Ophioglossum pycnostichum

Southern Adder's-tongue

Ophioglossaceae

Ophioglossum pycnostichum courtesy Alan Cressler, Lady Bird Johnson Wildflower Center

***Ophioglossum pycnostichum* 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

Ophioglossum pycnostichum (Southern Adder's-tongue) is a small perennial fern in the Ophioglossaceae, which is one of the oldest families of living ferns (Christenhusz and Chase 2014). The simple structure of plants in the adder's-tongue family, particularly those in the genus *Ophioglossum*, has made it notoriously difficult to delimit species (Clausen 1938) and the taxonomic status of *O. pycnostichum* is still under debate because it closely resembles the widespread *O. vulgatum* (see Synonyms and Taxonomy section). It is interesting to note that the chromosome counts in *Ophioglossum* are very high in comparison to other known organisms and the largest number reported for any plant was documented in *O. pycnostichum* (Wagner 1974, Otto and Whitton 2000, Wagner and Wagner 2020, Zhang and Zhang 2022). One additional *Ophioglossum* species, *O. pusillum*, is also present but rare (S3) in New Jersey (NJNHP 2024).

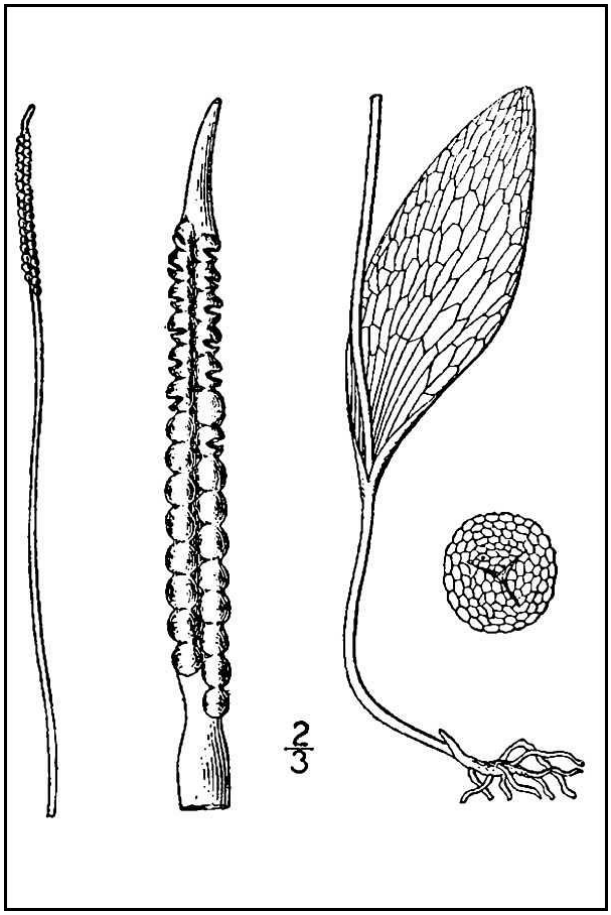
The life cycle of ferns includes two independent generations. Spores produced by mature plants initially develop into tiny gametophytes with structures that give rise to male and female reproductive cells (gametes). Male gametes (sperm) are formed in an antheridium and a female gamete (egg) develops in an archegonium. Fertilized female cells become 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).

The gametophytes of most ferns are free-living and photosynthetic but those of species in the Ophioglossaceae lack chlorophyll and develop underground. Consequently, they are completely dependent on mycorrhizal associations for their nutritional needs and will perish in the absence of a fungal partner (Clausen 1938, St. John 1950, McMaster 1994). *Ophioglossum* gametophytes are cylindrical and grow in a vertical position. In many species they are branched and/or studded with rhizoids. The sex organs (antheridia and archegonia) are located on the upper part of the gametophyte, where they are embedded in the tissue with only their tips exposed (Nayar and Kaur 1971). Due to their subterranean habit the gametophytes of *Ophioglossum* are seldom seen, although Pfeiffer (1916) found some that were still attached to developing sporophytes.

An *Ophioglossum pycnostichum* sporophyte consists of a single leaf divided into a narrow, long-stalked reproductive portion (sporophore) and a vegetative blade (trophophore). Total height can vary from 7–35 cm. The blade is firm, ovate, widest near the base, dark to bright green, 2.5–10 cm long, and 1.5–5.5 cm wide. The stalk of the sporophore is usually two to four times the length of the trophophore, and the large sporangia are arranged in two rows. (See Fernald 1939 & 1950, Lellinger 1985, Gleason and Cronquist 1991, Montgomery and Fairbrothers 1992, Wagner and Wagner 2020).

Ophioglossum pusillum differs from O. *pycnostichum* in having blades that are widest near the middle and dull pale green (Lellinger 1985, Isaac et al. 2004, Weakley et al. 2024). The color discrepancy is notable in living plants but may not be evident in dried specimens. Another difference between the two species, described in detail by McAlpin (1971), is the fate of the basal leaf sheath. The sheaths that protect developing *Ophioglossum* leaves are ruptured as the plants start to emerge. The remnant sheaths of *O. pusillum* are papery, about 1 mm long, and generally disappear during the growing season, but those of *O. pycnostichum* are leathery, approximately 2.5 mm long, and generally persistent. However, Gordon and Arsenault (2016)

noted that the helpful feature may be hidden beneath the soil surface. It is not clear whether *O. pycnostichum* and *O. pusillum* can hybridize but a Virginia colony with intermittent features was discovered by Wagner and Wagner (1966).



Left: Britton and Brown 1913, courtesy USDA NRCS 2025a. The illustration was labeled as *O. vulgatum* and the leaf shape is more typical of *O. pusillum*. Right: *O. pycnostichum* plants by Alvin Diamond, 2017.

Ophioglossum pycnostichum plants have a cluster of up to 20 sturdy roots that can store nutrients and serve as reproductive organs (St. John 1950, McAlpin 1971, Wagner and Wagner 2020). Vegetative proliferation has been documented in both *O. pycnostichum* and *O. pusillum*, and some adder's-tongues have been known to form extensive clonal stands (Wagner 1972, Cascio and Thomas 1993, McMaster 1996). *Ophioglossum* species spend a relatively short time above the ground, typically emerging in the spring and dispersing their spores by mid-summer (Pfeiffer 1916, Fernald 1939, Wagner and Wagner 2020, Weakley et al. 2024). Jędrzejczak et al. (2025) observed that *O. vulgatum* leaves usually last for about two to three months. By the time *Ophioglossum* plants begin to senesce, the leaves for the following growing season are already starting to break through their sheaths (McAlpin 1971). Adder's-tongues do not emerge every year and some may remain underground for multiple growing seasons. Mycorrhizal relationships established during the gametophyte phase are often perpetuated by the sporophytes and probably allow the plants to sustain dormancy over the longer periods (St. John 1950, Field

et al. 2015, Jędrzejczak et al. 2025). Arbuscular mycorrhizae were found in all of the *Ophioglossum* species that have been examined (Wang and Qiu 2006).

Pollinator Dynamics

Because *Ophioglossum pycnostichum* is a non-flowering plant, pollination does not take place. Instead, 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 flagellate sperm toward a receptive egg cell (Raven 1986).

St. John (1950) observed that the antheridia of *Ophioglossum* gametophytes are frequently positioned above the archegonia. He hypothesized that self-fertilization would be facilitated by the downward movement of water through the soil and that it was likely to be prevalent in the genus. Wagner et al. (1985) suggested that the potential for cross-fertilization in species with subterranean gametophytes had been underestimated, pointing out that the sperm were capable of swimming for distances up to 2 cm and might be carried farther by groundwater flow. McMaster (1994) agreed with St. John based on the low probability of gametophytes developing in close enough proximity for gene exchange. Genetic studies of plants in the adder's-tongue family have revealed high levels of inbreeding—supporting the idea that self-fertilization is predominant—but it is clear that some cross-fertilization also occurs (Soltis and Soltis 1986, Chung et al. 2013).

Seed Dispersal

Dispersal in *Ophioglossum* is carried out by spores rather than seeds. Members of the genus produce copious amounts of sulphur-yellow spores (Fernald 1950). Fern spores are primarily transported by wind and the majority are likely to be deposited locally although some may end up thousands of kilometers away (Kessler 2010). Larger spores typically travel for shorter distances (Raynor et al. 1976), and wind dispersal can also be limited by the structure of the surrounding vegetation (Peck et al. 1990). Spores that have landed on the ground may be moved farther by surface water following rain (Pfeiffer 1916) and viable spores can also be distributed by fern-eating herbivores (Boch et al. 2016). The latter two dispersal mechanisms are more likely to result in a clumped distribution that could facilitate cross-fertilization between gametophytes.

The development of *Ophioglossum* spores is inhibited by light (Whittier 1981). After landing, the propagules must make their way down into the soil to a depth of 1–5 cm before they can germinate. Germination may occur quickly or be deferred for a year or more until conditions are favorable and a fungal partnership has been established (Wagner 1974, McMaster 1994). Delayed germination has been documented in a variety of other ferns as well (Leck and Simpson 1987, Dyer and Lindsay 1992). The ferns in the adder's-tongue family grow slowly so they may remain in the gametophyte stage for several years before producing any sporophytes (Nayar and Kaur 1971).

Habitat

Ophioglossum gametophytes require continuous moisture (St. John 1950). Consequently, *O. pycnostichum* is most often found in sites that are mesic or moist but not continuously inundated such as bottomland forests, floodplains, rich woodlands, or wet meadows (Smith 1940, Steyermark 1959, Levy et al. 1963, Clarkson 1966, Clements and Wofford 1991, Grubbs and Fuller 1991, Witsell and Baker 2006, Rhoads and Block 2007, Philley 2019). It grows at elevations of 0–800 meters above sea level (Wagner and Wagner 2020). Southern Adder's-tongue has been documented on substrates that vary from sand to heavy clay, and it sometimes occurs in calcareous sites (Fernald 1939, Wagner and Wagner 1966, Carter et al. 1990, Sewell and Zomlefer 2014, NJNHP 2024). The fern is a generalist in terms of light requirements and is fairly tolerant of shaded conditions (Szakacs et al. 2022, Weakley et al. 2024).

Forested areas utilized by *Ophioglossum pycnostichum* may be dominated by hardwoods or consist of a mixture of deciduous and evergreen species (Cascio and Thomas 1993, Terry 2005, Sewell and Zomlefer 2014). Some examples of community types where the fern was found include *Juglans*/*Fraxinus*/*Aesculus*, *Fagus*, *Platanus*/*Tsuga*, *Quercus*/*Carya*, and *Quercus*/*Pinus* woodlands (Levy et al. 1963, Abbott and Thompson 2015, Witsell and Baker 2006). It has also been recorded in *Alnus* thickets and in open meadows dominated by *Sphagnum* spp., graminoids, and other wetland plants (Clarkson 1966, Witsell and Baker 2006). *O. pycnostichum* is occasionally associated with disturbed sites like ditches or old fields (Hayden et al. 1989, Weakley et al. 2024).

New Jersey records of *Ophioglossum pycnostichum* reflect a variety of growing conditions that range from wet to relatively dry. Natural habitats in the state include swamps and other forested lowlands. Populations have also been associated with disturbed sites around the ruins of old structures, an artificial clearing in a *Liquidambar*/*Ilex*/*Acer* woodland, and the edge of a road in a conifer-hardwood plantation. *O. pusillum* was also found at the latter location, although the distribution of the two fern species did not overlap (Montgomery 1982, Hough 1983, Gordon and Arsenault 2016, NJNHP 2024).

Wetland Indicator Status

Ophioglossum pycnostichum is a facultative wetland species, meaning that it usually occurs in wetlands but may occur in nonwetlands (U. S. Army Corps of Engineers 2022).

USDA Plants Code (USDA, NRCS 2025b)

The code for *Ophioglossum pycnostichum* is OPPY3. The USDA NRCS identifies Southern Adder's-tongue as *Ophioglossum vulgatum* (code OPVU).

Coefficient of Conservancy (Walz et al. 2020)

CoC = 6. 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 native range of *Ophioglossum pycnostichum* extends from the eastern and central United States to southern Mexico (POWO 2025). The map in Figure 1 depicts the extent of Southern Adder's-tongue in the United States and Canada.

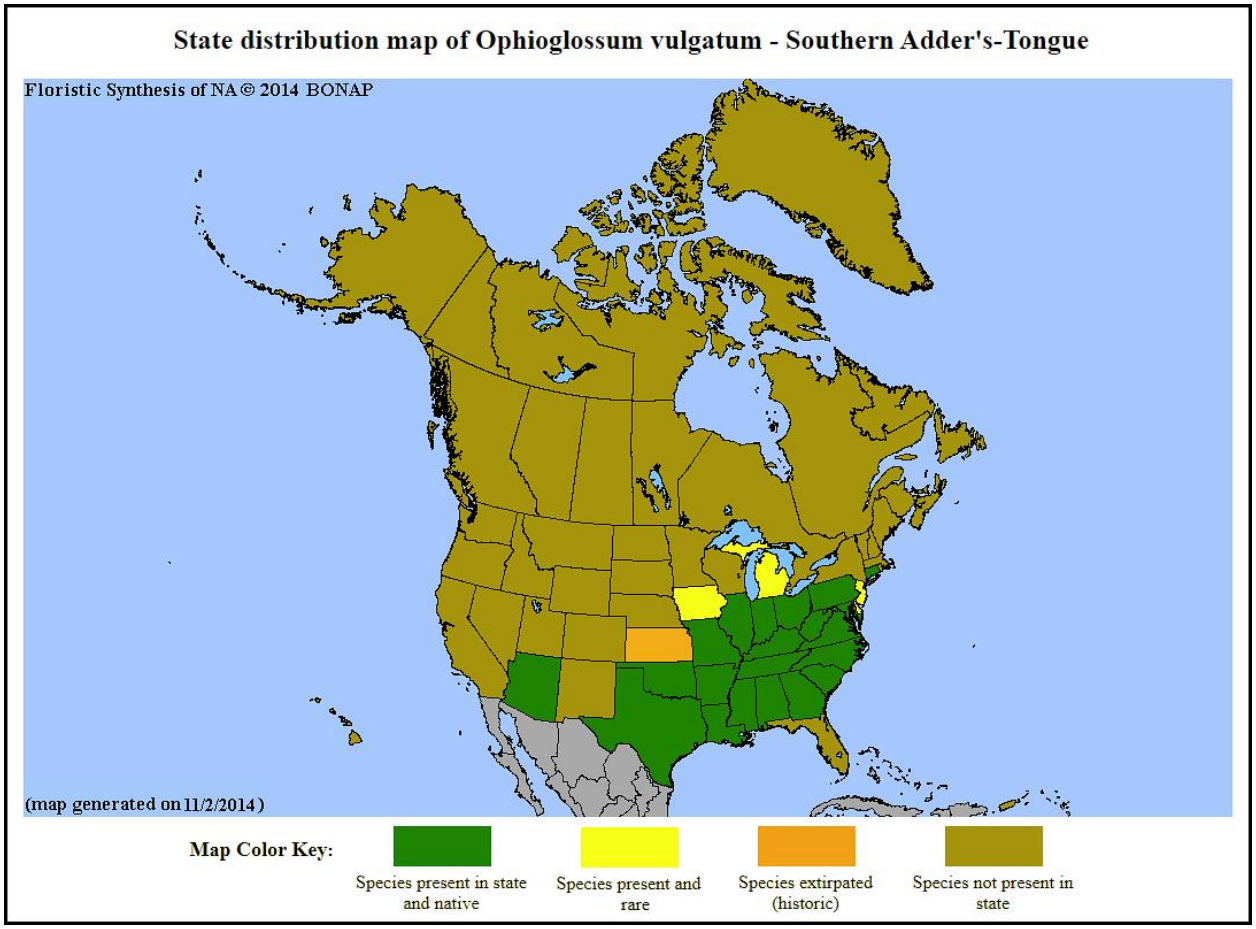


Figure 1. Distribution of O. pycnostichum in the United States and Canada, adapted from BONAP (Kartesz 2015).

The USDA PLANTS Database (2025b) shows *Ophioglossum pycnostichum* in all but two of New Jersey's counties (Figure 2 below). The state distribution is likely over-reported because *O. pycnostichum* was historically confused with another species (see Synonyms and Taxonomy section). There appear to be confirmed records, either current or historical, for seven counties: Atlantic, Burlington, Cape May, Cumberland, Gloucester, Salem, and Sussex (NJNHP 2024, Mid-Atlantic Herbaria 2025). However, there are quite a few ambiguously-labeled herbarium

specimens of *Ophioglossum* and some of those might be indicative of additional state locations for *O. pycnostichum*.

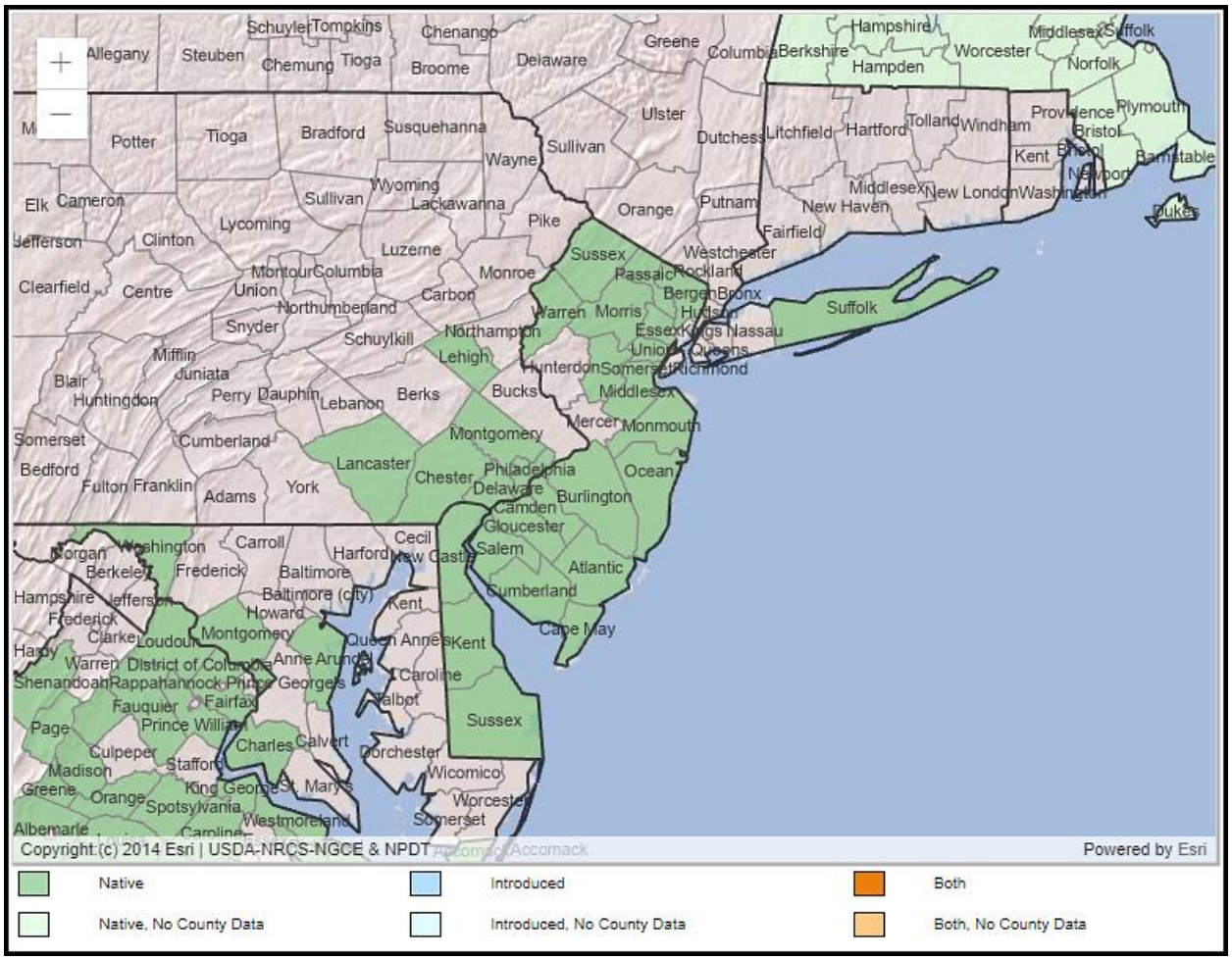


Figure 2. County records of O. vulgatum in New Jersey and vicinity (USDA NRCS 2025b).

Conservation Status

Ophioglossum pycnostichum is considered globally secure. The G5 rank means 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 (NatureServe 2025). The map below (Figure 3) illustrates the conservation status of *O. pycnostichum* in the United States and Canada. It is shown as unranked or apparently secure in most of the places it occurs, vulnerable (moderate risk of extinction) in two states, imperiled (high risk of extinction) in one state, and critically imperiled (very high risk of extinction) in one state. Some states may list the fern under a different name. Final recognition of the species as *Ophioglossum pycnostichum* by NatureServe is still pending.

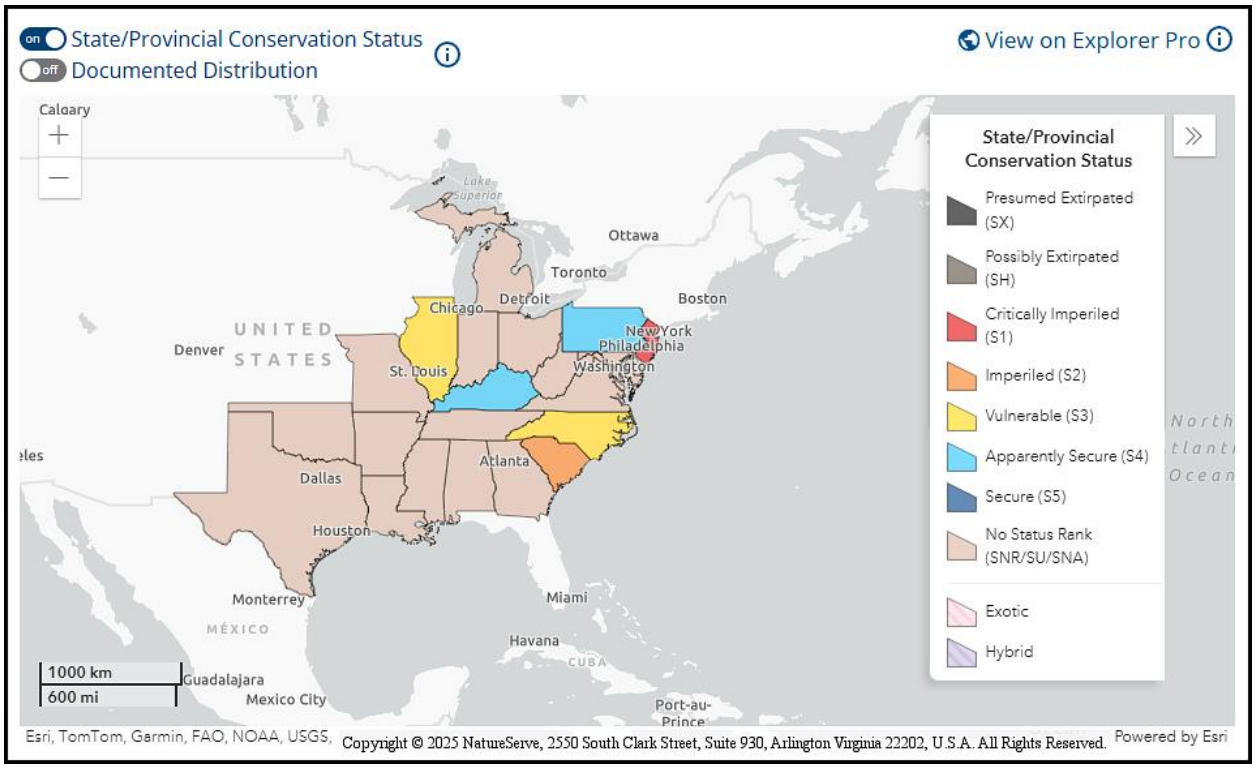


Figure 3. Conservation status of O. pycnostichum in the United States and Canada (NatureServe 2025).

Ophioglossum pycnostichum is critically imperiled (S1) in New Jersey (NJNHP 2024). The 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. *O. pycnostichum* 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 fern 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).

It is difficult to trace the early history of *Ophioglossum pycnostichum* in New Jersey because both of the adder's-tongue species in the state were initially lumped with *O. vulgatum* (e.g. Britton 1889, Stone 1911, Benedict 1914, Taylor 1915). Once it became clear that there were two distinct taxa present *O. pycnostichum* was identified as particularly rare in the state: It was only reported in Cumberland and Salem counties, where it had last been seen in 1963 (Montgomery 1982, Hough 1983, Montgomery and Fairbrothers 1992). *Ophioglossum pycnostichum* was included on the first official state list of endangered species, and for some time it was thought to be historical in New Jersey (NJONLM 1990, NJNHP 2001). Although it still appears to be absent from Cumberland, the fern has now been documented in Atlantic, Burlington, Cape May, Salem, and Sussex counties (Moore et al. 2016, NJNHP 2024).

Threats

Ophioglossum pycnostichum is particularly vulnerable during the gametophyte phase when developing plants can be destroyed by desiccation, soil compaction, or other substrate disturbances (St. John 1950, Peck et al. 1990). The greatest concern for established populations appears to be habitat loss to development or agriculture (Montgomery 1982). Potential threats cited for New Jersey occurrences of Southern Adder's-tongue include herbivory, successional changes, and the proliferation of invasive flora. However, it was noted that one population appeared to be thriving even though the site had been overrun by *Lonicera japonica* (NJNHP 2024).

The overabundance of deer poses a serious threat to many native understory plants in New Jersey (Kelly 2019) but it is not clear how vulnerable *Ophioglossum pycnostichum* is to grazing. Large mammals may overlook the tiny plants in favor of more substantial forage material. Herbivores have occasionally been known to browse on *Ophioglossum* sporophores but that may facilitate dispersal rather than posing a threat (McMaster 1994). It is equally unclear whether natural successional processes jeopardize *O. pycnostichum* populations. St. John (1950) observed that adder's-tongues could rapidly regenerate from rootstock after a fire and appeared to benefit from the reduced competition. A study of *O. vulgatum* in Poland found no effect on the species from simulated herbivory, while mowing reduced the development of sporiferous structures but stimulated vigorous clonal reproduction (Jędrzejczak et al. 2025). The susceptibility of *O. pycnostichum* to successional changes might be reduced by its ability to maintain mycorrhizal associations through all life stages.

Climate Change Vulnerability

Information from the references cited in this profile was used to evaluate the vulnerability of New Jersey's *Ophioglossum pycnostichum* populations 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). Overall the fern was assessed as Less Vulnerable, meaning that climate change is not expected to have a notable detrimental impact on its extent in New Jersey by 2050, but the exposure of individual populations is probably greater in certain locations.

As the climate continues to warm, plant communities in New Jersey are increasingly exposed to higher temperatures, shifting precipitation patterns that increase the frequency and intensity of local droughts and floods, and rising sea levels along the coast (Hill et al. 2020). Several populations of *Ophioglossum pycnostichum* in the state are situated in places where they are likely to be either inundated with salt water during severe coastal storms or directly affected by sea level rise (NJ Adapt 2025). The native range of Southern Adder's-tongue suggests that the species is well-adapted to warmer climactic conditions, and rising temperatures may even create an opportunity for a northward range expansion. The increasing occurrence of lengthy droughts is probably the greatest threat to *O. pycnostichum* throughout the state. Although the extent of

desiccation tolerance does not appear to be known for established plants, a steady moisture supply is essential for the survival of gametophytes.

Management Summary and Recommendations

Clausen and Edwards (1937) remarked that *Ophioglossum pycnostichum* plants can easily be overlooked and suggested that the species was probably more abundant in New Jersey than records indicated. The cryptic gametophytes and small, inconspicuous, somewhat ephemeral sporophytes of *O. pycnostichum* have led to similar conclusions in many other states where the fern occurs (e.g. Levy et al. 1963, Wagner and Wagner 1966, Carter et al. 1990, Isaac et al. 2004). Meticulous searches might relocate some historical occurrences or turn up additional populations in New Jersey. However, that would require some fortitude. According to Lellinger (1985), the best way to find small adder's-tongue plants involves "*crawling around on hands and knees in likely habitats during appropriate seasons of the year, a procedure that is as hilarious to onlookers as it is effective for collectors*."

In order to do meaningful conservation planning for Southern Adder's-tongue, clarity is needed regarding the taxonomic status of the species (see next section). It would also be helpful to have a better understanding of the effects of herbivory on *O. pycnostichum*, and of drought tolerance during the sporophyte stage.

Synonyms and Taxonomy

The accepted botanical name of the species is *Ophioglossum pycnostichum* (Fernald) Á. Löve & D. Löve. Some orthographic variants, synonyms, and common names are listed below (Löve and Löve 1977, Lellinger 1985, Weakley et al. 2024, POWO 2025).

Botanical Synonyms	**Common Names**
Ophioglossum vulgatum var. *pycnostichum* Fernald	Southern Adder's-tongue
Ophioglossum vulgatum L.	
Ophioglossum vulgatum f. *lanceolatum* S. F. Blake	

During the late 1800s and early 1900s, nearly all of the *Ophioglossum* plants encountered in the northeastern United States were identified as *Ophioglossum vulgatum*, a species that is widely distributed throughout Europe and Asia (e.g. Britton 1897, Benedict et al. 1915, Taylor 1915, Killip 1918). One exception was a new species (*O. arenarium*) described by Elizabeth Britton (1897) from a single colony in Cape May County, New Jersey but that was subsequently dismissed by other botanists as a depauperate form of *O. vulgatum* (Blake 1913, Fernald 1939).

Britton (1898) characterized *Ophioglossum vulgatum* as "very variable in size and in the time of maturing its sporangia, as well as in the shape of its sterile fronds." Blake (1913) laid the foundation for identifying different forms of *Ophioglossum vulgatum* in the northeast, and they in turn were described as North American varieties—*O. vulgatum* var. *pseudopodum* and *O.*

vulgatum var. *pycnostichum* (Farwell 1916, Fernald 1939, Wherry 1941). However, Fernald asserted that the European variety of *O. vulgatum* did not occur in North America whereas Wherry thought that var. *pycnostichum* was not reliably distinguishable from the European plants. Clausen (1938, 1942) continued to take a broad view of *Ophioglossum vulgatum*, noting that the differences between varieties were "trivial" and deeming the characters used to distinguish them "unsatisfactory".

During the latter part of the twentieth century both ferns were generally treated as varieties of *O. vulgatum*, but var. *pseudopodum* was eventually equated with Rafinesque's *Ophioglossum pusillum** and most current authors recognize Northern Adder's-tongue as a distinct species. Some also accept *O. pycnostichum* but others do not separate it from *O. vulgatum* (e.g. Kartesz 2015, Wagner and Wagner 2020, ITIS 2025, USDA NRCS 2025). Lellinger (1985) excluded *Ophioglossum vulgatum* from his manual of North American ferns and allies but recognized both *O. pusillum* and *O. pycnostichum*. According to Weakley et al. (2024) *O. vulgatum* is restricted to Eurasia, while the North American *O. pycnostichum* may actually encompass more than one species. Furthermore, the results of a global analysis of *Ophioglossum* by Zhang and Zhang (2022) indicate that (even with the exclusion of *O. pycnostichum*) *O. vulgatum* might not be monophyletic. Additional clarification is evidently needed.

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* Not to be confused with the *Ophioglossum pusillum* of Nuttall, an illegitimate name now treated as a synonym of another species that has taxonomic discrepancies of its own but thankfully does not occur in New Jersey (Kartesz 2015, POWO 2025).

References

Abbott, J. Richard and Ralph L. Thompson. 2015. Addendum to the vascular flora of the Hancock Biological Station, Murray State University, Calloway County, Kentucky, U.S.A. Journal of the Botanical Research Institute of Texas 9(1): 229–233.

Benedict, R. C. 1914. What is the habitat of *Ophioglossum vulgatum*. American Fern Journal 4(4): 121–122.

Benedict, R. C., C. A. Weatherby, Eugene T. Allen, Charles W. Jenks, E. J. Winslow, F. G. Floyd, H. E. Ransier, Stewart Henry Burnham, and F. L. Pickett. 1915. Where *Ophioglossum* grows (a multiple report). American Fern Journal 5(2): 42–50.

Blake, Sidney F. 1913. Forms of *Ophioglossum vulgatum* in eastern North America. Rhodora 15(169): 86–88.

Boch, Steffen, Matthias Berlinger, Daniel Prati, and Markus Fischer. 2016. Is fern endozoochory widespread among fern-eating herbivores? Plant Ecology 217(1): 13–20.

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, Elizabeth G. 1897. A revision of the North American species of *Ophioglossum*. Bulletin of the Torrey Botanical Club 24(12): 545–559.

Britton, Elizabeth G. 1898. The adder's tongue ferns. The Plant World 1(6): 85–89.

Carter, Richard, M. Wayne Morris, and Charles T. Bryson. 1990. Some rare or otherwise interesting vascular plants from the delta region of Mississippi. Castanea 55(1): 40–55.

Cascio, David Keith and R. Dale Thomas. 1993. Vegetative reproduction is common in *Ophioglossum pycnostichum*. American Fern Journal 83: 135.

Christenhusz, Maarten J. M. and Mark W. Chase. 2014. Trends and concepts in fern classification. Annals of Botany 113(4): 571–594.

Chung, Mi Yoon, Jordi López-Pujol, Jae Min Chung, Myung-Ok Moon, and Myong Gi Chung. 2013. Genetic diversity in the homosporous fern *Ophioglossum vulgatum* (Ophioglossaceae) from South Korea: Inference of mating system and population history. Journal of Heredity 104(2): 263–272.

Clarkson, Roy B. 1966. The vascular flora of the Monongahela National Forest, West Virginia. Castanea 31(1): 1–119.

Clausen, Robert T. 1938. A monograph of the Ophioglossaceae. Memoirs of the Torrey Botanical Club 19(2): 1–177.

Clausen, Robert T. 1942. *Ophioglossum vulgatum* on the inner coastal plain of Alabama. American Fern Journal 32(3): 105–108.

Clausen, R. T. and J. L. Edwards. 1937. The Ophioglossaceae of New Jersey, a study in local distribution. Bulletin of the Torrey Botanical Club 64(5): 269–285.

Clements, Richard K. and B. Eugene Wofford. 1991. The vascular flora of Wolf Cove, Franklin County, Tennessee. Castanea 56(4): 268–286.

Cressler, Alan. 2009. Cover photo of *Ophioglossum pycnostichum*. Courtesy of the Lady Bird Johnson Wildflower Center, https://www.wildflower.org/. Used with permission.

Cunningham, Bob. 2010. Final page image of *Ophioglossum pycnostichum*. Used with permission.

Diamond, Alvin. 2017. Photo of *Ophioglossum pycnostichum* plants from Alabama. Shared via iNaturalist at https://www.inaturalist.org/observations/19660022, licensed by https://creativecommons.org/licenses/by-nc/4.0/

Dyer, Adrian F. and Stuart Lindsay. 1992. Soil spore banks of temperate ferns. American Fern Journal 82(3): 89–123.

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

Farwell, Oliver Atkins. 1916. Fern Notes. Annual Report of the Michigan Academy of Science 18: 78–94.

Fernald, M. L. 1939. Contributions from the Gray Herbarium of Harvard University—No. CXXVIII: Last survivors in the flora of tidewater Virginia. Rhodora 41(490): 465–504.

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

Field, Katie J., Jonathan R. Leake, Stefanie Tille, Kate E. Allinson, William R. Rimington, Martin I. Bidartondo, David J. Beerling, and Duncan D. Cameron. 2015. From mycoheterotrophy to mutualism: Mycorrhizal specificity and functioning in *Ophioglossum vulgatum* sporophytes. New Phytologist 205: 1492–1502.

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.

Gordon, Ted and Joseph Arsenault. 2016. Flora of Burden Hill: A checklist for a Salem County, New Jersey landscape. Bartonia 69: 20–46.

Grubbs, Jeffrey T. and Marian J. Fuller. 1991. Vascular flora of Hickman County, Kentucky. Castanea 56(3): 193–214.

Hayden, W. John, Melanie L. Haskins, Miles F. Johnson, and James M. Gardner. 1989. Flora of Richmond National Battlefield Park, Virginia. Castanea 54(2): 87–104.

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.

Isaac, Bonnie L., Carl F. Chuey, and Joseph A. Isaac. 2004. The genus *Ophioglossum* in Pennsylvania. Bartonia 62: 45–54.

ITIS (Integrated Taxonomic Information System). Accessed January 31, 2025 at http://www.itis.gov

Jędrzejczak, Natalia, Paweł Olejniczak, and Zbigniew Celka. 2025. Allocation of resources to growth and spore production in a fern *Ophioglossum vulgatum* L.: Effects of mowing and simulated herbivory. Ecology and Evolution 15: e71555.

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)].

Kelly, Jay F. 2019. Regional changes to forest understories since the mid-twentieth century: Effects of overabundant deer and other factors in northern New Jersey. Forest Ecology and Management 444: 151-162.

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

Killip, E. P. 1918. A year's collecting in the northeastern United States. American Fern Journal 8(4): 121–126.

Leck, Mary Allessio and Robert L. Simpson. 1987. Spore bank of a Delaware River freshwater tidal wetland. Bulletin of the Torrey Botanical Club 144: 1–7.

Lellinger, David B. 1985. A Field Manual of the Ferns and Fern-allies of the United States and Canada. Smithsonian Institution Press, Washington, D.C. 454 pp.

Levy, Foster, Veda King, Clara Ousley, Tom Phillips, and David White. 1963. The ferns and fern allies of Pike County, Kentucky. Transactions of the Kentucky Academy of Science 44(1–2): 14–16.

Löve, Áskell and Doris Löve. 1977. New combinations in ferns. Taxon 26(2/3): 324–326.

McAlpin, Bruce W. 1971. *Ophioglossum* leaf sheaths: Development and morphological nature. Bulletin of the Torrey Botanical Club 98(4): 194–199.

McMaster, Robert T. 1994. Ecology, reproductive biology and population genetics of *Ophioglossum vulgatum* (Ophioglossaceae) in Massachusetts. Rhodora 96(887): 259–286.

McMaster, Robert T. 1996. Vegetative reproduction observed in *Ophioglossum pusillum* Raf. American Fern Journal 86(2): 58–60.

Mid-Atlantic Herbaria. 2025. Accessed at https://midatlanticherbaria.org/portal/index.php on June 15, 2025.

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

Moore, Gerry, Renee Brecht, and Dale Schweitzer. 2016. Additions and corrections to the checklist of vascular plants of Cumberland County, New Jersey. Bartonia 68: 1–59.

NatureServe. 2025. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed June 15, 2025 at https://explorer.natureserve.org/

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

NJ Adapt (New Jersey Climate Change Resource Center). 2025. Interactive map of flood hazard zones, accessed June 19, 2025 at https://www.njfloodmapper.org/

NJNHP (New Jersey Natural Heritage Program). 2001. List of Endangered Plant Species and Plant Species of Concern, September 2001. Biotics Database. NatureServe, Arlington, Virginia.

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.

NJONLM (New Jersey Office of Natural Lands Management). 1990. State of New Jersey Endangered Plant Species List. New Jersey Department of Environmental Protection, Division of Parks and Forestry, Trenton, NJ. 10 pp.

Otto, Sarah P. and Jeannette Whitton. 2000. Polyploid incidence and evolution. Annual Review of Genetics 34(1): 401–437.

Peck, J. H., C. J. Peck, and D. R. Farrar. 1990. Influences of life history attributes on formation of local and distant fern populations. American Fern Journal 80: 126–142.

Pfeiffer, Norma E. 1916. The prothallia of *Ophioglossum vulgatum*. Botanical Gazette 61: 518–522.

Philley, Kevin D. 2019. The vascular flora of Choctaw County, Mississippi, U.S.A. Journal of the Botanical Research Institute of Texas13(1): 319–348.

POWO. 2025. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Accessed June 15, 2025 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.

Raynor, Gilbert S., Eugene C. Ogden, and Janet V. Hayes. 1976. Dispersion of fern spores into and within a forest. Rhodora 78: 473–487.

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

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.

Sewell, Sabrina Y. S. and Wendy B. Zomlefer. 2014. Floristics of Piedmont Gabbro Upland Depression Forests in Jasper County, Georgia. Castanea 79(3): 195–220.

Smith, A. V. 1940. Some plants recently found on the coastal plain of Maryland. Rhodora 42(500): 277–280.

Soltis, Douglas E. and Pamela S. Soltis. 1986. Electrophoretic evidence for inbreeding in the fern *Botrychium virginianum* (Ophioglossaceae). American Journal of Botany 73: 588–592.

St. John, Edward P. 1950. The evolution of the Ophioglossaceae of the eastern United States. Quarterly Journal of the Florida Academy of Sciences 12(4): 207–219.

Steyermark, Julian A. 1959. *Ophioglossum vulgatum* in Missouri. American Fern Journal 48(2): 77–80.

Stone, Witmer. 1911. The Plants of Southern New Jersey. Quarterman Publications, Boston, MA. 828 pp.

Szakacs, Alexandria D., Alexander Krings, and Thomas R. Wentworth. 2022. Shade-tolerance classification of the upland herbaceous flora of the Carolina and Virginia Piedmont. The American Midland Naturalist 187(2): 113–147.

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.

Terry, Michael Austin. 2005. The Vascular Flora of Powhatan County, Virginia. Master's Thesis, University of Richmond, Richmond, VA. 93 pp.

U. S. Army Corps of Engineers. 2022. National Wetland Plant List, version 3.6. https://nwpl.sec.usace.army.mil/ 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). 2025a. *Ophioglossum vulgatum* 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). 2025b. PLANTS profile for *Ophioglossum vulgatum* (Southern Adderstongue). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed June 15, 2025 at http://plants.usda.gov

Wagner, W. H. Jr. 1972. Disjunctions in homosporous vascular plants. Annals of the Missouri Botanical Garden 59(2): 203–217.

Wagner, Warren H. Jr. 1974. Structure of spores in relation to fern phylogeny. Annals of the Missouri Botanical Garden 61(2): 332–353.

Wagner, W. H. Jr. and Florence S. Wagner. 1966. Pteridophytes of the Mountain Lake Area, Giles County, Virginia: Biosystematic studies, 1964-65. Castanea 31(2): 121–140.

Wagner, Warren H. Jr. and Florence S. Wagner. Page updated November 5, 2020. *Ophioglossum vulgatum* 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 June 17, 2025 at http://floranorthamerica.org/Ophioglossum_vulgatum

Wagner, W. H. Jr., F. S. Wagner, and J. M. Beitel. 1985. Evidence for interspecific hybridisation in pteridophytes with subterranean mycoparasitic gametophytes. Proceedings of the Royal Society of Edinburg, Section B, Biological Sciences 86: 273–281.

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.

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

Weakley, A. S. and Southeastern Flora Team. 2024. Flora of the Southeastern United States. Edition of March 4, 2024. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC. 2203 pp.

Wherry, Edgar T. 1941. The ferns and lycosphens of Pennsylvania. Bartonia 21: 11–37.

Whittier, P. 1981. Spore germination and young gametophyte development of *Botrychium* and *Ophioglossum* in axenic culture. American Fern Journal 71(1): 13–19.

Witsell, Theo and Brent Baker. 2006. Vascular flora of the South Fork Native Plant Reserve, Van Buren County, Arkansas. Journal of the Arkansas Academy of Science 60: 144–164.

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.

Zhang, Liang, and Li-Bing Zhang. 2022. Phylogeny, character evolution, and systematics of the fern family Ophioglossaceae based on Sanger sequence data, plastomes, and morphology. Molecular Systematics and Evolution 173: 107512.

O. pycnostichum colony by Bob Cunningham, 2010