

The phytogeography of *Ceratophyllum demersum* and *C. echinatum* (Ceratophyllaceae) in glaciated North America

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The present-day distributions of *Ceratophyllum demersum* and *C. echinatum* are useful in interpreting the Quaternary distributional history of aquatic plants. East–west North American disjunct distributions of submersed hydrophytes are probably due to incomplete interglacial migrations. Widespread species such as *C. demersum* have successfully bridged gaps formed when populations migrated into isolated southern refugia to escape glaciation. Species with narrower ranges, such as *C. echinatum*, are still in the process of doing so. Northern disjunct distributions of *C. demersum* indicate that the species also survived glaciation in northwest refugia. It is apparent that many submersed aquatic plants have endured the migrational pressures imposed during glacial periods. Their ability to do so is attributable to four factors: (i) long species durations, (ii) formerly continuous distributional ranges, (iii) high vagility, and (iv) adaptation to cold, oligotrophic conditions. Extant hydrophyte communities in glaciated North America may resemble those in existence during former interglacial periods.

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Les distributions actuelles de *Ceratophyllum demersum* et de *C. echinatum* sont utiles dans l'interprétation de l'histoire de la distribution quaternaire des plantes aquatiques. Les distributions disjointes des hydrophytes submergées de l'est à l'ouest de l'Amérique du Nord sont probablement dues à des migrations interglaciaires incomplètes. Des espèces répandues, tel que le *C. demersum*, ont comblé avec succès les lacunes laissées par les populations émigrant vers les refuges méridionaux isolés à la migration. Les distributions septentrionales disjointes du *C. demersum* indiquent que cette espèce a aussi survécu à la glaciation dans des refuges du nord-ouest. Manifestement, plusieurs plantes aquatiques submergées ont endured les pressions migratoires des périodes glaciaires. Qu'elles en aient été capables est attribuable à quatre facteurs: (i) de longues durées d'espèces, (ii) des portées distributionnelles qui étaient auparavant continues, (iii) une capacité prononcée de dissémination et (iv) l'adaptation au froid dans des conditions d'oligotrophie. Les communautés d'hydrophytes qui existent toujours dans les régions nord-américaines recouvertes par les glaces ressemblent peut-être à celles qui existaient pendant les périodes interglaciaires précédentes.

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Introduction

The phytogeography of aquatic plants has been a topic of interest since Darwin (1859) introduced the subject in his "Origin." Darwin attributed the vast ranges of hydrophytes to long-distance dispersal of seeds by freshwater birds, an explanation which continues to hold favor (Hutchinson 1975). Darwin (1859) also considered factors which may have influenced present distributional patterns of water plants. To explain disjunct patterns, he ventured the possibility that certain hydrophytes may have once covered "immense areas" in which intermediate populations became "extinct."

The aquatic genus *Ceratophyllum* is cosmopolitan (Sculthorpe 1967) and is represented on every major continent (except Antarctica) from arctic to tropic latitudes (Les 1980). *Ceratophyllum demersum* and *C. echinatum* are the only species of the genus with ranges extending into glaciated portions of North America, and both are more common at lower latitudes (30–50° N). The boreal distributions of these species are irregular. Ceska and Ceska (1980) pointed out the distinctive pattern of *Ceratophyllum echinatum* and other aquatic plant species, i.e., a generally eastern North American distribution with disjunct populations in the Pacific Northwest. Hulten's (1970) circumpolar distribution map of *Ceratophyllum demersum* indicates a similar east–west disjunction, as well as a "gap" in the northern range of the species; populations in Alaska, Yukon, and Northwest Territories are disjunct from the rest of the relatively continuous temperate distribution (Cwynar 1983). Hulten (1937) categorized *C. demersum* as a circumboreal species with distributional gaps in Iceland,

Greenland, and the Bering Sea islands, resulting from extermination of populations during Pleistocene glaciations. He observed that many species of this distributional type were aquatic and wetland plants and attributed the relationship to their ability for surviving close to the rim of ice during glacial advances.

This study reviews the North American distributions of *Ceratophyllum demersum* and *C. echinatum* and assesses the hypothesis that irregularities in these distributions are results of their Quaternary migrational history.

Methods

North American distribution maps were constructed for *Ceratophyllum demersum* and *C. echinatum* in preparation of a monograph of the genus *Ceratophyllum*. Specimens of these species were obtained from A, AAU, ALA, ALTA, B, BA, BH, BP, CAL, CAN, CU, CTES, DAO, DUKE, EMC, F, FSU, G, GH, GOET, HAL, HIB, JEPS, K, KKK, KY, LE, LIL, LKHD, LSU, MICH, MO, MSC, MT, MTMG, MUHW, NCS, NCU, NO, NY, OS, OSC, P, PENN, PH, QFA, QK, RB, SASK, SGO, SIUC, SLU, SMU, SP, SSME, TAI, TENN, TRT, TRTE, UARK, UBC, UNA, US, USF, UVIC, UW, V, VPI, WAG, WIB, WIN, WIS, WTU, and Z. All North American specimens of *Ceratophyllum demersum* and *C. echinatum* were identified by the author and mapped with dots to indicate their geographical origin (Figs. 1 and 2). The extreme northern distribution of *Ceratophyllum demersum* was mapped from data in Holmquist (1971). A complete listing of mapped specimens is available from the author. These maps were then modified by shading areas of closely situated dots (Figs. 3 and 4), which more clearly delimited the North American distributions of the species.

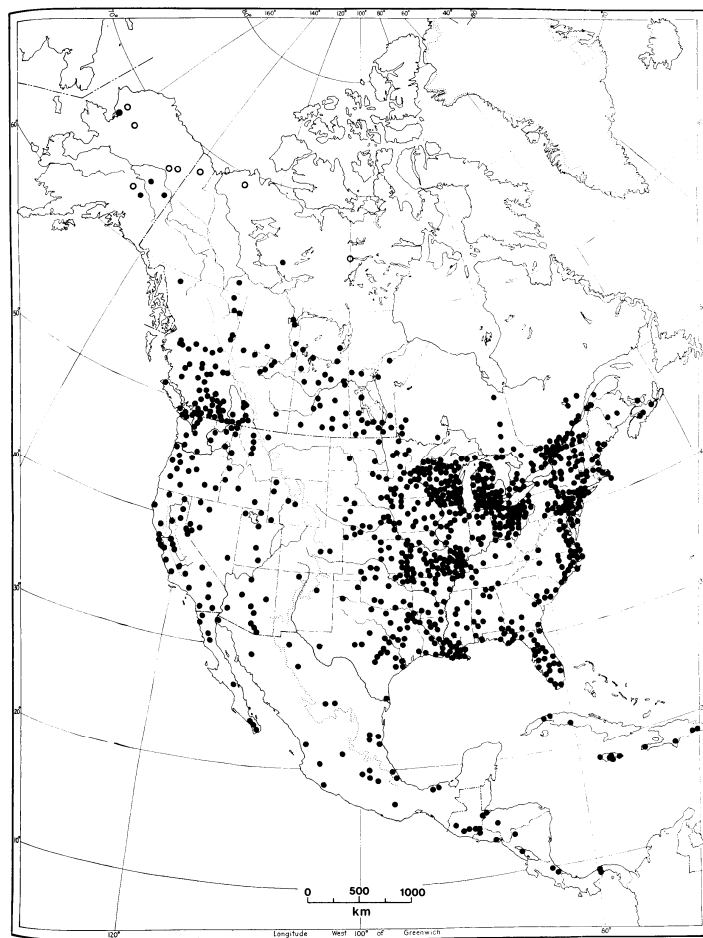


Fig. 1. Dot-distribution map of *Ceratophyllum demersum* in North America. ○, literature records from Holmquist (1971); ●, based upon specimens examined.

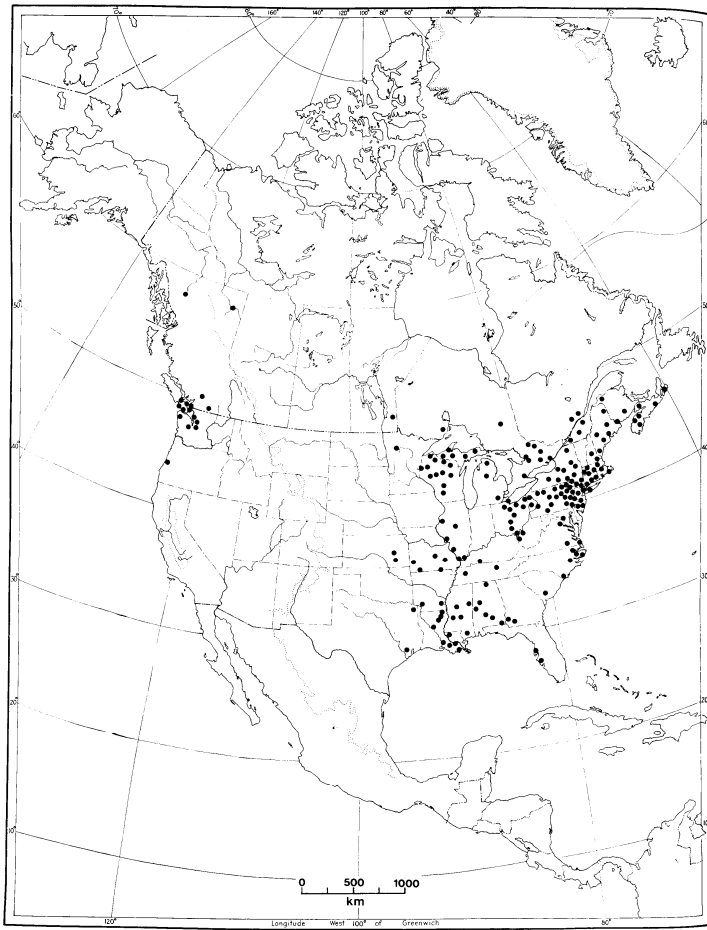


FIG. 2. Dot-distribution map of *Ceratophyllum echinatum* in North America based upon specimens examined.

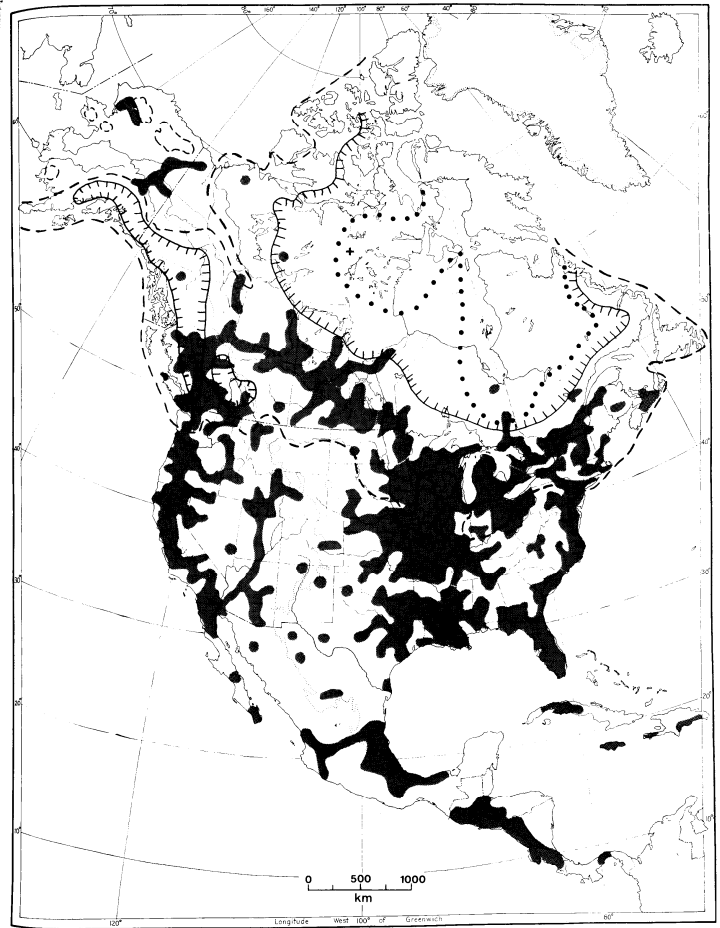


FIG. 3. Shaded distribution map of *Ceratophyllum demersum* in North America with glacial boundaries. Broken line, glacial maximum at 22 000 to 15 000 years BP (from Pewe 1983); solid, hatched line, glacial boundary at 10 000 years BP (from Pewe 1983); dotted line, glacial boundary at 8000 years BP (from Knox 1983); +, fossil site of approximately 5400 years BP (from Terasmae and Craig 1958).

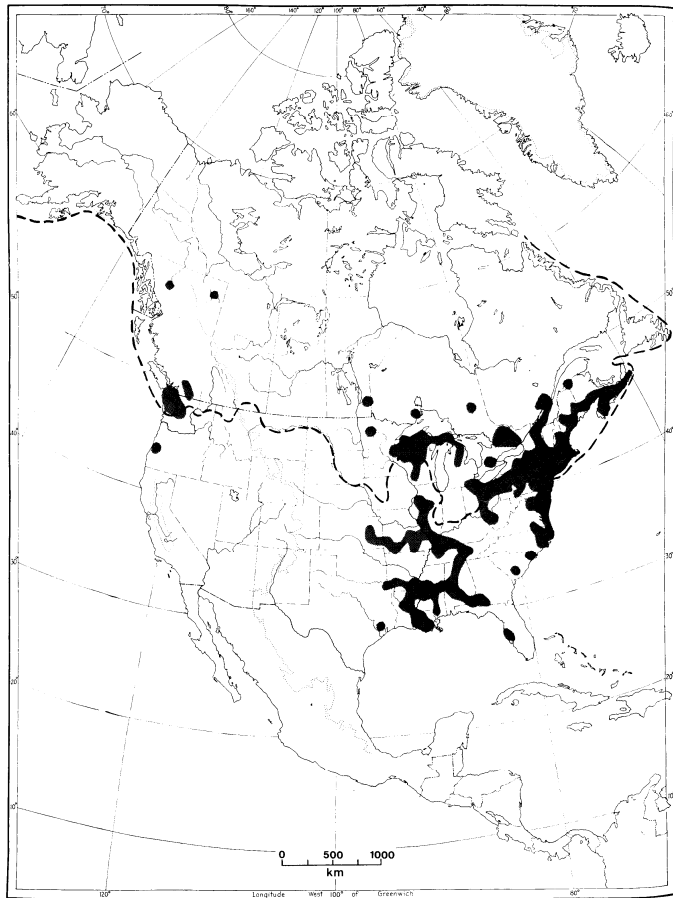


FIG. 4. Shaded distribution map of *Ceratophyllum echinatum* in North America with glacial boundary. Broken line, glacial maximum at 22 000 to 15 000 years BP (from Pewe 1983).

TABLE 1. Submersed aquatic plants with similar North American distributions

Species and growth form*	Reference	Cited in Aiken and Gillett, 1974	Cited in Ogdén et al., 1976
<i>Ceratophyllum echinatum</i> (V)	Ceska and Warrington 1976	-	+
<i>Heteranthera dubia</i> (V)	Ceska and Ceska 1980	+	+
<i>Lobelia dortmanna</i> (R)	McVaugh 1936	+	+
<i>Megalodonta beckii</i> (V)	Muenschler 1944	+	+
<i>Myriophyllum farwellii</i> (V)	Ceska and Warrington 1976	-	-
<i>Najas gracillima</i> (V)	Haynes 1979	-	-
<i>Potamogeton alpinus</i> (V)	Ogdén 1943	+	+
<i>P. amplifolius</i> (V)	Ogdén 1943	-	-
<i>P. ephedrus</i> (V)	Fernald 1932	+	+
<i>P. friesii</i> (V)	Fernald 1932	-	+
<i>P. oakstianus</i> (V)	Ceska and Ceska 1980	-	+
<i>P. pusillus</i> (= <i>P. berchtoldii</i>) (V)	Fernald 1932	+	+
<i>P. robbinsii</i> (V)	Muenschler 1944	+	+
<i>P. strictifolius</i> (V)	Ceska and Ceska 1980	-	-
<i>P. zosteriformis</i> (V)	Fernald 1932	+	-
<i>Ranunculus flabellaris</i> (V)	Muenschler 1944	-	+
<i>Scirpus subterminalis</i> (R)	Muenschler 1944	+	+
<i>Sparganium fluctuans</i> (R)	Ceska and Warrington 1976	-	+
<i>Subularia aquatica</i> (R)	Muenschler 1944	-	+
<i>Utricularia gibba</i> (V)	Ceska and Warrington 1976	+	+
<i>Vallisneria americana</i> (R)	D. H. Les, unpublished	+	-

*V, vivitate; R, rosulate.

Results and discussion

Distribution maps of *Ceratophyllum demersum* and *C. echinatum* (Figs. 1-4) confirm the existence of gaps in the boreal North American distribution of both species. The east-west North American disjunction of *C. demersum* indicated by Hulten (1970) was an artifact of insufficient collection data. Although there is a distinct gap in the Rocky Mountain region, the species is continuous through the Canadian prairie provinces by a narrow band of populations connecting east and west North American centers (Figs. 1 and 3). Alaskan and Canadian high-arctic populations of *C. demersum* are disjunct by more than 1000 km from this continuous portion of the species range (Figs. 1 and 3). Populations of *C. echinatum* in the Pacific Northwest are separated by more than 1700 km from the nearest population in the continuous range of the species (Figs. 2 and 4).

According to Hulten (1937), gaps in the distribution of boreal species were formed as the plants migrated onto refugia south of the ice front. Because the refugia were separated by physical barriers (such as mountain ranges), gaps developed wherever populations were trapped and exterminated between such barriers and the ice. Many species were able to fill the gaps during interglacial periods by migration out of southern refugia, although species with a lesser capacity to spread were unable to do so (Hulten 1937). Hulten's explanation of disjunction by glacial isolation followed by incomplete interglacial migration may apply not only to circumpolar species such as *C. demersum* but also to species of narrower ranges, such as *C. echinatum*. The pattern of a continuous eastern North American distribution with disjunct western populations occurs in at least 20 species of submersed aquatic plants (Table 1). The distribution of these species both north and south of the glacial boundary is an indication that they are presently in a phase of interglacial migration.

Aquatic plants and glaciation

Although some aquatic plants probably succumbed to Pleis-

tocene glaciation (Sculthorpe 1967; Tralau 1959), many were adapted for successful migration away from the oncoming ice and for later recolonization after glacial recession. Tremendous amounts of meltwater liberated during glacial recession created many fluvial and lacustrine habitats (Sculthorpe 1967). It is estimated that most lowland areas of the Yukon were inundated by meltwater lakes during the Pleistocene epoch (Matthews 1982). These habitats were conducive to hydrophyte colonization, particularly those species capable of establishment under oligotrophic conditions. The fossil record indicates that aquatic plants were capable of surviving close to the ice margins (Hulten 1937). This ability would enable hydrophytes to colonize rapidly the numerous new aquatic habitats formed as glacial ice receded. Aquatic plants fulfilled several requirements necessary for undergoing extensive Quaternary migrations: (i) a long species duration (dating back at least to the Pliocene); (ii) a distributional range continuous throughout boreal North America; (iii) high vagility (enabling migration both away from approaching ice sheets and into newly deglaciated regions); and (iv) adaptation to cold-water life and oligotrophic conditions (to endure habitat changes associated with glaciation).

There is little fossil evidence to document that particular aquatic plant species occurred in boreal North America prior to the Pleistocene. The lack of literature reports for Pliocene or older fossils within glaciated regions of North America is a result of glacial erosion of older sedimentary fossil-bearing deposits. In particular, the study of the genus *Ceratophyllum* poses a further difficulty. The early history of many plant species has been elucidated by their microfossil record; however, the pollen of *Ceratophyllum* probably does not fossilize (Pals et al. 1980). Macrofossils of *Ceratophyllum demersum* are known from Upper Pliocene deposits (Kirchheimer 1957) and it is likely that other extant aquatic plant species also date back to at least that period. Tiffney (1981) hypothesized that aquatic vascular plants have endured a species existence longer than most terrestrial plants, owing to their life in stable, well-

buffered aquatic environments, where abiotic selection is relatively low.

Because of the incomplete fossil record, it is difficult to furnish direct evidence that various aquatic plant species occurred continuously throughout boreal North America prior to Pleistocene glaciations; however, this assumption is reasonable. The observation that hydrophytes inhabit ranges relatively greater than their terrestrial counterparts was made by Arber (1920). Hutchinson (1975) suggested that wide ranges of water plants are a corollary to their efficient dispersal mechanisms, which have evolved in response to the geologically transitory nature of freshwater habitats. Hydrophytes have dispersal options (e.g., fragment carriage) not open to most terrestrial plants which require planting of fragmented parts (Hutchinson 1975). As a result of their great vagility, many hydrophytes are wide ranging within regions of their ecological tolerances (Hutchinson 1975). Indeed, the recent migrations of indigenous aquatic plants into glaciated North America are an indication that these species were once distributed more widely in the region than their present ranges imply.

Newly deglaciated habitats were probably similar limnologically to extant ponds and lakes of the tundra. Such habitats can be quite severe, often warming no higher than 10°C and characteristically containing low amounts of nutrients (Hobbie 1980). Aquatic plants with tolerances for these conditions could endure habitat cooling as glaciers advanced. This, in effect, would increase the time available for successful migration into less severe habitats. Plants not so adapted would probably have perished from the cold conditions before reaching suitable refugia. Such adaptations for cold-water survival would have been necessary for hydrophytes to persist close to advancing or retreating ice fronts, as Hulten (1937) suggested. Many temperate aquatic plants tolerate low water temperatures and, unlike terrestrial plants, are not often subjected to freezing. Even in arctic Alaska, lakes over 2 m deep do not usually freeze to the bottom (Holmquist 1971). Pure water reaches its greatest density at 4°C (Wetzel 1975); consequently, winter water temperatures seldom fall below this value in the benthic zone where rooted aquatic vegetation is able to survive. In one instance, healthy, green plants of *Eloidea canadensis* were dredged from 3 m depth in the St. Mary's River, United States (46°30' N latitude), where ice was 1 m thick and surface temperatures reached -29°C (D. H. Les, unpublished). Boylen and Sheldon (1976) found that in Lake George, New York (United States), nearly 40% of the submersed macrophytes not only maintained high viable biomass under winter ice cover but also carried on photosynthesis at rates from 10 to 20% of summer levels. To survive in shallower waters which may freeze completely, aquatic plants have evolved seeds and turions (Arber 1920) capable of withstanding periods of freezing. Because of these adaptations for cold-water survival, Hulten's (1937) suggestion that hydrophytes persisted close to advancing or retreating ice fronts is reasonable.

Both *Ceratophyllum demersum* and *C. echinatum* are tolerant to cold water. Imisch (1853) studied overwintering of *C. demersum* and noted that whole plants, as well as detached dormant apices, served as means of perennation in the species. His observations were confirmed by Muenscher (1944) and Stuckey et al. (1978), who observed living plants of *C. demersum* in ice-covered waters of ponds. *Ceratophyllum demersum* maintains sexual reproduction in cold climates. Flowering and fruiting in the species occur up to 68° N latitude in Europe (Julin and Luther 1959) and near 59° N latitude in North

America (D. H. Les, unpublished). Although Guppy (1895) concluded that water temperatures in excess of 27°C are necessary for *C. demersum* to mature fruits, the above findings, as well as observations of fruit maturation on plants at lower temperatures (18°C), refute Guppy's claims (Les 1980; D. H. Les, unpublished). *Ceratophyllum echinatum* overwinters by dormant apices (Les 1980), but it is not known whether the species can perennate as a whole plant. The apices of *C. echinatum* recover quickly from dormancy when temperatures and photoperiod increase. Dormant apices continuously illuminated and cultured at 24°C produced flowers in less than 2 weeks after their removal from the field (Les 1980). The extended distributions of both *C. demersum* and *C. echinatum* into cold climatic regions are a further indication of their tolerance to low water temperatures.

Glacial lakes originated as oligotrophic water bodies in clay, sand, or gravel basins (Neel 1963), habitats not ideally suited for colonization by aquatic plants. Although the habitats of northern aquatic plant species are often regarded as oligotrophic (Stuckey 1975), they are certainly more nutrient rich than were the newly exposed glacial habitats. Nevertheless, a knowledge of the present-day flora of these habitats can provide clues to what species may have first colonized new glacial habitats. According to Hutchinson (1975), oligotrophic lakes in the temperate northern hemisphere are inhabited generally by rosulate aquatics such as *Lobelia dortmanna*, *Isotetes*, and *Sagittaria*. As lakes evolve toward mesotrophic conditions, vittate species such as *Ceratophyllum*, *Najas*, and *Potamogeton* become more abundant (Hutchinson 1975). *Ceratophyllum demersum*, *C. echinatum*, and most of the submersed species with disjunct distributions (Table 1) are vittate, which suggests that these plants would have invaded glacial habitats after the nutrient status of the lakes had increased somewhat.

A comparison of the extant flora of lakes in glaciated North America with the submersed aquatic plants exhibiting disjunct east-west North American distributions is informative. Aiken and Gillett (1974) studied 21 lakes in Gattineau Park, Québec. Twelve of the 21 species (57%) listed in Table 1 occur in those lakes and often grow together. The aquatic flora of Lake George, New York (Ogden et al. 1987), includes 15 of the 21 species (71%, Table 1). In both studies, rosulate and vittate species occur together (Table 1) indicating that their ecological tolerances are relatively similar. During summer (1985) fieldwork in the Pacific Northwest, I noticed aggregations of several of these same species (e.g., *Ceratophyllum echinatum*, *Lobelia dortmanna*, *Megalodon beckii*, *Potamogeton amplifolius*, and *P. robbinsii*) in lakes of western Oregon and Washington (United States) and British Columbia (Canada). This group of submersed hydrophytes shares a similar Quaternary distributional history, as evidenced by their parallel patterns of disjunction. These plants also share similar habitat preferences, as indicated by their coexistence in extant communities. The survival of this group of species throughout the repeated Pleistocene glaciations is indicative of their well-developed ability for dispersal and establishment. Accordingly, this group of disjunct aquatics may have been a conspicuous element of many interglacial hydrophyte communities as they reformed in boreal North America throughout the glacial episodes. Whether similar communities existed in the region prior to glaciation is not ascertainable. Extant hydrophyte communities in boreal North America probably represent species selected for efficient migrational ability.

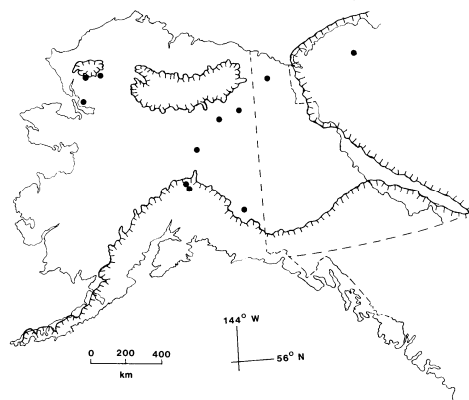


Fig. 5. Northwestern North American distribution of *Ceratophyllum demersum*. Solid, hatched line, maximum extent of Wisconsinan glaciation (from Coulter et al. 1965; Pewe 1983).

Probable migratory routes of *Ceratophyllum demersum* and *C. echinatum*

The present North American distribution of *Ceratophyllum demersum* is delimited in Fig. 3. During the Pleistocene, the species had to migrate south or westward to escape glaciation. In Fig. 3, the probable migratory pathways followed by the species are evident. Alpine glaciations presumably prevented its southward migration into the Rocky Mountains. The species may have moved south along the west coast of North America, where other populations extend northward from South America. The southward migration of *C. demersum* along both sides of the Appalachian Mountains is also likely to have occurred, as indicated by the presence of the species in both the Atlantic coastal plain and Mississippi embayment regions. After glacial recession, *C. demersum* migrated northward, and the populations once separated in eastern and western North American refugia became reunited. This union apparently occurred along the receding glacial front, which opened a corridor for plant migration between 22 000 and 10 000 years before present (BP) (Fig. 3).

The disjunct northern populations of *Ceratophyllum demersum* are probably relicts of a formerly wider North American range of the species throughout Alaska and western Canada. In Fig. 5, the northernmost distribution of *C. demersum* is superimposed on a map showing the extent of unglaciated portions of this region. The extant occurrences of the species correlate with unglaciated areas except for two populations in the Alaska Range and one in the Northwest Territories. Because these regions were glaciated during the Wisconsinan (Coulter et al. 1965), the sites probably represent dispersal from populations surviving in nearby unglaciated areas. Large glacial lakes existed in the Alaska Range region (Pewe 1975) and may have served as refugia for *C. demersum* and other hydrophytes. Populations of *C. demersum* in the Northwest Territories were

probably established by migrants from unglaciated parts of Alaska and Yukon Territory. Fossils of *C. demersum* from the north Canadian Shield (Terasmae and Craig 1958) support the idea of northwestern refugia for the species (see Fig. 3). The fossils were discovered in an area deglaciated 6000 years BP (Dotz and Batten 1976). The age of the fossil leaves is approximately 5500 years BP, indicating a rapid migration of the species into the deglaciated area. Migrants of *C. demersum* from nearby northwestern refugia could have quickly entered that area as they moved eastward along the receding ice front.

The northern distribution of *Ceratophyllum echinatum* probably ranged from eastern Québec to western British Columbia during the Pliocene. As Pleistocene glaciations progressed, migration southward occurred, probably along routes similar to those followed by *C. demersum* (Figs. 2 and 4). In the west, its southward migration may have been blocked by the Cascade Ranges, explaining why the present western range of the species extends no farther south than Siltcoos Lake, Oregon (United States). Unlike the wider ranging *C. demersum*, there were probably few populations of *C. echinatum* established previously to the south of this region. Paralleling routes taken by *C. demersum*, *C. echinatum* apparently migrated along both sides of the Appalachian Mountains to similar refugia. Unlike *C. demersum*, however, the east-west populations of *C. echinatum*, isolated earlier by glaciation, did not reunite. This discrepancy is probably due to the relative lack of populations in the south capable of serving as sources for northward migration.

Species of *Ceratophyllum* have undergone similar Quaternary migrations in Europe. It is commonly believed that *Ceratophyllum demersum* migrated progressively southward following the last glacial recession as continued cooling of northern habitats occurred (Sculthorpe 1967). This assumption was based upon the fact that fossils of the species had been

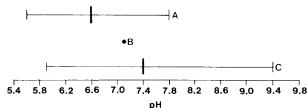


FIG. 6. Summary of water pH in 89 habitats of eastern North America *Ceratophyllum*. (A) Range (horizontal line) and mean (thick, vertical bar) of nine pH measurements made in *Ceratophyllum echinatum* habitats. (B) pH measurement from a habitat in southern Illinois (United States) where both *Ceratophyllum demersum* and *C. echinatum* occurred together. (C) Range (horizontal line) and mean (thick, vertical bar) of 80 pH measurements made in *Ceratophyllum demersum* habitats (compiled from Beal 1977; Hellquist and Crow 1984; D. H. Les, unpublished).

found considerably farther north of its present-day distribution (Backman 1943). Recent finds of extant localities of the species necessitate a revision of this hypothesis. *Ceratophyllum demersum* is now known to occur north of the arctic circle in both Eurasia and North America, a limit equalling or surpassing the northernmost subfossil finds on both continents (Julin and Luther 1959; Hulten 1970). Therefore, explanations for a southward migration of *C. demersum* may be superfluous. The formerly wider postglacial distribution of the species probably reflects the temporary nature of numerous, shallow habitats created upon retreat of glaciers. As succession progressed in these habitats, the submersed species would eventually have been exterminated. In North America, subfossils of *C. demersum* also have been found in a region not inhabited by extant populations. The fossilized plants lived originally in a shallow-water habitat where much peat deposition occurred (Terasma and Craig 1958), an indication of the transitory nature of such habitats. It is quite possible that aquatic plants such as *C. demersum* once thrived throughout newly deglaciated areas but continue to survive only in deeper or more permanent sites.

Influences of competition, habitat, and climate

Competition has undoubtedly played a part in influencing the present distributions of both *Ceratophyllum demersum* and *C. echinatum*. During observations of nearly 100 North American sites inhabited by *Ceratophyllum*, only 2 localities were found where both *C. demersum* and *C. echinatum* occurred together (D. H. Les, personal observation). In both instances, *C. demersum* was the more dominant species. Unlike congeneric species of morphologically diverse hydrophyte genera such as *Potamogeton*, *Ceratophyllum demersum* and *C. echinatum* are extremely similar in their growth habit and probably occupy very similar ecological niches. Therefore, the segregation of these species can be explained by Gause's principle of competitive exclusion which states that competition between species sharing the same niche will be severe in a stable environment, leading eventually to the elimination of one of them (Silvertown 1982). With respect to these species, it appears that overall, *C. demersum* is the better competitor. A similar situation has been noted for *Veronica beccabunga*, where competition with a closely related native species has apparently hindered the establishment of this introduced hydrophyte (Les and Stuckey 1985). Although *Ceratophyllum demersum* and *C. echinatum* are sympatric, *C. echinatum* persists in a fairly wide range. It is generally believed that closely related sympatric species avoid severe niche competition by the adaptive process of "character displacement"

(Dobzhansky et al. 1977). There is evidence that this process has occurred in *C. demersum* and *C. echinatum*. Both species rarely coexist and their habitat "preferences" differ. *Ceratophyllum demersum* is a plant of alkaline, nutrient-rich habitats (Eyles and Robertson 1944; Hutchinson 1975), whereas *C. echinatum* is most often associated with acidic, nutrient-poor sites (D. H. Les, personal observations). A summary of pH data measured in habitats of both species throughout the eastern United States supports these observations (Fig. 6). The mean pH of habitats in which *C. demersum* occurred was alkaline (7.4), whereas the mean for *C. echinatum* habitats was acidic (6.6). Interestingly, the pH of a habitat where both species occurred together was essentially halfway between these mean values (Fig. 6). Because of seasonal—diurnal variations, however, the mean values only estimate the optimal pH range of either species. Nevertheless, these data indicate that there has probably been character displacement between these species, in terms of their physiological tolerances to different habitat types. The extremely wide range of pH tolerance displayed by *C. demersum* indicates that in the absence of competition with *C. echinatum*, this species is able to persist in a variety of habitats. This tolerance to habitats correlates with the wide distributional range of *C. demersum*. During deglaciation, the spread of *C. echinatum* may have been limited by the availability of acidic habitats in which the species would have a competitive edge over *C. demersum*. *Ceratophyllum demersum*, however, was probably not as sensitive to habitat type, a factor which may account for its enhanced ability to spread in the newly exposed habitats.

Little is known about competition between these *Ceratophyllum* species and members of other aquatic genera. Because of the lack of controlled competition experiments, intergeneric competition can be assessed only from circumstantial evidence obtained by field observations. Throughout the North American ranges of both *C. demersum* and *C. echinatum*, their density varies from rare to abundant among sites (D. H. Les, personal observation), which may indicate differential responses to competition with other aquatic plants. There are other explanations for this variation, however, further complicating any assessment of how intergeneric competition may have influenced the present distribution of either species.

Climate has long been regarded as a major factor determining plant distributions (Good 1953). This conclusion, however, may be more fitting for terrestrial plants than for some submersed aquatic plants. *Ceratophyllum demersum* has a particularly wide range of climatic tolerances, as evidenced by its present cosmopolitan distribution in habitats ranging from sea level to elevations over 1700 m (Sculthorpe 1967), in arctic lakes (Holmquist 1971), and in desert oases (D. H. Les, personal observations). Because of this wide range of tolerances, it appears that climate has not been influential in regulating the distribution of this species. Even the narrower ranging *C. echinatum* spans fairly wide latitudinal and climatic ranges extending from humid subtropical to subarctic zones (Espenshade and Morrison 1975). Stuckey (1983), however, suggested that many submersed aquatics (including *C. echinatum*) may have succumbed to the drying effects of the xerothermic period as evidenced by their absence from the "prairie peninsula" region of the central United States. In fact, the modern distributions of both *C. demersum* and *C. echinatum* do exhibit gaps in this region (Figs. 1 and 2; approximately 40° N latitude; 90° W longitude). Because *C. echinatum* has an affinity for cooler climates, the warming period of the xer-

thermic may have been responsible for its absence from this region as Stuckey (1983) suggested. The absence of *C. demersum* from this same region is difficult to explain because of its demonstrated tolerance to warm climates. The correlation of extensive cropland with the prairie peninsula (Espenshade and Morrison 1975) is an indication that the modern absence of more tolerant aquatic species such as *C. demersum* may be an artifact of the extensive agricultural drainage of this area by early settlers. The warming of central North America during the xerothermic period may have restricted the spread of less tolerant boreal aquatic plants in that region and hindered the rejoining of their disjunct populations. Widespread species with broad environmental tolerances would not have been as susceptible to these climatic changes.

Alternate hypotheses

The disjunct distributions of *Ceratophyllum demersum* and *C. echinatum* are consistent with Hulten's (1937) view of Quaternary plant migrations. There are alternate explanations for their present distributional irregularities that warrant discussion, namely, introductions and long-distance dispersal.

It is unlikely that northernmost North American populations of *Ceratophyllum demersum* in Alaska and Canada have resulted from plant introductions in that region. These sites have been explored only recently (e.g., Holmquist 1971; Cwynar 1983) and are in areas isolated from populated centers. Also, these northern populations are diffusely scattered, an indication that they have not radiated from a particular site of introduction.

Ceska and Ceska (1980) regarded the disjunct populations of *Ceratophyllum echinatum* in British Columbia as native and attributed its belated discovery in western North America to inadequate collecting. They reported that the species is often undetected in lakes because of its tendency to grow anchored to the bottom at considerable depths. Early collections of *C. echinatum* were made in the region but remained misidentified as *C. demersum* or went unnoticed by authors of aquatic plant manuals for that area (Steward et al. 1960, 1963; Mason 1982). In preparing this work, western North American specimens were found dating back to 1892. Collection dates of the Pacific Northwest specimens gave no indication of radiation from a single point of origin, suggesting that the species is native to the region. Most of the specimens of *C. echinatum* from this area are sterile and require more than casual study for proper identification. Because the vegetative differences between *C. echinatum* and *C. demersum* are not often included in keys (Les 1980), it is apparent why the species was not recognized in the region until discovery of fruiting material (Ceska and Ceska 1980).

It is unlikely that long-distance dispersal is responsible for the disjunctions. *Ceratophyllum* is dispersed mainly by fragment carriage by waterfowl (Ridley 1930), a method effective only over short distances. The fruits of *Ceratophyllum* are categorized as "water-burs" (Van der Pijl 1982) and are probably dispersed locally by waterfowl. Because of their large size (3–5 mm excluding spines), however, their dispersal over long distances is unlikely. Long-distance dispersal by adhesion is limited to much smaller seeds and fruits (Ridley 1930). Evidence against the long-distance dispersal of *C. echinatum* can be obtained by examining waterfowl flyway routes. The most concentrated migration of ducks in North America is toward the Canadian prairie provinces, precisely the region in which *C. echinatum* is absent (Bellrose 1976).

The fact that many submersed aquatic plants possess similar

disjunct distributions (Table 1) also argues against both introduction and long-distance dispersal of these species. The possibility that all of these species were either introduced or dispersed to identical regions and were at the same time excluded from similar areas is negligible.

Summary and conclusions

The distributional patterns of *Ceratophyllum demersum*, *C. echinatum*, and other submersed aquatic plants reflect a similar Quaternary history. Prior to Pleistocene glaciations, hydrophyte communities consisting of vagile species with tolerance for cold, oligotrophic water probably existed transcontinentally in boreal North America. During glacial periods, these species migrated into refugia assisted by their efficient systems of dispersal and tolerances to changing climatic conditions. In recent time, aquatic plants have colonized deglaciated areas that occurred along the receding ice front. Species with widespread distributions, such as *Ceratophyllum demersum*, quickly moved into deglaciated habitats and have recovered much of what was probably their former North American range, assisted by source populations established previously south of the glacial boundary. These species characteristically have wide climatic tolerances and are fairly good competitors, factors which have assisted their spread. More restricted species such as *C. echinatum* were less successful in migrating northward, probably because of the smaller number of individuals reaching and surviving in refugia, their only source of migrants. Many of these species have more specific habitat requirements and narrower climatic tolerances and are relatively poorer competitors, factors which have hindered their recolonization of glacialated areas. These species characteristically show a disjunct east–west North American distribution which reflects the physical separation of glacial refugia. Similar Quaternary migrational histories have been suggested for terrestrial plants as well (Wood 1972; Marquis and Voss 1981). Aquatic plants may be a more conspicuous component of this type of distributional history because of their biological similarity as a group and the relative homogeneity of aquatic habitats. Although long-distance dispersal and plant introductions cannot be ruled out as explanations for the disjunct distributions of many temperate hydrophytes, the striking similarity of their distributional patterns is evidence against such coincidental explanations. In North America, the distributional range of widespread aquatic plants such as *C. demersum* is probably limited mostly by opportunity for dispersal. This conclusion is in agreement with Smith (1978), who stated that much vegetational change during the Quaternary was determined by ability and chance for plant dispersal and establishment.

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