

Status, Distribution, and Nomenclature of Northern Quillwort, *Isoetes septentrionalis* (Isoetaceae), in Canada

DANIEL F. BRUNTON^{1,4} and JOHN MCNEILL^{2,3}

¹216 Lincoln Heights Road, Ottawa, Ontario K1A 8A8 Canada

²Royal Botanic Garden, Edinburgh, 20A Inverleith Row, Edinburgh, Scotland EH3 5LR U.K.

³Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6 Canada

⁴Corresponding author: bruntonconsulting@rogers.com

Brunton, Daniel F., and John McNeill. 2015. Status, distribution, and nomenclature of Northern Quillwort, *Isoetes septentrionalis* (Isoetaceae) in Canada. *Canadian Field-Naturalist* 129(2): 174–180.

The lycophyte Northern Quillwort (*Isoetes septentrionalis* D. F. Brunton, *sp. nov.*) is the northern component of the Riverbank Quillwort (*I. riparia*) complex. It is locally abundant in southeastern Ontario and southwestern Quebec and is also widely distributed in the northeastern United States. In Canada, it is largely confined to river and lake shores along post-glacial drainage outlets within the limits of the post-glacial Champlain Sea. It is frequently found in association with other *Isoetes*, especially Dodge's Quillwort (*I. ×dodgei* A. A. Eaton), its sterile hybrid with Spiny-spored Quillwort (*I. echinospora* Durieu). The Canadian population of *I. septentrionalis* appears to be stable. Although first proposed at species level over a century ago, the nomenclature of this taxon has remained unresolved. It is clarified in the present study, in which *I. canadensis* var. *robbinsii* is lectotypified.

Key Words: Riverbank Quillwort; Northern Quillwort; *Isoetes septentrionalis*; *Isoetes riparia*; *Isoetes ×dodgei*; *Isoetes canadensis* var. *robbinsii*; Champlain Sea

Introduction

The Riverbank Quillwort, *Isoetes riparia* Engelmann ex A. Braun (Isoetaceae) complex consists of a number of tetraploid ($2n = 44$) aquatic emergent lycophytes (fern allies) that occur widely across eastern North America. *Isoetes riparia* (*s.l.*) is found predominantly close to and along the Atlantic Coastal Plain north from Virginia into southern Maine and then inland along major river and lake systems through eastern New England into the Champlain Sea lowlands of northern New York, southeastern Ontario, and southwestern Quebec (Taylor *et al.* 1993). It is typically uncommon to rare (Montgomery and Fairbrothers 1993; Tryon and Moran 1997; Taylor and Brunton 2000; Gerke *et al.* 2014). Although possibly more abundant within its Canadian rather than its adjacent United States range, it is considered a species of conservation concern in Ontario (Oldham and Brinker 2009) and potentially also in Quebec (Cody and Britton 1989).

Isoetes riparia (*s.l.*) is a complex taxon with a tangled nomenclatural history (Engelmann 1882; Eaton 1903a; Pfeiffer 1922; Proctor 1949; Kott and Britton 1983). Northern (typically inland) freshwater populations of robust plants (Figure 1) characterized by larger, more coarsely ornamented megaspores have been variously referenced as *I. riparia*, *I. dodgei* A. A. Eaton (as a species, not as a hybrid) and *I. canadensis* (Kott and Britton 1983; Britton and Brunton 1989). In at least parts of Canada, for many years *I. riparia* (*s.l.*) populations were also confused with the decaploid ($2n = 110$) *I. lacustris* Linnaeus (*I. macrospora* Durieu) (e.g., Marie-Victorin 1935; Boivin 1966; Gillett and White 1978). Kott and Britton (1983) clarified the differenti-

ation of *I. lacustris* from *I. riparia* (*s.l.*), noting especially the much larger megaspores of the former species, which also exhibit a more evenly reticulate ornamentation pattern. The identification of *I. ×jeffreyi* D. M. Britton & D. F. Brunton as the sterile, septaploid ($2n = 77$) hybrid between *I. lacustris* and northern *I. riparia* (*s.l.*) confirmed the distinction between these two species (Britton and Brunton 1992). For working purposes, the distinctive northern component of *I. riparia* (*s.l.*) has been known as *I. riparia* “canadensis” and will initially be so referenced in the following.



FIGURE 1. Mature, emergent plants of *Isoetes septentrionalis*, Madawaska River, Stewartville, Renfrew County, Ontario, Canada, 25 July 2013. Photo: D. F. Brunton.

Southern *Isoetes riparia* (*s. str.*) (*I. saccharata* Engelmann, including *I. riparia* var. *reticulata* (A. A. Eaton) Proctor) occurs in shallow brackish water and emergent tidal shores along the Atlantic coastal plain (Proctor 1949). The holotype of *I. riparia* (“gravelly shore, Dela-

A contribution towards the cost of this publication has been provided by the Thomas Manning Memorial Fund of the Ottawa Field-Naturalist's Club.

ware River near Philadelphia, Dr. Zantziger August 1844," MO) is from near the northernmost limit of the range of *I. riparia* (*s.str.*). The *I. riparia* complex is also considered to include the recently described freshwater aquatic *I. hyemalis* D. F. Brunton as its southernmost component (Caplen and Werth 2000a).

The distinction between the northern "canadensis" component of *Isoetes riparia* (*s.l.*) and the complex of southern components has been recognized for many years (Engelmann 1882; Clute 1904; Pfeiffer 1922). In addition to previously documented morphological and ecological differences, however, the investigation of *I. riparia* (*s.l.*) isozyme genotypes by Caplen and Werth (2000a, 2000b) provided strong evidence for the uniqueness of the northern "canadensis" taxon as an allopolyploid species arising from hybridization between the diploids ($2n = 22$) *I. echinospora* and *I. engelmannii* A. Braun. In contrast, they determined that southern *riparia* complex components most likely arose from different diploid ancestors, including *I. valida* (Engelmann) Clute, *I. mattaponica* L. J. Musselman & W. C. Taylor and *I. flaccida* A. Braun.

The following provides a review of the Canadian status of *Isoetes riparia* "canadensis" to evaluate its apparent relative abundance, identify distribution patterns, and report and evaluate recent additions to its previously known range. With the added weight of genetic evidence supporting long-standing arguments for this taxon to be treated at species level, the need for nomenclatural clarification is compelling. That clarification is provided below.

Methods

Observations on the ecological characteristics of *Isoetes riparia* "canadensis" were developed during field investigations conducted by the first author throughout the range of *I. riparia* (*s.l.*) since 1987. Distributional information and the physical attributes of preserved specimens were determined through the examination of over 300 voucher specimens in CAN, DAO, DUKE, FLAS, FSU, MB, MICH, MO, NYS, OAC, PH, PSU, TRT, UNA, US and the D. F. Brunton personal herbarium. Approximately 125 of these were from *I. riparia* "canadensis" populations. Scanning electron microscope (SEM) images and the cytology of a selection of these specimens were obtained by the late D. M. Britton of the University of Guelph, employing the techniques described in Britton and Brunton (1989, 1992).

Results and Discussion

Nomenclature

Most confusion over the existing nomenclature of Canadian *Isoetes riparia* (*s.l.*) arises from George Englemann's (1882) speculative application of "canadensis" as a working hypothesis. He suggested that northern populations, "might be [emphasis ours] designated as var. *Canadensis* [sic], but too little is known about it as yet to form a definite opinion." This does

not satisfy the requirements for valid publication, the name being "merely proposed in anticipation of the future recognition of the taxon" (McNeill *et al.* 2012: Article 36.1(b)). Engelmann (1882) cited two specimens that are morphologically and distributionally attributable to the northern component of *I. riparia* (*s.l.*). This account provided a weak but nonetheless nomenclaturally acceptable description of their distinction from the rest of the *I. riparia* complex: "with very few stomata on the leaves and apparently two weak bast-bundles, an upper and a lower one, very pale spots on the sporangia and smoothish microspores."

No further review of this complex occurred until 1898 when Alvah Eaton described *Isoetes dodgei* A. A. Eaton as a new species, close to but distinct from Engelmann's "canadensis" (Eaton 1898). Nonetheless, within a few years he revised that concept (Eaton 1901), concluding that Engelmann's "canadensis" warranted treatment at the species level and proposing "*Isoetes canadensis* (Engelmann) A. A. Eaton, *comb. nov.*" In fact, because Engelmann had not validly published the supposed basionym, this is not a new combination but publication of a new species, validated by Engelmann's brief description. In publishing this new species, however, Eaton also placed his recently described *I. dodgei* in synonymy under *I. canadensis*. Without designating a type from which to unequivocally distinguish "canadensis" from *I. dodgei*, *I. canadensis* thus became a nomenclatural synonym of the previously described *I. dodgei* (McNeill *et al.* 2012: Article 7.5). Eaton soon appreciated this himself, and acknowledged that nomenclatural priority rules prescribed the use of *I. dodgei* over *I. canadensis* (Eaton 1908).

The name *Isoetes dodgei* (and thus *I. canadensis*) was lectotypified by Kott and Britton (1983). Britton and Brunton (1989) subsequently established that most *I. dodgei* specimens, including the lectotype, represent the triploid hybrid *I. echinospora* × *I. riparia* Engelmann (*s.l.*). It was accordingly revised to *I. ×dodgei* A. A. Eaton, *pro. sp.* (Britton and Brunton 1989), the hybrid taxon to which the name *I. canadensis* applies as a synonym. The *I. riparia* of Britton and Brunton (1992) is the *I. riparia* "canadensis" taxon discussed here.

Pfeiffer's (1922) "var. *canadensis* Engelmann" published under *Isoetes riparia*, while constituting the first valid publication of *I. riparia* var. *canadensis* Engelmann ex Pfeiffer, is also illegitimate because Pfeiffer included *I. canadensis* var. *robbinsii* A. A. Eaton (Eaton 1903b) in synonymy. She thus should have adopted the latter, previously published, epithet. As Pfeiffer also included *I. canadensis* A. A. Eaton in the synonymy of *I. riparia* var. *canadensis*, she definitely indicated a different type (that of *I. canadensis* = *I. ×dodgei*) from that of *I. canadensis* var. *robbinsii* (McNeill *et al.* 2012: Article 7.5 and example 6). *Isoetes canadensis* var. *robbinsii* A. A. Eaton (*I. dodgei* var. *robbinsii* (A. A. Eaton) A. A. Eaton in Eaton (1908) and *I. riparia* var. *robbinsii* (A. A. Eaton) Proctor in Proctor (1949)) has

been shown to have been applied to both *I. ×novae-angliae* D. F. Brunton & D. M. Britton (the sterile tetraploid hybrid *I. riparia* “canadensis” × *I. tuckermanii* A. Braun) and *I. riparia* “canadensis” (Brunton and Britton 2006). To eliminate this ambiguity with “robbinsii,” we designate here the following as lectotype for *Isoetes canadensis* var. *robbinsii* A. A. Eaton (Eaton 1903b: 279): UNITED STATES, MASSACHUSETTS, Watson’s Pond, Taunton, 15 September 1905, A. A. Eaton 308, MICH ex herb A. A. Eaton [middle plant (*I. ×novae-angliae*) on mixed sheet between two *I. septentrionalis* plants (to left) and two *I. tuckermanii* plants (to right)]; sheet labeled “Type” in Eaton’s handwriting. In this way the various varietal names with the epithet “robbinsii” become synonyms of *I. ×novae-angliae*.

The previously described taxonomic and nomenclatural confusion surrounding *Isoetes riparia* “canadensis” was due in large measure to the existence of undetected sterile hybrids, which present ambiguous, intermediate morphological characteristics. Until the nature of such hybrids was recognized in the *I. riparia* complex (Britton and Brunton 1989, 1992), the misinterpretation of hybrids often contributed to the presentation of conflicting taxonomic interpretations.

This analysis of the complex nomenclatural history of the northern “canadensis” component of the *Isoetes riparia* complex indicates that no validly published name is available for it at species level. Accordingly, the following is proposed.

***Isoetes septentrionalis* D. F. Brunton, sp. nov.** (Figures 1 and 2). TYPE: CANADA, ONTARIO, City of Ottawa, 45.373850°N, 75.788695°W, 250 m east of water purification plant along south shore of Ottawa River, Britannia Conservation Area, 26 July 1998 *Daniel F. Brunton 13 646* (Holotype: OAC; Isotypes: ODU, FSU, D. F. Brunton personal herbarium). The epithet “septentrionalis” refers to the northernmost geographic position of this species within the *I. riparia* complex.

The species has previously been recognized under the following names, none of which correctly apply to

it: *Isoetes riparia* “var. *canadensis* Engelmann” (Engelmann 1882); *I. canadensis sensu* Eaton (1901, 1903a, 1903b) *pro parte*, non *I. canadensis* A. A. Eaton; *I. riparia* var. *canadensis sensu* Pfeiffer (1922) *pro parte*, non *I. riparia* var. *canadensis* Engelmann ex Pfeiffer; *I. riparia* Engelmann f. *canadensis sensu* Proctor (1949) *pro parte*, non *I. riparia* f. *canadensis* Proctor. (The type of all the names with the epithet “canadensis” is referable to *I. ×dodgei* (*I. echinospora* × *I. septentrionalis*.)

HABIT: Short (< 25 cm tall), aquatic and emergent plant arising from a rounded, two-lobed corm 0.75–1.7 cm wide; **LEAVES:** simple, erect to recurved, semi-evergreen, gradually tapering to the tip, shiny to (usually) dull olive green with sporangia inset into the inner side of widened, whitish-green to white bases; **SPORANGIA:** brown-streaked to completely brown with velum covering 25–40% of sporangium wall; **MEGASPORE:** round, about 545 μm (343–682 μm [720 μm], Kott and Britton 1983) in diameter, triradial hemisphere with a pattern of short, broken to loosely anastomosing ridges and with spines frequently occurring along the ridges (Figure 2a), distal hemisphere with an open pattern of short, irregular, loosely anastomosing ridges and no equatorial band of spines (Figure 2b); **MICROSPORES:** white to grayish in mass, round to oval, about 31 μm (24–38 μm [42 μm], Kott and Britton 1983) in length with numerous tubercles on a smooth perispore (Figure 2c); **CYTOLOGY:** $2n = 44$ (Kott and Britton 1983; Britton and Brunton 1989; Britton and Brunton 1992).

PARATYPES:

CANADA, ONTARIO, Hastings County: Canada West, Crow [sic] River, *J. Macoun s.n.*, 18 July 1864 (MO); 44.49036°N, 77.68920°W, 620 m west of Iron Works dam ruins along east shore of Crow [sic] River, Marmora, 24 September 2002, *D. F. Brunton 15 341* (OAC, TTC, CAN, D. F. Brunton personal herbarium); Leeds & Grenville County: Champagne Point, Thousand Islands, 23 September 1908, *E. P. Bicknell II 393* (NYS); Renfrew County: 46.17171°N, 77.62674°W, Meilleurs Bay by Highway 17 rest stop near Rolphton, Laurentian Hills, 16 August 2007, *D. F. Brunton 17 078* (D. F.

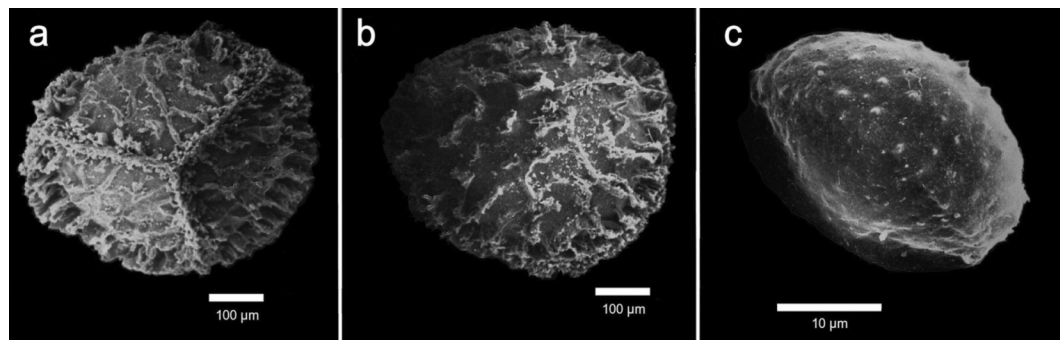


FIGURE 2. Spores of *Isoetes septentrionalis*: (a) triradial hemisphere of megaspore (*J. A. Calder and W. J. Cody 1,685*, 9 September 1947, Fitzroy Harbour, Ontario, DAO); (b) distal hemisphere of megaspore (*L. and E. Kott 622a*, 19 August 1978, Fitzroy Harbour, Ontario, OAC); (c) microspore (*L. and E. Kott 622a*, 19 August 1978, Fitzroy Harbour, Ontario, OAC).

Brunton personal herbarium); [45.3061°N, 76.7108°W], shore of Calabogie Island, Calabogie, Madawaska River, 24 July 1990, *W. D. Bakowsky s.n.* (D. F. Brunton personal herbarium); QUEBEC. Comté de Pontiac: [45.834°N, 76.751°W], Rive de la rivière des Outaouais, sud-ouest de Fort-Coulonge, 3 September 1997, *M. Blondeau et M. J. Oldham OUT-013* (QFA); Gatineau County: [45.38755°N, 75.79421°W] 1 km below Deschênes Rapids, Aylmer, 12 September 1988, *D. F. Brunton 8629* (OAC) [determined $2n = 44$, D. M. Britton, 1988]; UNITED STATES. CONNECTICUT. Fairfield County: mill race in Mill River, Fairfield. *E. H. Eames 8624*, 8 September 1912 (NY); MASSACHUSETTS. Barnstable County: Watson's Pond, Taunton. *A. A. Eaton s.n.*, 15 September 1903 (MICH); NEW HAMPSHIRE. Grafton County: [Powow Pond, Powow River], Kingston, *A. A. Eaton 942*, September 1897 (MICH); NEW JERSEY. Morris County; in Passaic River near Pompton Plains. *R. W. Storer 380*, 30 August 1939 (MICH); NEW YORK. Washington County: along Hudson River, town of Easton. *H. D. House 23,885*, 26 August 1936 (PH); PENNSYLVANIA. Lycoming County: 41.20250°N, 77.25166°W, Susquehanna River below and beside

the Main Street Bridge, Jersey Shore, 6 July 1992, *Daniel F. Brunton and Karen L. McIntosh 11 179* (OAC, MIL, D. F. Brunton personal herbarium) [sampled for analysis in Caplen and Werth 2000a, 2000b]; VERMONT. Caledonia County: Comerford Reservoir near Waterford town line, Barnet, 3 August 1993, *A. V. Gilman 93-189* (MICH). At least one representative paratype is identified for all states and provinces in which the species occurs, except Maine and Rhode Island from which no specimens were seen.

The following modification of a portion of the *Isoetes* key in the Flora of North America (FNA) treatment (Taylor *et al.* 1993) is provided to assist in the identification of *I. septentrionalis* specimens. A couplet addressing *I. septentrionalis* is inserted in that portion of the key treating aquatic, eastern North American *Isoetes* that do not possess echinate megaspores and have velum coverage over less than half of their sporangia. The numbering of the otherwise unaltered 1993 FNA key is retained to simplify comparison. The term "girdle" in the key is equivalent to "equatorial band" used in this paper.

10. Megaspores averaging less than 500 µm diameter; reticulate with unbroken lamellate ridges . . . *Isoetes engelmannii*
10. Megaspores averaging more than 500 µm diameter; reticulate, rugulate, or cristate with isolated broken ridges.
 11. Megaspores with densely papillate or smooth girdle; leaves olive green to reddish-brown.
 12. Megaspores with densely papillate girdle, reticulate to cristate with ridges having irregular and roughened crests *Isoetes tuckermanii*
 12. Megaspores with smooth girdle, rugulate to reticulate with ridges having rounded and smooth crests *Isoetes acadimensis*
 11. Megaspores with obscure girdle; leaves bright green.
 13. Megaspores cristate with isolated and branching lamellate ridges; plants of northeastern North America and eastern seaboard.
 - 13A. Megaspores with short, broken to loosely anastomosing ridges; no equatorial band of spines; freshwater habitat *Isoetes septentrionalis*
 - 13B. Megaspores with densely crowded (rarely, low and broad), anastomosing ridges; equatorial band of spines obscure to conspicuous; tidal beach habitat *Isoetes riparia* (*s.str.*)

Distribution and Status in Canada

As noted above, *Isoetes septentrionalis* occupies the northernmost geographic position of any component of the *I. riparia* complex. In Canada, Cody and Britton (1989) identify *I. septentrionalis* (as *I. riparia*) as occurring in the lower Ottawa River valley of Ontario and Quebec from Ottawa, Ontario, and Gatineau, Quebec, downstream for approximately 200 km to Montreal, Quebec, and downstream along the St. Lawrence River for another approximately 100 km to Sorel. Outliers are known inland in Ontario in the Tweed–Marmora area of Hastings County (approximately 150 km west of the Ottawa River) and along the St. Lawrence River in Leeds & Grenville County (180 km upstream from Montreal). Sites away from the St. Lawrence River in Quebec include the north end of Lake Champlain (approximately 50 km south of the river) and the Thetford Mines area of the Eastern Townships (approximately 65 km southeast of the river).

Our knowledge of the distribution of *Isoetes septentrionalis* in Canada has expanded in the last 20 years, notably in and about the Ottawa Valley of Ontario and Quebec (Figure 3). Recent discoveries have extended its known range more than 100 km upstream along the Ottawa River. As noted in Figure 3, these include the Pontiac County, Quebec, population supported by specimens from Fort Coulonge (*M. Blondeau et M. J. Oldham OUT-013*) and Renfrew County, Ontario, populations supported by specimens from Rolphton (*D. F. Brunton 17 078*) and Calabogie (*Bakowsky, s.n.*). *Isoetes septentrionalis* was subsequently found to be common in and about Calabogie and downstream along the Madawaska River at Stewartville. An additional, "inland" Ontario population from Lanark County is inferred from a specimen of *I. ×dodgei* (45.13326°N, 76.15200°W) west shore of Mississippi River 1.0 km downstream of Highway 7, Carleton Place, Beckwith

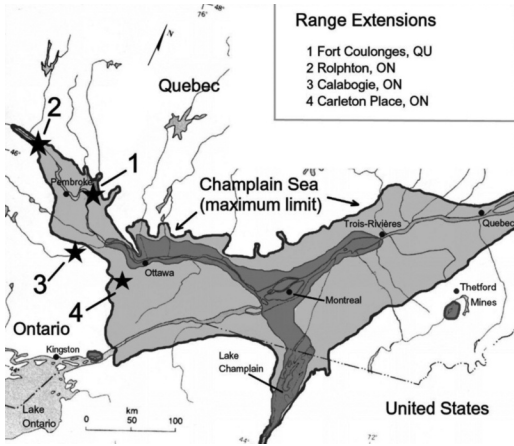


FIGURE 3. Distribution of *Isoetes septentrionalis* in Canada (excludes disjunct Hasting County, Ontario, populations 150 km to the west). Generalized extent of core range (darkest shading) is based on Cody and Britton (1989) and herbarium specimens, as cited in Methods; Champlain Sea maximum limit adapted from Occhietti (1989).

Township, 17 September 2014, *D. F. Brunton and H. Bickerton 18,871* (*D. F. Brunton* personal herbarium).

The core area for *Isoetes septentrionalis* in Canada is the lower Ottawa River and upper St. Lawrence River (Figure 3) where several dozen populations have been documented in a more or less continuous distribution. This core range is within or closely adjacent to the limits of the post-glacial Champlain Sea, an Atlantic Ocean embayment that was present in the lower Great Lakes region 10 000–12 000 years ago (Occhietti 1989). It is presumably not coincidental that the recent range extensions described above are within or immediately adjacent to the maximum reach of the former sea (Figure 3).

Isoetes septentrionalis occurs in a habitat similar to the other *Isoetes* species of Ontario and Quebec; it is typically found in shallow (< 1.25 m deep), fresh water

(Figure 4a) or emergent on shores in sterile sand or fine gravel, often among boulders (Figure 4b), in a sparse association with other aquatic vegetation. A distinctive characteristic of most Canadian *I. septentrionalis* populations is the presence of clay in the substrate immediately below the thin mantle of sand and gravel. Deposition of marine clay during the Champlain Sea era established an abundance of such habitat in eastern Ontario and western Quebec (Chapman and Putnam 1984).

Beneficial aspects of these otherwise uncommon substrate conditions are presumed to have contributed to the abundance of *Isoetes septentrionalis* in the core area. Hundreds if not thousands of plants occur at sites in western Ottawa (Britannia Conservation Area) and Gatineau (Deschênes) amongst the relatively numerous populations found along the lower Ottawa River.

Ontario and Quebec populations also appear to be persistent. That the large population below the Deschênes Rapids in Gatineau has been known from that location for over a century is inferred by the long-term presence of *Isoetes* × *dodgei* (*W. H. Harrington, s.n.*, 1 August 1908 (CAN)) and the contemporary presence of both the hybrid (1 km below Deschênes Rapids, Ottawa River, Aylmer, 12 September 1988, *D. F. Brunton 8628* (OAC)) and *I. septentrionalis* (*D. F. Brunton 8629*). Indeed, the population from which the 1864 John Macoun collection cited in Engelmann (1882) was taken is still thriving after 150 years (*D. F. Brunton 15 341*).

In Canada, *Isoetes septentrionalis* is frequently found in association with *I. echinospora* and rarely also with *I. lacustris*. The presence of sterile hybrids between *I. septentrionalis* and associated species is common. Indeed, hybrids occur in most larger *I. septentrionalis* populations, sometimes in greater numbers than either parent. At the Britannia (Ottawa, Ontario) holotype location of *I. septentrionalis*, for example, a mixed population of 23,000 hybrids, 6,000 *I. septentrionalis*, and 1,000 *I. echinospora*, was estimated to be present

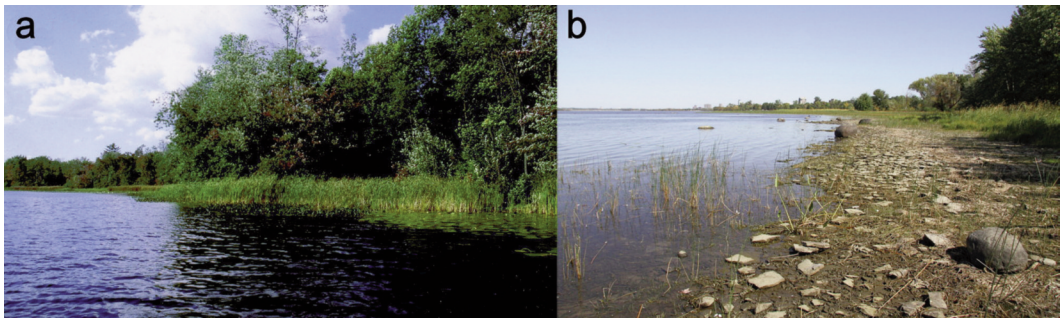


FIGURE 4. Habitat of *Isoetes septentrionalis* in Canada: (a) fully aquatic habitat (shallow, flowing water before marshy fringe), above Marmora, Ontario Iron Works ruins (site of 1864 J. Macoun collection), 24 September 2002, (b) emergent, amphibious habitat (silty sand and clay among open cobble), Britannia Conservation Area, Ottawa, Ontario (holotype location), 25 September 2011. Photos: *D. F. Brunton*.

on 20 July 1993 (personal observation) in an area 350 m long by 25 m wide.

The more robust stature of hybrids has often led to their detection before that of the parent species at particular sites and thus, their disproportionately higher representation in herbaria (Brunton and Britton 2006). No *Isoetes septentrionalis* hybrids are known to occur in the absence of one or (almost always) both diploid parents at any of the sites surveyed in Canada or the United States.

Not conforming closely to this distribution pattern are a cluster of sites in south-central Ontario, despite occurring in similar sites characterized by clay under sterile sand substrate in fresh, flowing water. Thriving populations exist along the banks of the Crowe and Skootamatta Rivers in Hastings County, Ontario, well west of the core area. There is no obvious phytogeographic connection between these western, apparently disjunct populations and those in the core area within the limits of the Champlain Sea. Curiously, although occurring frequently with *Isoetes septentrionalis* populations in the core range, *Isoetes* \times *dodgei* is not known from any of the Hastings County populations, despite *I. echinospora* being commonly found in the vicinity.

The thriving, distributionally atypical Hastings County populations include one of the two occurrences cited by Engelmann in his original (1882) speculation about *Isoetes riparia* “canadensis” (*John Macoun s.n.*). Although not constituting a range extension, the 2001 re-discovery of that population along the Crowe River in Marmora is useful, not only for permitting the contemporary examination of material identical to that used by Engelmann, but also as proof of the longevity of particular *I. septentrionalis* populations.

The Leeds & Grenville County, Ontario, occurrence is based on a more than century-old record (*E. P. Bicknell* 11, 393). Although the site is intact (personal observation), no *Isoetes* have subsequently been found there. The existence of pre-1940 specimens from adjacent St. Lawrence County, New York (NYS), however, supports the interpretation of the Leeds & Grenville County record representing a former natural occurrence rather than a mislabeled specimen from elsewhere.

Notwithstanding densely urbanized sites which have succumbed to development and/or associated water pollution, most Canadian *Isoetes septentrionalis* populations appear to be enduring. Few historic specimen records are not confirmable by contemporary field investigations.

The distribution of *Isoetes septentrionalis* in the United States was determined from the examination of herbarium specimens during the present study (as cited above) to include at least Connecticut, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, and Vermont (Figure 5). Previous *I. riparia* reports from Rhode Island and Maine are also presumed to represent *I. septentrionalis*, although specimens from those states were not examined during this study. It appears to be uncommon to rare throughout much or

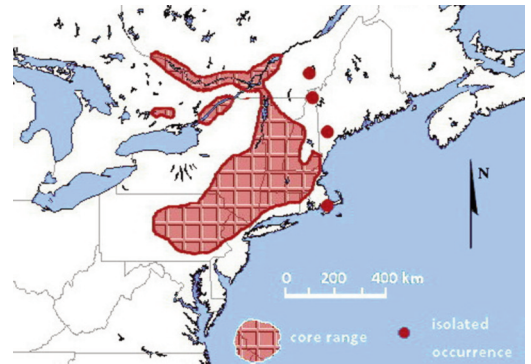


FIGURE 5. North American distribution of *Isoetes septentrionalis* (from Angelo and Boufford 2015; Weldy *et al.* 2015; Rhodes and Klein 1993; Taylor *et al.* 1993; this study).

all of its American range (Gerke *et al.* 2014; Rhodes and Block 2000; Young 2010; Arthur Haines, personal communication).

Conclusions

In Canada, populations of *Isoetes septentrionalis*, the northern representative of the *I. riparia* complex, are concentrated in a core area within the limits of the former post-glacial Champlain Sea. Although typically scattered and modest in size (50–100 plants), the presence of some large and long-persisting populations within the core area imply that the overall Canadian population is substantial and stable. The distribution pattern illustrated by the combination of long-documented and recently discovered occurrences, however, suggests that *I. septentrionalis* will remain rare and local beyond the limits of the former Champlain Sea.

No explanation for the occurrence of several robust and long-persisting populations well to the west of the core area is evident. The presence and abundance of a number of discrete populations in essentially pristine sites within two distinct watersheds (the Skootamatta and Crowe River systems), however, suggests that these are natural occurrences. This situation invites further phytogeographic investigation.

Acknowledgements

The cooperation of the collection managers of the cited herbaria is appreciated. Thanks are also due the late Donald Britton (1923–2012) of the University of Guelph who produced the scanning electron microscope images and granted permission for their use. He also produced the cytological data used here and shared both his insights and frustrations with this complex group. Arthur Haines, New England Wild Flower Society, Framingham, Maine, also provided helpful information on the contemporary status of *Isoetes* in New England. The review comments of Arthur Haines, W. Carl Taylor, National Museum of Natural History, Suitland, Maryland, and Paul M. Catling, Agriculture Canada, Ottawa, Ontario, are much appreciated.

Documents Cited

- Angelo, R., and D. E. Boufford.** 2015. *Isoetes riparia*. In Atlas of the Flora of New England: Pteridophytes. Accessed 22 May 2015. <http://neatlas.org/Pterid.html>. http://www.google.com/cse?cx=008785917149153578800:z3t5hr5rxegs&q=isoetes%20riparia&oq=isoetes%20riparia&gs_l=partner.12...0.0.2.280310.0.0.0.0.0.0.0.0.gsnos%2Cn%3D13...0.0.1.ac..25.partner.0.0.0.#gsc.tab=0&gsc.q=isoetes%20riparia&gsc.page=1.
- Weldy, T., D. Werier, and A. Nelson.** 2015. New York Flora Atlas: *Isoetes riparia* var. *canadensis*. New York Flora Association, Albany, New York, USA. Accessed 22 May 2015. <http://newyork.plantatlas.usf.edu/Plant.aspx?id=7055>.

Literature Cited

- Boivin, B.** 1966. Énumération des plantes du Canada. Naturaliste Canadien [Part 1] 93: 253–273.
- Britton, D. M., and D. F. Brunton.** 1989. A new *Isoetes* hybrid (*I. echinospora* × *riparia*) for Canada. Canadian Journal of Botany 67: 2995–3002.
- Britton, D. M., and D. F. Brunton.** 1992. *Isoetes* × *jeffreyi*, *hyb.nov.*, a new *Isoetes* (*Isoetes macrospora* × *Isoetes riparia*) from Quebec, Canada. Canadian Journal of Botany 70: 447–452.
- Brunton, D. F., and D. M. Britton.** 2006. *Isoetes* × *novae-angliae* (Isoetaceae), an additional hybrid quillwort from New England. Rhodora 108: 228–241.
- Caplen, C. A., and C. R. Werth.** 2000a. Isozymes of the *Isoetes riparia* complex. I. Genetic variation and relatedness of diploid species. Systematic Botany 25: 235–259.
- Caplen, C. A., and C. R. Werth.** 2000b. Isozymes of the *Isoetes riparia* complex. II. Ancestry and relationships of polyploids. Systematic Botany 25: 260–280.
- Chapman, L. J., and D. F. Putnam.** 1984. The Physiography of Southern Ontario. Third Edition. Ontario Geological Survey Special Volume 2, Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.
- Clute, W. N.** 1904. The Fern Allies of North America North of Mexico. Frederick A. Stokes Co., New York, New York, USA.
- Cody, W. J., and D. M. Britton.** 1989. The Ferns and Fern Allies of Canada. Publication 1829E. Agriculture Canada Research Branch, Ottawa, Ontario, Canada.
- Eaton, A. A.** 1898. A new *Isoetes*. Fern Bulletin 6: 5–7.
- Eaton, A. A.** 1901. *Isoetes* L. Pages 649–651 in A List of the Ferns and Fern Allies of North America North of Mexico, with Principal Synonyms and Distribution. Edited by W. Maxon. Proceedings of the United States National Museum 23. Smithsonian Institution Press, Washington DC, USA.
- Eaton, A. A.** 1903a. *Isoetes riparia* Canadensis and *Isoetes* Dodgei. Bulletin of the Torrey Botanical Club 30: 359–362.
- Eaton, A. A.** 1903b. Three new varieties of *Isoetes*. Rhodora 5: 277–280.
- Eaton, A. A.** 1908. Nomenclatural changes in *Isoetes*. Rhodora 10: 42.
- Engelmann, G.** 1882. The genus *Isoetes* in North America. Transactions of the Academy of Science of St. Louis 4: 358–390.
- Gerke, J. M., E. J. Farnsworth, and W. E. Brumback.** 2014. Fifteen years of change: what a comparison of the two Flora Conservanda lists can tell us about rare plants in the New England landscape. Rhodora 116: 428–493.
- Gillett, J. M., and D. J. White.** 1978. Checklist of Vascular Plants of the Ottawa-Hull Region, Canada. National Museum of Natural Sciences, Ottawa, Ontario, Canada.
- Kott, L. S., and D. M. Britton.** 1983. Spore morphology and taxonomy of *Isoetes* in northeastern North America. Canadian Journal of Botany 61: 3140–3163.
- Marie-Victorin, Frère.** 1935. Flore Laurentienne. Imprimerie de la Salle, Montréal, Quebec, Canada.
- McNeill, J., F. R. Barrie, W. R. Buck, V. Demoulin, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, K. Marhold, J. Prado, W. F. Prud'homme van Reine, G. F. Smith, J. H. Wiersema, and N. J. Turland.** 2012. International code of nomenclature for algae, fungi, and plants (Melbourne Code). Adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Koeltz Scientific Books, Koenigstein, Germany.
- Montgomery, J. D., and D. E. Fairbrothers.** 1993. New Jersey Ferns and Fern Allies. Rutgers University Press, New Brunswick, New Jersey, USA.
- Occhietti, S.** 1989. Quaternary geology of St. Lawrence Valley and adjacent Appalachian subregion. Pages 350–389 in Quaternary Geology of Canada and Greenland. Edited by R. J. Fulton. Geological Survey of Canada, Ottawa, Ontario, Canada.
- Oldham, M. J., and S. R. Brinker.** 2009. Rare Vascular Plants of Ontario. Fourth edition. Natural Heritage Information Centre, Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada.
- Pfeiffer, N. E.** 1922. Monograph on the Isoetaceae. Annals of the Missouri Botanical Garden 9: 79–233.
- Proctor, G. R.** 1949. *Isoetes riparia* and its variants. American Fern Journal 39: 110–121.
- Rhoads, A. F., and T. A. Block.** 2000. The Plants of Pennsylvania, an Illustrated Manual. University of Pennsylvania Press, Philadelphia, Pennsylvania, USA.
- Rhoads, A. F., and W. M. Klein, Jr.** 1993. The Vascular Flora of Pennsylvania: Annotated Checklist and Atlas. American Philosophical Society, Philadelphia, Pennsylvania, USA.
- Taylor, W. C., and D. F. Brunton.** 2000. Isoetaceae Quillwort family. Pages 62–63 in The Plants of Pennsylvania: an Illustrated Manual. Edited by A. F. Rhoads and T. A. Block. University of Pennsylvania, Philadelphia, Pennsylvania, USA.
- Taylor, W. C., N. T. Luebke, D. M. Britton, R. J. Hickey, and D. F. Brunton.** 1993. *Isoetaceae* Reichenbach – Quillwort family. Pages 64–75 in Flora of North America, Volume 2: Pteridophytes and Gymnosperms. Edited by Flora of North America Editorial Committee. Oxford University Press, New York, New York, USA.
- Tryon, A. F., and R. C. Moran.** 1997. The Ferns and Allied Plants of New England. Massachusetts Audubon Society, Lincoln, Massachusetts, USA.
- Young, S. M.** 2010. New York Natural Heritage Program rare plant status lists. New York Natural Heritage Program, Department of Environmental Conservation, Albany, New York, USA.

Received 11 March 2015

Accepted 26 May 2015