Distribution and taxonomy of *Isoetes tuckermanii* subsp. *acadiensis*, comb. nov. (Isoetaceae) in North America

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Abstract

Isoetes acadiensis is an emergent aquatic lycophyte of freshwater shores found in a narrow range along the Atlantic coast of northeastern North America where it frequently coexists with *Isoetes tuckermanii* (*sensu stricto* [*s. str.*]). Apparently fertile plants with intermediate morphology occur commonly in mixed populations. No sterile hybrids between the two taxa have been detected. Although *I. acadiensis* maintains a distinctive geographic distribution (within and smaller than that of *I. tuckermanii* [*s. str.*]), exhibits molecular evidence of genetic distinctiveness, and has morphologically distinctive features in most populations, the weight of evidence suggests it is not distinct from *I. tuckermanii* at a species level. Accordingly, *I. tuckermanii* subsp. *acadiensis*, comb. nov. is proposed as the appropriate designation for this biogeographically important Acadian endemic.

Key words: *Isoetes tuckermanii* subsp. *acadiensis*; *Isoetes acadiensis*; *Isoetes tuckermanii*; taxonomy; distribution; Acadian endemic; lycophyte

Introduction

Interspecific relationships within the lycophyte group Quillworts (*Isoetes*; Isoetaceae) have received considerable attention in North America since the 1980s (Kott and Britton 1983; Taylor and Luebke 1988; Taylor *et al*. 1993; Brunton and Britton 1997; Musselman *et al.* 1997; Brunton and McNeill 2015). However, the infraspecific relationships of these *Isoetes* have received less attention because of the group's reputation for difficult identification (Tryon and Tryon 1982; Cody and Britton 1989). Subspecific classification is applied to separate the common North American *Isoetes echinospora* M. Durieu subsp. *muricata* (M. Durieu) A. Löve & D. Löve (Taylor *et al.* 1993) from Eurasian *I. echinospora* (*sensu stricto* [*s. str.*]) populations, but only one North American *Isoetes* subspecies has been described in recent years: *Isoetes melanopoda* M. Durieu subsp. *silvatica* D.F. Brunton & D.M. Britton in the southern United States (Brunton and Britton 2006; Troia and Rouhan 2018).

Acadian Quillwort, *Isoetes acadiensis* L.S. Kott, was separated from *Isoetes tuckermanii* A. Braun (Kott 1981) during a period of particularly dramatic re-evaluation of the genus in North America (Brunton and Troia 2018). Since that time, increases in the quantity and quality of *Isoetes* field data in North America have enhanced taxonomic clarity within the group in general and the *I. tuckermanii – acadiensis* complex in particular.

Recent distributional, morphological, and ecological evidence suggests that *I. acadiensis* may not be specifically distinct from *I. tuckermanii.* In some recent publications these taxa have been combined without nomenclatural distinction (Taylor *et al.* 2016). Based on extensive field and herbarium studies over several decades supported by enhanced and more abundant imagery than was available in the past, this study evaluates that concept and presents evidence for a reconsideration of the taxonomic status of *I. acadiensis*.

Methods

Kott (1981) identified three attributes that distinguish *I. acadiensis* from *I. tuckermanii*: megaspore and microspore ornamentation patterns and leaf colour. Over 300 herbarium specimens were examined for these and other definitive morphological and/or ecological attributes. Other features that have been useful in discriminating closely related *Isoetes* taxa, such as plant size, root and corm form and structure, spore size and colour, velum coverage of the sporangia, and sporangial pigmentation (Taylor *et al.* 1993, 2016; Brunton 2015), were found not to differ between *I. acadiensis* and *I. tuckermanii* (*s. str.*) (Kott 1981; Kott and Britton 1983; this study) and were not evaluated further.

Between 1989 and 2017, I examined 33 *Isoetes tuckermanii* (*sensu lato* [*s. l.*]) populations in the field in New Brunswick (NB), Newfoundland and Labrador (NL), Nova Scotia (NS), including the *I. acadiensis* type location, Ontario (ON), Connecticut, Maine (ME), Massachusetts (MA), and New Hampshire. These observations provide insight into the site ecology, population structure, and infraspecific abundance within individual populations throughout the range of the taxon.

Scanning electron microscope (SEM) images were taken of microspores and megaspores of selected specimens of *I. tuckermanii* (*s. l.*) from contemporary collections and herbarium specimens using the standard methods of Britton and Brunton (1992) and Brunton and Britton (2006). Herbaria reviewed for *I. tuckermanii* and related taxa include Acadia University (ACAD),

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Canadian Museum of Nature (CAN), Agriculture and Agri-Food Canada (DAO), Duke University (DUKE), University of Michigan (MICH), Milwaukee Public Museum (MIL), Missouri Botanical Garden (MO), Université de Montréal (MT), University of New Hampshire (NHA), Nova Scotia Museum of Natural History (NSPM), New York Botanical Garden (NY; selected specimens), New York State Museum (NYS), University of Guelph (OAC), Academy of Natural Sciences (PH), and author's private collection (DFB).

The concept of subspecies employed here is consistent with the traditional view of it as a geographically coherent component of a species with morphological distinctions that can intergrade (Davis and Heywood 1963; Kapadia 1963; Mayr and Ashlock 1991). This is more explicitly defined by USDA (2010) as "a grouping within a species used to describe geographically isolated variants, a category above variety".

The infraspecific term "variety" was used widely in earlier North American *Isoetes* literature (Engelmann 1867, 1882; Proctor 1949; Reed 1953). It was applied rather loosely however, to geographically randomized morphological variants; most of these have subsequently been synonymized or dismissed as forms. Article 25 of the International Code of Nomenclature (Shenzhen Code) states that varieties are components of subspecies but not equivalent to them (Turland *et al.* 2018).

Results

Isoetes tuckermanii is a locally common tetraploid ($2n = 4x = 44$), shallow-water aquatic/emergent of freshwater lake and river shores in northeastern North America (Taylor *et al.* 1993), growing in acidic or subacidic substrates. *Isoetes acadiensis* (also tetraploid) was distinguished from *I. tuckermanii* by Kott (1981) based on several key characters:

- megaspore ornamentation—lower, broader muri (Figure 1a) in a more open pattern than with *I. tuckermanii* (Figure 1b) and completely lacking the latter's equatorial band (girdle) of spines;
- microspore ornamentation—a densely echinate or coarsely papillate perispore (surface; Figures 2a,b) compared with a smooth to densely fine-papillate perispore in *I. tuckermanii* (Figures 2c,d);
- leaf colour—darker green, rarely exhibiting the reddish-brown colour typical of *I. tuckermanii*;
- restricted distribution—confined to a narrow band along the Atlantic coast (Figure 3).

Morphological variation and genetic distinction

Field and herbarium research undertaken in the current study indicates that several of the stated *I. acadiensis* attributes are also common in *I. tuckermanii* (*s. str.*) populations. Leaf colour, for example, was found to be uniformly reddish-brown in all 18 mixed populations (several thousand plants) examined *in situ* in NS and NB, including those at the type location for *I. acadiensis* in Halifax County, NS (Figure 4). Extensive examinations of SEM images obtained since 1981 have also determined that, although *I. acadiensis* plants routinely exhibit the densely echinate microspore ornamentation described in Kott (1981), such ornamentation is also frequently found on plants with typical *I. tuckermanii* megaspore ornamentation (e.g., Lake George, York County, NB, D.M. Britton and A. Anderson 11,915, [OAC]). Conversely, the smooth to papillate microspore ornamentation typical of *I. tuckermanii* is found on plants with typical *I. acadiensis* megaspore ornamentation (e.g., Uniake Lake, Hants County, NS, M.L. Fernald *et al.* 23,107 [GH] and Trefry Lake, Yarmouth County, NS, M.L. Fernald *et al.* 19,618, [NSPM]). Some *I. tuckermanii* (*s. l.*) specimens

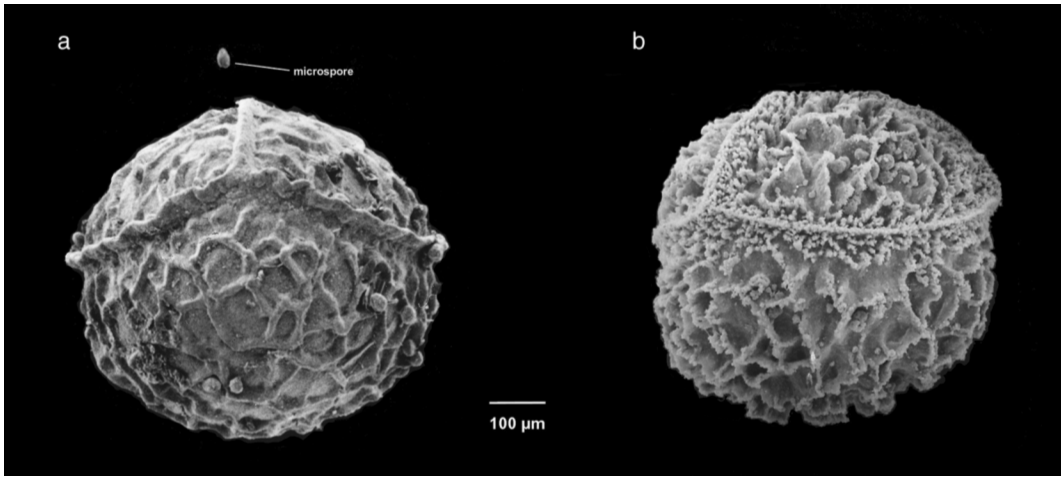

FIGURE 1. Typical megaspores of *Isoetes tuckermanii* (*s. l.*). a. *I. acadiensis*, Grand Lake Shubenacadie, Halifax County, Nova Scotia, R. Bidwell s. n., 11 August 1945 (Topotype) (NYPM); b. *I. tuckermanii* (*s. str.*), Taunton, Massachusetts, A.A. Eaton s. n., 15 September 1903 (MICH). Photos: Donald M. Britton.

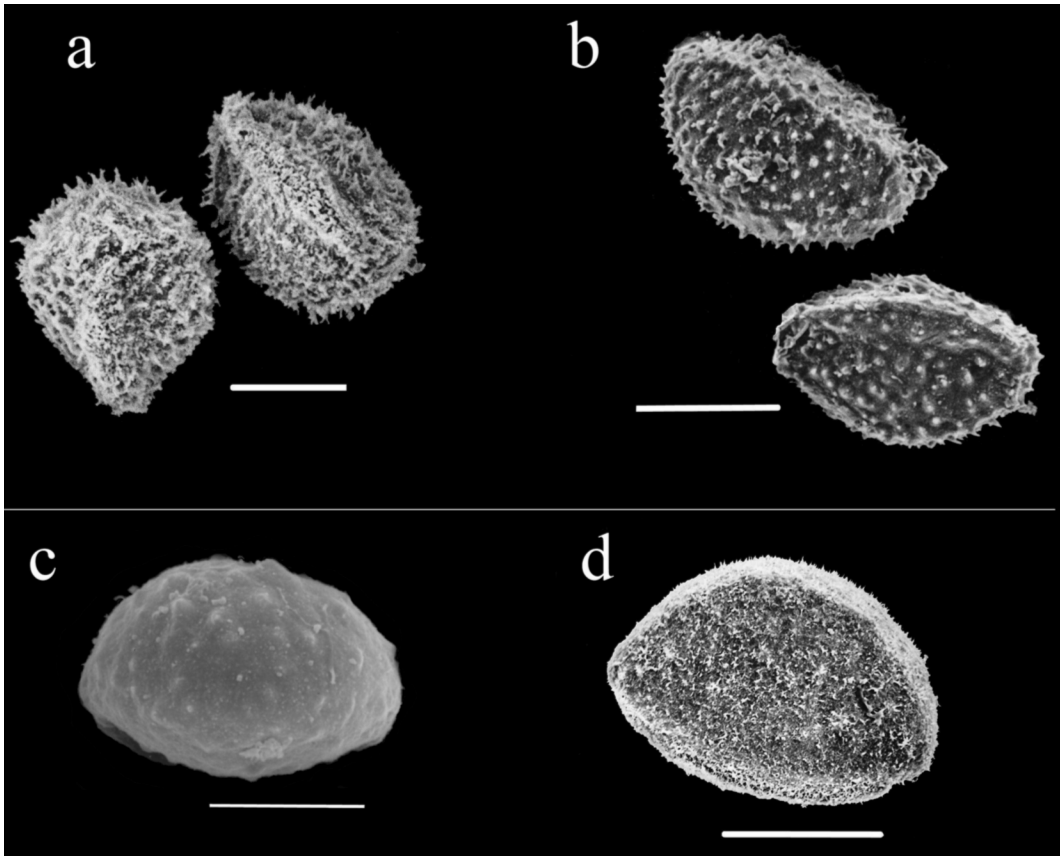

FIGURE 2. Typical microspores of *Isoetes tuckermanii* (*s. l.*). *I. acadiensis*: a. Short papillate–echinate type (Gavelton, Yarmouth County, Nova Scotia [NS], M.L. Fernald, B. Long & D.H. Linder 19,626, 4 August 1920 [NSPM]); b. Roughly echinate type (Grand Lake Shubenacadie, Halifax County, NS, R. Bidwell s. n., 11 August 1945 [NYPM]). *I. tuckermanii* (*s. str.*): c. Plain to smooth type (Taunton, Massachusetts, A.A. Eaton s. n., 15 September 1903 [MICH]); d. Densely fine-papillate type (Gray Lake, Muskoka District, Ontario, J. Goltz and P. Papoulidis 1,447, 11 August 1988 [OAC, DFB]). Scale bar = 10 µm. Photos: Donald M. Britton.

were found to contain microspores with both smooth to papillate and densely echinate ornamentation patterns (Figure 5). Consistent with most other polyploids in North America (Taylor *et al.* 1993; pers. obs.), no significant differences in megaspore or microspore size were detected between these two tetraploids (Kott and Britton 1983; this study).

That said, the extremes of megaspore ornamentation expression between *I. tuckermanii* (*s. str.*) and *I. acadiensis* can be dramatic, with the low, broad muri and a plain, unornamented equatorial band (girdle) typical of *I. acadiensis* (Figure 1b) contrasting sharply with the thin, high-walled muri and dense band of equatorial spines of *I. tuckermanii* (*s. str.*) (Figure 1a). Even this characteristic is ambiguous, however. I have found that many plants (a majority in some cases) in at least eight of 21 Canadian *I. acadiensis* populations considered to be that taxon on the basis of other characters to exhibit intermediate megaspore ornamentation (Figure 6).

No plants with the aborted megaspores indicative of sterile hybrids (Taylor and Luebke 1988; Britton and Brunton 1989, 1992) have been detected in mixed *I. acadiensis–I. tuckermanii* populations. Similarly, aborted megaspores have not been observed amongst the numerous (200+) plants with intermediate megaspore and/or microspore ornamentation observed in this study.

Strikingly, however, plants with typical *I. acadiensis* megaspore ornamentation as per Kott (1981) appear to be almost entirely confined to the Acadian region of northeastern North America (viz., the Maritime provinces of Canada and the adjacent northeastern United States; Figure 3).

Megaspore ornamentation patterns of particular populations remain true to form over many years. An example of this is provided by the consistent megaspore ornamentation pattern exhibited by *I. acadiensis* plants in Trefry Lake, Yarmouth County, NS, over the last century, starting in 1920 (M.L. Fernald & B. Long 19,614

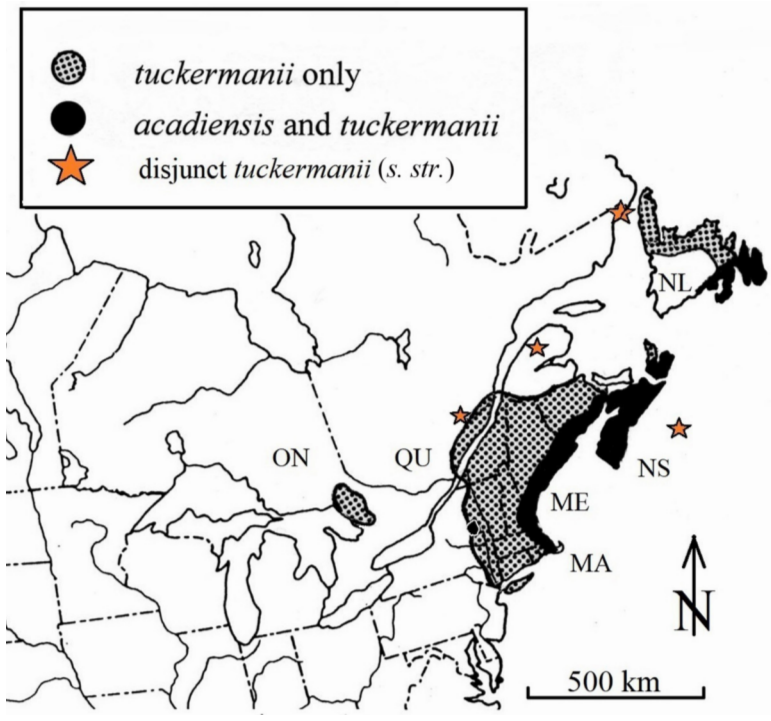

FIGURE 3. Distribution of *Isoetes tuckermanii* (*s. l.*) in North America (adapted from Taylor *et al.* 1993).

FIGURE 4. *Isoetes acadiensis* plants at type location, Grand Lake Shubenacadie, Halifax County, Nova Scotia, 18 July 2016. Coin is 27 mm across. Photo: D.F. Brunton.

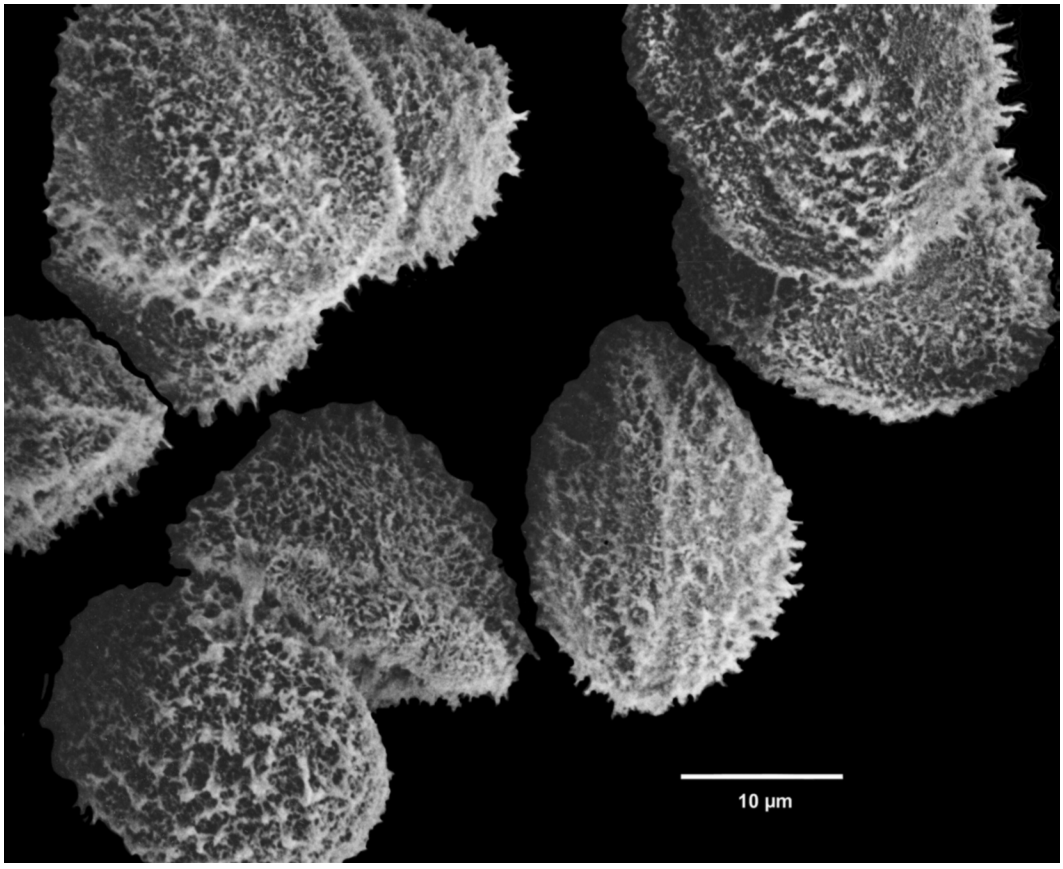

FIGURE 5. *Isoetes tuckermanii* (*s. l.*) microspores on a single plant with intermediate ornamentation ranging from finely papillate *I. tuckermanii* (*s. str.*) type (top left) to coarsely echinate *I. acadiensis* type (below, left, and right); Tusket River, Yarmouth County, Nova Scotia, J.S. Erskine 51.1436, 28 August 1951 [NSPM]). Photos: Donald M. Britton.

[NSPM]) through 1995 (D.F. Brunton and K.L. McIntosh 12,342 [OAC, DFB]) to 2015 (D.F. Brunton and K.L. McIntosh 19,400 [NY, DFB]). Currently however, plants showing megaspore ornamentation intermediate between "classic" *I. acadiensis* and *I. tuckermanii* (*s. str.*) appear to be the most commonly represented individuals at this site (pers. obs.).

Genetic evidence in support of particular taxonomic interpretations is unclear and perhaps contradictory. Based on DNA sequencing, Hoot *et al.* (2004) found a subtle but evident genetic distinction between *I. tuckermanii* (*s. str.*) and *I. acadiensis*. That study also found that despite a substantial (~800 km) oceanic gap between the two, genetic affinities (shared parental genomes) were evident between *I. acadiensis* and the European *Isoetes azorica* M. Durieu. Based on morphological characteristics, this relationship was alluded to earlier by Britton and Brunton (1996; see also Discussion, below). Recent data from contemporary Next Gen sequencing also suggests that insufficient justification exists for the treatment of *I. acadiensis* as specifically distinct from *I. tuckermanii* (P. Schafran pers. comm. July 2018). In contrast, however, the sequence data reported by Pereira *et al.* (2018) suggests species status distinctions based on different origins for *I. acadiensis* and *I. tuckermannii* (*s. str.*).

Isoetes acadiensis is reported as being of disjunct occurrence in brackish marshes in eastern Virginia, there providing the tetraploid parent for the sterile triploid ($2n = 3x = 33$) hybrid *I.* ×*carltaylorii* L.J. Musselman (*I. acadiensis* × *engelmannii* A. Braun). The tetraploid taxon involved in this hybrid, however, appears to be *Isoetes riparia* M. Durieu var. *reticulata* A.A. Eaton, a rare Atlantic coastal taxon with atypically subdued megaspore ornamentation which mimics that of *I. acadiensis* (Brunton 2015). *Isoetes acadiensis* has not otherwise been reported south of MA, 650 km to the north.

Decaploid ($2n = 10x = 110$) *Isoetes lacustris* L. forma *hieroglyphica* (A.A. Eaton) W.N. Clute is confused with *I. acadiensis* as well. It has megaspores ornamented with low, broad muri and a plain, unornamented equatorial band (Kott and Britton 1983; Tryon and Moran 1997; Haines 2011). The former is identical in all other respects to *I. lacustris* (*s. str.*) however. Most importantly,

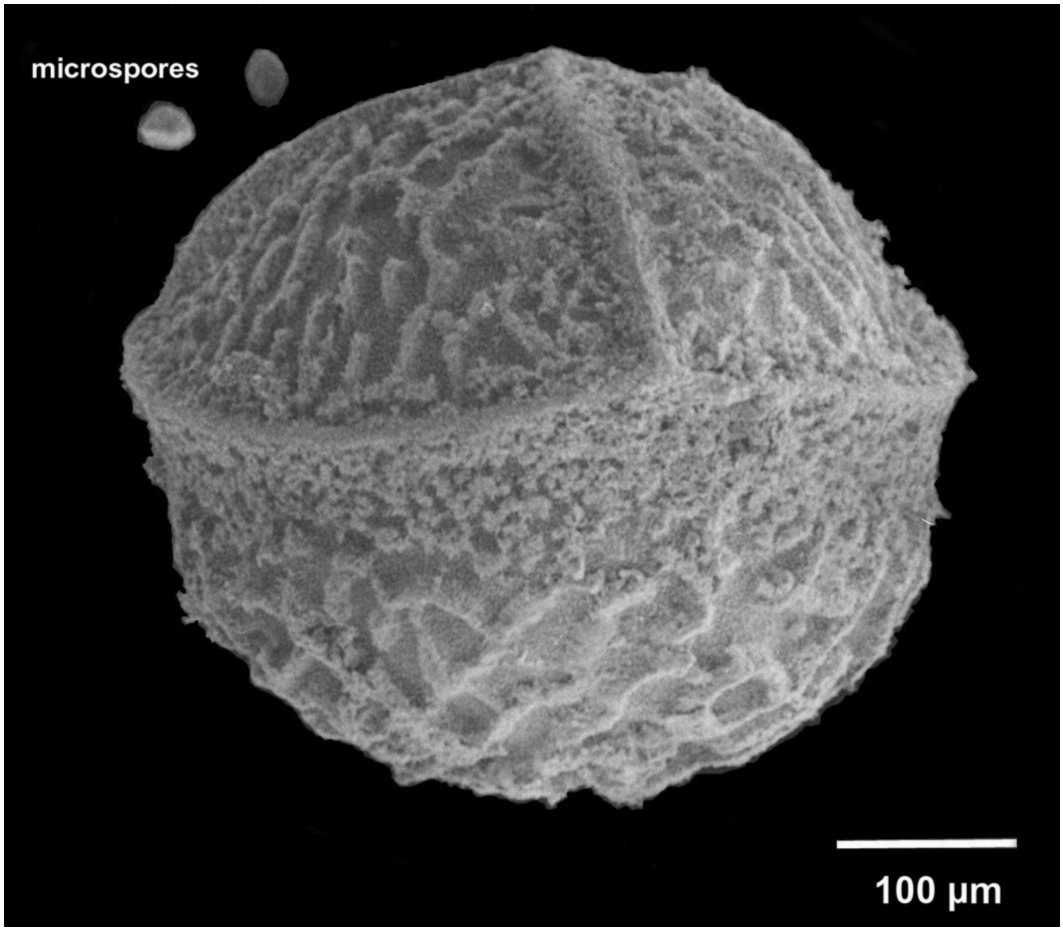

FIGURE 6. *Isoetes tuckermanii* (*s. l.*) with intermediate megaspore ornamentation, exhibiting the equatorial band of spines of *I. tuckermanii* (*s. str.*) and the lower, broader, less congested distal muri of *I. acadiensis* (Jassy Lake, Yarmouth County, Nova Scotia, R.C. Bean, D. White and D.H. Linder 19,615, 29 July 1920 [NSPM]). Photos: Donald M. Britton.

decaploid forma *hieroglyphica* has much larger (≥650 µm) megaspores than those (~520 µm) of tetraploid *I. tuckermanii* (*s. l.*) (Kott and Britton 1983; Taylor *et al.* 2016). Although found predominately in the Maritime provinces of Canada and adjacent New England, forma *hieroglyphica* rarely if ever forms pure populations and is found randomly across most of the range of *I. lacustris* (*s. l.*) as far west as central ON (Boshkung Lake, Stanhope Township, Haliburton County, ON, D.F. Brunton, K.L. McIntosh, W.C. Taylor & C.A. Caplen 13,349C, 9 August 1997 [OAC]).

Ecological segregation

Although plants of *I. acadiensis* and *I. tuckermanii* (*s. str.*) were most often found randomly in the 18 mixed populations examined in this study, some habitat differentiation has been noted. Transects conducted across large mixed populations in Yarmouth County, NS, in 1990, for example, indicated that plants with *I. acadiensis* megaspore ornamentation patterns occurred disproportionately in very shallow water or on emergent shores, while those with *I. tuckermanii* megaspore ornamentation patterns most commonly occurred in deeper water (0.5–1 m; pers. obs.). However, an exactly reversed situation was observed along similar transects conducted in mixed populations in Barnstable and Plymouth Counties, MA, in 1989 (pers. obs.). Accordingly, while some ecological segregation appears to be occurring within individual populations, no consistent pattern has been established.

Discussion

The herbarium, SEM, and field investigations described above, as well as most of the molecular evidence noted here, suggest that *I. acadiensis* constitutes a genetically distinct taxon (with European affinities) within *I. tuckermanii* (*s. l.*) and is almost exclusively confined within a restricted geographic range. A collection from Stoner Lake, Fulton County, New York (R.T. Clausen 5518, 17 August 1941 [NYS]) represents the only sig-

nificantly inland report of this taxon (Figure 3). This distributional evidence, the absence of diagnostic morphological characters, ambiguous genetic evidence, and the apparent absence of sterile hybrids within populations that frequently (more than 60%) are mixed, indicate that *I. acadiensis* is not specifically distinct from the more wide-ranging *I. tuckermanii* (*s. str.*). The available evidence suggests that a subspecific ranking is the most appropriate designation for this taxon; that is proposed here.

Isoetes tuckermanii A. Braun **subsp. *acadiensis*** (L.S. Kott) D.F. Brunton, **comb. et stat. nov.**

Basionym: *Isoetes acadiensis* L.S. Kott; Canadian Journal of Botany 59: 2592. 1981.

Isoetes tuckermanii subsp. *acadiensis* may represent a relatively recent evolutionary "experiment" dating from the Wisconsinan or middle Sangamonian continental glaciation period (<110 000 years before present). During this period, extensive areas of the now-submerged continental shelf were exposed and available for colonization by coastal plain taxa (Fulton 1989). The identification of genetic affinities of *I. tuckermanii* subsp. *acadiensis* with *I. azorica* by Hoot *et al.* (2004) supports this, suggesting the former might once have occurred across a much larger area of the exposed continental shelf coastal plain. Accordingly, it likely was considerably more common at that time than it is today. Comparably, the rare Acadian quillwort endemic *Isoetes prototypus* D.M. Britton (Britton and Goltz 1991), may also have been more widely distributed across that larger glacial era Atlantic coastal plain.

Individual *I. tuckermanii* subsp. *acadiensis* populations are large—often consisting of hundreds or even thousands of plants (pers. obs.)—but it is found in relatively few individual populations overall. It is accordingly designated to be of conservation concern in NL (S1), NB (S2S3), NS (S3), ME (S2), and MA (S1) (NatureServe 2019). In addition to this significance, the taxon presents considerable potential for evolutionary and biogeographic research.

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