Isoetes lacustris

Lake Quillwort

Isoetaceae

Isoetes lacustris by Samuel Brinker, 2018

Isoetes lacustris **Rare Plant Profile**

New Jersey Department of Environmental Protection
State Parks, Forests & Historic Sites
Forests & Natural Lands
Office of Natural Lands Management
New Jersey Natural Heritage Program

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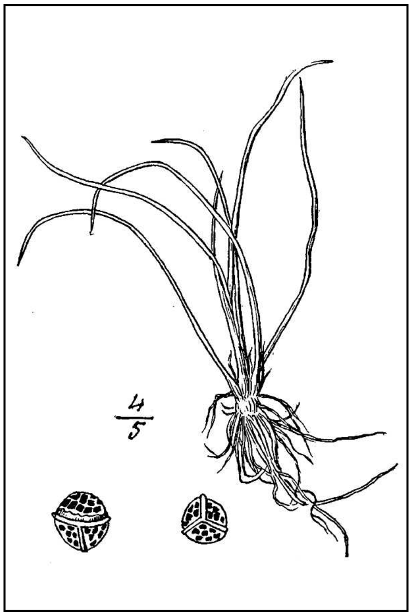
Life History

Isoetes lacustris (Lake Quillwort) is a submerged aquatic plant in the Isoetaceae. The family consists of a single genus which includes about 150 species around the globe, but only two dozen of them occur in North America (Taylor et al. 2020). Like other pteridophytes, *Isoetes* has a life cycle with two distinct generations. Spores produced by mature plants (sporophytes) develop into tiny gametophytes that form structures which produce reproductive cells (gametes). Male gametes (sperm) develop in an antheridium and a female gamete (egg) develops in an archegonium. Fertilized eggs develop into the recognizable quillwort plants that produce spores for the next generation (Raven et al. 1986).

The spores and gametophytes of *Isoetes* are either male or female. The microspores (male) and megaspores (female) are produced on separate leaves (microsporophylls and megasporophylls) of mature quillwort plants (Raven et al. 1986). Müller (1848) described the early development of an *Isoetes lacustris* megaspore and provided detailed illustrations of the process, although he viewed the megaspores as ovules that were developing asexually. A better understanding of reproduction in *Isoetes* arose later in the 1800s following work by German scientists Wilhelm Hofmeister and Karl Goebel so subsequent developmental descriptions of *I. lacustris* recognized the presence and functions of the unisexual spores and gametophytes (eg. Farmer 1890, Campbell 1891).

Unlike the free-living gametophytes of most ferns and allies, those of *Isoetes* species form inside of the spores (Renzaglia and Garbary 2001). An *Isoetes* microgametophyte is a simple structure consisting of a few-celled wall and a single-celled antheridum that divides to create four sperm (Pfeiffer 1922, Renzaglia and Garbary 2001). The megagametophytes may have 1–4 archegonia, which are typically produced singly until one has been fertilized. *Isoetes* gametophytes can develop while the spores are still located on the plants or after they have been released (Farmer 1889 & 1890, Pfeiffer 1922, Kott and Britton 1982). Female gametophytes appear to be reliant on nutrient reserves in the megaspores and thus they could be relatively short-lived (Campbell 1891); however, Čtvrtlíková et al. (2014) reported that *I. lacustris* megagametophytes which formed late in the growing season were able to winter over or even persist for several seasons before the sporophytes began to develop.

Isoetes sporophytes have a relatively uncomplicated structure, with a cluster of quill-like leaves arising from a short, fleshy underground stem (corm). The spores are produced in chambers at the widened bases of the leaves (Raven et al. 1986). The simplicity of quillworts can make species identification challenging so close observation of features like megaspore size and texture or extent of the velum (a small flap of tissue that partly or fully covers the sporangium) is required (Taylor and Hickey 1992, Taylor et al. 2020). The sporophytes of *Isoetes lacustris* have 10–40 stiff, dark green leaves that may reach 25 cm in length and 2 mm in width: Husák et al. (2000) indicated that 20–30 leaves is typical. Because the species is restricted to submerged habitats its leaves lack stomata (Keely 1982). The basal sporangia of *I. lacustris* are 3–5 mm long and less than half of their length is covered by velum. The microspores are tiny (33–45 µm) and appear as a gray mass. The macrospores are white and larger than those of most other *Isoetes* species—they are typically 550–750 µm in diameter and generally average more than 600 µm in a given sample. Raised ridges divide each macrospore into two subequal parts and also divide the upper part into three faces, and the interior surfaces are covered with a network of rough projections that irregularly branch or form cross-connections. (See Britton and Brown 1913, Fernald 1950, Fassett 1957, Kott and Britton 1983, Gleason and Cronquist 1991, Montgomery and Fairbrothers 1992, Taylor et al. 2020).



Left: Britton and Brown 1913, courtesy USDA NRCS 2024a. Right: Samuel Brinker, 2017.

Eight species of *Isoetes* have been documented in New Jersey but three are currently listed as historic and two others are rare in the state (Kartesz 2015, NJNHP 2024). In the northeastern United States and Canada, *Isoetes lacustris* often co-occurs with other quillworts including *I. echinospora, I. engelmannii, I. riparia, I. septentrionalis,* and *I. tuckermanii* (Taylor and Hickey 1992, Brunton and McNeill 2015). *Isoetes* species hybridize frequently, further complicating identification. Many quillworts appear to have evolved via hybridization, and Taylor (1992) noted that all of the species that occur in New Jersey are polyploid. *Isoetes* ×*fairbrothersii* is the only hybrid involving *I. lacustris* that has been documented in the state—the other parent species being *I. engelmannii*—and to date it has not been found anywhere else (Montgomery and Fairbrothers 1992, Montgomery and Taylor 1994, Brunton and Sokoloff 2020). In other parts of Lake Quillwort's range it has been known to hybridize with *Isoetes echinospora*, *I. riparia*, and *I. tuckermanii* (Taylor and Leubke 1988, Brunton and McNeill 2015).

The best time to identify *Isoetes* plants is when fully developed spores are present. In New Jersey and other parts of the northeastern United States the spores of *I. lacustris* mature from August to October (Hough 1983, Kott and Britton 1983). In *Isoetes*, the more distinctive megaspores are usually located on the outer leaves while the tiny microspores are situated on inner leaves (Campbell 1891, Raven et al. 1986). As evergreen species like *I. lacustris* age they typically retain individual leaves for multiple seasons, discarding some older leaves around the periphery and replacing them with new leaves at the center (Kott and Britton 1983, Husák et al. 2000). As with the leaves, young roots are also produced near the center of the plants (Müller 1848, Boston and Adams 1987). Because megasporophylls develop earlier in the growing season (Smith 1900) they occupy the outermost positions. The majority of leaf production in *I.*

lacustris takes place during the summer months and growth is seldom observed in the winter (Kansanen and Niemi 1974, Boston and Adams 1987, Gacia and Ballersteros 1994).

E. T. Wherry, 1938.

Samuel Brinker, 2017.

Four life stages were described for *Isoetes lacustris* sporophytes by Husák et al. (2000). The categories were Early Juvenile (small plants with about three leaves that had not yet formed rosettes), Late Juvenile (immature plants with fewer than ten leaves in a developing rosette), Mature (fertile plants with rosettes of more than ten leaves), and Senile (infertile plants with no fresh leaves). New leaves may be identified by coloration: They are typically pale green in color and have white bases, in contrast with older leaves that are dark green with brownish basis and often have a coating of algae (Kansanen and Niemi 1974). Quillworts do not reproduce clonally, so the relative abundance of juvenile and senile plants can indicate whether an I. *lacustris* population is expanding or declining (Vöge 2014, Čtvrtlíková et al. 2023).

Pollinator Dynamics

Because *Isoetes lacustris* is a non-flowering plant, pollination does not take place. Fertilization occurs during the gametophyte phase and is dependent on water, which allows the movement of the multi-flagellated sperm cells toward receptive egg cells. The sperm of quillworts have approximately 20 flagella (Raven et al. 1986, Renzaglia and Garbary 2001) and they are produced in abundance. Smith (1900) estimated that a single *Isoetes* microsporangium contains between 150,000–300,000 microspores, and each of those has the potential to generate four sperm.

<u>Seed Dispersal and Establishment</u>

Dispersal in *Isoetes* is carried out by spores rather than seeds and because their gametophytes develop inside of the spores—often while still attached to the generative plants—quillworts may also be dispersed as gametophytes or even as early-stage sporophytes. The establishment of a new *Isoetes* colony requires either the movement of a fertilized megagametophyte or the deposition of both male and female spores/gametophytes at the same location (Troia 2016). Ungerminated *Isoetes* spores may be dispersed in a coordinated manner, with the tiny microspores clinging to the larger macrospores. Kramer (1977) proposed that the rough texture of the macrospores could facilitate such attachment and Musselman (2002) noted that *Isoetes* megaspores have often been observed with numerous microspores attached. The high rates of hybridization in *Isoetes* suggest that many species are likely to be self-compatible, but polyploidy might mitigate inbreeding effects (Troia 2016).

Pfeiffer (1922) indicated that spore release in *Isoetes* is contingent on disintegration of the sporangia, which often results in an accumulation of propagules around the bases of established plants, although decaying quillwort leaves can be somewhat buoyant and may occasionally be carried to new locations by water movement (Smith 1900). Long-distance dispersal of quillworts is likely to depend on animals, particularly waterfowl, either by attachment or ingestion (Taylor 1992, Troia 2016). Silva et al. (2021) recently found *Isoetes* megaspores in the fecal material of teal and ducks.

Not all of the spores in a given *Isoetes lacustris* sporophyll mature simultaneously and some may remain viable for several years. The dispersal of propagules from living leaves is also staggered and may occur throughout the year (Vöge 2006, Čtvrtlíková et al. 2014). Gametophyte development is governed by temperature and most activity occurs during the summer and early fall. Kott and Britton (1983) noted that the megaspores do not require a cold period but germinate in response to rising temperatures. Microspores can germinate at lower temperatures than macrospores, which permits prompt fertilization of the macrospores when they develop and become receptive (Čtvrtlíková et al. 2014).

As previously noted, young *Isoetes* plants pass through several distinct developmental stages so it takes several years for the sporophytes to become reproductive (Szmeja 1994, Husák et al. 2000). Some *I. lacustris* plants form fungal associations, although they are not obligate. Sudová et al. (2011) found mycorrhizal fungi in the roots of *I. lacustris* but noted that colonization rates were low and variable. The investigators also observed dark septate endophytic fungi in *I. lacustris* roots. Dark septate endophytes are frequently associated with stressful environments and can benefit their hosts by facilitating nutrient uptake and growth (Santos et al. 2021, Malika et al. 2022).

Habitat

Isoetes lacustris, like many other isoetid species, is a poor competitor so it is usually found in low-light, low-nutrient habitats where few other plants can grow (Ballesteros et al. 1989, Vöge 2014). Murphy et al. (1990) pointed out that the characteristics of freshwater aquatic plants which utilize the stress-tolerant life strategy described by Grime in 1977 often include a perennial evergreen habit, a high root:shoot ratio, slow biomass turnover, tolerance of limited light availability, and CAM metabolism. *Isoetes lacustris* displays all of those attributes. In addition to CAM metabolism, which allows *I. lacustris* to synthesize carbon at night, the species is able to obtain CO_2 from the sediments rather than the water column (Keeley 1982, Boston and Adams 1987, Madsen 1987, Raven et al. 1988).

Throughout its range, *Isoetes lacustris* grows on the bottom of cold, freshwater lakes that are often ice-covered during the winter months. The lakes usually have clear water and low nutrient content (Toivonen and Lappalainen 1980, Hough 1983, Boston and Adams 1987, Madsen 1987, Montgomery and Fairbrothers 1992, Břízová 2011, Taylor et al. 2020, Staniforth and Brunton 2022). Although the quillwort can grow in water with pH ranging from 4.0–9.0, the pH values are normally between 5.3 and 7.0 (Kott and Britton 1983, Mäkirinta et al. 1997, Ronowski et al. 2020).

Depths where *Isoetes lacustris* have been found extend from the shoreline (Toivonen and Lappalainen 1980, Boston and Adams 1987, Murphy et al. 1994) to 8 meters below the surface (Břízová 2011). Depths of 1–3 meters are typical and appear to be the most favorable for Lake Quillwort (Madsen 1987, Ballesteros et al. 1989, Gacia and Ballesteros 1993, Murphy et al. 1994, Rørslett and Johansen 1995, Husák et al. 2000). *I. lacustris* is usually sparsely distributed when growing in shallow areas that are subject to ice erosion, and the plants in that zone are smaller (Toivonen and Lappalainen 1980, Kott and Britton 1983, Gacia and Ballesteros 1993, Mäkirinta et al. 1997). Gacia and Ballesteros (1994) indicated that *I. lacustris* plants growing at depths of 2.3 meters received more than enough light to meet their requirements, and when growing at optimum depths *I. lacustris* populations can achieve densities up to around 2,500 plants per square meter (Toivonen and Lappalainen 1980) and have a root:shoot ratio of 25–40% (Kansanen and Niemi 1974). As depth increases light availability becomes more limited and the plants make a larger investment in leaf length but produce fewer leaves and roots (Kansanen and Niemi 1974, Gacia and Ballesteros 1996). Since leaf number is an indicator of reproductive potential in *I. lacustris* (Husák et al. 2000) the populations at depths of greater than 3 meters are likely to be smaller.

In New Jersey, *Isoetes lacustris* formed several colonies a single lake. The plants were observed growing at depths of 0.2–2.0 meters, mostly on sand or gravel substrate but sometimes on organic matter. Associated species included *Brasenia schreberi*, *Eleocharis acicularis*, *Eriocaulon aquaticum*, *Isoetes engelmannii*, and several *Potamogeton* spp. (Montgomery and Taylor 1994). *Eleocharis acicularis* also co-occurred with *I. lacustris* at some locations in Europe and northern Russia. Typical associates reported from Eurasian sites included three species that were formerly documented in New Jersey but are no longer present in the state: *Lobelia dortmanna*, *Sparganium angustifolium*, and *Ranunculus flammula* var. *reptans*. Other common associates noted in Eurasia included *Isoetes echinospora*, *Littorella uniflora*, and

Subularia aquatica (Ballesteros et al. 1989, Murphy et al. 1994, Mäkirinta et al. 1997, Dynowski et al. 2012). In one lake in Poland, *I. lacustris* was found growing in shallow water near a transitional bog where it was embedded in a submerged lawn of *Sphagnum auriculatum*. In that habitat the quillwort plants were smaller than those situated in deeper parts of the lake but their reproductive capacity was not diminished (Szmeja 1994).

Wetland Indicator Status

Isoetes lacustris is an obligate wetland species, meaning that it almost always occurs in wetlands (U. S. Army Corps of Engineers 2020).

USDA Plants Code (USDA, NRCS 2024b)

ISLA

Coefficient of Conservancy (Walz et al. 2020)

CoC = 10. Criteria for a value of 9 to 10: Native with a narrow range of ecological tolerances, high fidelity to particular habitat conditions, and sensitive to anthropogenic disturbance (Faber-Langendoen 2018).

Distribution and Range

The global range of *Isoetes lacustris* encompasses much of the northern hemisphere, including parts of Asia, Europe, Greenland, Canada, and the United States (POWO 2024). The map in Figure 1 depicts the extent of the quillwort in the United States and Canada. In the past, North American populations of *Isoetes lacustris* were generally identified as a separate species (*I. macrospora*). When describing *Isoetes macrospora* Durieu de Maisonneuve (1864) noted the species' close resemblance to the European *I. lacustris*, and the possibility of conspecificity was raised by later botanists (eg. Kott and Britton 1983). Although the name *I. macrospora* is still occasionally employed, experts have found no morphological basis for the distinction (Taylor et al. 2020).

The USDA PLANTS Database (2024b) shows records of *Isoetes lacustris* in one New Jersey county: Sussex County (Figure 2). The map accurately reflects the current distribution of the species.

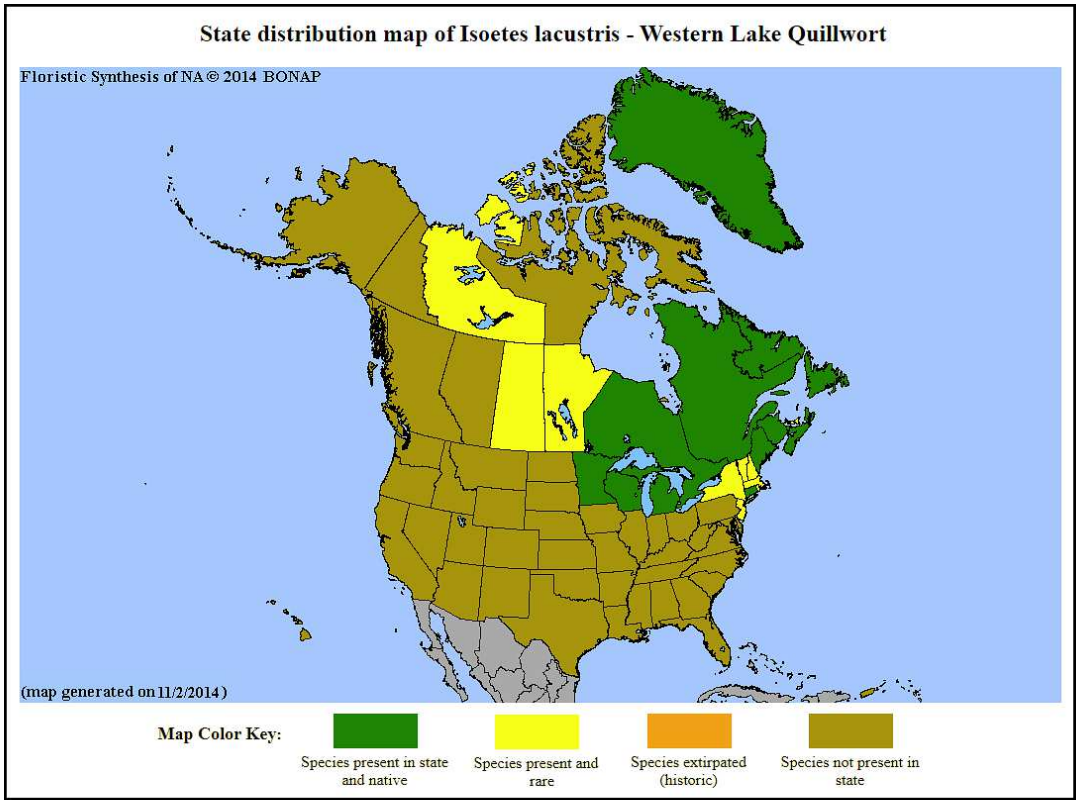


Figure 1. Distribution of I. lacustris in North America, adapted from BONAP (Kartesz 2015).

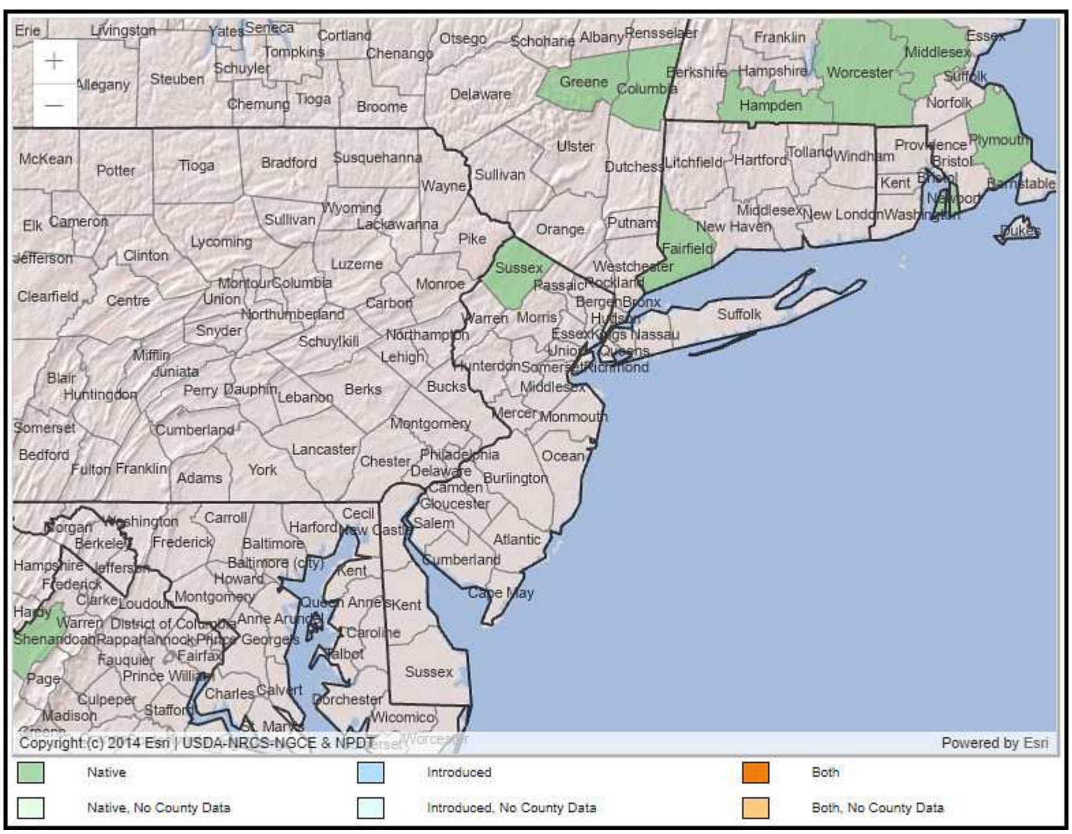


Figure 2. County records of I. lacustris in New Jersey and vicinity (USDA NRCS 2024b).

Conservation Status

Isoetes lacustris is considered globally secure, although NatureServe (2024) indicates that its status is in need of review. A G5 rank signifies that the species has a very low risk of extinction or collapse due to a very extensive range, abundant populations or occurrences, and little to no concern from declines or threats. There is some evidence that the quillwort is decreasing in parts of Eurasia. Analyses of macrofossil data showed that *I. lacustris* was once widespread in Bulgaria, but it is now restricted to a small part of the country (Stefanova and Ivanoca 2000). It formerly occurred in Greece and Romania but is presently considered extinct in those nations (POWO 2024). There is only one extant site in the Czech Republic (Břízová 2011), and it is vulnerable in Poland (Dynowski et al. 2012) and rare in Russia (Borisova et al. 2020).

The map below (Figure 3) illustrates the conservation status of Lake Quillwort in the United States and Canada. *I. lacustris* is vulnerable (moderate risk of extinction) in one province, imperiled (high risk of extinction) in three provinces, critically imperiled (very high risk of extinction) in one province and four states, and possibly extirpated in Virginia, New Hampshire, and Nunavut. The species appears to be secure in other provinces where it occurs although it has not been ranked in a number of states.

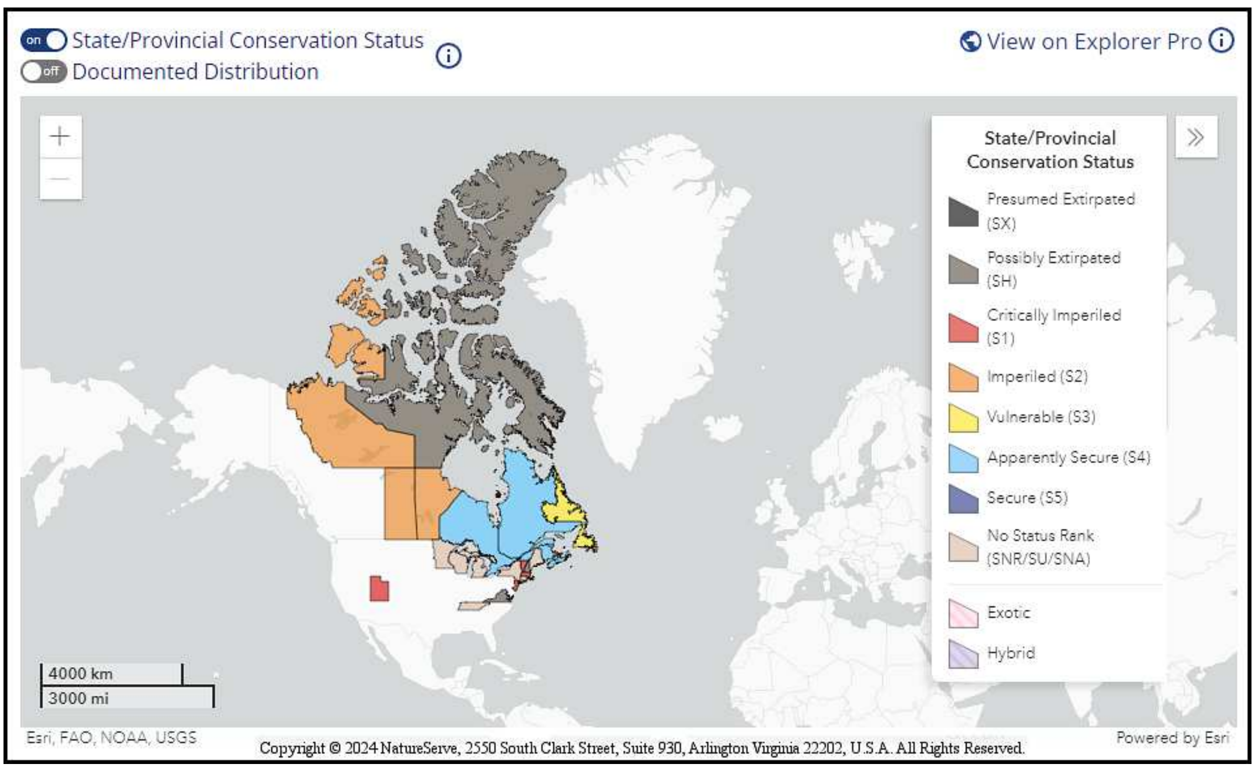


Figure 3. Conservation status of I. lacustris in the United States and Canada (NatureServe 2024).

Isoetes lacustris is ranked S1.1 in New Jersey (NJNHP 2024), meaning that it is critically imperiled due to extreme rarity. A species with an S1.1 rank has only ever been documented at a single location in the state. *I. lacustris* is also listed as an endangered species (E) in New Jersey, meaning that without intervention it has a high likelihood of extinction in the state. Although the presence of endangered flora may restrict development in certain communities such as wetlands or coastal habitats, being listed does not currently provide broad statewide protection for the plants. Additional regional status codes assigned to the quillwort signify that the species is eligible for protection under the jurisdictions of the Highlands Preservation Area (HL) and the New Jersey Pinelands (LP) (NJNHP 2010).

The earliest reports of *Isoetes lacustris* in New Jersey were based on plants collected by Britton (1889) at two Sussex County sites, but Taylor (1915) indicated that the species' presence in the greater New York area had not been confirmed outside of the Catskill Mountains and herbarium records indicate that Britton's specimens were later determined to be *I. engelmannii* (Mid-Atlantic Herbaria 2024). Lake Quillwort was eventually documented in New Jersey in 1937 and the site where it was found continues to be the sole known occurrence in the state (Fairbrothers and Hough 1973, Montgomery 1982, NJNHP 2024).

Threats

Isoetes lacustris is very sensitive to changes in water level and water quality (Vlasov 2012). Fairbrothers and Hough (1973) noted that water pollution could eliminate the species. Heavy sediment loads can bury established quillwort plants or reduce light availability (Boston and Adams 1987, Gacia and Ballesteros 1993, Dynowski et al. 2012, Borisova et al. 2020). Eutrophication has frequently been cited as one of the primary causes for declines in *I. lacustris* populations, and it can favor the growth of other aquatic species that similarly reduce the amount of light reaching the quillworts (Roelofs 1983, Grzybowski et al. 2008, Dynowski et al. 2012, Chappuis et al. 2015, Borisova et al. 2020, Ronowski et al. 2020, Čtvrtlíková et al. 2023). Because *Isoetes lacustris* plants are rooted and develop slowly, significant water level shifts can take a toll on established populations. During an experimental study on the effects of raising water levels, *I. lacustris* plants declined rapidly as a result of reduced sunlight and extensive shoot death was observed. Even when the original water levels were restored after a month the quillworts continued to experience high rates of mortality (Rørslett and Johansen 1995). Substantial decreases in the size of natural populations exposed to long-term flooding have also been reported (Gacia and Ballesteros 1996 & 1998, Riera et al. 2017). Steep reductions in water level are equally harmful to *I. lacustris* and can favor the establishment of other plants that are likely to replace the quillworts (Vandel et al. 2014 & 2016, Vaasma et al. 2015). Declines in *I. lacustris* have resulted from the dense growth of *Sparganium angustifolium* (Ballesteros et al. 1989), *Myriophyllum spicatum* (Montgomery and Taylor 1994), and *Elodea* spp. (Murphy et al. 1990 & 1994, Borisova et al. 2020).

Certain kinds of herbivory may be harmful to *Isoetes lacustris*. The species is subject to grazing by crayfish, although that rarely results in plant mortality (Boston and Adams 1987). Animals that feed on the corms and rootstocks can do more extensive damage because the plants are unable to regenerate. Such herbivores include muskrats, ducks, and geese (Pfeiffer 1922, Taylor 1992). *I. lacustris* plants can also be inadvertently destroyed by human recreational activities: Examples include trampling by swimmers or mechanical damage resulting from anchors or nets (Vlasov 2012).

Climate Change Vulnerability

Information from the references cited in this profile was used to evaluate the vulnerability of New Jersey's *Isoetes lacustris* population to climate change. The species was assigned a rank from NatureServe's Climate Change Vulnerability Index using the associated tool (Version 3.02) to estimate its exposure, sensitivity, and adaptive capacity to changing climactic conditions in accordance with the guidelines described by Young et al. (2016) and the state climactic computations by Ring et al. (2013). Based on available data *I. lacustris* was assessed as Highly Vulnerable, meaning that it is likely to experience a significant decrease in abundance or range extent throughout New Jersey by 2050.

Isoetes lacustris has a primarily northern distribution on the North American continent (Figures 1 and 3). Montgomery (1982) indicated that the quillwort reached the southern limit of its range in New Jersey and although it was later discovered as a site in Virginia it was subsequently extirpated from that state (Musselman and Knepper 1994, Weakley et al. 2022). Growth and development in *I. lacustris* is closely tied to climactic conditions. According to Taylor (1992) Lake Quillwort plants need several month of temperatures below 4.5ºC (40ºF) in order to remain healthy. They are dormant during that cold period but require temperatures above 10ºC (50ºF) to grow and produce sphorophylls (Gacia and Ballesteros 1994, Vöge 2006). Temperatures are rising at an unprecedented rate in New Jersey, with the increase being particularly notable during the winter months, and changes in global circulation patterns are also contributing to more unpredictable and extreme weather patterns (Hill et al. 2020). Warmer winters can disrupt the normal dormancy and growth cycle of *Isoetes lacustis*. An increase in the frequency of intense storms may cause more sediment to be deposited in aquatic systems. Climate warming is also likely to exacerbate habitat degradation resulting from eutrophication (Jeppesen et al. 2010, Nazari-Sharabian et al. 2018) and to favor the growth of species such as *Myriophyllum spicatum* that can outcompete the quillwort (Patrick et al. 2012).

Management Summary and Recommendations

New Jersey's sole occurrence of *Isoetes lacustris* has not been observed since 1991, at which time the population appeared be declining (NJNHP 2024). An updated assessment is required in order to evaluate the present status of the quillwort and determine whether active management is necessary. The monitoring visit can also be used to note habitat changes and identify threats.

Generally speaking, *I. lacustris* populations would benefit from actions that maintain extant water levels and preserve water quality such as land preservation or buffers that reduce the impacts of offsite activities. Depending on the locations of the plants, some efforts to direct human recreational pursuits away from their immediate vicinity might also be beneficial.

Synonyms

The accepted botanical name of the species is *Isoetes lacustris* L. Orthographic variants, synonyms, and common names are listed below (ITIS 2024, POWO 2024, Taylor et al. 2020, USDA NRCS 2024b). The genus name is also written as *Isoëtes*. At least seven varieties of *I. lacustris* have been described but none are currently accepted (POWO 2024).

Botanical Synonyms	**Common Names**
Isoetes hieroglyphica A. A. Eaton	Lake Quillwort
Isoetes macrospora Durieu	Deep-water Quillwort
Isoetes moorei Moore	
Calamaria lacustris (L.) Kuntze	

References

Ballesteros, E., E. Gacia, and L. Camerero. 1989. Composition, distribution and biomass of benthic macrophyte communities from Lake Baciver, a Spanish alpine lake in the central Pyrenees. Annales de Limnologie 25(2): 177–184.

Borisova, Elena, Nikita Konotop, Julia Vinogradova, Dmitriy Markov, and Alexey Sivukhin. 2020. About the reasons for the rare plant species disappearance in the Upper Volga region. E3S Web of Conferences 169, 03003. https://doi.org/10.1051/e3sconf/202016903003

Boston, Harry L. and Michael S. Adams. 1987. Productivity, growth, and photosynthesis of two small 'Isoetid' plants, *Litorella uniflora* and *Isoetes macrospora*. Journal of Ecology 75(2): 333–350.

Brinker, Samuel. 2017. Two photos of *Isoetes lacustris* from Ontario. Shared via iNaturalist at https://www.inaturalist.org/observations/8009286, licensed by https://creativecommons.org/licenses/by-nc/4.0/

Brinker, Samuel. 2018. Cover photo of *Isoetes lacustris* from Ontario. Shared via iNaturalist at https://www.inaturalist.org/observations/13992241, licensed by https://creativecommons.org/licenses/by-nc/4.0/

Britton, N. L. 1889. Catalogue of plants found in New Jersey. Geological Survey of New Jersey, Final report of the State Geologist 2: 27–642.

Britton, N. L. and A. Brown. 1913. An Illustrated Flora of the Northern United States and Canada in three volumes: Volume I (Ferns to Buckwheat). Second Edition. Reissued (unabridged and unaltered) in 1970 by Dover Publications, New York, NY. 680 pp.

Břízová, Eva. 2011. Quillwort (*Isoëtes*), a mysterious plant from the Czech Republic. Acta Musei Nationalis Pragae, Series B - Historia Naturalis 67(1–2): 25–34.

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.

Brunton, Daniel Francis and Paul Clayton Sokoloff. 2020. A review of North American *Isoetes engelmannii* (Isoetaceae) complex hybrids, including the description of *I.* ×*fernaldii*, hyb. nov. and *I.* ×*karenae*, hyb. nov. Journal of Plant Taxonomy and Geography 75(1): 35–50.

Campbell, Douglas Houghton. 1891. Contributions to the life-history of *Isoetes*. Annals of Botany 5(19): 231–258.

Chappuis, E., A. Lumbreras, E. Ballesteros, and E. Gacia. 2015. Deleterious interaction of light impairment and organic matter enrichment on *Isoetes lacustris* (Lycopodiophyta, Isoetales). Hydrobiologia 760: 145–158.

Čtvrtlíková, M., P. Znachor, and J. Vrba. 2014. The effect of temperature on the phenology of germination of *Isoëtes lacustris*. Preslia 86(3): 279–292.

Čtvrtlíková, Martina, Jiří Kopáček, Jiří Nedoma, Petr Znachor, Petr Hekera, and Jaroslav Vrba. 2023. Aquatic quillworts, *Isoëtes echinospora* and *I. lacustris* under acidic stress—A review from a temperate refuge. Ecology and Evolution 13(3): e9878.

Durieu de Maisonneuve, M. 1864. Notes sur quelques espèces nouvelles d'*Isoetes* de l'Amérique du Nord et de l'Australie. Bulletin de la Société Botanique de France 11: 100–105.

Dynowski, Piotr, Anna Źróbek-Sokolnik, Hanna Ciecierska, Jan Dziedzic, and Ryszard Piotrowicz. 2012. The use of GIS tools in the generation of maps illustrating the distribution of protected submerged species - The case of *Isoetes lacustris*. GIS for Geoscientists, Zagreb, Croatia: 123–129.

Faber-Langendoen, D. 2018. Northeast Regional Floristic Quality Assessment Tools for Wetland Assessments. NatureServe, Arlington, VA. 52 pp.

Fairbrothers, David E. and Mary Y. Hough. 1973. Rare or Endangered Vascular Plants of New Jersey. Science Notes No. 14, New Jersey State Museum, Trenton, NJ. 53 pp.

Farmer, J. Bretland. 1889. Preliminary note on the morphology and development of *Isoëtes lacustris*, Linn. Annals of Botany 3(9): 131–134.

Farmer, J. Bretland. 1890. On *Isoetes lacustris*, L. Annals of Botany 5(17): 37–62.

Fassett, Norman C. 1957. A Manual of Aquatic Plants. Second Edition. University of Wisconsin Press, Madison, WI. 405 pp.

Fernald, M. L. 1950. Gray's Manual of Botany. Dioscorides Press, Portland, OR. 1632 pp.

Gacia, Esperança and Enric Ballesteros. 1993. Population and individual variability of *Isoetes lacustris* L. with depth in a Pyrenean lake. Aquatic Botany 46(1): 35–47.

Gacia, Esperança and Enric Ballesteros. 1994. Production of *Isoetes lacustris* in a Pyrenean lake: Seasonality and ecological factors involved in the growing period. Aquatic Botany 48(1): 77–89.

Gacia, E. and E. Ballesteros. 1996. The effect of increased water level on *Isoetes lacustris* L. in Lake Baciver, Spain. Journal of Aquatic Plant Management 34: 57–59.

Gacia, E. and E. Ballesteros. 1998. Effects of building up a dam in a shallow mountain lake (Baciver, Central Pyrenees). Oecologia Aquatica 11: 55–66.

Gleason, H. A. and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Second Edition. The New York Botanical Garden, Bronx, NY. 910 pp.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111(982): 1169–1194.

Grzybowski, Mirosław, Zbigniew Endler, and Bożena Jaworska. 2008. Disappearance of *Isoëtes lacustris* localities and changes in the phytolittoral of Lake Długie near Łukta. Limnological Review 8(1-2): 69–77.

Hill, Rebecca, Megan M. Rutkowski, Lori A. Lester, Heather Genievich, and Nicholas A. Procopio (eds.). 2020. New Jersey Scientific Report on Climate Change, Version 1.0. New Jersey Department of Environmental Protection, Trenton, NJ. 184 pp.

Hough, Mary Y. 1983. New Jersey Wild Plants. Harmony Press, Harmony, NJ. 414 pp.

Husák, Štěpán, Margrit Vöge, and Cletus Weilner. 2000. *Isoëtes echinospora* and *I. lacustris* in the Bohemian Forest lakes in comparison with other European sites. Silva Gabreta 4: 245–252.

ITIS (Integrated Taxonomic Information System). Accessed January 4, 2024 at http://www.itis.gov

Jeppesen, Erik, Brian Moss, Helen Bennion, Laurence Carvalho, Luc DeMeester, Heidrun Feuchtmayr, Nikolai Friberg, Mark O. Gessner, Mariet Hefting, Torben L. Lauridsen, Lone Liboriussen, Hilmar J. Malmquist, Linda May, Mariana Meerhoff, Jon S. Olafsson, Merel B. Soons, and Jos T. A. Verhoeven. 2010. Interaction of climate change and eutrophication. In M. Kernan, R. Battarbee, and B. Moss (eds.). Climate Change Impacts on Freshwater Ecosystems. First edition. Blackwell Publishing Ltd, Hoboken, NJ.

Kansanen, Airi and Reino Niemi. 1974. On the production ecology of isoetids, especially *Isoëtes lacustris* and *Lobelia dortmanna*, in Lake Pääjärvi, southern Finland. Annales Botanici Fennici 11(2): 178–187.

Kartesz, J. T. 2015. The Biota of North America Program (BONAP). Taxonomic Data Center. (http://www.bonap.net/tdc). Chapel Hill, NC. [Maps generated from Kartesz, J. T. 2015. Floristic Synthesis of North America, Version 1.0. Biota of North America Program (BONAP) (in press)].

Keeley, J. E. 1982. Distribution of diurnal acid metabolism in the genus *Isoetes*. American Journal of Botany 69: 254–257.

Kott, L. S. and D. M. Britton. 1982. A comparative study of spore germination of some *Isoëtes* species of northeastern North America. Canadian Journal of Botany 60: 1679–1687.

Kott, L., and D. M. Britton. 1983. Spore morphology and taxonomy of *Isoetes* in northeastern North America. Canadian Journal of Botany 61: 3140–3163.

Kramer, K. U. 1977. Synaptospory: A hypothesis - A possible function of spore sculpture in pteridophytes. The Gardens' Bulletin, Singapore 30(4): 79–83.

Madsen, Tom Vindbæk. 1987. Interactions between internal and external CO_2 pools in the photosynthesis of the aquatic CAM plants *Litorella uniflora* (L.) Aschers and *Isoetes lacustris* L. New Phytologist 106: 35–50.

Mäkirinta, Urho, Marja Sipola, and Petra Nuotio. 1997. On the aquatic flora and vegetation of the northern half of the isoetid Lake Hiitehenjärvi in the Kostomuksha Nature Reserve. In Tapio Lindholm, Raimo Heikkilä and Marjo Heikkilä (eds.). Ecosystems, Fauna and Flora of the Finnish-Russian Nature Reserve Friendship. Finnish Environment Institute, Helsinki, Finland.

Malika, Monika, Franco Magurno, and Zofia Piotrowska-Seget. 2022. Plant association with dark septate endophytes: When the going gets tough (and stressful), the tough fungi get going. Chemosphere 302: 134830.

Mid-Atlantic Herbaria. 2024. Accessed at https://midatlanticherbaria.org/portal/index.php on January 18, 2024.

Montgomery, James D. 1982. Habitat preservation and rare pteridophytes in New Jersey. In William J. Cromartie (ed.). New Jersey's Endangered Plants and Animals. Stockton State College Center for Environmental Research, Pomona, NJ.

Montgomery, J. D. and D. E. Fairbrothers. 1992. New Jersey Ferns and Fern Allies. Rutgers University Press, New Brunswick, NJ. 293 pp.

Montgomery, James D. and W. Carl Taylor. 1994. Confirmation of a hybrid *Isöetes* from New Jersey. American Fern Journal 84(4): 115–120.

Müller, Karl. 1848. An account of the germination of *Isoëtes lacustris*. The Annals and Magazine of Natural History 2(8): 81–95,181–188, and 322–329.

Murphy, K. J., B. Rorslett, and I. Springue. 1990. Strategy analysis of submerged lake macrophyte communities: An international example. Aquatic Botany 36: 303–323.

Murphy, K. J., K. D. Hudson, and J. Mitchell. 1994. Freshwater and wetland plant communities of Loch Lomond. Hydrobiologia 290: 63–74.

Musselman, Lytton John. 2002. Ornamentation of *Isoetes* (Isoetaceae, Lycophyta) microspores. Botanical Review 68(4): 2002.

Musselman, Lytton J. and David A. Knepper. 1994. Quillworts of Virginia. American Fern Journal 84(2): 48–68.

NatureServe. 2024. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed January 18, 2024 at https://explorer.natureserve.org/

Nazari-Sharabian, Mohammad, Sajjad Ahmad, and Moses Karakouzian. 2018. Climate change and eutrophication: A short review. Engineering, Technology and Applied Science Research 8(6): 3668-3672.

NJNHP (New Jersey Natural Heritage Program). 2010. Explanation of Codes Used in Natural Heritage Reports. Updated March 2010. Available at https://nj.gov/dep/parksandforests/natural/docs/nhpcodes_2010.pdf

NJNHP (New Jersey Natural Heritage Program). 2024. Biotics 5 Database. NatureServe, Arlington, VA. Accessed March 15, 2024.

Patrick, D. A., N. Boudreau, Z. Bozic, G. S. Carpenter, D. M. Langdon, S. R. LeMay, S. M. Martin, R. M. Mourse, S. L. Prince, and K. M. Quinn. 2012. Effects of climate change on late-season growth and survival of native and non-native species of watermilfoil (*Myriophyllum* spp.): Implications for invasive potential and ecosystem change. Aquatic Botany 103: 83–88.

Pfeiffer, Norma E. 1922. Monograph of the Isoetaceae. Annals of the Missouri Botanical Garden 9(2): 79–233.

POWO. 2024. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Accessed January 4, 2024 at http://www.plantsoftheworldonline.org/

Raven, Peter H., Ray F. Evert and Susan E. Eichhorn. 1986. Biology of Plants. Worth Publishers, New York, NY. 775 pp.

Raven, John A., Linda L. Handley, Jeffrey J. MacFarlane, Shona McInroy, Lewis McKenzie, Jennifer H. Richards, and Goran Samuelsson. 1988. Tansley Review No. 13. The role of CO_2 uptake by roots and CAM in acquisition of inorganic C by plants of the isoetid life-form: A review, with new data on *Eriocaulon decangulare* L. The New Phytologist 108(2): 125–148.

Renzaglia, Karen S. and David J. Garbary. 2001. Motile gametes of land plants: Diversity, development, and evolution. Critical Reviews in Plant Sciences 20(2): 107–213.

Riera, Joan Lluís, Enric Ballesteros, Cristina Pulido, Eglantine Chappuis, and Esperança Gacia. 2017. Recovery of submersed vegetation in a high mountain oligotrophic soft-water lake over two decades after impoundment. Hydrobiologia 794: 139–151.

Ring, Richard M., Elizabeth A. Spencer, and Kathleen Strakosch Walz. 2013. Vulnerability of 70 Plant Species of Greatest Conservation Need to Climate Change in New Jersey. New York Natural Heritage Program, Albany, NY and New Jersey Natural Heritage Program, Department of Environmental Protection, Office of Natural Lands Management, Trenton, NJ, for NatureServe #DDCF-0F-001a, Arlington, VA. 38 pp.

Roelofs, J. G. M. 1983. Impact of acidification and eutrophication on macrophyte communities in soft waters in the Netherlands. I. Field observations. Aquatic Botany 17: 139–155.

Ronowski, Rafał P., Krzysztof Banaś, Marek Merdalski and Józef Szmeja. 2020. Plant replacement trend in soft-water lakes with isoetids. Oceanological and Hydrobiological Studies 49(2): 157–167.

Rørslett, Bjørn and Stein W. Johansen. 1995. Dynamic response of the submerged macrophyte, *Isoëtes lacustris*, to alternating light levels under field conditions. Aquatic Botany 51: 223–242.

Santos, Mila, Ignacio Cesanelli, Fernando Diánez , Brenda Sánchez-Montesinos, and Alejandro Moreno-Gavíra. 2021. Advances in the role of dark septate endophytes in the plant resistance to abiotic and biotic stresses. Journal of Fungi 7: 939.

Silva, Giliandro G., Andy J. Green, Pedro Hoffman, Vinícius Weber, Cristina Stenert, Ádám Lovas-Kiss, and Leonardo Maltchik. 2021. Seed dispersal by neotropical waterfowl depends on bird species and seasonality. Freshwater Biology 66(1): 78–88.

Smith, R Wilson. 1900. The structure and development of the sporophylls and sporangia of *Isoetes*. Botanical Gazette 29(5): 323–346.

Stefanova, Ivanka and Daniela Ivanova. 2000. On systematics and history of the Bulgarian representative of genus *Isoetes* L. Phytologia Balcanica 61(1): 31–42.

Sudová, Radka, Jana Rydlová, Martina Ctvrtlíková, Pavel Havránek, and Lubomír Adamec. 2011. The incidence of arbuscular mycorrhiza in two submerged *Isoëtes* species. Aquatic Botany 94: 183–187.

Staniforth, R. J. and D. F. Brunton. 2022. A synopsis of the lycophytes in Manitoba, Canada: Their status, distribution, abundance and habitats. Canadian Field-Naturalist 136: 107–121.

Szmeja, Józef. 1994. Effect of disturbances and interspecific competition in isoetid populations. Aquatic Botany 48(3-4): 225–238.

Taylor, Norman. 1915. Flora of the vicinity of New York - A contribution to plant geography. Memoirs of the New York Botanical Garden 5: 1–683.

Taylor, W. Carl. 1992. *Isoetes*. In James D. Montgomery and David E. Fairbrothers. New Jersey Ferns and Fern Allies. Rutgers University Press, New Brunswick, NJ.

Taylor, W. Carl and R. James Hickey. 1992. Habitat, evolution, and speciation in *Isoetes*. Annals of the Missouri Botanical Garden 79(3): 613–622.

Taylor, W. C, and N. T. Luebke. 1988. *Isoetes ×hickeyi*: A naturally occurring hybrid between *I. echinospora* and *I. macrospora*. American Fern Journal 78: 6–13.

Taylor, W. Carl, Neil T. Luebke, Donald M. Britton, R. James Hickey, and Daniel F. Brunton. Page updated November 5, 2020. *Isoëtes lacustris* Linnaeus. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico [Online]. 22+ vols. New York and Oxford. Accessed January 4, 2024 at http://floranorthamerica.org/Iso%C3%ABtes_lacustris

Toivonen, Heikki and Teuvo Lappalainen. 1980. Ecology and production of aquatic macrophytes in the oligotrophic, mesohumic Lake Suomunjärvi, eastern Finland. Annales Botanici Fennici 17(1): 69–85.

Troia, Angelo. 2016. Dispersal and colonization in heterosporous lycophytes: Palynological and biogeographical notes on the genus *Isoetes* in the Mediterranean region. Webbia: Journal of Plant Taxonomy and Geography 71(2): 277–281.

U. S. Army Corps of Engineers. 2020. National Wetland Plant List, version 3.5. https://cwbi-app.sec.usace.army.mil/nwpl_static/v34/home/home.html U. S. Army Corps of Engineers Research and Development Center, Cold Regions Research and Engineering Laboratory, Hanover, NH.

USDA, NRCS (U. S. Dept. of Agriculture, Natural Resources Conservation Service). 2024a. *Isoetes lacustris* illustration from Britton, N. L. and A. Brown, 1913, An illustrated flora of the northern United States, Canada and the British Possessions, 3 vols., Kentucky Native Plant Society, New York, Scanned By Omnitek Inc. Image courtesy of The PLANTS Database (http://plants.usda.gov). National Plant Data Team, Greensboro, NC.

USDA, NRCS (U. S. Dept. of Agriculture, Natural Resources Conservation Service). 2024b. PLANTS profile for *Isoetes lacustris* (Lake Quillwort). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed January 4, 2024 at http://plants.usda.gov

Vaasma, Tiit, Jaanus Terasmaa, and Egert Vandel. 2015. Changes in sedimentation and aquatic vegetation caused by drastic lake level fluctuation. Lakes, Reservoirs and Ponds 9(1): 29–42.

Vandel, Egert, Tiit Vaasma, Jaanus Terasmaa, Tiiu Koff, and Marko Vainu. 2014. Effect of human induced drastic water-level changes to ecologically sensitive small lakes. 2nd

International Conference - Water resources and wetlands. 11–13 September, 2014 Tulcea (Romania); Available online at http://www.limnology.ro/water2014/proceedings.html

Vandel, Egert, Tiit Vaasma, Tiiu Koff, and Jaanus Terasmaa. 2016. Impact of water-level changes to aquatic vegetation in small oligotrophic lakes from Estonia. Lakes, Reservoirs and Ponds 10(1): 9–26.

Vlasov, Boris P. 2012. Geoecological features of Belarus lakes - The habitats of relict species *Isoëtes lacustris* L. Acta Geographica Silesiana 12: 57–64.

Vöge, Margrit. 2006. The reproductive phenology of *Isoetes lacustris* L.: Results of field studies in Scandinavian lakes. Limnologica 36: 228–233.

Vöge, Margrit. 2014. Monitoring the vitality of *Isoëtes lacustris* by using a non-destructive method. Limnological Review 14(3): 153–158.

Walz, Kathleen S., Jason L. Hafstad, Linda Kelly, and Karl Anderson. 2020. Floristic Quality Assessment Index for Vascular Plants of New Jersey: Coefficient of Conservancy (CoC) Values for Species and Genera (update to 2017 list). New Jersey Department of Environmental Protection, New Jersey Forest Service, Office of Natural Lands Management, Trenton, NJ.

Weakley, A. S. and Southeastern Flora Team. 2022. Flora of the Southeastern United States. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC. 2022 pp.

Wherry, E. T. 1938. Specimen of *Isoetes lacustris* collected in New Jersey on August 7, 1938. Image of herbarium sheet courtesy of New York Botanical Garden Steere Herbarium via MidAtlantic Herbaria. Accessed January 4, 2024 at https://midatlanticherbaria.org/portal/index.php. Licensed by https://creativecommons.org/licenses/by/3.0/. Image modified to remove location.

Young, Bruce E., Elizabeth Byers, Geoff Hammerson, Anne Frances, Leah Oliver, and Amanda Treher. 2016. Guidelines for Using the NatureServe Climate Change Vulnerability Index, Release 3.02, 1 June 2016. NatureServe, Arlington, VA. 65 pp.