

# Charophytes of Insular Newfoundland II: *Chara evoluta* and *Chara canescens*

HENRY MANN and E. M. V. NAMBU DIRI

Environmental Science/Biology, Sir Wilfred Grenfell College, Memorial University of Newfoundland, Corner Brook, Newfoundland and Labrador A2H 6P9 Canada

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The rare Newfoundland disjuncts *Chara evoluta* and *Chara canescens* are compared morphologically, ecologically, and geographically. Although very similar morphologically, they can readily be distinguished by their monoecious/dioecious nature, cortical cell features and coronula size. Ecological differences are more subtle and difficult to quantify. In Newfoundland the two species are restricted to coastal saline lagoons in the southwest region of the Island, with *C. evoluta* exhibiting an association with *Chara aspera*. The flora and fauna of these unique habitats are poorly documented even though it is known that they are associated with other rare species including the Piping Plover and the Banded Killifish. Consideration of some degree of protection as special habitats within the provincial ecological reserve strategy is suggested. An updated key to all species of charophytes known to inhabit Newfoundland and Labrador is included, and a brief overview of their ecological distributions is provided.

Key Words: charophytes, Characeae, *Chara evoluta*, *Chara canescens*, *Chara aspera*, coastal lagoons, Newfoundland.

The first survey of the charophytes of Newfoundland (Mann 1989) described ten taxa, three of *Nitella* and seven of *Chara*. Distribution maps and a key were provided. Subsequently *Tolypella glomerata* (Desv.) Leonh. was reported from the Great Northern Peninsula (Mann 1994a). In 1995 *Chara evoluta* T. F. Allen was discovered as well as a second site for *Chara canescens* Desv. & Lois. in Lois, and these were added to the list for Insular Newfoundland (Mann 1998, 2000\*; Mann et al. 1999). A search of saline coastal lagoons and estuaries on the southwest coast of Newfoundland identified several more sites for *C. evoluta*, but no more for *C. canescens*. Information, including morphological, taxonomic, geographical and ecological, has never been published for this disjunct population of *C. evoluta* in Newfoundland. Because the two species are so similar morphologically and ecologically, and because both *C. evoluta* and *C. canescens* are considered rare species in Newfoundland, eastern Canada, and *C. evoluta* in eastern North America, the two will be treated together in a comparative way. They also need to be distinguished and reported as separate taxa, a problem which arose since the publication of Wood's (1965) monograph where they were merged under *C. canescens*, a concept which is no longer defensible (Proctor 1980). Due to the disjunct nature of Newfoundland populations it is important to determine whether local populations exhibit any features differing from those elsewhere in North America. This is also necessary for future studies comparing similar Asian taxa. T. F. Allen's (1882) original description of *C. evoluta* and those of Robinson (1906), and Wood's chosen lectotype in Wood and Imahori (1964) are the basic sources for this species supplemented with North American specimens on loan from

the New York Botanical Garden (NY). It may be assumed that features not here described or elaborated upon are consistent with those in the above reports.

A new key is prepared incorporating species not included in the original work (Mann 1989) and based on current concepts of charophyte taxonomy and nomenclature.

Material of *C. evoluta* and *C. canescens* is housed in the Sir Wilfred Grenfell College Herbarium (SWGCH) as liquid preserved specimens and herbarium sheets. Voucher specimens have been deposited with the Newfoundland Museum (NFM), the Canadian Museum of Nature, Ottawa (CAN), and the Phycological Herbarium of Memorial University (NFLD), (*C. evoluta*, Mann numbers 228, 282; *C. canescens*, Mann number 229). Herbarium acronyms are as in Holmgren et al. (1990), except for the Sir Wilfred Grenfell College (SWGCH) which is not yet listed. Vascular plant nomenclature follows Crow and Helquist (2000), that of invertebrate groups, Barnes (1994), and fishes, Scott and Crossman (1973). Methods for gametangial measurements and illustrations are consistent with those described in Mann (1994b). Spore preparation for the SEM followed the method of John and Moore (1987).

## Study Area and Habitat

The study area where *C. evoluta* and *C. canescens* are located includes south-western Newfoundland extending from Port aux Basques in the south and northward to the Port au Port Peninsula (Figure 1). All sites are coastal saline lagoons or salt ponds, sometimes designated as "barachois" locally. The southernmost cluster of five lagoons can be located on Canadian Topographic Map 11-0/11, "Port aux Basques". Codroy Estuary Pond has UTM map co-ordinates of 314E

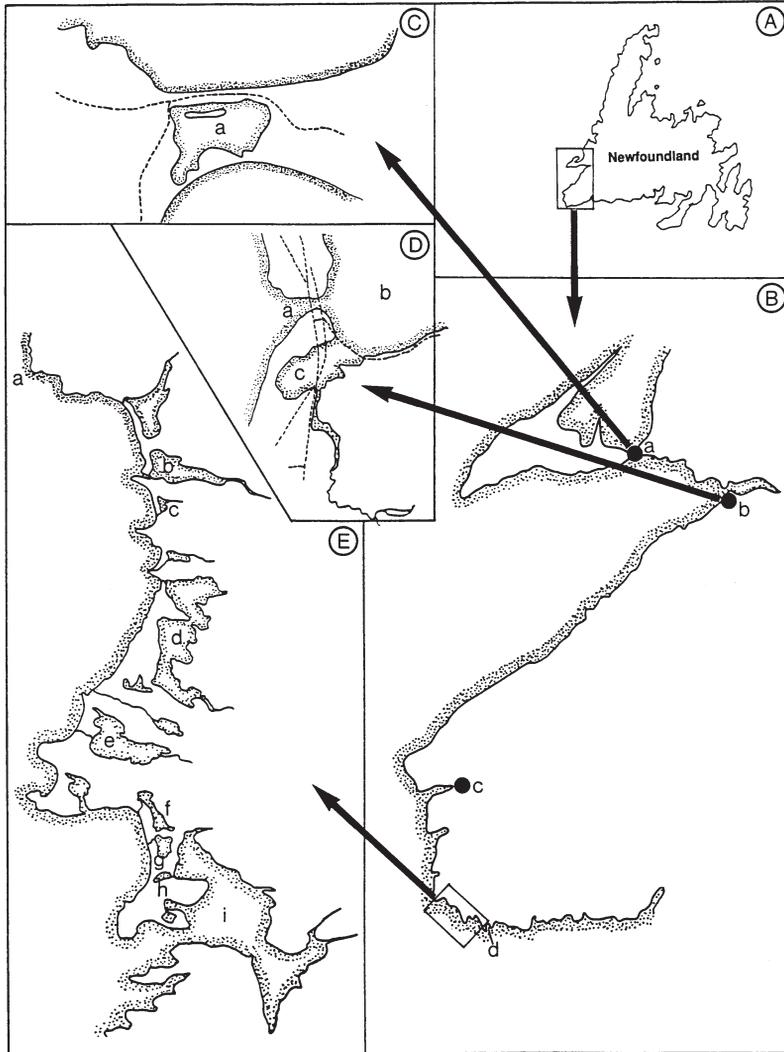


FIGURE 1. Location of collection sites in Insular Newfoundland.

- A. Study area of southwestern Newfoundland inset.
- B. Coastal Newfoundland from Port aux Basques to the Port au Port Peninsula: (a) Gravels Pond, (b) St. George's Pond, (c) Codroy Estuary Pond, (d) Port aux Basques.
- C. Isthmus of the Port au Port Peninsula: (a) Gravels Pond. Dashed lines indicate roads.
- D. St. George's Bay: (a) Main Gut, (b) Estuary, (c) St. George's Pond. Dashed lines indicate roads and a railway embankment.
- E. Coastal Newfoundland from Cape Ray to Grand Bay: (a) Cape Ray, (b) Little Barachois, (c) Osmond Pond, (d) Big Barachois, (e) Rocky Barachois, (f) Salt Water Pond, (g) Second Pond, (h) First Pond, (i) Grand Bay.

and 018N on map 11-0/14, "Codroy". The more northern Gravels Pond is indicated on map 12-B/10, "Stephenville", and the St. George's Lagoon on map 12-B/8, "Main Gut".

The southern five lagoons from Grand Bay to Cape Ray Cove are formed behind sandy beach and dune deposits. All have breachways to the ocean, but the channels are not active during most of the year and no

seawater exchange is apparent normally, except for First Pond where exchange may occur more often. Outflow occurs during spring runoff, but there is evidence that some saltwater influx occurs to maintain their brackish nature. All of these ponds drain freshwater from inland peatlands and heath barrens. The small Codroy Estuary Pond is in the floodplain of the estuary, but is isolated from estuarine water except

during spring flooding. St. George's Lagoon is separated from the ocean by a sand barrier of 100 meters in width. Originally connected to the estuary, it is now separated by highway and railway embankments, but still receives some influx via culverts where saline estuarine water intermixes with the freshwaters of Little River draining the interior peatlands. Gravels Pond in the narrow isthmus of the Port au Port Peninsula is separated on either side from the ocean by a narrow cobble/shingle barrier.

Coastal lagoons in this study are non-tidal, but only semi-isolated systems receiving some periodic seawater influx. As such, the salinity of their waters varies with the seasons and is also subject to rapid fluctuations because of heavy rains, storm surges, salt spray, and perhaps some percolation through the barrier as possibly occurs in Gravels Pond. Because of irregular sporadic episodes of varying intensity they are habitats extremely difficult to characterize and compare other than through intensive long-term monitoring (Barnes 1980). In 1995 Gravels Pond ranged in specific conductance ( $\mu\text{mhos} = \mu \text{ siemens}$ ) from 10 000 in July, 15 200 in August, to 22 200 in September. According to the salinity scale of Cowardin et al. (1979), Gravels Pond is in the brackish mesohaline category. First Pond, Second Pond, and Saltwater Pond exhibited single readings of 26 400, 18 000, and 27 000  $\mu\text{mhos}$  respectively in July 1999, also categorizing them as mesohaline. St. George's Lagoon had the lowest readings ranging from 400 to 7500  $\mu\text{mhos}$  characterizing it as fresh to oligohaline. Internally, lagoons are often not uniform with regard to salinity, possessing zones depending on the location and volume of freshwater entry as well as periodic marine influx (Barnes 1980).

The Newfoundland lagoons which are separated from the ocean by a sandy barrier have extensive shallow sandy-bottomed areas on their seaward sides due to windblown sand drift from the outer beaches and gradually deepen to several meters on their landward sides. This produces an unstable sandy shifting substrate subject to wave action where vascular vegetation is sparse or absent, but to some extent successfully colonized by charophytes. On these shallow flats, charophytes form open scattered stands where individual plants tend to be tiny, only a few centimeters, and deeply embedded in the sand substrate. In deeper areas or sheltered locations with more stable substrates, denser beds of larger charophytes and beds of vasculars occur.

Aquatic vasculars largely consist of broad-ranging and saline tolerant species including Sago Pondweed (*Potamogeton pectinatus* L. = *Stuckenia pectinata* (L.) Borner), Widgeon-grass (*Ruppia maritima* L.), and Horned Pondweed (*Zannichellia palustris* L.). In zones of lower salinity Claspingleaved Pondweed (*Potamogeton perfoliatus* L.) and Mare's-tail (*Hippuris vulgaris* L.) are occasionally found. Eelgrass (*Zostera marina* L.) is absent from these charophyte dominated lagoons, but is common and forms extensive stands

in tidal lagoons which also occur in the area (e.g., Big Barachois, Figure 1). Charophytes have not been located in the tidal lagoons, but potentially may occur near freshwater inlets.

Although the aquatic fauna was not systematically sampled, the following organisms were commonly noted: amphipods, water boatman, snails, opossum shrimps, aquatic beetles, and a variety of insect larvae forms. Two fish species were encountered. The Threespine Stickleback (*Gasterosteus aculeatus* L.) is common in all lagoons amongst the charophytes. As well, in First Pond the Banded Killifish (*Fundulus diaphanus* Leseur) was commonly in the charophyte beds.

Species diversity decreases with increased salinity in inland waters (Cole 1994), but in addition, coastal lagoons often present a widely fluctuating ionic environment which cannot be tolerated by most marine organisms as well as most freshwater derived inland forms. Biodiversity, therefore, tends to be low and lagoons are inhabited by organisms that have a broad tolerance to fluctuating conditions. Lagoons also tend to contain a narrow range of niches and mainly favour a suite of organisms adapted to shallow, soft sediment habitats (Barnes 1994; 1999). Nevertheless, like estuaries, lagoons are highly productive and important feeding and migratory sites for waterfowl and shorebirds (Nelson-Smith 1977; Barnes 1980; Gillespie et al. 1991).

## Morphology

Newfoundland *Chara evoluta* produces a cluster of axes arising from an enlarged basal node anchored in the substrate by rhizoids. Axes up to 23 cm. in length and 520  $\mu\text{m}$  in diameter have been observed from depths of one to several meters, but in very shallow waters plants of only 2 to 3 cm. in length can be commonly found. Main axes are basically haplostichous, that is, having only vertical rows of cortical cells equal in number to the number of branchlets in a whorl. These cortical rows of cells are all primary rows with all rows containing spine cell clusters. Although the haplostichous condition may be quite regular, invariably in this species small secondary cells can be found along the axis between the primary cells producing an imperfect haplostichous condition and showing a tendency towards the diplostichous condition (Figure 2A). Spine cells are produced at the nodes of the cortical cells, sometimes singly, but more often in clusters of two or three. Characteristically, at least one spine cell at a node will be long, up to twice the diameter of the axis, whereas the other one or two are shorter, often being quite tiny and rudimentary (Figure 2A, 2D). Two rows of stipulodes are produced at the base of the branchlets, the cells of the upper row being slightly longer than the lower (Figure 2A, 2B).

Whorls of 9 to 10 branchlets occur at intervals along the axis. Branchlets are corticated with whorls of bract cells at the nodes (Figure 2B). A small ecorticate end cell arises from the terminal whorl. In some collections

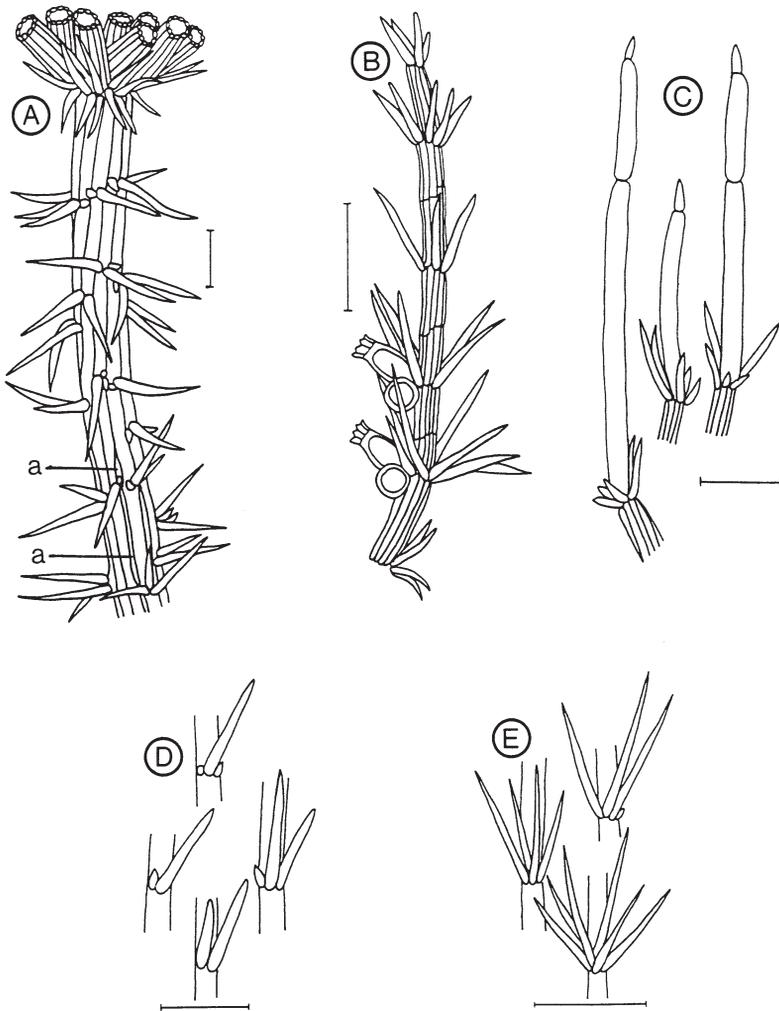


FIGURE 2. Morphological features of *C. evoluta* and *C. canescens*.

- A. *C. evoluta* axis - a. secondary cortical cells. Scale bar = 500  $\mu$ m.
- B. *C. evoluta* branchlet. Scale bar = 1000  $\mu$ m.
- C. *C. evoluta* variation in ecorticate end cells of branchlets; unusual, ecologically induced. Scale bar = 1000  $\mu$ m.
- D. *C. evoluta* typical spine cell clusters. Scale bar = 500  $\mu$ m.
- E. *C. canescens* typical spine cell clusters. Scale bar = 1000  $\mu$ m.

an elongated branchlet extension occurs of 2 or 3 ecorticate end cells (Figure 2C). Invariably these plants have been heavily intermingled with filamentous algal growth so this feature is probably a stress reaction to local biotic or abiotic conditions. This feature is not seen in normal vigorous material growing without obvious competition.

Gametangia, antheridia and oogonia are conjoined at the lowest 2 to 3 branchlet nodes (Figure 2B). Although the antheridia are produced below the oogonia at the nodes, in plants with very short branchlets

the internodes are too short to allow antheridia and oogonia to line up above each other and a superficial appearance of two rows is produced with antheridia and oogonia lateral to each other. The two bracteoles on either side of the oogonium are usually shorter or as long as the mature oogonium whereas the bract cells tend to be much longer. Gametangial measurements of *C. evoluta* are listed in Table 1 and compared to those of the lectotype provided by Wood and Imahori (1964). Newfoundland measurements compare favourably with this originally described material from west-

TABLE 1. Gametangial and oospore features of *Chara evoluta* and *Chara canescens*. Measurements are presented as means ( $\mu\text{m}$ ) with range values in parentheses.

	<i>C.</i> <i>evoluta</i> Newfoundland	<i>C. evoluta</i> Wood and Imahori 1964	<i>C.</i> <i>canescens</i> Newfoundland	<i>C.</i> <i>canescens</i> Wood and Muenscher 1956	<i>C.</i> <i>canescens</i> Krause 1997
Oogonium					
length*	931 (816 – 1002)	690 – 810*	759 (620 – 878)	710	550 – 800*
width	474 (372 – 548)	420 – 450	400 (341 – 455)	464	300 – 450
coronula height	128 (103 – 155)	90 – 105	71 (62 – 83)	71	50 – 80
coronula width	249 (207 – 279)	200 – 220	137 (103 – 165)	178	100 – 200
convolutions	(12 – 15)	(13 – 15)	(10 – 15)	(12 – 13)	(11 – 15)
Oospore					
length	601 (517 – 661)	585 – 645	557 (444 – 671)	535	400 – 700
width	338 (227 – 403)	320 – 360	299 (258 – 341)	357	200 – 400
Number of ridges <sup>+</sup>	(9 – 12)	(10 – 12)	(10 – 14)	11	(10 – 13)
fossae width <sup>+</sup>	55 (47 – 65)	51	50 (42 – 55)	–	–
Antheridium					
diameter	348 (310 – 393)	300 – 330	–	–	500 – 700

\* Length measurements include coronula length except Wood and Imahori (1964) and Krause (1967) which do not.

<sup>+</sup> Number of measurements (n) are 100 in all Nfld. features, except oospore No. of ridges (n = 50) and oospore fossae width (n = 30).

ern Canada. Wood and Imahori (1964) state that the antheridia may be 4 scutate, but indicate with a (?) their uncertainty. No other reports mention this feature. All members of the genus *Chara* at present are considered octoscutate with the exception of *C. zeylanica* Klein ex Willd. which is tetrascutate (Proctor et al. 1971). Determining the number of antheridial plates (scutes) in dried herbarium material is often not possible and scutes of liquid preserved material of this species are even difficult to separate clearly. Newfoundland material is distinctly octoscutate and we suspect this is equally true for the lectotype. Characteristic of the oospore are the very low, almost inconspicuous ridges, and the claws of the cage which are almost always present at the base (Figure 3D, 3E). The number of ridges (striae) per oospore ranged from 9 to 12, but most oospores (72%) had 10 or 11.

*Chara canescens* Desv. & Lois. in Lois. is morphologically very similar to monoecious *C. evoluta*, but is not known to produce antheridia in North America, instead producing oospores parthenogenetically. Besides the obvious absence of plants with antheridia, a number of other morphological differences occur, although some being quite subtle unless one is familiar with both species. The best, most obvious, and most constant of these is the comparative size of the coronulas (Table 1, Figure 3C, 3F). Coronulas of *C. evoluta* are almost double the size of *C. canescens* and there is no overlapping in the range values. The tips of the spiral cells just beneath the coronula also tend to enlarge considerably more at maturity in *C. evoluta* than in *C. canescens*. Detached oogonia of the two species can easily be distinguished by these features. Other gametangial measurements (Table 1) are consistently lower in *C. canescens* but not sufficiently to be taxonomically

useful. Oospores of *C. canescens* tend to exhibit more ridges with 72% of the oospores having 11 or 12 striae. The striae are also more pronounced than those of *C. evoluta* (Figure 3A, 3D), a feature readily seen with the compound light microscope as well. Basal claws are normally absent, but normally present in *C. evoluta*. Oospore membranes of both species are indistinctly and minutely granular (Figure 3B, 3E). Comparative measurements of North American *C. canescens* are provided by Wood and Muenscher (1956) from New York State (Table 1). European measurements are also given from Krause (1997) although these combine sexual dioecious and parthenogenetic forms as will be discussed in the taxonomic section. All three sets of measurements are fairly consistent for *C. canescens*.

Several subtle vegetative differences also occur between the species. *C. canescens* produces a more perfectly uniform haplostichous axis, only rarely are tiny secondary cells formed between primary cortical rows. Up to 4 to 6 spine cells are normally produced in a cluster (Figure 2E) and all or most tend to be equally long, often twice as long as the axis diameter producing a very spiny appearance. On the other hand, *C. evoluta* normally produces 1 to 3 cells per cluster, one or two often much smaller (Figure 2D).

### Taxonomy

*Chara evoluta* T. F. Allen was first described by T. F. Allen from the Red Deer Lakes and the saline ponds west of the Saskatchewan River (Alberta) based on material collected by J. Macoun (Allen 1882). Founded on a belief that the monoecious/dioecious conditions are not good indicators of species boundaries, Wood (1965) combined *C. evoluta* with dioecious and parthenogenetic taxa under *C. canescens*

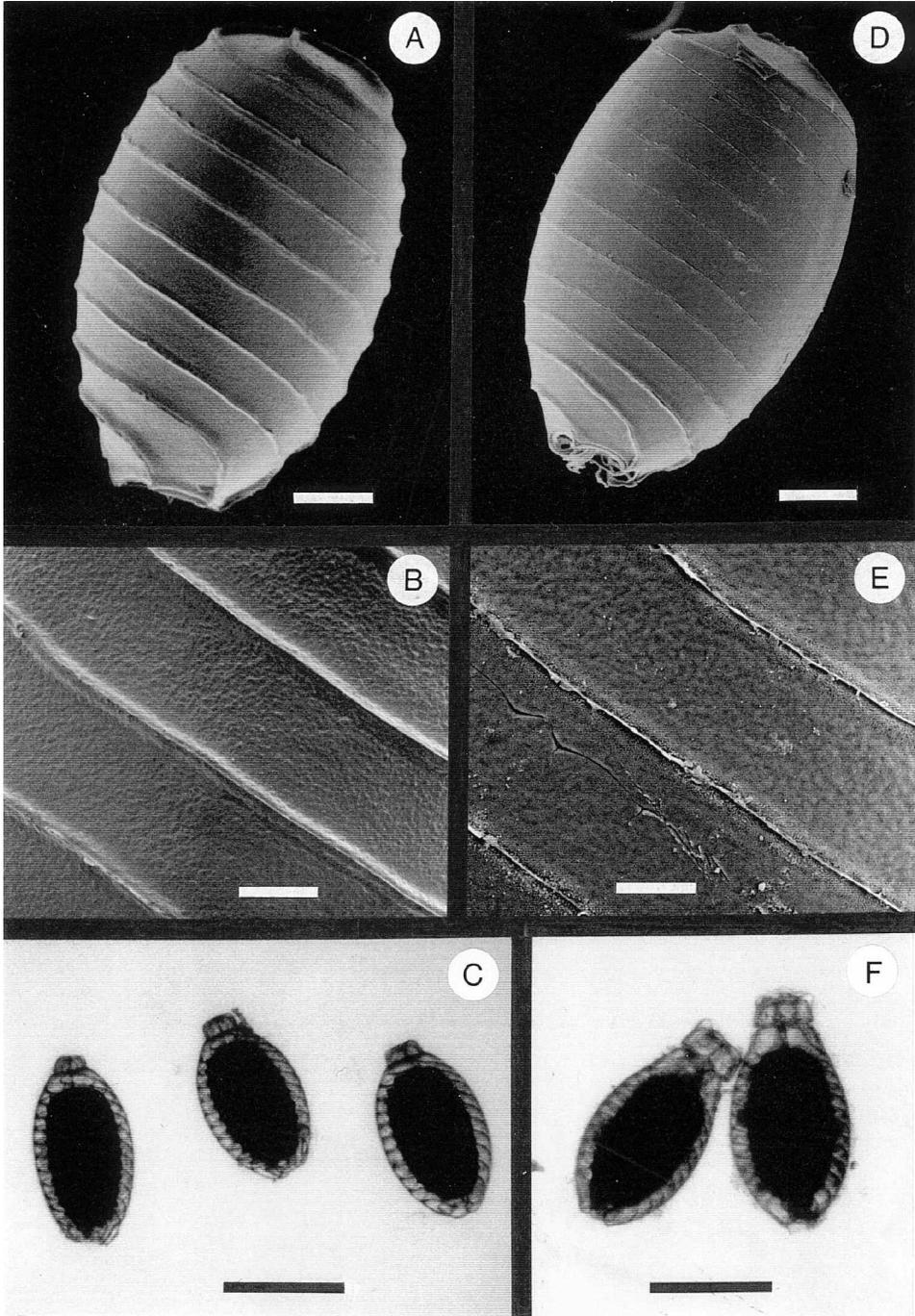


FIGURE 3. Oogonium and oospore features of *C. evoluta* and *C. canescens*.

- A. *C. canescens* spore (SEM). Scale bar = 120  $\mu\text{m}$ .
- B. *C. canescens* spore membrane (SEM). Scale bar = 30  $\mu\text{m}$ .
- C. *C. canescens* oogonia (Light Microscope). Scale bar = 500  $\mu\text{m}$ .
- D. *C. evoluta* spore (SEM). Scale bar = 100  $\mu\text{m}$ .
- E. *C. evoluta* spore membrane (SEM). Scale bar = 24  $\mu\text{m}$ .
- F. *C. evoluta* oogonia (Light Microscope). Scale bar = 500  $\mu\text{m}$ .

Desv. & Lois. In Lois. Subsequently it has been adequately demonstrated that monoecious and dioecious morphologically similar species pairs in charophytes are not conspecific and that Wood's views on this matter are no longer tenable (Proctor 1980). Nevertheless, this combining has led to continuing difficulty in distinguishing taxa in literature reports ever since, a matter especially troublesome for biogeographic purposes.

T. F. Allen (1900) described a very similar taxon which he designated as *Chara hirsuta* from a freshwater pond in California. It is a more robust plant to 60 cm. in height with somewhat larger oospores, more striae, and somewhat more prominent ridges. By comparing the descriptions based on the same material collected from Lakeside, California, by Allen (1900) and others (Robinson 1906; Wood 1965) it becomes apparent that considerable overlap exists in the morphological features of *C. hirsuta* and *C. evoluta*. It has long been understood that morphological variants of charophyte species can often be encountered in isolated bodies of water, but that these minor ecological or genetic variants probably do not indicate reproductive isolation (Robinson 1906; Moore 1986). One report of *C. hirsuta* occurs from Nebraska (Daily and Kiener 1956) and one from Wyoming (Daily and Porter 1961), however, Daily and Kiener (1956) suggest that *C. evoluta* and *C. hirsuta* are probably conspecific. That view was also taken by Proctor (1990) and is accepted here as well, although no evidence other than morphological is available to support this conjecture.

A monoecious, morphologically similar taxon to North American *C. evoluta* has been reported from Asia designated as *C. altaica* A.Br. = *C. sibirica* Mig. (Wood 1965; Hollerbach and Krassavina 1983). The *C. evoluta* taxon has also been reported from China (Han and Li 1994). In light of Proctor's (1980) conjecture that most charophytes are endemic to a single land mass, it remains to be seen whether the North American and Asian taxa are conspecific. To our knowledge no such comparative studies of a morphological, genetic, molecular, or of a breeding nature have yet been undertaken.

North American *Chara canescens* is parthenogenetic; no males have ever been seen. In Europe and Asia there are probably two isolated taxonomic entities within the broadly designated species, a dioecious male/female sexually reproducing entity of restricted range from south-central Europe through central Asia and China and the parthenogenetic entity more widespread across the continent (Krause 1997). Whether male *C. canescens* can fertilize parthenogenetic *C. canescens* has never been demonstrated. The concept of conspecificity is not applicable to parthenogenetic populations which is exemplified by a mutant ecorticate vegetatively reproducing form of *C. canescens* from Svalbard coexisting in the same springpool as a more normal parthenogenetic form (Langangen 2000).

In Newfoundland and elsewhere in North America *C. canescens* and *C. evoluta* sometimes inhabit the same pond. Although the theoretical potential for *C. evoluta* to fertilize *C. canescens* may be suggested, the morphological differences as described previously in this paper remain distinct and no indication of intergradation of features has ever been noted in these situations. This is strong evidence that the two are reproductively isolated and that hybridization does not and cannot occur.

### Distribution and Ecology

*Chara evoluta* in North America has essentially a western distribution, west of the interstate borders connecting the eastern state line of North Dakota with the eastern state line of Texas (Figure 4). Almost all states west of this line have reports in the literature and/or specimens in major herbaria. It is also known from southern British Columbia, Alberta, and Saskatchewan in Canada, but not east of Saskatchewan. It then reappears in a single disjunct location in coastal Rhode Island (Wood 1965; Wood and Palmatier 1954) and again in southwestern Newfoundland. Although thorough charophyte surveys have not been conducted in many areas of North America, some eastern jurisdictions have been variously investigated and *C. evoluta* has not been recorded, further supporting its general absence in the east. These studies include Iowa (Crum 1975), Illinois (Ebinger and Vogel 1977), Indiana (Daily 1953), Minnesota, Wisconsin (Prescott 1962), New York (Wood and Muenscher 1956), West Virginia, Virginia, Tennessee, North Carolina, South Carolina, Georgia, Alabama, Mississippi, Louisiana, Florida (Choudhary and Wood 1973), and others.

Most reports indicate that *C. evoluta* is a species of saline coastal or inland waters. Its western distribution seems to reflect the climatic conditions of low rainfall where rates of evapotranspiration often exceed precipitation to produce saline lakes and ponds which are often closed systems. In some regions geological deposits are also sources of salts (Hammer 1986). Within the stippled region of Figure 4, *C. evoluta* only occurs locally where such saline conditions exist. East of this region rainfall increases, few inland saline habitats occur, and all known collections are from coastal locations influenced by sea water.

Inland and coastal saline waters often differ significantly in their ionic composition. For example, Waldsea Lake, Saskatchewan, is a magnesium-sodium sulphate lake (Hammer 1984) as opposed to marine salinity where sodium and chloride predominate as in the Newfoundland lagoons. Waldsea water has a conductivity and pH in the same range as the Newfoundland lagoons and both *C. evoluta* and *C. canescens* are known to occur in Waldsea Lake as well as *C. buckelii* G. O. Allen. Hammer et al. (1983) indicate that the Na/Mg ratio plays an important role in governing the occurrence of algal species in lakes. *C. evoluta* appears

to be capable of adapting to chemically different saturations, but also to a wide range of salinities. Winter and Kirst (1991) and Winter et al. (1996) determined that *C. canescens* has an upper salinity tolerance in the mesohaline range of approximately 20 parts per thousand (ppt) and a lower limit of 1.5 ppt in the low oligohaline range. It may be assumed that this is equally probable for *C. evoluta* since both are often associates in inland and coastal waters. A few authors report *C. evoluta* from non-saline freshwater habitats (Allen 1900; Leake 1945). Also V. W. Proctor (personal communication) indicates that both species can be successfully cultured under low salinity conditions to produce viable oospores. Brock (1986), however, suggests that for submerged aquatic plants in saline environments, extremes of tolerance are not the primary factors in determining the flora, but rather evolved life cycle mechanisms which allow survival under widely fluctuating conditions. Thus fluctuating salinities and/or ephemeral habitats would foster different floras than permanent water bodies with little salinity fluctuation.

Some degree of salinity and/or particular ionic composition appears to be required by *C. evoluta* (and *C. canescens*), but within this broad tolerance range from lower oligohaline (oligosaline) to mesohaline (mesosaline), presence or absence in water bodies may be a function of biotic community structure. This concept suggests that salinity may set the extreme boundaries for such species, but that community structure including competition, predation, herbivory, allelopathy, and others may determine the colonization ability of any given species. Barnes (1999) states that there is evidence that brackish water communities are not physically structured by salinity, but by biotic processes such as predation and competition. Although it is tempting to suggest that *C. evoluta*'s apparent absence from continental eastern North America is due to the absence of any significant saline waters, this may be an oversimplification. Even when dispersed, ability to establish, grow, and reproduce in complexly evolved communities may not be possible despite favourable physical parameters. For example, a relationship between the presence of certain invertebrate herbivores and the distribution of charophyte species has been demonstrated by Proctor (1990, 1999).

In Newfoundland *C. evoluta* grows in association with *Chara aspera* in the five southernmost lagoons and Codroy Estuary Pond (Table 2). In these lagoons *C. aspera* is very common, as is *C. evoluta*, but no other charophytes occur. This *C. evoluta/C. aspera* association is also recorded from interior British Columbia (Allen 1951), Rhode Island (Wood and Palmatier 1954), and Nebraska (Daily and Kiener 1956). In the two northern lagoons (Gravels Pond and St. George's Pond) *C. evoluta* grows with *C. canescens*, but *C. aspera* is absent. The *C. evoluta/C. canescens* association is reported from Waldsea Lake, Saskatchewan, and Roses Pond (Sweets Lake), British Columbia, where they both grow with *Chara buckellii*, but *C.*



FIGURE 4. Distribution of *Chara evoluta* in North America. The stippled area indicates its western distribution. The two dots indicate the only known eastern sites.

*aspera* is apparently absent. The *C. canescens/C. aspera* combination is recorded for Rhode Island (Wood 1950) and reported as a common associate in both North America and Europe (Allen 1882; Krause 1997). *C. canescens* has not yet been collected in association with *C. aspera* in Newfoundland, and neither here, nor in any other reports have all three species ever been reported from the same body of water. Based on two well-known ecological principles of competitive exclusion and of coexistence, it is tempting to try and ascribe some ecological significance to this apparent pattern of species associations, but such an attempt may be premature without a thorough comparison of site conditions, both biotic and abiotic.

*Chara aspera* has a broad North American range, commonly occurring in permanent sites from coast to coast in southern Canada and tapering to and becoming more infrequent in Mexico (Croy 1982). It occurs more commonly in freshwater situations than either *C. canescens* and *C. evoluta*, but has an extremely broad salt tolerance (Langangen 1974). It is common in the Newfoundland upper estuaries of the Little Codroy and the Codroy River, however has not been collected further north. Ripe oospores have not yet been observed for this species in Newfoundland despite collections ranging over many years and all summer seasons. Dispersal by waterfowl via the many round white bulbils produced on the rhizoids of this species

TABLE 2. Charophytes present in the coastal lagoons/ponds of southwestern Newfoundland investigated in this study.

	<i>C. evoluta</i>	<i>C. canescens</i>	<i>C. aspera</i>	<i>C. globularis</i>
Gravels Pond	X	X		
St. George's Pond	X	X		X
Codroy Estuary Pond	X		X	
Osmond Pond	X		X	
Rocky Barachois	X		X	
Saltwater Pond	X		X	
Second Pond	X		X	
First Pond	X		X	

may be considerably more haphazard and infrequent than dispersal by spores and may account for its absence in the two northern lagoons. However, other abiotic/biotic differences as yet undetermined may also be involved.

*Chara globularis* Thuill. (= *C. delicatula* Agardh) grows in St. George's Lagoon, the site with the lowest recorded salinity. Although this species is normally associated with fresh water, it has quite a broad tolerance range and is occasionally reported from low salinity waters (Winter and Kirst 1991). It is the most common *Chara* in Newfoundland.

Relatively few vascular taxa inhabit brackish waters. Those associated with charophytes in all the Newfoundland lagoons include Sago Pondweed, Horned Pondweed, and Widgeon-grass. These cosmopolitan vasculars of saline coastal and inland waters all belong to closely related families and are important food sources for waterfowl, as are charophytes. These vasculars are common throughout their ranges wherever brackish conditions occur (Melack 1988) although all can also occur in alkaline freshwaters (Hammer and Heseltine 1988).

It is well accepted that charophyte spores are readily dispersed by waterfowl and shore birds, even great distances (Kristiansen 1996). The disjunct Rhode Island *C. evoluta* site may be attributed to such long distance dispersal as considerable east-west exchange also occurs in addition to the normal north-south migratory routes of waterfowl (Bellrose 1976). Undoubtedly more coastal populations of *C. evoluta* occur along the Atlantic seaboard wherever suitable conditions exist. The Newfoundland populations are almost certainly a northward dispersal since the last glaciation via the Atlantic Flyway.

North American parthenogenetic *C. canescens* exhibits a similar range to *C. evoluta*, but tends to have a more sporadic occurrence as one moves south from western Canada. It ranges up the eastern seaboard into Newfoundland, Greenland, Svalbard, and into Europe and Asia where many forms and varieties have been described. It too is reported occasionally from fresh or oligohaline waters (Olsen 1944; Prescott 1962; Winter and Kirst 1991; Langangen 2000). Langangen (2000) suggests that the reason that *C. canescens* is not nor-

mally found at low salinities in Europe may be due to competition from other plants which flourish at low salinities, but are excluded at higher salinities. It might also be suggested that at the lower salinities, increased herbivore pressure may also become a factor (Proctor 1999).

As there are no distinct morphological differences between *C. canescens* of the eastern seaboard and that of Newfoundland lagoons (Table 1) it can be assumed that this species, like *C. evoluta*, entered Newfoundland from the south via the Atlantic Flyway. However, because of its northern distribution an arctic route cannot be ruled out (Mann 1994a).

**Key to Newfoundland Species**

The following key is provided specifically to identify the taxa known to occur in Newfoundland and Labrador. For an explanation of charophyte structure and terminology we recommend Groves and Bullock-Webster (1920, 1924), G. O. Allen (1950), and Moore (1986). Recommended more general keys to the entire North American charophyte flora include Robinson (1906) for the Genus *Chara*, Wood (1948) for the Genus *Nitella*, and G. O. Allen (1954) for Genera *Nitella* and *Tolypella*. Wood (1965, 1967) and Wood and Imahori (1964) are essential references for advanced studies, but the combining of some species in these works discourages the reporting of many good taxa. It is recommended that Newfoundland workers identify taxa using the currently supplied key and when uncertain, consult a specialist. There is always the possibility that species new to the province may be discovered in the future, but such will almost certainly be rare or uncommon in our flora.

- 1a Coronula of 5 cells in one tier, cortical cells usually present on the main axis, stipulodes present - (*Chara*) ..... 5
- 1b Coronula of 10 cells in two tiers of 5, axes always without cortication, stipulodes absent ..... 2
- 2a Oogonia and oospores round in cross section, branchlets consisting of a main axis with smaller laterals - *Tolypella* ..... *Tolypella glomerata* (Desv.) Leonh.  
This is our only known *Tolypella*
- 2b Oogonia and oospores somewhat flattened in cross-section, branchlets forking usually equally one or more times (*Nitella*) ..... 3

- 3a Unbranched end segments of branchlets (dactyls) of more than one cell, end cell tiny and pointed  
.....*Nitella confervacea* (Breb.) A. Braun
- 3b Unbranched end segments of branchlets (dactyls) of one cell (*N. flexilis* group) ..... 4
- 4a Plants monoecious (antheridia and oogonia on same plants) ..... *Nitella flexilis* (L.) Agardh
- 4b Plants dioecious (antheridia and oogonia on separate plants) ..... *Nitella opaca* Agardh
- 5a Axial cortex composed only of primary rows of cells (all rows contain spine cells = haplostichous), Axes bristly with many long spines ..... 6
- 5b Axial cortex of primary rows with spine cells alternating with one or two secondary rows without spine cells, Axes not greatly spiny ..... 7
- 6a Plants monoecious (antheridia and oogonia on same plants), coronula width over 180 µm  
.....*Chara evoluta* T. F. Allen
- 6b Plants only with oogonia, no males with antheridia known in North America, coronula less than 180 µm wide  
.....*Chara canescens* Desv. & Lois. in Lois.
- 7a Axial cortex having each primary row alternating with one secondary row (diplostichous) ..... 8
- 7b Axial cortex having each primary row alternating with two secondary rows (triplostichous) ..... 9
- 8a Primary axial cortical rows of cells more prominent than the secondary rows  
.....*Chara contraria* A. Brown ex Kütz
- 8b Primary axial cortical rows of cells less prominent than the secondary rows .... *Chara vulgaris* L.
- 9a Plants dioecious, upper and lower stipulodes well developed, rhizoids often with tiny spherical white bulbils  
.....*Chara aspera* Deth.ex Willd
- 9b Plant monoecious, stipulodes especially lower ones rudimentary, globular; rhizoids without bulbils ..... 10
- 10a Primary cortical rows more prominent than secondary rows (tylacanthous), upper row of stipulodes more elongate than globular lower row (sometimes only slightly)  
.....*Chara delicatula* Agardh non Desv.\*
- 10b Primary cortical row and secondary rows equal in size (isostichous), both upper and lower stipulode rows of rudimentary globular cells  
.....*Chara globularis* Thuill (= *C. fragilis* Desv.)\*

\* These two taxa may show ecologically induced intergrading forms and in some treatments are combined under *C. globularis* Thuill. They should, however, always be distinguished separately whenever possible until their taxonomy can be more precisely defined.

## Discussion

Insular Newfoundland has a depauperate vascular flora compared to the adjacent mainland largely due to dispersal difficulty across the straits and to climatic and edaphic factors resulting in less diverse habitats (Damman 1965). On the other hand, the charophyte

flora compares favorably numerically with many other parts of northern North America (Mann et al. 1999). It is well known that charophytes are rapid early colonizers of disturbed habitats (Olsen 1944) suggesting that dispersal is not a significant limiting factor for this group, especially within a single land mass. Almost invariably if suitable habitat exists, it will become colonized by charophyte species normally occupying those particular biotic and abiotic parameters.

Those Newfoundland taxa with broad ecological tolerances commonly occur across North America, including *C. globularis*, *C. delicatula*, *C. contraria*, *C. vulgaris*, *N. flexilis*, and *N. opaca*. These are species of permanently inundated and relatively stable habitats after formation. *C. globularis* and *C. delicatula* as defined in this paper, in addition to *N. flexilis* and *N. opaca*, are most tolerant of oligotrophic acid waters and are ubiquitous across the Island (Mann 1989). Of this group, *C. delicatula* is the most tolerant of saline conditions and can commonly be found in coastal areas subject to some marine influence. *C. contraria* and *C. vulgaris* are species of high pH waters, commonly the limestone areas of the west coast, but also in very high pH serpentine pools and of coastal low-saline habitats.

The other portion of the Newfoundland charophyte flora is made up of species with more narrowly defined habitats, where habitats are rare on the Island and therefore the species themselves are rare. The three species featured in this paper (*C. evoluta*, *C. canescens*, *C. aspera*) are restricted to soft-bottomed, fluctuating saline habitats which are only relatively common on the southwest coast. *Tolypella glomerata* is restricted to coastal freshwater ephemeral sites or their equivalents which are decidedly uncommon here. *Nitella confervacea* is restricted to two west coast sites whose common ecological features are still unclear. In all of these five rare species, fluctuating and regular habitat disturbance are common factors, and all are of coastal distribution because this is the only area where habitat suitable for their growth occurs. These five rare species exhibit a disjunct distribution with the New England states. None have yet been reported for the maritime provinces or adjacent Quebec. If suitable habitat for these species exists in the Maritimes, this disjunct distribution may prove to be an illusion of insufficient field observation.

It has been determined that disjunct Newfoundland *Chara evoluta* and *Chara canescens* populations are morphologically and ecologically similar to their counterparts elsewhere in North America suggesting relatively recent introductions from the south. The two taxa can readily be distinguished by their monoecious/dioecious (parthenogenetic) conditions respectively and by oospore and oogonial features. However, other subtle differences also may suggest the possibility that at least some morphology may be due to convergent adaptation rather than divergent evolution from recent com-

mon ancestors. Their distribution in North America is ascribed to their affinity for saline waters. Although ecologically similar, there is some indication that their niches do not totally overlap and that their salinity tolerance ranges far exceed their actual ecological ranges leading one to suspect that biotic factors may be equally important in determining presence or absence in a given body of water, and therefore their total biogeography.

The coastal lagoons of south-west Newfoundland are unique habitats adding to the provincial biodiversity by harbouring highly disjunct charophyte species within the North American continental perspective. Three species, *C. evoluta*, *C. canescens*, and *C. aspera* are restricted to this region and have been accorded rare status in Newfoundland (Mann 2000\*). Along with estuaries in the region (Gillespie et al. 1991), lagoons provide important feeding and migratory habitat for waterfowl and shorebirds, including the endangered Piping Plover which nests on the sandy outer beaches (Hancock, J. 2001\*; Knox et al. 1994). The Banded Killifish listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2000\*) as a species of special concern in Newfoundland also occurs in the lagoons. Much is still unknown about the detailed flora/fauna and the community structure in these saline water bodies. Being sites that can easily be altered and degraded by human activity (Martin et al. 2002; Barnes 1980), their unique features need to be further documented in detail and some degree of protection should be considered within the developing provincial strategy.

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### Documents Cited [marked \* in text]

- COSEWIC.** 2000. Canadian species at risk, November 2000. Committee on the status of endangered wildlife in Canada, Canadian Wildlife Service, Ottawa.
- Hancock, J.** 2001. Status of the Piping plover (*Charadrius melodus*) in Newfoundland, Canada. Internal Report, Inland fish and Wildlife Division, Department of Forest Resources and Agrifoods, Government of Newfoundland and Labrador, St. John's, Newfoundland.
- Mann, H.** 2000. General status of charophytes of the island of Newfoundland. Report for the Newfoundland Rare Plant Project, Endangered Species and Biodiversity Section,

Inland Fish and Wildlife Division, Government of Newfoundland and Labrador, St. John's, Newfoundland.

### Literature Cited

- Allen, G. O.** 1950. British Stoneworts (Charophyta). The Haslemere Natural History Society, Surrey, England.
- Allen, G. O.** 1951. Notes on charophytes from British Columbia. Linnean Society of London Proceedings 162: 148-152.
- Allen, G. O.** 1954. An annotated key to the Nitelleae of North America. Bulletin of the Torrey Botanical Club 81: 35-60.
- Allen, T. F.** 1882. Development of the cortex in *Chara*. Bulletin of the Torrey Botanical Club 9: 37-46, plus plates 15-22.
- Allen, T. F.** 1900. Three new *Charas* from California. Bulletin of the Torrey Botanical Club 27: 299-304, plus plates 10-15.
- Barnes, R. S. K.** 1980. Coastal lagoons. Cambridge University Press, Cambridge.
- Barnes, R. S. K.** 1994. The brackish-water fauna of north-western Europe. Cambridge University Press, Cambridge.
- Barnes, R. S. K.** 1999. The conservation of brackish-water systems: priorities for the 21<sup>st</sup> century. Aquatic Conservation: Marine and Freshwater Ecosystems 9: 523-527.
- Bellrose, F. C.** 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, Pennsylvania.
- Brock, M. A.** 1986. Adaptation to fluctuations rather than to extremes of environmental parameters. In Limnology in Australia. Edited by P. De Deckker and W. D. Williams. CSIRO, Melbourne, Australia.
- Choudhary, M. C., and R. D. Wood.** 1973. The Characeae of southeastern United States. American Midland Naturalist 90: 413-446.
- Cole, G. A.** 1994. Textbook of Limnology. Waveland Press, Prospect Heights, Illinois.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. La Roe.** 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish and Wildlife Service, Washington, D.C.
- Crow, G. E., and C. B. Hellquist.** 2000. Aquatic and wetland plants of northeastern North America. Volumes I and II. University of Wisconsin Press, Madison.
- Croy, C. D.** 1982. *Chara aspera* (Charophyta): breeding pattern in the northern hemisphere. Phycologia 21: 243-246.
- Crum, G. H.** 1975. Distribution, taxonomy, and ecology of charophytes in Iowa. Ph.D. thesis, Iowa State University, Ames.
- Daily, F. K.** 1953. The Characeae of Indiana. Butler University Botanical Studies 11: 5-49.
- Daily, F. K., and W. Kiener.** 1956. The Characeae of Nebraska: additions and changes. Butler University Botanical Studies 13: 36-46.
- Daily, F. K., and C. L. Porter.** 1961. A key and annotations for some Characeae collected in Wyoming. Butler University Botanical Studies 14: 29-37.
- Damman, A. W. H.** 1965. The distribution patterns of northern and southern elements in the flora of Newfoundland. Rhodora 67: 363-392.
- Ebinger, J. E., and R. L. Vogel.** 1977. Distribution of *Chara* species in Illinois. Transactions, Illinois State Academy of Science 70: 96-100.
- Gillespie, D. I., H. Boyd, and P. Logan.** 1991. Wetlands for the world: Canada's Ramsar Sites. Canadian Wildlife Service, Ottawa.
- Groves, J., and G. R. Bullock-Webster.** 1920. The British Charophyta. I. Nitelleae. Ray Society, London.

- Groves, J., and G. R. Bullock-Webster.** 1924. The British Charophyta. II. Chareae. Ray Society, London.
- Hammer, U. T.** 1984. The saline lakes of Canada. In lakes and reservoirs, ecosystems of the world 23. Edited by F. B. Taub. Elsevier, Amsterdam.
- Hammer, U. T.** 1986. Saline lake ecosystems of the world. Junk Publishers, The Netherlands.
- Hammer, U. T., and J. M. Heseltine.** 1988. Aquatic macrophytes in saline lakes of the Canadian prairies. *Hydrobiologia* 158: 101-116.
- Hammer, U. T., J. Shames, and R. C. Haynes.** 1983. The distribution and abundance of algae in saline lakes of Saskatchewan, Canada. *Hydrobiologia* 105: 1-26.
- Han, F. S., and Y. Y. Li.** 1994. Flora algarum sinicarum aquae dulcis. Tomus 3. Charophyta. Consilio Florarum Cryptogamarum Sinicarum Academiae Sinicae edita. Science Press (in Chinese).
- Hollerback, M. M., and L. K. Krassavina.** 1983. Flora of freshwater algae in the USSR, 14: Charoic algae – Charophyta. Leningrad, Russia (in Russian).
- Holmgren, P. K., N. H. Holmgren, and L. C. Barnett.** 1990. Index Herbariorum, Part I: The herbaria of the world. New York Botanical Garden, Bronx, New York.
- John, D. M., and J. A. Moore.** 1987. An SEM study of the oospore of some *Nitella* species (Charales, Chlorophyta) with descriptions of wall ornamentation and assessment of taxonomic importance. *Phycologia* 26: 334-355.
- Knox, K., J. Brazil, and R. Etcheberry.** 1994. The Piping Plover census in Newfoundland and St. Pierre-et-Miquelon (France). In The 1991 International Piping Plover Census in Canada. Edited by S. Flemming. Canadian Wildlife Service, Occasional Paper Number 82.
- Krause, W.** 1997. Charales (Charophyceae). In Süßwasserflora von Mitteleuropa, Band 18. Gustav Fischer, Jena.
- Kristiansen, J.** 1996. Dispersal of freshwater algae – a review. *Hydrobiologia* 336: 151-157.
- Langangen, A.** 1974. Ecology and distribution of Norwegian charophytes. *Norwegian Journal of Botany* 21: 31-52.
- Langangen, A.** 2000. Charophytes from the warm springs of Svalbard. *Polar Research* 19: 143-153.
- Leake, D. V.** 1945. The algae of Crystal Lake, Cleveland County, Oklahoma. *American Midland Naturalist* 34: 750-768.
- Mann, H.** 1989. Charophytes of insular Newfoundland. *Canadian Field-Naturalist* 103: 34-42.
- Mann, H.** 1994a. The genus *Tolypella* (Characeae) in insular Newfoundland. *Canadian Field-Naturalist* 108: 297-304.
- Mann, H.** 1994b. Charophytes of Crooked Lake, Saskatchewan. *Canadian Field-Naturalist* 108: 413-427.
- Mann, H.** 1998. Newfoundland Charophytes. In Assessing the state of the environment of Gros Morne National Park. Edited by D. W. Anions and A. R. Berger. Gros Morne National Park, Rocky Harbour, Newfoundland.
- Mann, H., V. W. Proctor, and A. S. Taylor.** 1999. Towards a biogeography of North American Charophytes. *Australian Journal of Botany* 47: 445-458.
- Martin, A., L. Carvalho, and A. J. Downie.** 2002. Rare charophytes in Scotland's coastal saline lagoons. *Botanical Journal of Scotland* 54(1): 23-35.
- Melack, J. M.** 1988. Aquatic plants in extreme environments. In Vegetation of inland waters. Edited by J. J. Symoens. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Moore, J. A.** 1986. Charophytes of Great Britain and Ireland. Handbook Number 5. Botanical Society of the British Isles, London.
- Nelson-Smith, A.** 1977. Estuaries. In The Coastline. Edited by R. S. K. Barnes. John Wiley and Sons, London.
- Olsen, S.** 1944. Danish Charophyta: chorological, ecological, and biological investigations. Det Kongelige Danske Videnskaberne Selskab, Biologiske Skrifter 3: 1-240.
- Prescott, G. W.** 1962. Algae of the western Great Lakes area. Wm. C. Brown Company, Dubuque, Iowa.
- Proctor, V. W.** 1980. Historical biogeography of *Chara* (charophyta): an appraisal of the Braun- Wood classification plus a falsifiable alternative for future consideration. *Journal of Phycology* 16: 218-233.
- Proctor, V. W.** 1990. Characeae of Llano Estacado (Texas and adjacent New Mexico) Playas. *Journal of Biogeography* 17: 75-84.
- Proctor, V. W.** 1999. Charophytivory, playas y papalotes, a local paradigm of global relevance. *Australian Journal of Botany* 47: 399-406.
- Proctor, V. W., D. G. Griffin III, and A. T. Hotchkiss.** 1971. A synopsis of the genus *Chara*, series *Gymnobasalia* (Subsection *Willdenowia* RDW). *American Journal of Botany* 58: 894-901.
- Robinson, C. B.** 1906. The Chareae of North America. *Bulletin of the New York Botanical Garden* 4: 244-308.
- Scott, W. B., and E. J. Crossman.** 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Ottawa.
- Winter, U., and G. O. Kirst.** 1991. Partial turgor pressure regulation in *Chara canescens* and its implications for a generalized hypothesis of salinity response in Charophytes. *Botanica Acta* 104: 37-46.
- Winter, U., I. Soulié-Marsche, and G. O. Kirst.** 1996. Effects of salinity on turgor pressure and fertility in *Tolypella* (Characeae). *Plant, Cell and Environment* 19: 869-879.
- Wood, R. D.** 1948. A review of the genus *Nitella* (Characeae) of North America. *Farlowia* 3: 331- 398.
- Wood, R. D.** 1950. Stability and zonation of Characeae. *Ecology* 31: 642-647.
- Wood, R. D.** 1965. Monograph of the Characeae. In A revision of the Characeae, Volume I. By R. D. Wood and K. Imahori. Cramer, Weinheim.
- Wood, R. D.** 1967. Charophytes of North America. Stella's Printing, West Kingston, Rhode Island.
- Wood, R. D., and K. Imahori.** 1964. Iconograph of the Characeae. In A revision of the Characeae, Volume II. By R. D. Wood and K. Imahori. Cramer, Weinheim.
- Wood, R. D., and W. C. Muenscher.** 1956. The Characeae of the State of New York. Memoir 338, Cornell University Agricultural Experiment Station, Ithaca, New York.
- Wood, R. D., and E. A. Palmatier.** 1954. Macroscopic algae of the coastal ponds of Rhode Island. *American Journal of Botany* 41: 135-142.

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