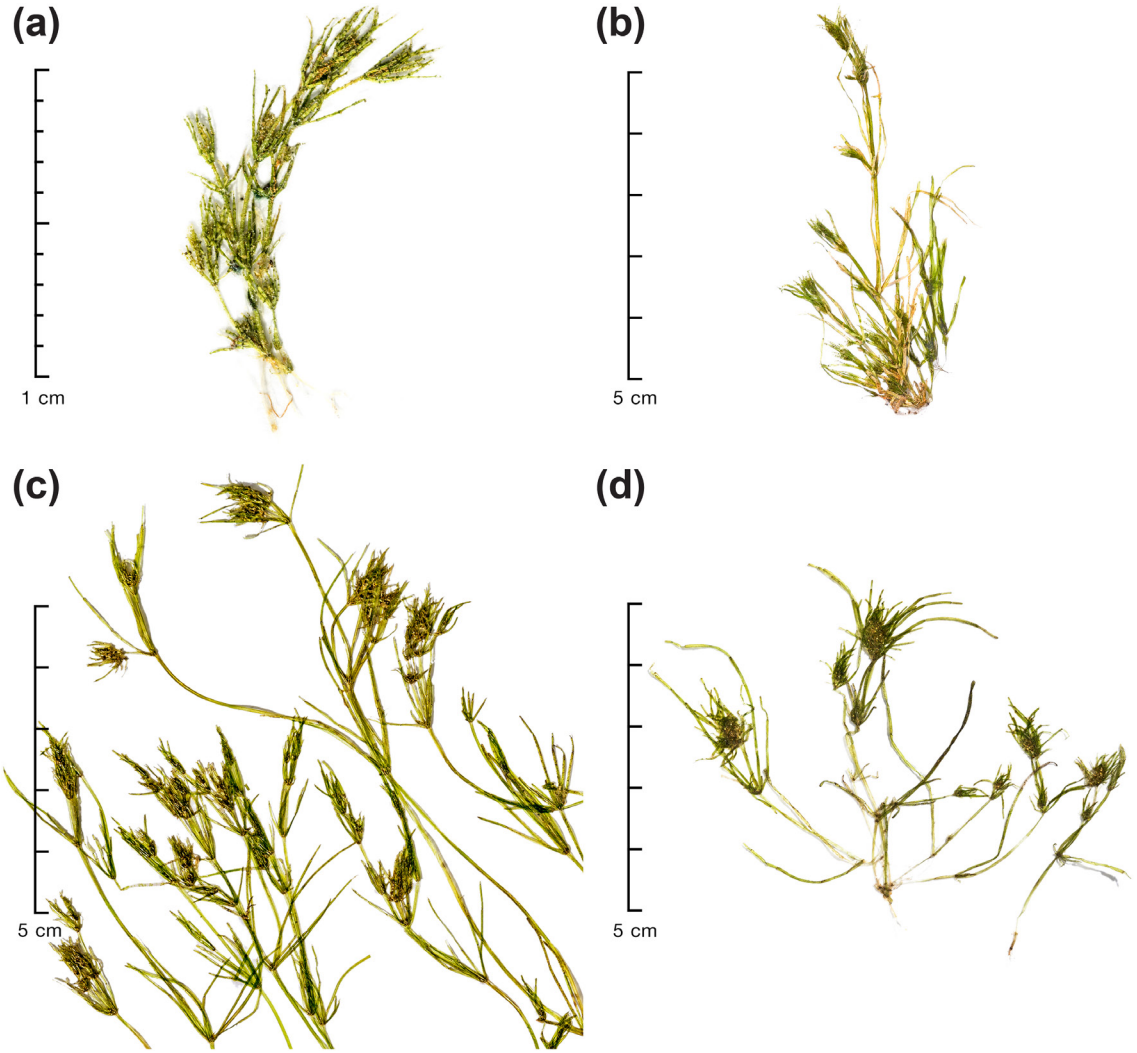


Figure 2. Preserved specimens of the four charophyte species new to Iceland: (a) *Chara aspera* from Lake Skúmsstaðavatn, south Iceland, (b) *Chara contraria* from Lake Vatnshlíðarvatn, north Iceland, (c) *Tolypella canadensis* from Lake Úlfsvatn, north Iceland, (d) *Tolypella glomerata* from Lake Vatnshlíðarvatn, north Iceland. Photos by Ragnar Th.

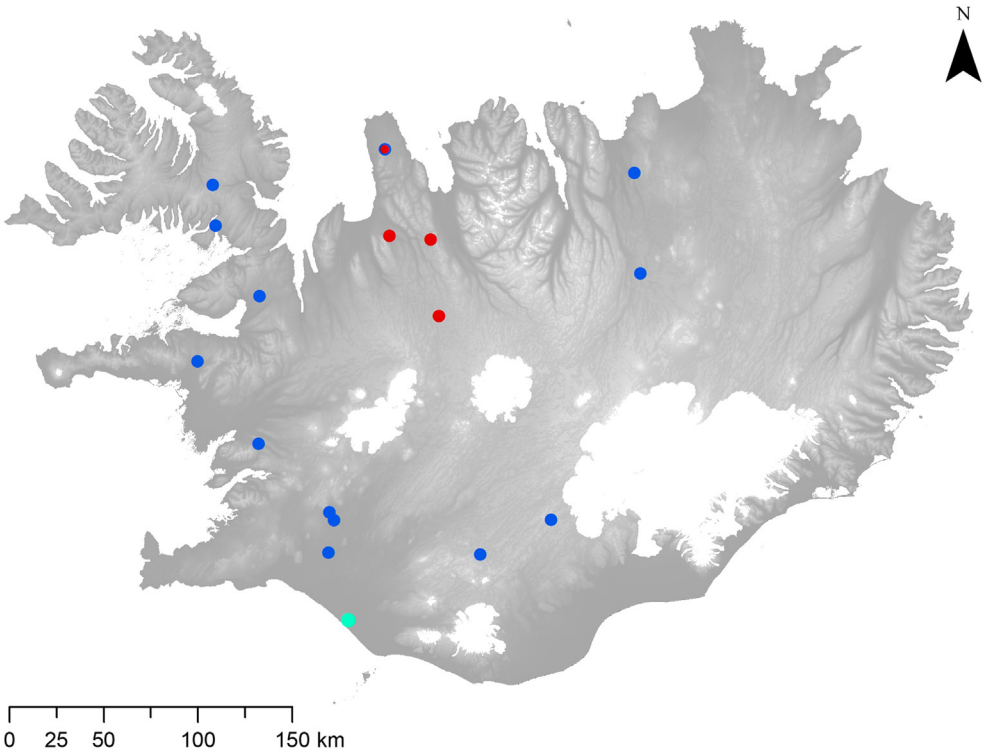


Figure 3. Distribution of *Chara aspera* (light blue dot), *Chara contraria* (red dots) and *Chara* spp. (blue dots) in Iceland. See also Supplementary material Appendix 1.

Chara contraria Braun ex Kützing * (Fig. 2b)

Short description of species. Up to 25 cm long and commonly encrusted, green to grey in colour (Langangen 2007). Axis up to 0.5 mm in diameter. Cortex diplostichous, tylacanthous. Spine-cells solitary, papillous, up to twice the stem diameter in length. Monoecious. Oogonia up to 1 mm long. Oospores black. Antheridia reddish-yellow, solitary, up to 0.45 mm in diameter (Langangen 2007).

Description of specimens from Iceland. Up to 14 cm long and not encrusted. Diplostichous, tylacanthous cortex. Spine-cells papillous. Branchlets ecorticate or cortex only on the lowest internodium. Sterile or poorly fertile, with small oogonia and antheridia up to 0.38 mm in diameter.

Occurrence in Iceland. Four lakes; Blönduvatn, Vatnshlíðarvatn, Langavatn, Svínavatn (Fig. 3, Table 1).

Lake depth of species occurrences. At 0.9–2.9 m depth (average 2.2 m), mostly on soft sediment bottom, also sand, gravel and cobbles.

Remarks. The four lakes where *Chara contraria* is found are at 126–488 m a.s.l. and of variable surface area and depth. The content of calcium in the lake water, where data are available, is prominently high (10 mg l^{-1}) compared to Icelandic lakes in general (Karst-Riddoch et al. 2009).

Chara globularis Thuiller

Short description of species. 5–50 cm long, commonly green in colour, but encrusted and grey in calcareous waters (Langangen 2007). Axis up to 0.5 mm in diameter. Cortex triplostichous, isostichous. Spine-cells lacking or papillous. Monoecious. Oogonia solitary and up to 1.2 mm long. Oospores black. Antheridia up to 0.5 mm in diameter. Known from both brackish water and freshwater (Langangen 2007).

Occurrence in Iceland. 14 localities (Fig. 4, Supplementary material Appendix 1).

Lake depth of species occurrences. At 0.2–2.7 m depth on soft sediment bottom (information available for five localities only).

Remarks. *Chara globularis* occurs mainly in lowland lakes and ponds, but throughout most parts of Iceland, although with only a single record in the east. Two old records are from tepid or warm springs; Laugarnes in Reykjavík and Reykhólar, WF (Supplementary material Appendix 1) but water temperature is not mentioned.

Chara virgata Kützing

Short description of species. 3–15 (30) cm long, encrusted or not, grey to green in colour (Langangen 2007). Axis up

Table 1. The 13 Icelandic lakes where the four charophyte species new to Iceland were found along with their environmental, physical and chemical characteristics. Based on Jensdóttir Fjeld et al. (2016), except for Kleifarvatn (unpublished data from 2005) and Víkurvatn. Measurements of calcium in lake water (Ca^{2+}) were taken in the period 1992–2003 and originate in Karst-Riddoch et al. (2009).

Lake	DMS Latitude	DMS Longitude	Sampling date dd/mm/yyyy	*Chara aspera*	*Chara contraria*	*Tolypella canadensis*	*Tolypella glomerata*	Altitude m	Lake area km^2	Z mean m	Lake temperature °C	pH	Specific conductivity µS cm^{-1}	P total mg l^{-1}	N total mg l^{-1}	Chl-a µg l^{-1}	Ca^{2+} mg l^{-1}
Ásbjarnarvötn, N	65°02′28.7″N	18°47′17.2″W	17/07/2013			×		777	0.6	0.7	8.9	9.54	76.6	0.024	0.23	2.4	4.3
Blönduvatn, N	65°09′15.1″N	19°31′45.5″W	18/07/2013		×	×		488	1.1	3.0	11.3	7.84	84.6	0.002	0.10	0.7	–
Frostastaðavatn, S	64°01′07.3″N	19°03′33.1″W	21/07/2012			×		570	2.6	4.5	13.3	9.12	91.4	0.006	0.09	1.2	4.4
Högnavatn, WF	65°44′47.0″N	22°09′54.7″W	20/08/2012			×		410	0.3	1.2	10.3	7.9	37.8	0.008	0.10	1.0	1.2
Kleifarvatn, W	63°55′32.9″N	21°58′27.5″W	15/07/2013			×		140	10	29	6.6	8.4	173	0.002	0.04	1.3	8.1
Langavatn, N	65°56′34.8″N	20°10′33.6″W	10/07/2013		×			214	3.1	2.2	11.5	8.05	90.9	0.002	0.07	1.7	–
Reyðarvatn, N	65°06′46.1″N	18°31′23.5″W	17/07/2013			×		707	1.0	0.6	9.4	7.49	53.8	0.008	0.11	1.0	6.8
Skúmsstaðavatn, S	63°41′57.1″N	20°28′31.8″W	23/07/2012	×				3	1.9	0.3	14.9	9.0	275	0.179	0.31	7.7	–
Svínavatn, N	65°31′58.8″N	20°06′18.4″W	10/07/2013		×		×	126	12	12.5	11.9	7.62	96.9	0.002	0.13	0.6	9.3
Úlfsvatn, N	64°53′34.1″N	20°35′11.4″W	20/07/2013			×	×	435	4.1	1.2	11.4	7.79	75.2	0.006	0.17	2.4	4.2
Vatnshlíðarvatn, N	65°31′02.3″N	19°37′47.6″W	11/07/2013		×		×	286	0.7	1.6	12.8	8.34	89.5	0.015	0.28	4.2	9.8
Vestara-Friðmundarvatn, N	65°17′34.4″N	19°51′14.0″W	18/07/2013			×		441	5.1	0.8	12.5	9.0	68.1	0.019	0.39	5.5	4.6
Víkurvatn, E	65°01′31.8″N	13°44′23.3″W	22/07/1959			×		276			–	–	–	–	–	–	–

to 0.5 mm in diameter. Cortex triplostichous, tylacanthous. Spine-cells solitary and papillous. Monoecious. Oogonia up to 1.1 mm long, and up to 0.7 mm in diameter. Oospores black. Antheridia up to 0.35 mm in diameter. Multicellular bulbils are often found (Langangen 2007).

Occurrence in Iceland. 18 localities (Fig. 4, Supplementary material Appendix 1).

Lake depth of species occurrences. At 0.1–10.2 m depth (average 2.6 m), mostly on soft sediment bottom, also in sand, gravel and peat.

Remarks. *Chara virgata* occurs mainly in lowland lakes and ponds, but throughout most parts of Iceland except for the east. An old record is from a peat pit, Silfurtún (Supplementary material Appendix 1).

Chara spp. L.

Occurrence in Iceland. 13 localities (Fig. 3, Supplementary material Appendix 1).

Remarks. These records were filed as unidentified *Chara* sp. No specimens were collected and thus species identification is not possible. In some instances these are the only records for the genus *Chara* at the locality.

Nitella flexilis (L.) C.A. Agardh

Short description of species. See description of *Nitella opaca*. *Nitella flexilis* differ from *Nitella opaca* by being monoecious. It is not possible to separate the two species in sterile condition (Langangen 2007).

Occurrence in Iceland. 14 localities (Fig. 5a, Supplementary material Appendix 1).

Lake depth of species occurrences. At 0.6–18.3 m depth (average 4.2 m), primarily on soft sediment bottom, also in sand and gravel.

Remarks. *Nitella flexilis* occurs in lowland and highland lakes (20–662 m a.s.l.) in most parts of the country (Supplementary material Appendix 1).

Nitella opaca (C.A. Agardh ex Bruzelius) C.A. Agardh

Short description of species. 5–50 cm long and green (Langangen 2007). Axis up to 1 mm in diameter. Branchlets simple or once divided with one-celled end segments. Dioecious. Oogonia solitary or geminate, up to 0.7 mm long and 0.6 mm in diameter. Oospores chestnut brown to black in colour. Antheridia up to 0.8 mm in diameter (Langangen 2007).

Occurrence in Iceland. 40 localities (Fig. 5a, Supplementary material Appendix 1).

Lake depth of species occurrences. At 0.1–20 m depth (average 2.6 m), primarily on soft sediment bottom, also in sand, gravel and peat.

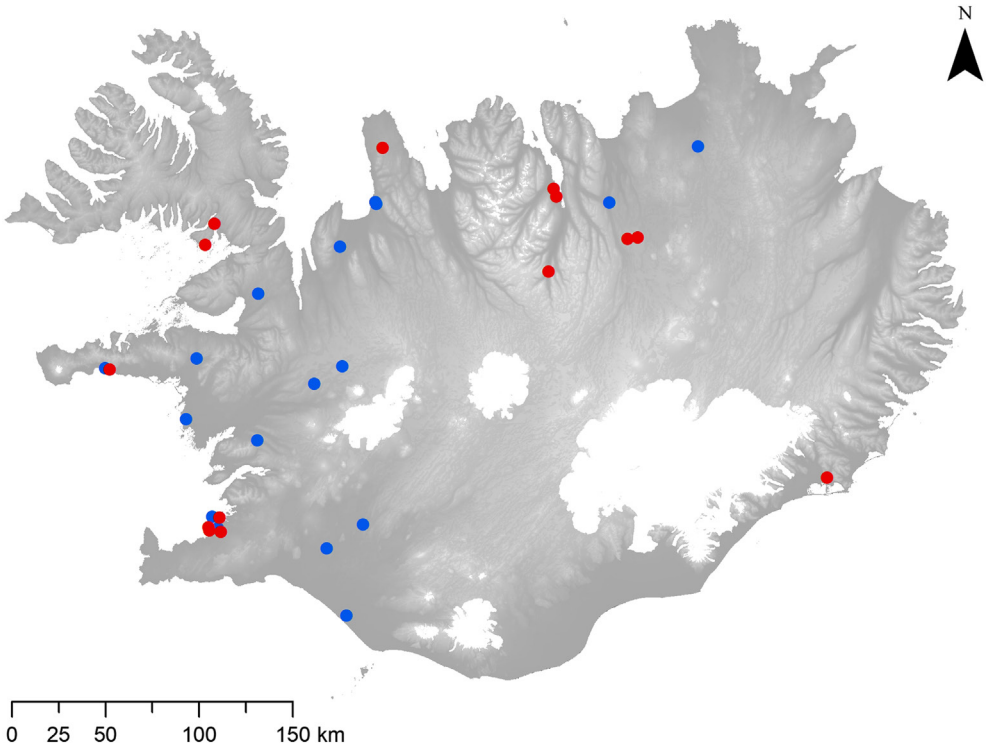


Figure 4. Distribution of *Chara globularis* (red dots) and *Chara virgata* (blue dots) in Iceland. See also Supplementary material Appendix 1.

Remarks. *Nitella opaca* occurs in lowland and highland lakes (3–777 m a.s.l.) in all parts of the country (Supplementary material Appendix 1).

Nitella opaca vel *flexilis*

Short description of species. These are sterile specimens of either *Nitella opaca* or *N. flexilis*. The two species cannot be separated if sterile as their reproductive state and gametangia size are the clearest distinguishing features between these taxa (Bryant and Stewart 2002, Langangen 2007).

Occurrence in Iceland. 80 localities (Fig. 5b, Supplementary material Appendix 1).

Lake depth of species occurrences. At 0.05–24 m (average 4.7 m), primarily on soft sediment bottom, also in sand, gravel and peat.

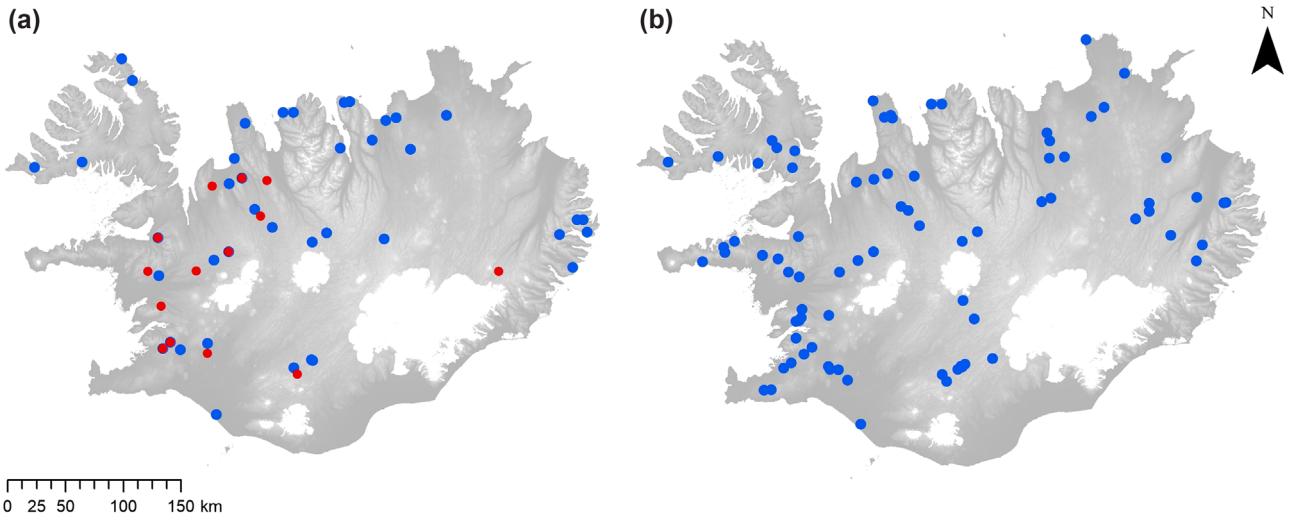


Figure 5. Distribution of (a) *Nitella flexilis* (red dots) and *N. opaca* (blue dots), (b) *Nitella opaca* vel *flexilis* in Iceland. See also Supplementary material Appendix 1.

Remarks. The taxon occurs in lowland and highland lakes (0–777 m a.s.l.) in all parts of the country (Supplementary material Appendix 1).

Tolypella canadensis Sawa * (Fig. 2c)

Short description of species. 4–20 cm long (Langangen 2007). Axis up to 0.4 mm in diameter. Plants green, unencrusted and *Nitella*-like. Sterile branchlets simple, with 2–3 segments. Fertile branchlets commonly have gametangia in dense heads. End cells forming a mucro (an important character). Monoecious. Oogonia 1–4 together, up to 0.7 mm long and often stalked. Oospores brown. Antheridia up to 0.4 mm in diameter and stalked. Two forms were described by Langangen (1993): f. *glomdalensis*, *Nitella*-like and up to 27 cm long, and f. *hasslowi* which is up to 10 cm long, in tufted colonies (Langangen 2007).

Description of specimens from Iceland. The common form in Iceland is f. *hasslowi* with specimens up to 8 cm long, 3–5 plants together. In Úlfsvatn the specimens were up to 25 cm long (f. *glomdalensis*) and with axis up to 1 mm in diameter. The end cells are mucronate (pointed). Sterile branchlets long, once divided, of 4–5 segments. Fertile branchlets small, short. Monoecious. Oogonia up to 0.50 mm long and stalked. Oospores up to 0.40 mm long, brown to dark brown. Antheridia up to 0.35 mm in diameter and stalked.

Occurrence in Iceland. Nine lakes; Ásbjarnarvötn, Blönduvatn, Frostastaðavatn, Högnavatn, Kleifarvatn, Reyðarvatn, Úlfsvatn, Vestara-Friðmundarvatn, Víkurvatn (Fig. 6, Table 1).

Lake depth of species occurrences. At 0.4–4.2 m depth (average 1.6 m), but at around 6 m depth in Kleifarvatn. Substrate at stations mostly soft sediment, also sand.

Remarks. The species is found in remote and oligotrophic lakes, primarily in the highlands (276–777 m a.s.l.), except for Lake Kleifarvatn, at 140 m a.s.l., a large lake mainly fed by cold groundwater springs.

Tolypella glomerata (Desvaux) Leonhardi * (Fig. 2d)

Short description of species. 10–20 cm long, green or grey if encrusted (Langangen 2007). Axis up to 1 mm in diameter, without cortex. Sterile branchlets simple, 3–5 celled. End cells rounded. Some whorls forming heads. Monoecious. Oogonia 1–3 together, stalked and up to 0.6 mm long. Oospores less than 0.4 mm long, brown to dark brown. Antheridia up to 0.4 mm in diameter (Langangen 2007).

Description of specimens from Iceland. Up to 7 cm long, 3–5 plants together. Axis up to 1 mm in diameter. End cells rounded. Sterile branchlets long, once divided, of 4–5 segments. Fertile branchlets small, short. Monoecious. Specimens from Svínavatn and Vatnshlíðarvatn were richly fertile. Oogonia up to 0.5 mm and oospores up to 0.36 mm long, brown. Antheridia up to 0.3 mm in diameter, stalked.

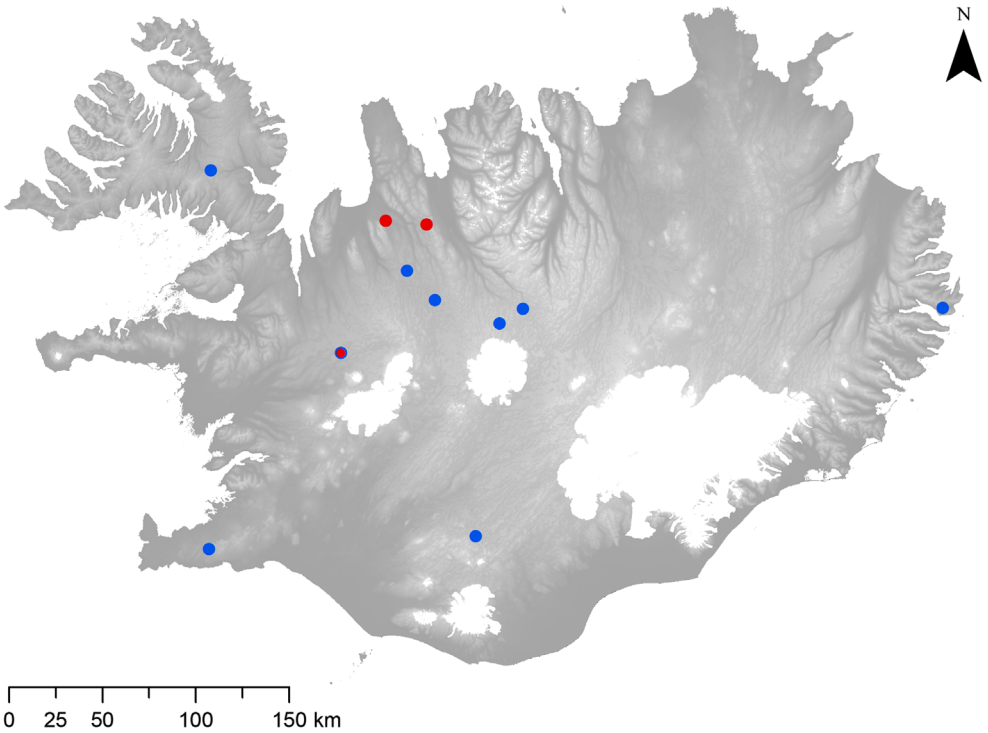


Figure 6. Distribution of *Tolypella canadensis* (blue dots) and *Tolypella glomerata* (red dots) in Iceland. See also Supplementary material Appendix 1.

Occurrence in Iceland. Three lakes; Svínavatn, Úlfsvatn, Vatnshlíðarvatn (Fig. 6, Table 1).

Lake depth of species occurrences. At 1.1–2.1 m depth on a substrate of soft sediment.

Remarks. The three lakes where *T. glomerata* is found are at 126–435 m a.s.l. and of variable area and depth. The content of calcium in the lake water is relatively high compared to Icelandic lakes in general (Karst-Riddoch et al. 2009).

Discussion

In this article we report the findings of four new species of charophytes in Iceland: *Chara aspera*, *C. contraria*, *Tolypella canadensis* and *T. glomerata*. Combined with earlier published findings of charophyte species, i.e. *Nitella opaca*, *N. flexilis*, *Chara globularis* and *C. virgata* (Langangen 1972, Hallgrímsson 2007) the number of observed species of charophytes in Iceland is now eight.

Charophytes are widespread in Iceland according to the present compilation of records revealing 126 localities (Fig. 1). The four new species were mainly found in the western part of Iceland (Fig. 3, 6), at localities surveyed in 2012 and 2013. In that survey the primary focus was on the occurrence and distribution of macrophytes, i.e. charophytes and vascular plants. To get at better knowledge of the full distribution of Icelandic charophytes a similar survey should also be done in the eastern part of the country.

The four new charophyte species reported here have a wide distribution range, either found worldwide or throughout the northern hemisphere.

Chara aspera is found in the northern hemisphere with its main distribution in Europe (Langangen 2007). It is widespread in the Nordic countries and the British Isles (Moore 1986, Langangen 2007). The species has not been reported from Greenland (Langangen et al. 1996) but there are scattered records from North America (Wood 1965, Mann 1989, Mann and Nambudiri 2005). The single Icelandic locality is a shallow lake near the sea with relatively high pH and specific conductivity, conditions which reflect the known habitat preferences of the species in Europe, i.e. limerich and brackish areas (Langangen 2007). The lake and its surroundings are an important staging area for waterbirds like whooper swan *Cygnus cygnus* and geese *Anser anser* and *Anser brachyrhynchus* (Skarphéðinsson et al. 2016), and a documented stop-over site for white-fronted goose *Anser albifrons flavirostris* on its way between the breeding areas in west Greenland and the wintering areas in Britain and Ireland (Francis and Fox 1987, Fox et al. 1999).

Chara contraria is a cosmopolitian species (Corillion 1957), frequent in calcareous waters throughout Europe and common in the Nordic countries and the British Isles (Bryant and Stewart 2002, Langangen 2007). In the Nearctic, the species is reported from West Greenland (Langangen et al. 1996) and Canada from Quebec and insular Newfoundland (Robinson 1906, Mann 1989). In Iceland, limestone areas do not occur, however, the species was found in lakes with prominently high content of calcium.

Tolypella canadensis has a northern circumpolar distribution and is typical for oligotrophic lakes with low water temperature (Langangen and Zhakova 2002, Langangen 2007, Romanov and Kopyrina 2016). It has been found in northern Fennoscandia (Langangen 2007), Russia (Langangen and Zhakova 2002, Romanov and Kopyrina 2016), Greenland (Langangen et al. 1996), Canada (Sawa 1973), and scattered in the USA (Langangen 2001, Perez 2014). In Iceland, the species occurs in remote and oligotrophic highland lakes in association with *Nitella opaca* and *N. flexilis*, which concurs with the known habitat preferences of the species.

Tolypella glomerata is a cosmopolitan species, frequent in alkaline waters, widespread in central Europe and North America (Corillion 1957, Mann 1994, Krause 1997). The species is scattered in the British Isles and is concidered nationally scarce (Bryant and Stewart 2002, Stewart 2004). In the Nordic countries it is restricted to southern Sweden and Denmark, and has disappeared from many previous sites in both countries (Blindow 2009). These have been considered the northern limits of the distribution in Europe (Langangen 2007). In Iceland the species was found in lakes of various types with relatively high content of calcium and along with *Chara contraria* in two lakes out of three. The new find of *T. glomerata* in Iceland is at present the northernmost limit of the distribution (Fig. 7).

The four most frequently encountered species in Iceland, i.e. *Chara globularis*, *C. virgata*, *Nitella flexilis* and *N. opaca*, are all cosmopolitan, and widespread in Europe, including the Nordic countries and the British Isles (Bryant and Stewart 2002, Langangen 2007, Scribailo and Alix 2010). In Europe these species are common in a wide range of freshwater and brackish habitats (Langangen 2007). As such, they may be more likely to encounter possible agents of dispersal than other species, and are also more likely to succeed in new habitats. The two *Nitella* species seem to prefer clear oligotrophic, often high-mountain lakes (Langangen 2007), which is reflected in the Icelandic occurrences. Furthermore, *Nitella opaca* is considered a typical deep-water species (Langangen 2007, Urbaniak and Gabka 2014), in Iceland reaching down to a depth of 20 m or more, and forming dense underwater mats, sometimes along with *Tolypella canadensis*.

It is notable that among the five taxa of *Chara* there is only one record in east Iceland (*C. globularis*) according to the present compilation of records. This could partly be explained by the majority of sampled localities in the east being above 330 m a.s.l., and partly by lack of research in suitable habitats for *Chara* in the area.

Compared to the neighbouring countries, the occurrence of eight charophyte species in Iceland is low. In the the Nordic countries, charophytes are represented with 20 species in Finland, 26 in Norway and Denmark and 35 species in Sweden (Langangen et al. 2002, Langangen 2007). In the British Isles 30 species are recorded (Moore 1986, Bryant

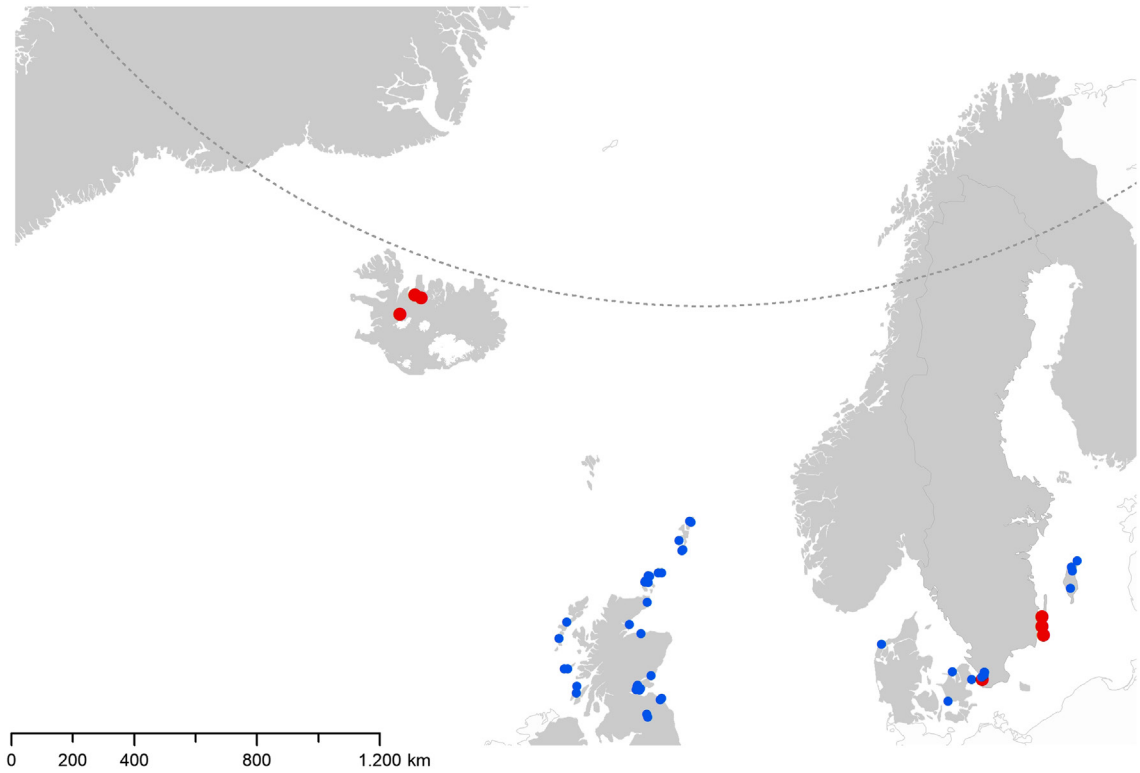


Figure 7. Present distribution of *Tolypella glomerata* in the northernmost part of Europe. Based on this study, Olsen (1944), Blindow (2009) and NBN Atlas website. Red dots denote recent and confirmed records. Blue dots denote old or unconfirmed records, i.e. finds in Denmark prior to 1940, in Sweden prior to 1961 and unconfirmed records from Scotland according to the NBN Atlas website.

and Stewart 2002), and 39 species in Canada (Scribailo and Alix 2010). However, in the Faroe Islands and Greenland the number of charophyte species is similar to that found in Iceland, i.e. 6 and 10 species respectively (Langangen 1996, Langangen et al. 1996). This result is in line with previous findings for the Icelandic flora (Þórhallsdóttir 2010), as well as the freshwater fauna (Gíslason 2005, Hrafnsdottir 2005) and terrestrial mammals (Hersteinsson 2004), and can be explained by the country's geographically isolated location in the North Atlantic Ocean.

When considering possible ways of dispersal of charophytes to Iceland, long-distance transfer with migrating waterbirds seems to be the most plausible way for these submerged organisms. Waterbirds are considered major dispersers of aquatic organisms, including charophytes, as they ingest and transport propagules of plants, algae and invertebrates in their guts, and attached to their bodies (Imahori 1954, Proctor 1962, 1967, 1968, Vlaming and Proctor 1968, Figuerola and Green 2002, Charalambidou and Santamaría 2005). Furthermore, both waterfowls (Anatidae) and waders (Charadridae, Scolopacidae) migrate over long distances and therefore have the capacity for long-distance dispersal.

Every spring migrating birds arrive at their breeding grounds in Iceland predominantly from Europe (Petersen 1998). Among waterbirds which may be considered possible vectors for long-distance and frequent dispersal of charophytes are geese *Anser anser* and *Anser brachyrhynchus*, whooper swan *Cygnus cygnus* and ducks, e.g. *Anas crecca*, *Aythya fuligula* and *Aythya marila*. Furthermore, Iceland is an important stopover site for many passage migrants, like *Anser albifrons flavirostris*, *Branta leucopsis* and *Branta bernicla hrota*, on their way between their wintering areas in Scotland and Ireland and the breeding areas in Greenland and NE-Canada (Fox et al. 1999, Guðmundsson 2009).

Other ways of dispersal of charophytes to Icelandic freshwaters might be by unvoluntary introduction connected with human activities in freshwaters, e.g. by fishing nets which the early settlers brought along or by angling gear in more recent times. However, this would only be sporadic introductions and we believe that frequent and continuous introductions with migrating waterbirds are more likely.

Additional charophyte species can be expected in Iceland with more research. Two possible candidates are *Chara canescens* and *Chara baltica*, both found in coastal areas in northern Europe, Greenland and North America (Langangen 2007). These species live in brackish water which is a poorly investigated habitat in Iceland as far charophytes are concerned.

Acknowledgements – We wish to thank Irmgard Blindow for the confirmation of *Tolypella glomerata*. Thanks are due to Theo Bakker, John Bruinsma and Klaus van de Weyer for identifying and reporting the find of *T. canadensis* from Lake Kleifarvatn, W-Iceland on 15 July 2013. Special thanks to the Icelandic Institute

of Natural History for loan of herbaria specimens (ICEL, AMNH) and for providing data on unpublished records on charophytes. The distribution maps are based on geographic data from the National Land Survey of Iceland (<www.lmi.is>). Thanks are due to Þóra Björg Andrésdóttir for producing the distribution maps.
Funding – The survey on macrophytes in Icelandic lakes was partly supported by the European Union's IPA-fund.

References

Blindow, I. 2009. Åtgärdsprogram för hotade kransalger: arter i småvatten/periodiska vatten 2008–2011. – Naturvårdsverket. Rapport 5849, in Swedish with an English summary.

Blindow, I. et al. 2007. Bestämningsnyckel för kransalger i Sverige. – Sv. Bot. Tidskr. 101: 165–220, in Swedish with an English abstract.

Bryant, J. A. and Stewart, N. F. 2002. Order Charales. – In: John, D. M. et al. (eds), The freshwater algal flora of the British Isles: an identification guide to freshwater and terrestrial algae. Cambridge Univ. Press, pp. 593–612.

Charalambidou, I. and Santamaría, L. 2005. Field evidence for the potential of waterbirds as dispersers of aquatic organisms. – Wetlands 25: 252–258.

Corillion, R. 1957. Les charophycées de France et d'Europe Occidentale. – Travaux du Lab. Bot. Fac. Scienc. D'Angers.

Einarsson, M. Á. 1984. Climate of Iceland. – In: van Loon, H. (ed.), Climates of the oceans. Elsevier, pp. 673–697.

Figuerola, J. and Green, A. J. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. – Freshwater Biol. 47: 483–494.

Fox, A. D. et al. 1999. Phenology and distribution of Greenland white-fronted geese *Anser albifrons flavirostris* staging in Iceland. – Wildfowl 50: 29–43.

Francis, I. S. and Fox, A. D. 1987. Spring migration of Greenland white-fronted geese through Iceland. – Wildfowl 38: 7–12.

Georgsdóttir, G. I. et al. 2016. Vistgerðir í fjöru. – In: Ottósson, J. G. et al. (eds), Vistgerðir á Íslandi. Fjölrit Náttúrufræðistofnunar nr. 54, pp. 170–213, in Icelandic with an extended English summary.

Gíslason, G. M. 2005. The origin of the freshwater fauna of the North-Atlantic Islands. Present distribution in relation to climate and possible migration routes. – Verh. Internat. Verein. Limnol. 29: 198–203.

Guðmundsson, G. A. 2009. Fargestir á Íslandi. – Bliki 30: 1–8, in Icelandic with an English summary.

Hallgrímsson, H. 1975. Íslenskir kransþörungar (Charophyta). – Náttúrufræðingurinn 45: 142–150, in Icelandic with an English summary.

Hallgrímsson, H. 2007. Þörungatal. Skrá yfir vatna- og landþörunga á Íslandi samkvæmt heimildum. – Fjölrit Náttúrufræðistofnunar nr. 48, in Icelandic with an English abstract.

Hersteinsson, P. (ed) 2004. Íslensk spendýr. – Vaka-Helgafell.

Hrafnsdottir, Th. 2005. Diptera 2 (Chironomidae). – Zool. Iceland III 48b: 1–169.

Imahori, K. 1954. Ecology, phytogeography and taxonomy of Japanese Charophyta. – Kanazawa Univ.

Jensdóttir Fjeld, M. et al. 2016. Vistgerðir í ferskvatni. – In: Ottósson, J. G. et al. (eds.), Vistgerðir á Íslandi. Fjölrit Náttúrufræðistofnunar nr. 54, pp. 170–213, in Icelandic with an extended English summary.

Jeppesen, E. et al. 2010. Chapter 6. Interaction of climate change and eutrophication. – In: Kernan, M. et al. (eds), Climate change impacts on freshwater ecosystems. Wiley-Blackwell, pp. 119–151.

Kairesalo, T. et al. 1992. Metabolism and community dynamics within *Nitella opaca* (Charophyceae) beds in Thingvallavatn. – Oikos 64: 241–256.

Karst-Riddoch, T. et al. 2009. Relationships between freshwater sedimentary diatoms and environmental variables in Subarctic Icelandic lakes. – Fund. Appl. Limnol. 175: 1–28.

Krause, W. 1997. Charales (Charophyceae). – In: Süsswasserflora von Mitteleuropa, bd. 18. Gustav Fischer Verlag.

Langangen, A. 1972. The charophytes of Iceland. – Astarte 5: 27–31.

Langangen, A. 1993. *Tolypella canadensis*, a charophyte new to the European flora. – Cryptogamie, Algol. 14: 221–231.

Langangen, A. 1996. Some charales (Chlorophyta, Charophyceae) from the Faroes. – Cryptogam. Algol. 17: 259–263.

Langangen, A. 2001. Some charophytes (Chlorophyta, Charales) from Alaska, USA. – Acta Mus. Nat. Pragae B Hist. Nat. 56: 51–56.

Langangen, A. 2007. Charophytes of the Nordic countries. – Saeculum ANS.

Langangen, A. and Zhakova, L. 2002. *Tolypella canadensis* Sawa (Charales), a charophyte new to the flora of Russia, with remarks on its ecology and distribution. – J. Nat. Mus. Nat. Hist. Ser. 171: 85–88.

Langangen, A. et al. 1996. The charophytes of Greenland. – Cryptogam. Algol. 17: 239–257.

Langangen, A. et al. 2002. The charophytes of Finland. – Memoranda Soc. Fauna Flora Fenn. 8: 17–48.

Malmquist, H. J. et al. 2005. Information about the ESIL-project: ecological survey of Icelandic lakes: a standardized database. – <www.researchgate.net/publication/242543198_ECOLOGICAL_SURVEY_OF_ICELANDIC_LAKES_A_STANDARDIZED_DATABASE_ESIL-Project_teamfounders_and_board>, accessed 25 January 2019.

Mann, H. 1989. Charophytes of insular Newfoundland. – Can. Field. Nat. 10: 34–42.

Mann, H. 1994. The genus *Tolypella* (Characeae) in insular Newfoundland. – Can. Field. Nat. 108: 297–304.

Mann, H. and Nambudiri, E. M. V. 2005. Charophytes of insular Newfoundland II: *Chara evoluta* and *Chara canescens*. – Can. Field. Nat. 119: 26–37.

Moore, J. A. 1986. Charophytes of Great Britain and Ireland. – B.S.B.I. Handbook no. 5.

NBN Atlas website. – <https://species.nbnatlas.org/species/NBNSYS0000039876>, accessed 14 February 2019.

Olsen, S. 1944. Danish Charophyta. – Det kongelige danske videnskabernes selskab, Biologiske skrifter 3: 1–240.

Ottósson, J. G. et al. (eds) 2016. Vistgerðir á Íslandi. – Fjölrit Náttúrufræðistofnunar nr. 54, in Icelandic with an extended English summary.

Perez, W. 2014. A systematic revision of North American *Tolypella* A. Braun (Charophyceae, Charophyta). – CUNY Academic Works. <https://academicworks.cuny.edu/gc_etds/269>.

Petersen, Æ. 1998. Íslenskir fuglar. – Vaka-Helgafell.

Proctor, V. W. 1962. Viability of *Chara* oospores taken from migratory waterbirds. – Ecology 43: 528–529.

Proctor, V. W. 1967. Storage and germination of *Chara* oospores. – J. Phycol. 3: 90–92.

Proctor, V. W. 1968. Long-distance dispersal of seeds by retention in digestive tract in birds. – Science 160: 321–322.
Robinson, C. B. 1906. The Chareae of North America. – Bull. N. Y. Bot. Gard. 4: 244–308.
Romanov, R. E. and Kopyrina, L. I. 2016. *Tolypella canadensis* (Charales, Charophyceae) in Asia: final evidence of its circumpolar distribution. – Nova Hedwigia 102: 423–427.
Sæmundsson, K. 1979. Outline of the geology of Iceland. – Jökull 29: 7–28.
Sawa, T. 1973. Two new species of *Tolypella* (Characeae) from North America. – J. Phycol. 9: 472–482.
Scribailo, R. W. and Alix, M. S. 2010. A checklist of North American Characeae. – Charophytes 2: 38–52.
Skarphéðinsson, K. H. et al. 2016. Mikilvæg fuglasvæði á Íslandi. – Fjölrit Náttúrufræðistofnunar nr. 55, in Icelandic with an extended English summary.

Supplementary material (available online as Appendix njb-02111 at <www.nordicjbotany.org/appendix/njb-02111>). Appendix 1.

Stewart, N. F. 2004. Important stonewort areas of the United Kingdom. An assessment of the best areas for stoneworts in the United Kingdom (summary). – Plantlife Int.
Urbaniak, J. and Gabka, M. 2014. Polish charophytes. An illustrated guide to identification. – Wroclaw Univ. Environ. Life Sci.
Vlaming, V. L. de and Proctor, V. W. 1968. Dispersal of aquatic organisms: viability of seeds recovered from the droppings of captive killdeer and mallard ducks. – Am. J. Bot. 55: 20–26.
Wood, R. D. 1965. Monograph of the Characeae. – In: Wood, R. D. and Imahori, K. (eds), A revision of the Characeae, Vol. 1. Cramer, pp. 1–904.
Þórhallsdóttir, Þ. E. 2010. Um tegundaauðgi og einkenni íslensku flórunnar: Hvað segir samanburður við aðrar eyjur um sögu hennar og aldur? – Náttúrufræðingurinn 79: 102–110.