Asplenium pinnatifidum

Lobed Spleenwort

Aspleniaceae

Asplenium pinnatifidum, courtesy Alan Cressler, Lady Bird Johnson Wildflower Center

***Asplenium pinnatifidum* Rare Plant Profile**

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

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Life History

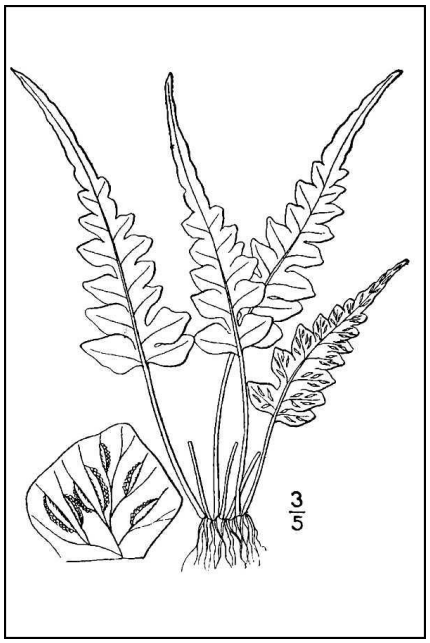
Asplenium pinnatifidum (Lobed Spleenwort) is a small fern in the Aspleniaceae. A number of the *Asplenium* species in the eastern United States are very closely related and have similar life histories and somewhat overlapping morphological characteristics. Wagner (1954) outlined the relationships within the group, identifying three 'basic' species from which the others were derived: *A. montanum* (Mountain Spleenwort), *A. platyneuron* (Ebony Spleenwort), and *A. rhizophyllum* (Walking Fern). Wagner's proposal that *Asplenium pinnatifidum* initially arose as a fertile hybrid of *A. montanum* and *A. rhizophyllum* was subsequently confirmed by a genetic analysis (Werth et al. 1985). In fact, Werth and his colleagues found some evidence suggesting that *A. pinnatifidum* may have arisen more than once in that manner.

The life cycle of ferns includes two independent generations. Spores produced by mature plants initially develop into tiny free-living gametophytes with structures that produce male and female reproductive cells (gametes). Male gametes (sperm) develop in an antheridium and a female gamete (egg) develops in an archegonium. Fertilized female cells develop into the leafy plants (sporophytes) that produce the spores for the next generation, and once the sporophytes are large enough to be self-sufficient the gametophytes disintegrate (Raven et al. 1986). Apogamy—the development of a sporophyte from a gametophyte without fertilization—has been reported in some species (e.g. *Asplenium unilaterale*) but is not common in the spleenwort family (Nayar and Kaur 1971).

Gametophytes of ferns in the Aspleniaceae establish on top of the substrate. The tiny plants are flat, somewhat heart-shaped, and green with a lighter-colored midrib. In some spleenworts they are hairy (Nayar and Kaur 1971, Wagner et al. 2020). There is limited information available regarding the gametophyte phases of many ferns in natural settings (Farrar 1976) but the stage was studied in *Asplenium rhizophyllum*, one of the parent species of Lobed Spleenwort. The spores of *A. rhizophyllum* matured between June and October (Pickett 1914a) and gametophytes were observed during the autumn months (Pickett 1914b). The gametophyte stage was typically brief and mature gametes usually developed within 10–12 weeks of spore germination, although in protected sites gametophytes sometimes persisted throughout the winter before producing sporophytes (Pickett 1914a, 1914b). Although clonal reproduction at the gametophyte stage is not common in ferns (Nayar and Kaur 1971), the studies of *A. rhizophyllum* indicated that some vegetative regeneration is possible following damage (Pickett 1914b). As with its parent species, the spores of *Asplenium pinnatifidum* mature from late June through October (Hough 1983) and it is likely that its gametophyte generation follows a similar trajectory.

The sporophyte of *Asplenium pinnatifidum* is perennial from a short rootstock that produces a dense cluster of stems. Total frond length ranges from 7–20 cm. The leaf petiole (or stipe) is dark at the base but become greener toward the blade and the portion that extends through the center of the blade (rachis) is also green. The leaves are usually lanceolate in outline and pinnate near the base but unlobed near the tips. Lobes at the lower end of the fronds may be bluntly toothed. The clusters of sporangia (sori) are linear and straight or slightly curved. (See Britton and Brown 1913, Fernald 1950, Gleason and Cronquist 1991, Montgomery and Fairbrothers 1992, Wagner et al. 2020). Both the sterile and fertile fronds of *A. pinnatifidum* are evergreen (Wacker 1905, Wherry 1957). One of its parent species, *A. montanum*, is also considered

evergreen but the leaves can sometime become discolored or desiccated so that the plants appear brown until new fronds emerge the following spring (NYNHP 2022).



Left: Britton and Brown 1913, courtesy USDA NRCS 2022a. Right: Frond with sori by John Hilty, Illinois Wildflowers (undated).

Vegetative reproduction by leaf tip propagation is most often associated with *Asplenium rhizophyllum* but, although less frequent, it can also occur in *A. pinnatifidum*, *A. platyneuron*, and *A. ebenoides* (Wacker 1905). Wagner (1960) discovered an *A. pinnatifidum* colony in Kentucky in which all of the plants were developing reproductive structures near the tips of their leaves and made detailed notes. Subterminal buds developed on the upper sides of prolonged leaf tips, and those were accompanied by varying combinations of leaves, roots and sporangia. Sporangia were present on half of the reproductive structures observed, while only about a third had leaves. Roots were only found when leaf tips were in contact with the ground. According to Morlang (1967), vegetative reproduction in *Asplenium* species is triggered by parent vigor and not by contact with the substrate.

Identification of spleenworts may be complicated by both hybridization and intraspecific variability. A key for distinguishing the most similar species and their hybrids is available in Wagner and Darling (1957). *Asplenium pinnatifidum* is known to cross with *A. montanum* (*A.* × *trudellii*), *A. bradleyi* (*A.* × *gravesii*), *A. platyneuron* (*A.* × *kentuckiense*) and *A. trichomanes* (*A.* × *herb-wagneri*), forming mostly sterile hybrids (Wagner et al. 2020). However, Wherry (1925) reported some evidence of self-perpetuation in both *A.* × *trudellii* and *A.* × *gravesii*. To date, *A.* × *trudellii* is the only confirmed *A. pinnatifidum* hybrid in New Jersey (Kartesz 2015), and that was known from a single occurrence documented in 1908 which could not subsequently be relocated (Montgomery and Fairbrothers 1992).

Wherry (1925) called *Asplenium pinnatifidum* a "remarkably variable species", describing a form with acute segments that was found among more typical plants. Earlier botanists had also

observed variation in leaf shapes within *A. pinnatifidum* populations (e.g. Copeland 1902), and Graves (1923) reported the collection of Lobed Spleenwort plants with leaves that were so deeply cut that they were bipinnate. Mohlenbrock (1955, 1956) described and illustrated a form of *A. pinnatifidum* that produced sori along the rachis and only rudimentary pinnae, and Wagner (1966) found a Lobed Spleenwort population that developed unusual crested leaf tips during a single growing season but not previously or afterward. Identification of rare forms of *A. pinnatifidum* was usually based on stipe and rachis colors as well as their occurrence within populations of more conventional plants.

Pollinator Dynamics

Because *Asplenium pinnatifidum* is a non-flowering plant, pollination does not take place. Antheridia on the gametophytes release their gametes through a pore-like opening that develops in the cap cell (Nayar and Kaur 1971). Fertilization is dependent on water, which allows the movement of the multiflagellate sperm toward a receptive egg cell (Raven 1986).

Some pteridophytes can manipulate the sequence of gamete development in order to promote cross-fertilization, but it is not clear if this occurs in *A. pinnatifidum*. The Hart's-tongue Fern (*A. scolopendrium*) utilizes a mixed mating system, outcrossing when circumstances permit but self-fertilizing when necessary. The latter strategy permits the colonization of a new site by a single spore (Wubs et al. 2010). Genetic variability is low in young colonies of *A. ruta-muraria* but it increases as the populations age (Schneller and Holderegger 1996). The authors suggested that for *A. ruta-muraria* and similar species that occur in small, isolated colonies genetic variation is probably less important to the maintenance of populations than ecological and demographic factors.

Seed Dispersal and Establishment

Dispersal in *Asplenium pinnatifidum* is carried out by spores rather than seeds. Lobed Spleenwort develops 64 spores in each sporangium (Wagner et al. 2020). The dust-like spores are transported by wind and may be deposited nearby or thousands of kilometers away (Kessler 2010). Many ferns disperse their spores slowly over a long period, sometimes continuing into the following spring (Farrar 1976). Pickett (1914a) successfully grew gametophytes from spores that had been retained on the leaves of *A. rhizophyllum* throughout the winter, confirming their extended viability, and Darling (1957) successfully germinated *A. pinnatifidum* spores he had collected from wild plants during January.

The early development of *Asplenium pinnatifidum* has not been well described but the process has been studied in a number of other *Asplenium* species and it appears to be fairly consistent within the genus. Once spores have been released some germinate rapidly but others may remain dormant for 3–4 months. Staggering the release times and germination periods of the spores helps to reduce losses that might result from severe conditions such as freezing or drought (Pickett 1914b). When conditions are favorable the spores absorb water and swell to twice their size and then rupture to release their contents (Pickett 1914a). Morlang (1967) reported that an

unidentified type of bacteria facilitated germination in three related ferns: *A. rhizophyllum*, *A. montanum*, and *A. platyneuron*. Germination initially produces a rhizoid and a filament 4-8 cells long and one cell wide (Nayar and Kaur 1971, Testo and Watkins 2011). Chloroplasts quickly appear near the surface of the cells and additional rhizoids are formed that anchor the developing gametophyte to the substrate (Pickett 1914a).

Asplenium spores sown in laboratories typically germinated in 5–28 days (Pickett 1914a, Herraro et al. 1993, Pangua et al. 1994, Testo and Watkins 2011). Germination times were at the longer end of the spectrum in shade (Pickett 1914a) and at lower temperatures (Pangua et al. 1994). In comparison to an average germination period of 1–3 weeks under laboratory conditions germination in the field took longer, with gametophytes appearing after 4–8 weeks for *A. trichomanes* and 8–12 weeks for *A. ruta-muraria* (Pangua et al. 1994). Archegonia and antheridia were present six weeks after germination (Pickett 1914a, Herraro et al. 1993), at which point the average size of gametophytes was ~0.5 mm^2 (Pangua et al. 1994). *Asplenium* gametophytes can be bisexual, exclusively male, or exclusively female, and Pangua and her colleagues noted that fully developed gametophytes with archegonia were always the largest (6–10 mm^2) while those with only antheridia typically reached maximum sizes of 1–2 mm^2. As previously noted, sporophyte development may proceed rapidly or the ferns may remain in the gametophyte stage for several months depending on environmental conditions (Pickett 1914a, 1914b).

Mycorrhizal associations have not been reported for *Asplenium pinnatifidum*. Development of mycorrhizae is highly variable in the genus, and roughly half of the species in Aspleniaceae are non-mycorrhizal (Wang and Qiu 2006). Ferns that inhabit isolated rock outcroppings and crevices often lack mycorrhizae (Berch and Kendrick 1982).

Habitat

Asplenium pinnatifidum grows in rocky environments on cliff faces, ledges, boulders, bluffs, and outcrops at elevations up to 1000 meters. The fern is often associated with sandstone, but it has also been reported on gneiss, granite, phyllite, and schist (Graves 1921, Wherry 1927, McCoy 1938, Mohlenbrock 1955, McDowell 1965, Duncan 1966, Tryon 1971, Hanson and Hanson 1979, Weakley 2015, PANHP 2019, Wagner et al. 2020). Rhoads and Block (2007) specified that the preferred substrate was noncalcareous rock, and Mohlenbrock (1981) observed that while two of its hybrids (*A.* × *kentuckiense* and *A.* × *trudellii*) were found on limestone cliffs *A. pinnatifidum* itself was not present. The sites occupied by Lobed Spleenwort are frequently described as acidic or sub-acidic (Fairbrothers and Hough 1973, Hanson and Hanson 1979, Montgomery 1982), and Wherry (1927) reported that the optimum substrate for *A. pinnatifidum* was medi-acid with a specific acidity of 300 using parameters that he had previously defined (see Wherry 1919).

Asplenium pinnatifidum is typically found beneath overhangs or tucked into cracks and crevices that offer some protection from the elements (Fairbrothers and Hough 1973, Hanson and Hanson 1979). The array of climactic conditions reported for an Illinois occurrence included heavy spring rainfalls followed by two months of extreme drought with regional temperatures ranging

from summer highs of 40°C to winter lows of -31°C (Wherry 1927). Wherry (1927) observed that *A. pinnatifidum* avoided extreme desiccation by growing on the shady side of cliffs, Hanson and Hanson (1979) remarked that the majority of populations were found at east or north facing sites, and other botanists have also indicated that the spleenwort favors shaded or lightly shaded locations (Duncan 1966, Rhoads and Block 2007). An absence of accumulated litter in the rock crevices occupied by *A. pinnatifidum* was noted by Hanson and Hanson (1979).

Microhabitat of *A. pinnatifidum* by Joe Brehm (left) and John Hilty, Illinois Wildflowers (right).

Mohlenbrock (1955) remarked that Lobed Spleenwort was not common in Illinois but could occasionally be abundant in suitable habitat. Graves (1923) reported that he often found *Asplenium pinnatifidum* growing in the same location as *A. bradleyi*, a fern with similar habitat preferences that is also endangered in New Jersey. However, the two species have not been observed co-occurring in the state (NJNHP 2022).

Wetland Indicator Status

Asplenium pinnatifidum is not included on the National Wetlands Plant List (NWPL). Any species not on the NWPL is considered to be Upland (UPL) in all regions where it occurs. The UPL designation means that it almost never occurs in wetlands (U. S. Army Corps of Engineers 2020).

USDA Plants Code (USDA, NRCS 2022b)

ASPI

Coefficient of Conservatism (Walz et al. 2018)

CoC = 8. Criteria for a value of 6 to 8: Native with a narrow range of ecological tolerances and typically associated with a stable community (Faber-Langendoen 2018).

Distribution and Range

The worldwide distribution of *Asplenium pinnatifidum* is restricted to the central and eastern United States (POWO 2022). The map in Figure 1 shows the global extent of Lobed Spleenwort.

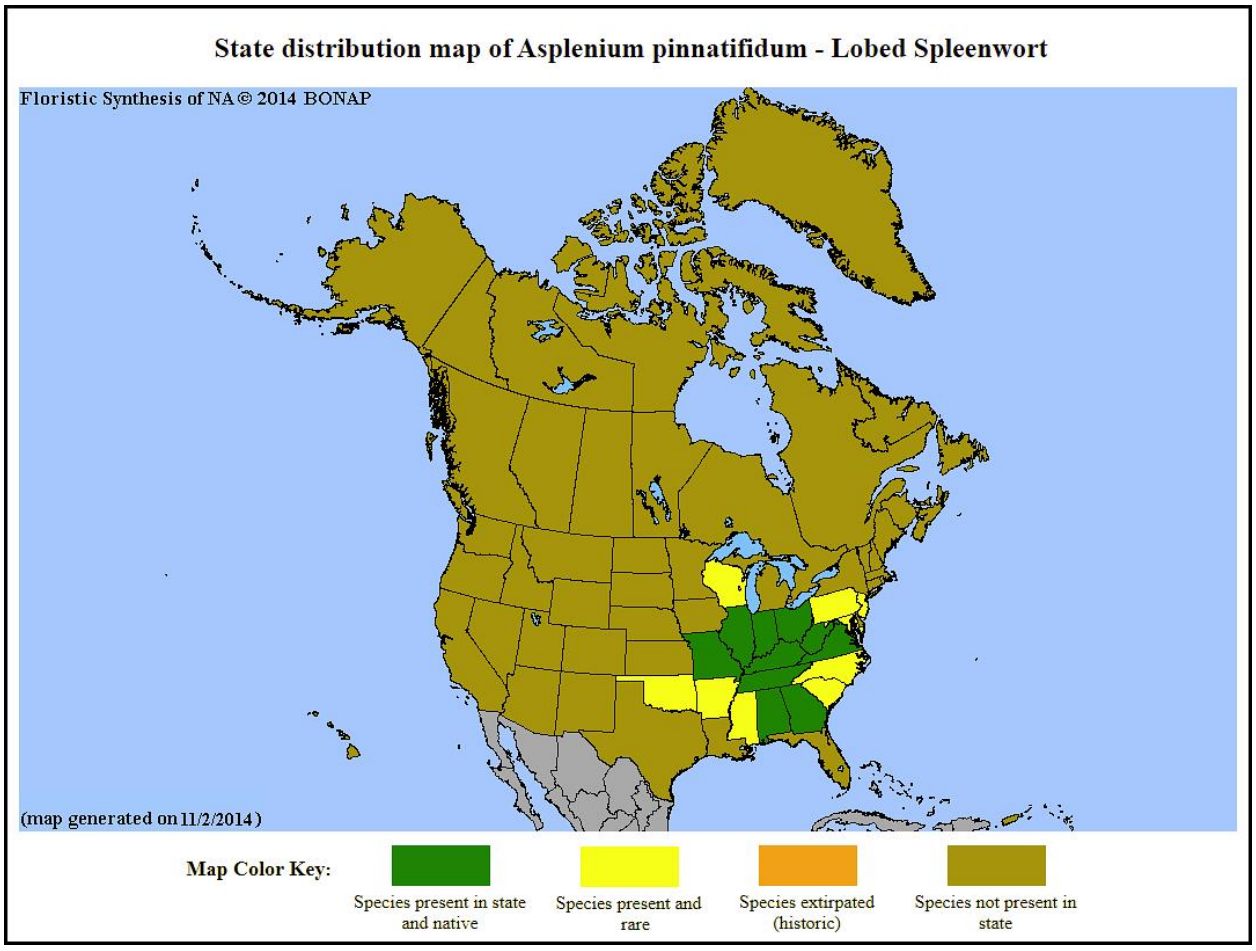


Figure 1. Distribution of A. pinnatifidum in North America, adapted from BONAP (Kartesz 2015).

The USDA PLANTS Database (2022b) shows records of *Asplenium pinnatifidum* in three New Jersey counties: Hunterdon, Sussex, and Warren (Figure 2 below). The data include historic observations and do not reflect the current distribution of the species.

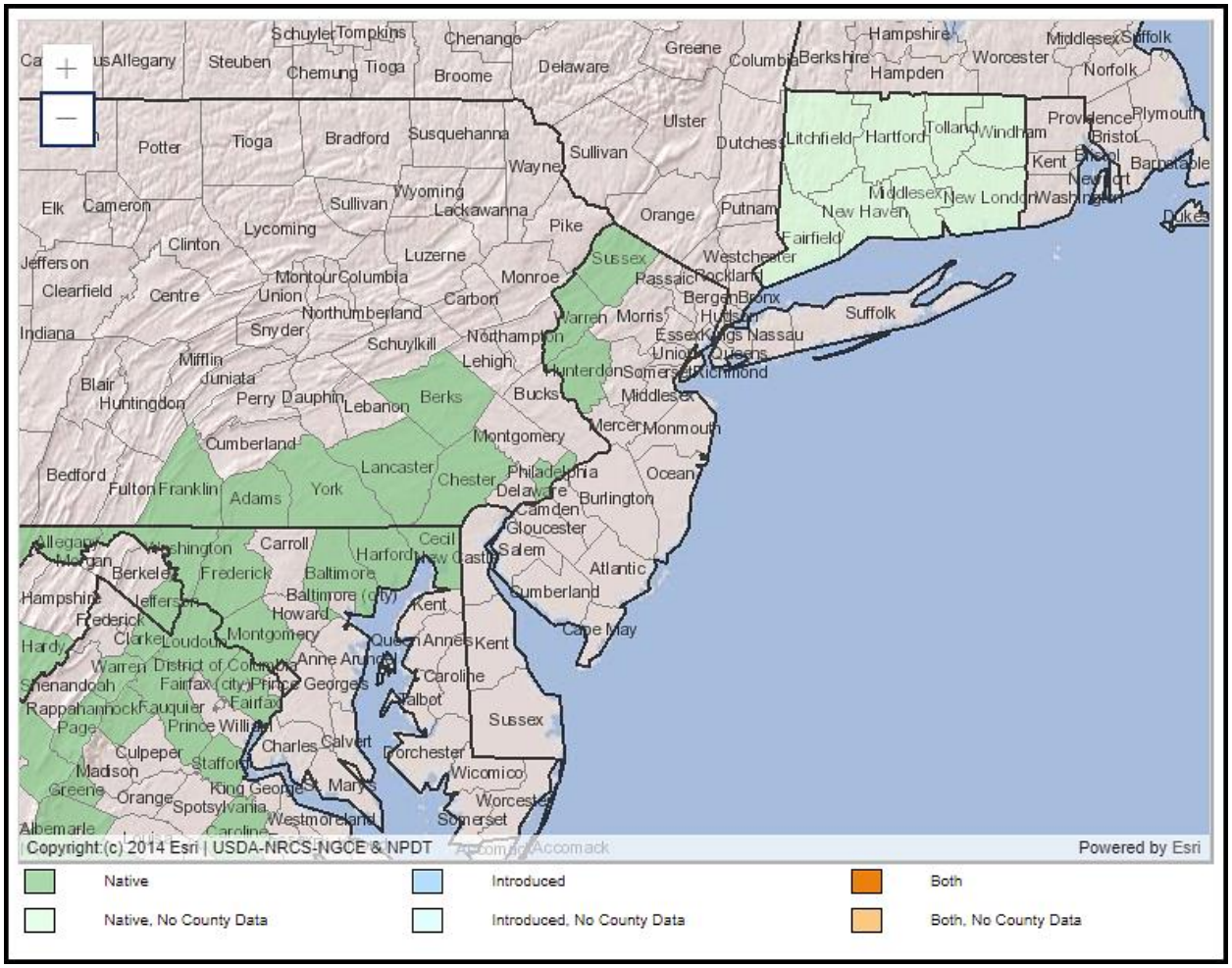


Figure 2. County records of A. pinnatifidum in New Jersey and vicinity (USDA NRCS 2022b).

Conservation Status

Asplenium pinnatifidum is apparently secure at a global scale. The G4 rank means the species is at fairly low risk of extinction or collapse due to an extensive range and/or many populations or occurrences, although there is some cause for concern as a result of recent local declines, threats, or other factors (NatureServe 2022). The map below (Figure 3) illustrates the conservation status of *A. pinnatifidum* throughout its range. Lobed Spleenwort is critically imperiled (very high risk of extinction) in seven states, imperiled (high risk of extinction) in one state, vulnerable (moderate risk of extinction) in four states, and presumed extirpated in New York. The species is ranked as apparently secure in three states and is unranked in five other states where it has been reported.

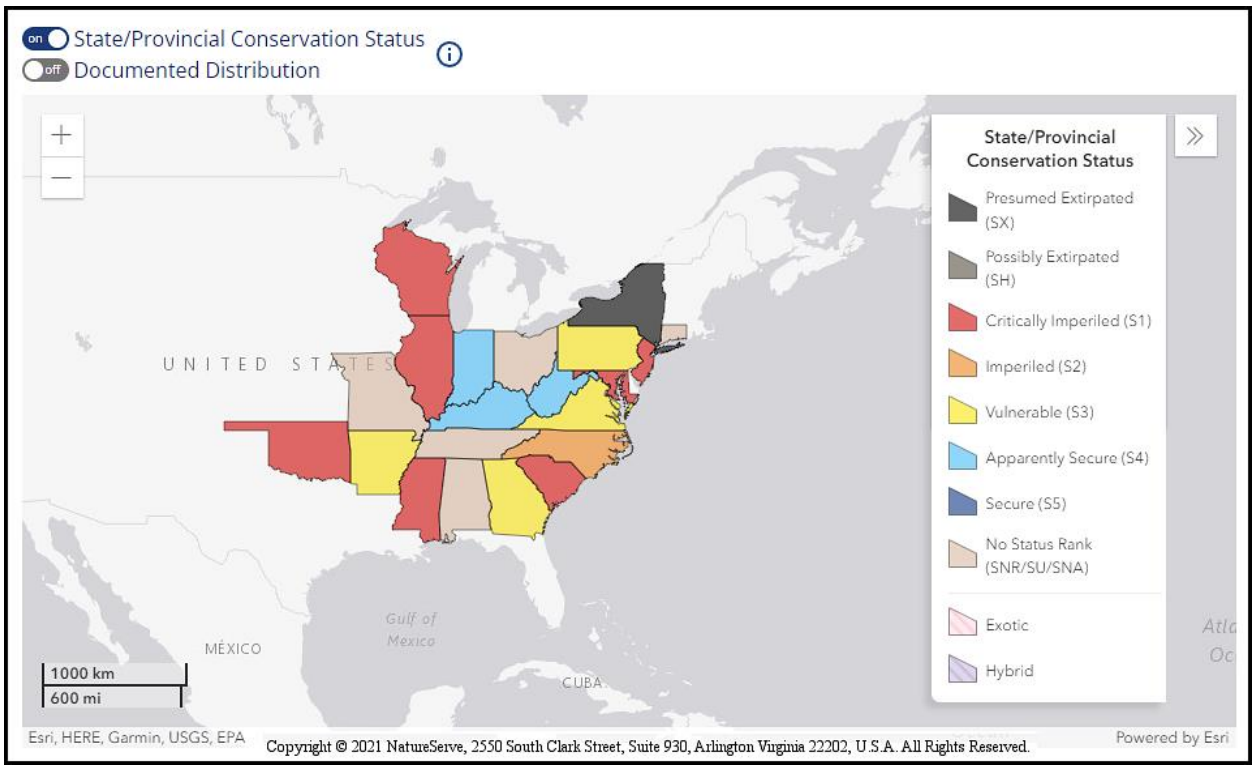


Figure 3. Conservation status of A. pinnatifidum in North America (NatureServe 2022).

New Jersey is one of the states where *Asplenium pinnatifidum* is critically imperiled (NJNHP 2022). The S1 rank signifies five or fewer occurrences in the state. A species with an S1 rank is typically either restricted to specialized habitats, geographically limited to a small area of the state, or significantly reduced in number from its previous status. *A. pinnatifidum* 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, being listed does not currently provide broad statewide protection for plants. Additional regional status codes assigned to Lobed Spleenwort signify that the fern is eligible for protection under the jurisdictions of the Highlands Preservation Area (HL) and the New Jersey Pinelands (LP) (NJNHP 2010).

Asplenium pinnatifidum was first reported in New Jersey from a specimen collected in Warren County (Taylor 1915) but the account was later determined to be based on a misidentification (Fairbrothers and Hough 1973). The specimen was actually a hybrid of *A. pinnatifidum* and *A. montanum* (*Asplenium* × *trudellii*), so Kobbé and Davis (1928) took that as evidence that the parent species was growing somewhere nearby. However, further searches in Warren County failed to turn up *A. pinnatifidum* or relocate *A.* × *trudellii* (Montgomery and Fairbrothers 1992). Lobed Spleenwort was discovered in both Sussex and Hunterdon Counties between 1939 and 1941 (NJNHP 2022) but it was only known from one occurrence in each district (Fables 1957). Fairbrothers and Hough (1973) noted that the species seemed to be disappearing, and for a time the New Jersey populations were thought to be lost (Snyder 1985). Both sites were subsequently rediscovered as a result of extensive searches carried out by some intrepid botanists who faced encounters with venomous snakes and bears and climbed cliff faces and trees in order to locate

the small ferns (Snyder 1993, NJNHP 2022). At one of the sites six hours of searching only turned up a single plant, while just four plants were observed at the second site (NJNHP 2022).

Threats

Asplenium pinnatifidum is likely to be shielded from many typical anthropogenic disturbances because of the steep, rocky, and often inaccessible habitat in which it occurs. At some locations quarrying may be a threat (PANHP 2019). Populations could also be affected by development on the summit of cliffs. One of New Jersey's occurrences is situated on the side of a mountain below a residential development (NJNHP 2022) where its habitat could be altered by runoff that contains herbicides, fertilizers, or road salts. Potential threats were identified for *A. montanum*—a species with similar life history characteristics and habitat preferences—from recreational rock-climbing and bouldering. In addition to directly damaging extant plants, climbers may inadvertently introduce invasive species or alter the chemistry of ledges by depositing chalk (Minicuci 2019).

Rising temperatures and extended periods of drought associated with climate change are likely to have a detrimental impact on *Asplenium pinnatifidum*. Fairbrothers and Hough (1973) suggested that an observed decline in the species could have been precipitated by drought or by changes in microclimate resulting from the removal of trees. Although the impacts of weather conditions on *A. pinnatifidum* have not been evaluated, some inferences may be drawn from studies of similar species. Pickett (1914b) found that gametophytes of *A. rhizophyllum* could survive and recover from experimentally induced desiccation that lasted for periods of 4–6 days. The observation was confirmed by Testo and Watkins (2013), who also documented a comparable response in *A. trichomanes* gametophytes. In natural settings *Asplenium* gametophytes are likely to tolerate extended periods of drought if they are not exposed to excessive sunlight, taking advantage of the occasional showers that facilitate fertilization to develop sporophytes (Pickett 1914b). However, spleenworts may be less tolerant of climate extremes at the sporophyte stage, as Pickett (1914b) also reported both mortality and impaired spore production in mature *A. rhizophyllum* plants following a summer characterized by unusually high temperatures and drought.

Management Summary and Recommendations

Asplenium pinnatifidum does not appear to require a lot in the way of active management. The most important step that can be taken for the protection of Lobed Spleenwort is conservation of its habitat in areas where the fern occurs. Depending on the location, a buffer area may be needed to maintain the characteristics of microsites where *A. pinnatifidum* has become established, particularly to avoid loss of tree cover or limit development uphill from the plants. At sites where the fern could be harmed by recreational activities, trails or climbing routes should be redirected to avoid damage to the plants. Occurrences should be monitored periodically for emerging threats from disturbance or invasive species. There may be undiscovered populations of *A. pinnatifidum* in New Jersey or other places where suitable habitat is present. While seeking out new occurrences can be relatively costly in terms of time and

effort, focused searches for the species should be prioritized at sites where suitable habitat could be impacted by nearby development, right-of-way establishment, or resource extraction.

A number of *Asplenium* species share a common developmental pathway and *A. pinnatifidum* might reasonably be expected to follow the same general pattern. However, the spleenworts also display individual differences in characteristics such as the timing and sequence of gamete development or responses to climactic conditions. Research focused specifically on the habits, requirements, and tolerances of *A. pinnatifidum* would be beneficial. An unusual amount of plasticity in the sporophytes of Lobed Spleenwort has been described but not explained, and it would be interesting to learn what induces variation in the mature plants. Understanding whether the species is capable of establishing from a single spore via self-fertilization or apogamy would also be valuable.

Synonyms

The accepted botanical name of the species is *Asplenium pinnatifidum* Nutt. Orthographic variants, synonyms, and common names are listed below (ITIS 2021, USDA NRCS 2022b, POWO 2022).

Botanical Synonyms	Common Names
Asplenium pinnatifidum f. *elongatum* C. V. Morton	Lobed Spleenwort
Antigramma pinnatifida (Nutt.) Alph. Wood	
× *Asplenosorus pinnatifidus* (Nutt.) Mickel	
Athyrium pinnatifidum Shafer	
Camptosorus pinnatifidus (Nutt.) Alph. Wood	
Chamaefilix pinnatifida Farw.	
Scolopendrium pinnatifidum Diels	

References

Berch, Shannon M. and Bryce Kendrick. 1982. Vesicular-arbuscular mycorrhizae of southern Ontario ferns and fern-allies. Mycologia 74(5): 769–776.

Brehm, Joe. 2019. Photo of *Asplenium pinnatifidum* from Ohio. Shared via iNaturalist at https://www.inaturalist.org/observations/33869019, licensed by https://creativecommons.org/licenses/by-nc/4.0/

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.

Copeland, Edwin Bingham. 1902. Two fern monstrosities. Botanical Gazette 34(2): 142–144.

Cressler, Alan. 2014. Cover photo of *Asplenium pinnatifidum*. Courtesy of the Lady Bird Johnson Wildflower Center, https://www.wildflower.org/. Used with permission.

Darling, Thomas Jr. 1957. In search of the rock-fern hybrid *Asplenium gravesii*. American Fern Journal 47(2): 55–66.

Duncan, Wilbur H. 1966. Asplenium × kentuckiense on granitic gneiss in Georgia. American Fern Journal 56(4): 145–149.

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

Fables, David Jr. 1957. Caesarian flora and fauna, Number 3. Published posthumously in Bartonia 32(1961–62): 7–10.

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.

Farrar, Donald R. 1976. Spore retention and release from overwintering fern fronds. American Fern Journal 66(2): 49–52.

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

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.

Graves, E. W. 1921. An interesting trip. American Fern Journal 11(3): 86–88.

Graves, E. W. 1923. Is *Botrychium dissectum* a mutant? American Fern Journal 13(3): 87–89.

Hanson, Martha G. and Robert P. Hanson. 1979. The northernmost station for *Asplenium pinnatifidum*. Wisconsin Academy of Sciences, Arts, and Letters 67: 165–170.

Herraro, Alberto, Carmen Prada, Emilia Pangua, Adrian Escudero, Agustin Rubio, and Santiago Pajaron. 1993. Gametophyte morphology of four subspecies of *Asplenium trichomanes* L. Botanica Complutensis 18: 67–77.

Hilty, John. Undated. Two images of *Asplenium pinnatifidum* from Illinois Wildflowers http://www.illinoiswildflowers.info/grasses/plants/lb_spleenwort.html used with permission https://www.illinoiswildflowers.info/files/photo_use.html

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

ITIS (Integrated Taxonomic Information System). Accessed November 13, 2021 at http://www.itis.gov

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)].

Kessler, Michael. 2010. Biogeography of Ferns. In K. Mehltreter, L. R. Walker, and J. M. Sharpe. Fern ecology. Cambridge University Press, Cambridge, United Kingdom. Available at https://www.zora.uzh.ch/id/eprint/42711/9/Kessler_Fern_Ecology_Book_2010.pdf

Kobbé, F. W. and W. A. Davis. 1928. A note on *Asplenium pinnatifidum* Nuttall. American Fern Journal 18(1): 21–23.

McCoy, Thomas N. 1938. The ferns and fern allies of Kentucky (concluded). American Fern Journal 28(3): 101–110.

McDowell, Gladstone W. 1965. Shorter notes. American Fern Journal 55(2): 81–83.

Minicuci, Lee. 2019. *Asplenium montanum* Rare Plant Profile. New Jersey Department of Environmental Protection, Division of Parks and Forestry, New Jersey Forest Service, Office of Natural Lands Management, New Jersey Natural Heritage Program, Trenton, NJ. 11 pp.

Mohlenbrock, Robert H. 1955. The pteridophytes of Jackson County, Illinois. American Fern Journal 45(4): 143–150.

Mohlenbrock, Robert H. 1956. An unusual form of *Asplenium pinnatifidum*. American Fern Journal 46(2): 91–83.

Mohlenbrock, Robert H. 1981. Ferns of the Shawnee National Forest (Illinois). Rhodora 83(835): 433–440.

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.

Morlang, Charles Jr. 1967. Hybridization, polyploidy and adventitious growth in the genus *Asplenium*. American Journal of Botany 54(7): 887–897.

NatureServe. 2022. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed July 27, 2022 at https://explorer.natureserve.org/

Nayar, B. K. and S. Kaur. 1971. Gametophytes of homosporous ferns. Botanical Review 37(3): 295–396.

NJNHP (New Jersey Natural Heritage Program). 2010. Special Plants of NJ - Appendix I - Categories & Definitions. Site updated March 22, 2010. Available at https://nj.gov/dep/parksandforests/natural/docs/nhpcodes_2010.pdf

NJNHP (New Jersey Natural Heritage Program). 2022. Biotics 5 Database. NatureServe, Arlington, VA. Accessed February 1, 2022.

NYNHP (New York Natural Heritage Program). 2022. Online conservation guide for *Asplenium montanum*. Available at https://guides.nynhp.org/mountain-spleenwort/.

Pangua, Emilia, Stuart Lindsay, and Adrian Dyer. 1994. Spore germination and gametophyte development in three species of *Asplenium*. Annals of Botany 73: 587–593.

PANHP (Pennsylvania Natural Heritage Program). 2019. Species and Natural Features List. Fact sheet for *Asplenium pinnatifidum* available at https://www.naturalheritage.state.pa.us/factsheets/15825.pdf

Pickett, F. L. 1914a. The development of the prothallia of *Camptosorus rhizophyllus*. Botanical Gazette 57: 228–238.

Pickett, F. L. 1914b. Some ecological adaptations of certain fern prothallia - *Camptosorus rhizophyllus* Link., *Asplenium platyneuron* Oakes. American Journal of Botany 1(9): 477–498.

POWO. 2022. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Retrieved July 27, 2022 from 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.

Rhoads, Ann Fowler and Timothy A. Block. 2007. The Plants of Pennsylvania. University of Pennsylvania Press, Philadelphia, PA. 1042 pp.

Schneller, Johann Jakob and Rolf Holderegger. 1996. Genetic variation in small, isolated fern populations. Journal of Vegetation Science 7: 113–120.

Snyder, David B. 1985. Additions to New Jersey's Flora. Bartonia 51: 95–98.

Snyder, David B. 1993. Extinct, extant, extirpated or historical? Or in defense of historical species. Bartonia 57 Supplement: 50–57.

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.

Testo, Weston L. and James E. Watkins Jr. 2011. Comparative development and gametophyte morphology of the Hart's-tongue Fern, *Asplenium scolopendrium* L. Journal of the Torrey Botanical Society 138(4): 400–408.

Testo, Weston L. and James E. Watkins Jr. 2013. Understanding mechanisms of rarity in Pteridophytes: Competition and climate change threaten the rare fern *Asplenium scolopendrium* var. *americanum* (Aspleniaceae). American Journal of Botany 100(11): 2261–2270.

Tryon, Alice F. 1971. American Fern Society: A report of the 1970 fern foray. American Fern Journal 61(1): 44–47.

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). 2022a. *Asplenium pinnatifidum* 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). 2022b. PLANTS profile for *Asplenium pinnatifidum* (Lobed Spleenwort). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed July 27, 2022 at http://plants.usda.gov

Wacker, Alma H. 1905. Ecological notes on Ohio pteridophytes. The Ohio Naturalist V(5): 295–297.

Wagner, Warren H. Jr. 1954. Reticulate evolution in the Appalachian *Aspleniums*. Evolution 8: 103–118.

Wagner, W. H. Jr. 1960. The proliferations of *Asplenium pinnatifidum*. Castanea 25(2): 74–79.

Wagner, W. H. Jr. 1966. Illustrations of transient fern forms. American Fern Journal 56(3): 101–107.

Wagner, W. H. and Thomas Darling, Jr. 1957. Synthetic and wild *Asplenium gravesii*. Brittonia 9(1): 57–63.

Wagner, Warren H. Jr., Robbin C. Moran, and Charles R. Werth. Page updated November 5, 2020. *Asplenium pinnatifidum* Nuttall. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico [Online]. 22+ vols. New York and Oxford. Accessed July 28, 2022 at http://floranorthamerica.org/Asplenium_pinnatifidum

Walz, Kathleen S., Linda Kelly, Karl Anderson and Jason L. Hafstad. 2018. Floristic Quality Assessment Index for Vascular Plants of New Jersey: Coefficient of Conservativism (CoC) Values for Species and Genera. New Jersey Department of Environmental Protection, New Jersey Forest Service, Office of Natural Lands Management, Trenton, NJ. Submitted to United

States Environmental Protection Agency, Region 2, for State Wetlands Protection Development Grant, Section 104(B)(3); CFDA No. 66.461, CD97225809.

Wang, B., and Y. L. Qiu. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16(5): 299–363.

Weakley, A. S. 2015. Flora of the southern and mid-Atlantic states, working draft of May 2015. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC.

Werth, Charles R., Sheldon I. Guttman, and W. Hardy Eshbaugh. 1985. Electrophoretic evidence of reticulate evolution in the Appalachian *Asplenium* complex. Systematic Botany 10(2): 184–192.

Wherry, Edgar T. 1919. The statement of acidity and alkalinity, with special reference to soils. Journal of the Washington Academy of Sciences 9(11): 305–309.

Wherry, Edgar T. 1925. The Appalachian *Aspleniums*. American Fern Journal 15(2): 46–54.

Wherry, E. T. 1927. Recent fern literature. American Fern Journal 17(4): 133–135.

Wherry, Edgar T. 1957. Which northeastern ferns are evergreen? American Fern Journal 47(3): 93–95.

Wubs, E. R. Jasper, G. Arjen de Groot, Heinjo J. During, Johannes C. Vogel, Michael Grundmann, Piet Bremer, and Harald Schneider. 2010. Mixed mating system in the fern *Asplenium scolopendrium*: implications for colonization potential. Annals of Botany 106: 583–590.