Diplazium pycnocarpon

Glade Fern

Dryopteridaceae

Diplazium pycnocarpon by Bob Cunningham, 2011

Diplazium pycnocarpon **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

501 E. State St.
PO Box 420
Trenton, NJ 08625-0420

Prepared by:
Jill S. Dodds
jsdodds@biostarassociates.com

April, 2023

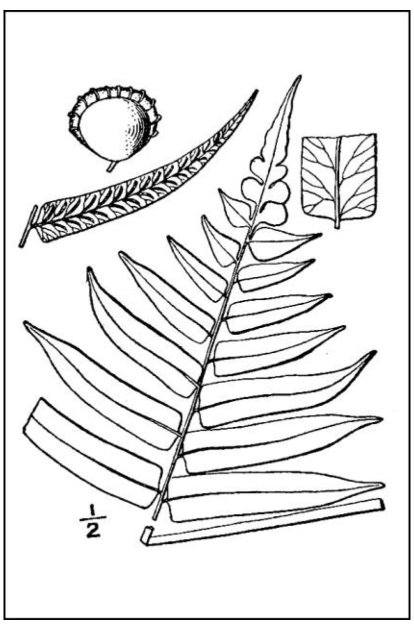
For:
New Jersey Department of Environmental Protection
Office of Natural Lands Management
New Jersey Natural Heritage Program
natlands@dep.nj.gov

This report should be cited as follows: Dodds, Jill S. 2023. *Diplazium pycnocarpon* 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, Trenton, NJ. 16 pp.

Life History

Diplazium pycnocarpon (Glade Fern) is a perennial fern that has traditionally been included in the Dryopteridaceae. Like most other ferns, its life cycle 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 documented in many species of *Diplazium* (Kato 2020).

Gametophytes of plants in the wood fern family are relatively large when compared to those in many other fern groups, often reaching widths of a centimeter or more. They are thin, flat, and oval in shape with a notch on one side and a median midrib that may be 4–8 cells thick. Most dryopterid gametophytes have a short life span, producing sporophytes in less than eight months (Nayar and Kaur 1971). The gametophytes of *Diplazium pycnocarpon* are able to exhibit some developmental plasticity in response to environmental conditions. In favorable habitats the gametophytes can grow larger and persist longer but when conditions are stressful their life expectancies are shorter so more resources are allocated to reproduction, allowing them to reach sexual maturity faster and increase their chances of producing offspring (Greer and McCarthy 1999).



Left: Britton and Brown 1913, courtesy USDA NRCS 2023a. Right: Courtesy Alan Cressler, Lady Bird Johnson Wildflower Center.

The sporophytes of *Diplazium pycnocarpon* have stout horizontal rhizomes that are unbranched or simply forked (Johnson 1986). Vigorous clonal growth can occur in favorable habitats (Coddington and Field 1978, Wade et al. 2009). Johnson (1986) reported that a typical *D.*

pycnocarpon rhizome can be up to 31 cm long and support 1.8–4.7 leaf bases per centimeter. Glade Fern fronds are 0.6–1.2 meters long and pinnately divided, with 20–30 pairs of smooth-edged, unlobed pinnae. The primary fronds are 8–25 cm wide, lance-shaped in outline, and somewhat spreading while the fertile fronds are comparable but narrower and more upright. Pinnae of the fertile fronds bear 20–40 elongate sori that may be straight or slightly curved. Thin lateral outgrowths (indusia) shield the developing sori. (See Britton and Brown 1913, Fernald 1950, Cody 1978, Gleason and Cronquist 1991, Montgomery and Fairbrothers 1992, Kato 2020).

The bases of *Diplazium pycnocarpon* leaf petioles are modified for the storage of starch. The enlarged leaf bases, known as trophopods, persist after the fronds decay and some additional trophopods may form at the base of aborted leaves (Wagner and Johnson 1983, Vasco et al. 2013). Close examination of *D. pycnocarpon* sporophytes showed that the ferns also accumulate starches in their root-bases and rhizomes but the trophopods generally double a plant's storage capacity. Individual trophopods are light to dark reddish brown and can vary from 5.5–16.5 mm in length and 3.5–5.6 mm in width. The structures are difficult to detect when fronds are present but they may be seen at the base of new shoots early in the spring or later in the season following leaf senescence (Johnson 1986).

Diplazium pycnocarpon can continue to produce new fronds throughout the growing season (Hamilton 1992) but its spore-bearing fronds are generally late to emerge. Wagner (1955) observed that the furled tops of young fertile fronds were not yet evident in early July and spore production did not begin until August. In New Jersey spores are most likely to be present on *D. pycnocarpon* from late August through mid-September, although many populations are primarily vegetative and rarely develop fertile fronds (Hough 1983). Glade Fern fronds begin to turn yellow in late summer and are deciduous in the fall (Montgomery and Fairbrothers 1992). Experimental work in Michigan showed that *D. pycnocarpon* was inactive during the winter but not fully dormant, as plants that were moved into a greenhouse could rapidly begin to grow (Hill 1976).

Pollinator Dynamics

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

Fern gametophytes can be functionally female (producing only archegonia), male (producing only antheridia) or hermaphroditic (producing both types of reproductive cells). Each spore is capable of following multiple developmental paths, and the sex of the gametophyte is not determined until after the spore has germinated (Banks 1999). In three populations of *Diplazium pycnocarpon* studied by Greer and McCarthy (1999) all of the gametophytes initially developed as females. The female gametophytes of many ferns, including *D. pycnocarpon*, release a hormone (antheridiogen) that induces male development in nearby undifferentiated gametophytes. Antheridiogen can also stimulate the germination of nearby spores beneath the soil surface, which then develop as males or hermaphrodites (Banks 1999, Greer and McCarthy 1999). The system benefits the species by utilizing spores that would otherwise fail to germinate, promoting rapid reproduction in low-quality microsites, and increasing the likelihood of cross-fertilization (Schneller et al. 1990, Hamilton and Lloyd 1991a, Hamilton 1992).

Seed Dispersal and Establishment

Dispersal in *Diplazium pycnocarpon* is carried out by spores rather than seeds. *Diplazium* indusia usually wither at maturity, exposing the sori (Butters 1917). The spores of *D. pycnocarpon* are dark brown and tiny, with a mean diameter of 31.2 × 25.5 μm (Kato and Darnaedi 1988). A detailed illustration is available in Oliver (1968). Many ferns disperse their spores slowly over a long period, sometimes continuing into the following spring (Farrar 1976). The dust-like spores are transported by wind and the majority are likely to be deposited locally but some can end up thousands of kilometers away (Hamilton 1988, Kessler 2010).

A high rate of spore germination has been observed in *Diplazium pycnocarpon* (Greer and McCarthy 1999). Hamilton (1998) confirmed that the species can maintain a spore bank in the soil. Although light is generally required for the germination of ferns, *D. pycnocarpon* spores that have been buried in the soil or litter can also be triggered to develop by the release of antheridiogen from newly established female gametophytes (see previous section).

Earthworms can act as agents of spore burial and re-emergence and may play an important role in bringing buried spores to the surface and placing them in favorable sites for germination. Experiments with container-grown ferns (*Deparia acrostichoides*) demonstrated that spore germination and the establishment and reproductive success of gametophytes were enhanced in the presence of earthworms. In addition to repositioning the spores in the soil, the worms removed fungi and algae that could inhibit the growth of the young plants (Hamilton and Lloyd 1991b). It is not clear whether Glade Fern forms mycorrhizae during either the gametophyte or sporophyte phase, although they have been documented in several other species of *Diplazium* (Wang and Qiu 2006).

Habitat

Diplazium pycnocarpon can occur at elevations of 150–1000 meters above sea level (Kato 2020). The fern is typically found in moist, shady places such as woodlands or thickets. The substrate is generally rich and it may be circumneutral but it is frequently calcareous. Glade Fern can grow on the sloping sides or bottoms of ravines, and populations are sometimes situated along stream borders (Taylor 1915, Fernald 1941, Cobbe 1943, Coddington and Field 1978, Graves and Monk 1982, Hough 1983, Gaddy 1990, Hill 1992, Ware and Ware 1992, Angelo and Boufford 1996, Greer and McCarthy 1999, Leopold 2005, Rhoads and Block 2007, LADWF 2009, Wade et al. 2009). Occurrences on two salt dome islands along the gulf coast of Louisiana are probably the southernmost populations in the species' range—those also are located in deep, sheltered ravines (Reese and Thieret 1996).

All of New Jersey's *Diplazium pycnocarpon* populations are associated with limestone substrate. The occurrences are located in rich, wet or moist woods. They are variously situated adjacent to streams, in rocky ravines, and at the bases of ridges, outcrops, or talus slopes (Fairbrothers and Hough 1973, Montgomery 1982, Montgomery and Fairbrothers 1992, NJNHP 2022).

Hamilton (1992) characterized *Diplazium pycnocarpon* as an early-successional species, but once established the populations can be long-lived (Coddington and Field 1978) and the fern has been found in remnants of old-growth forest (Cobbe 1943, Dolan and Moore 2017). Greer et al. (1997) noted that *D. pycnocarpon* habitats were high in moisture, pH, nutrients, and canopy cover. In Massachusetts, Glade Fern was cited as an indicator species of Rich Mesic Forest, an *Acer saccharum* dominated community that is usually associated with calcareous bedrock and nutrient-rich soils (Bellemare et al. 2005).

Wetland Indicator Status

Diplazium pycnocarpon is a facultative species, meaning that it occurs in both wetlands and nonwetlands (U. S. Army Corps of Engineers 2020).

USDA Plants Code (USDA, NRCS 2023b)

DIPY

Coefficient of Conservatism (Walz et al. 2018)

CoC = 9. 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 *Diplazium pycnocarpon* is restricted to the United States and Canada (POWO 2023). The map in Figure 1 depicts the extent of Glade Fern in North America.

The USDA PLANTS Database (2023b) shows records of *Diplazium pycnocarpon* in three New Jersey counties: Bergen, Sussex, and Warren (Figure 2). The data include historic observations and do not reflect the current distribution of the species.

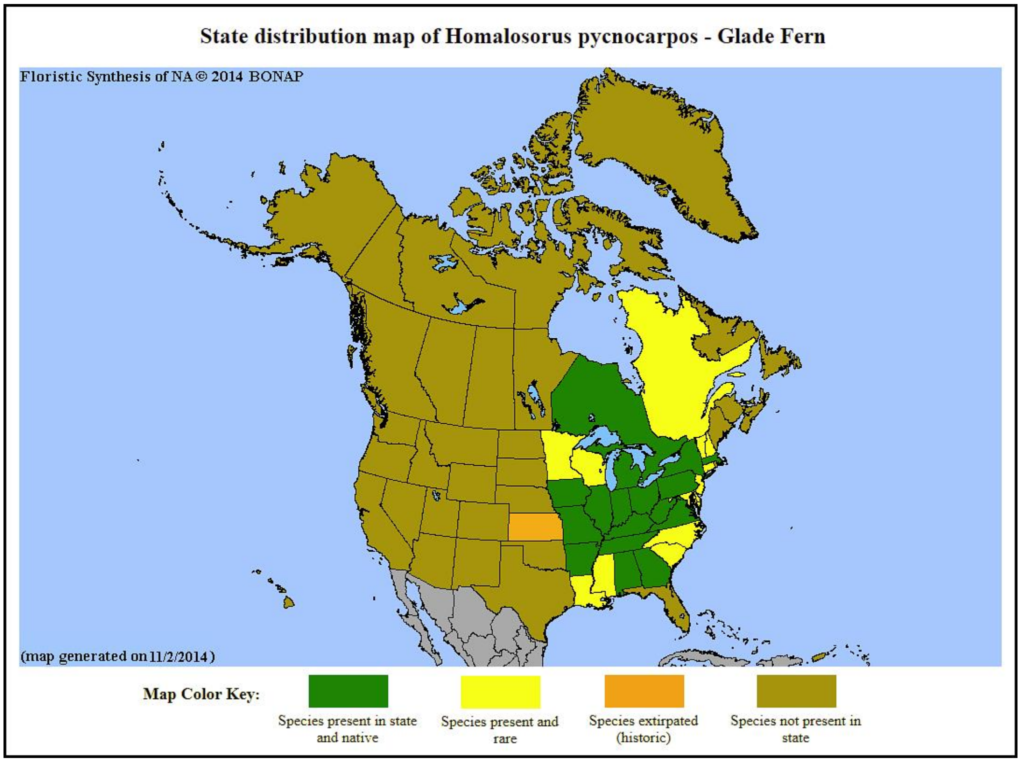


Figure 1. Distribution of D. pycnocarpon in North America, adapted from BONAP (Kartesz 2015).

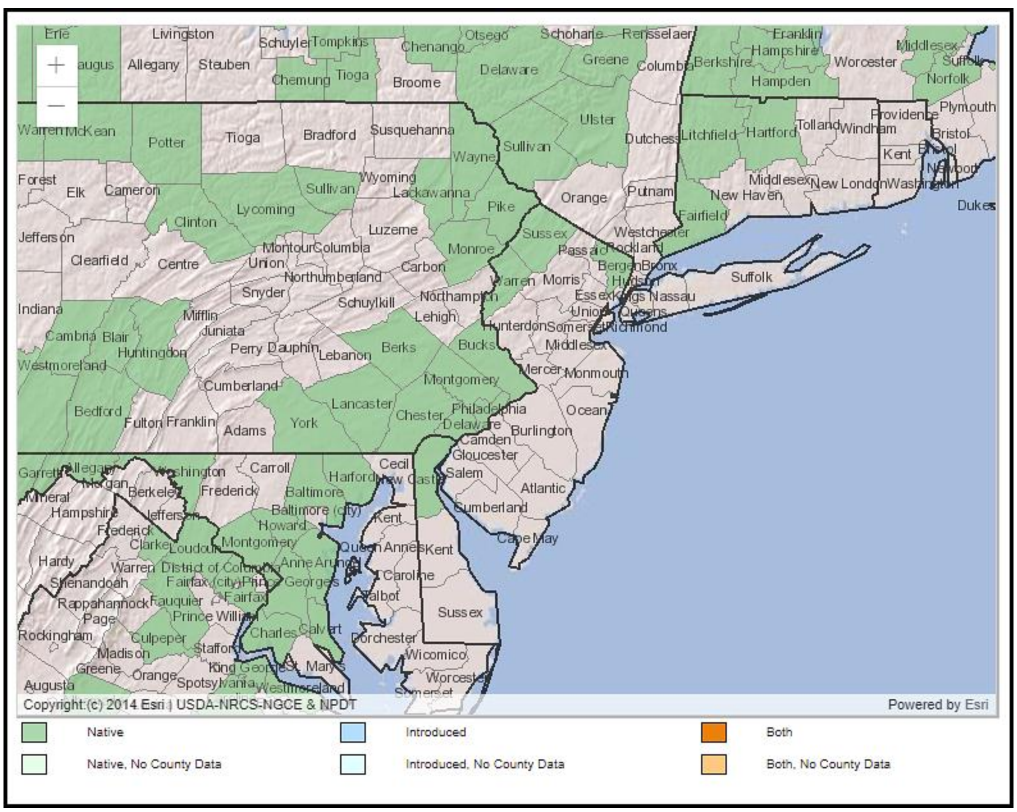


Figure 2. County records of D. pycnocarpon in New Jersey and vicinity (USDA NRCS 2023b).

Conservation Status

Diplazium pycnocarpon 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 2023). The map below (Figure 3) illustrates the conservation status of *D. pycnocarpon* throughout its range. The fern is critically imperiled (very high risk of extinction) in six states, imperiled (high risk of extinction) in five states and one province, vulnerable (moderate risk of extinction) in six states, and possibly extirpated in Kansas. In other places where *D. pycnocarpon* occurs it is secure, apparently secure, or unranked.

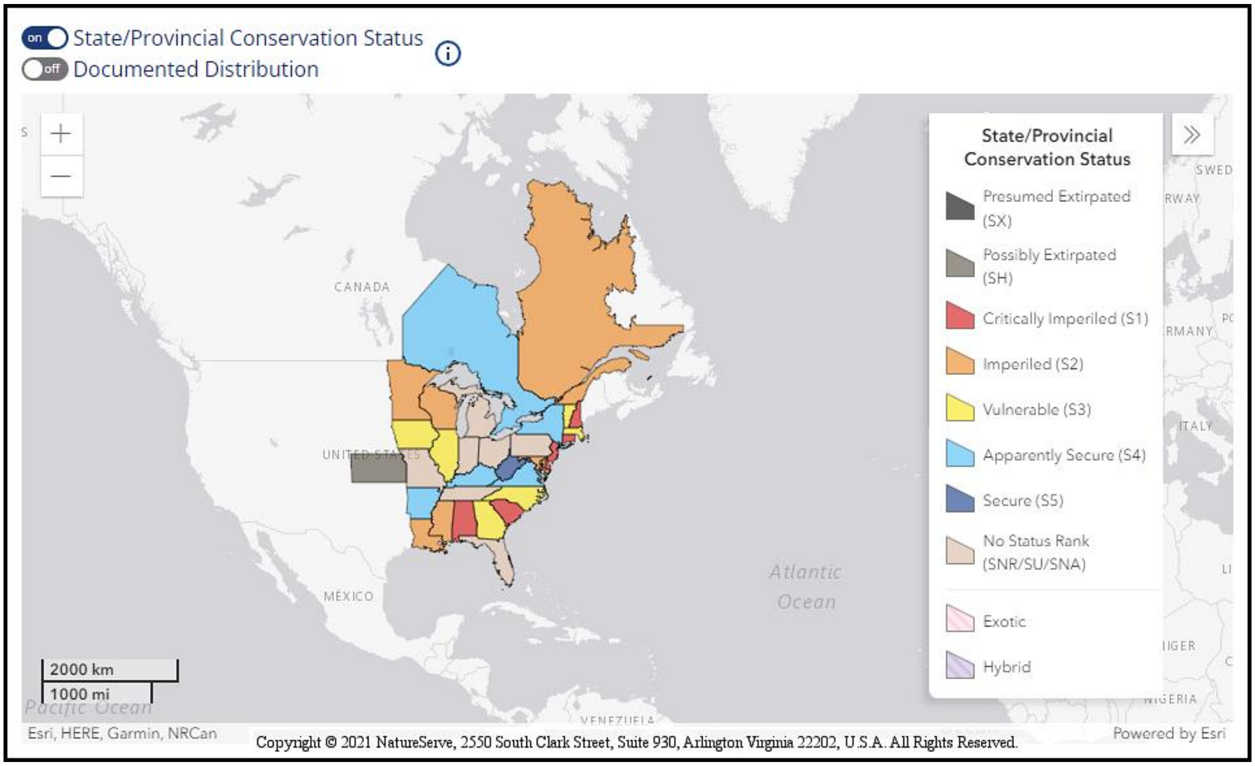


Figure 3. Conservation status of D. pycnocarpon in North America (NatureServe 2023).

Diplazium pycnocarpon is critically imperiled (S1) in New Jersey (NJNHP 2022). 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. Glade Fern 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 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).

Diplazium pycnocarpon has been documented at ten locations in New Jersey but two of the populations are known to be extirpated and two others are considered historical. Although six occurrences are potentially extant, two of those were limited to a few scattered plants when last viewed several decades ago (NJNHP 2022). Fairbrothers and Hough (1973) reported that the state's populations of *D. pycnocarpon* were mostly in decline and at least one had been infertile for years. Montgomery and Fairbrothers (1992) also observed that fertile fronds were rarely produced in New Jersey populations and that has continued to be the case for the majority of the state's occurrences, although vigorous vegetative reproduction has been noted at some of the sites (NJNHP 2022).

Threats

There is no single threat that has been widely identified as a concern for *Diplazium pycnocarpon*. Throughout the range of the species, individual populations may be in danger of habitat loss or degradation resulting from land use conversion, forest management practices, erosion, livestock grazing, or feral hogs (LADWF 2009, Smith 2021, NatureServe 2023).

Invasive plants were identified as a general menace to *Diplazium pycnocarpon* in Louisiana (LADWF 2009) and as a threat to a specific occurrence in New Jersey (NJNHP 2022). During 2021 it was noted that the habitat at the New Jersey site had been overrun by nonnative flora, particularly barberry (*Berberis thunbergii*). In addition to forming dense stands that crowd out other plants, the decaying leaves of *Berberis* can alter soil chemistry and make the habitat less suitable for native shrubs, herbs, and fungi (Kaufman and Kaufman 2007).

Young *Diplazium pycnocarpon* fronds can occasionally be damaged by slugs or snails (NCCE 2023), but the plants appear to have some natural defenses that deter herbivory. When tested by Markham et al. (2006), proteins that had been extracted from the species and applied to soybean leaves were found to notably decrease leaf damage by moth larvae. The *D. pycnocarpon* proteins also significantly increased caterpillar mortality and caused a decline in larval growth rates. Although White-tailed Deer (*Odocoileus virginianus*) occasionally browse on the fern's leaves (Hilty 2020), no reports of extensive mammalian herbivory on *D. pycnocarpon* were found.

New Jersey populations of *Diplazium pycnocarpon* may be expected to have a relatively low level of vulnerability to climate change because the fern has been found in both cooler and warmer climates and seems to tolerate some variation in moisture conditions. However the fronds can turn brown if the soil dries out and remains dry for an extended period of time (NCCE 2023) and since New Jersey is experiencing more frequent and prolonged droughts as a result of rising temperatures and altered precipitation patterns (Hill et al. 2020), *D. pycnocarpon* populations could be affected. Loss of leaves during the growing season may reduce photosynthetic activity and consequently decrease energy storage and overall vigor. Low genetic diversity could also make populations of Glade Fern less able to adapt as conditions continue to change. One *D. pycnocarpon* population examined by Hamilton (1992) included 200 individual ramets but only four genotypes. Comparable limited diversity is likely in New Jersey colonies, most of which are thought to be maintained primarily by clonal reproduction (Montgomery and Fairbrothers 1992, NJNHP 2022).

Management Summary and Recommendations

Only one of the six potentially extant New Jersey populations of *Diplazium pycnocarpon* has been monitored in recent years and updated site visits are needed in order to assess current population status and viability. Since the spore-bearing structures of Glade Fern develop late in the season the best time to monitor the species would be late summer (August-September) when fertile fronds are most likely to be present.

Generally speaking, *Diplazium pycnocarpon* is a species that could benefit greatly from land conservation and habitat protection because populations can persist for a long time when conditions are favorable. Conservation planning for the species might be appreciably enhanced by new research. Few details are available regarding suitable microenvironments for the gametophyte stage or the factors which trigger development of fertile fronds in populations that are primarily vegetative. It is possible that similar circumstances are advantageous for both spore production and gametophyte development. *D. pycnocarpon*'s potential mycorrhizal relationships and competitive interactions with other species are also suggested as areas for further study.

Synonyms and Taxonomy

The accepted botanical name of the species is *Diplazium pycnocarpon* (Spreng.) Broun. Orthographic variants, synonyms, and common names are listed below (ITIS 2023, POWO 2023, USDA NRCS 2023b). Glade Fern was placed in the genus *Athyrium* during the mid-1800s and although Butters (1917) observed that the species was more closely aligned with *Diplazium* many botanists continued to include it in *Athyrium* throughout the 1900s (eg. Gleason and Cronquist 1991, Montgomery and Fairbrothers 1992). Detailed morphological and genetic studies have determined that *D. pycnocarpon* is more closely related to some Asian ferns (*Diplazium flavoviride, Diplaziopsis* spp.) than to any of the North American *Athyrium* species (Kato and Darnaedi 1988, Chunxiang et al. 2011). Some sources now identify Glade Fern as *Homalosorus pycnocarpos* (eg. Kartesz 2015, POWO 2023). Pichi Sermolli (1977) was credited with the establishment of the monotypic genus *Homalosorus* to accommodate this species (Chunxiang et al. 2011): A similar strategy had been proposed earlier by Small (1935) but the name was not adopted because it had not been validly published (Weatherby 1936, POWO 2023).

Botanical Synonyms	**Common Names**
Homalosorus pycnocarpos (Spreng.) Pichi Sermolli	Glade Fern
Diplaziopsis pycnocarpa (Spreng.) M. G. Price	Narrow-leaved Spleenwort
Diplazium angustifolium (Milde) Butters	
Asplenium pycnocarpon Spreng.	
Athyrium angustifolium Milde	
Athyrium pycnocarpon (Spreng.) Tidestr.	

References

Angelo, Ray and David E. Boufford. 1996. Atlas of the flora of New England: Pteridophytes and gymnosperms. Rhodora 98(893): 1–79.

Banks, Jo Ann. 1999. Gametophyte development in ferns. Annual Review of Plant Physiology and Plant Molecular Biology 50(1): 163–186.

Bellemare, Jesse, Glenn Motzkin, and David R. Foster. 2005. Rich mesic forests: Edaphic and physiographic drivers of community variation in western Massachusetts. Rhodora 107(931): 239–283.

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.

Butters, Frederic K. 1917. Taxonomic and geographic studies in North American Ferns. Rhodora 19(225): 169–216.

Chunxiang, Li, Lu Shugang, Sun Xiaoyan, and Yang Qun. 2011. Phylogenetic positions of the enigmatic Asiatic fern genera *Diplaziopsis* and *Rhachidosorus* from analyses of four plastid genes. American Fern Journal 101(3): 142–155.

Cobbe, Thomas J. 1943. Variations in the Cabin Run Forest, a climax area in southwestern Ohio. The American Midland Naturalist 29(1): 89–105.

Coddington, Jonathan and Katharine G. Field. 1978. Rare and endangered vascular plant species in Massachusetts. Report prepared by the New England Botanical Club, Cambridge, MA. 67 pp.

Cody, William J. 1978. Ferns of the Ottawa District. Canada Department of Agriculture Publication 974. 120 pp.

Cressler, Alan. 2011. Photo of *Diplazium pycnocarpon*. Courtesy of the Lady Bird Johnson Wildflower Center, https://www.wildflower.org/. Used with permission.

Cunningham, Bob. 2011. Cover photo of *Diplazium pycnocarpon*. Used with permission.

Dolan, Rebecca W. and Marcia E. Moore. 2017. Floristic inventory of Woollen's Gardens Nature Preserve, Indianapolis, Marion County, Indiana, USA, with quantitative vegetation sampling of permanent plots in 2003 and 2016. Proceedings of the Indiana Academy of Science 126(2): 185–199.

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.

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

Fernald, M. L. 1941. Contributions from the Gray Herbarium of Harvard University - No. CXXXIX: Another century of additions to the flora of Virginia. Rhodora 43(514): 485–553.

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

Gaddy, L. L. 1990. Glade Fern Ravine, a rich fern site in the Blue Ridge province of South Carolina. Castanea 55(4): 282–285.

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, James H. and Carl D. Monk. 1982. Herb-soil relationships on a lower north slope over marble. Bulletin of the Torrey Botanical Club 109(4): 500–507.

Greer, Gary K. and Brian C. McCarthy. 1999. Gametophytic plasticity among four species of ferns with contrasting ecological distributions. International Journal of Plant Sciences 160(5): 879–886.

Greer, Gary K., Robert M. Lloyd, and Brian C. McCarthy. 1997. Factors influencing the distribution of pteridophytes in a southeastern Ohio hardwood forest. The Journal of the Torrey Botanical Society 124(1): 11–21.

Hamilton, Robert G. 1988. The significance of spore banks in natural populations of *Athyrium pycnocarpon* and *A. thelypterioides*. American Fern Journal 78(3): 96–104.

Hamilton, Robert G. 1992. Allozyme variation and ramet distribution in two species of athyrioid ferns. Plant Species Biology 7(2-3): 69–76.

Hamilton, R. G. and R. M. Lloyd. 1991a. Antheridiogen in the wild: The development of fern gametophyte communities. Functional Ecology 5(6): 804–809.

Hamilton, R. G. and Robert M. Lloyd. 1991b. An experimental study on the effects of earthworms on the ecological success of fern gametophytes. American Fern Journal 81(3): 95–98.

Hill, Royce H. 1976. Cold requirements of several ferns in southeastern Michigan. American Fern Journal 66(3): 83–88.

Hill, Steven R. 1992. Calciphiles and calcareous habitats of South Carolina. Castanea 57(1): 25–33.

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.

Hilty, John. 2020. *Diplazium pycnocarpon*. Illinois Wildflowers. Accessed April 8, 2023 at https://www.illinoiswildflowers.info/grasses/plants/glade_fern.htm

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

ITIS (Integrated Taxonomic Information System). Accessed April 2, 2023 at http://www.itis.gov

Johnson, David M. 1986. Trophopods in North American species of *Athyrium* (Aspleniaceae). Systematic Botany 11(1): 26–31.

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)].

Kato, Masahiro. Page updated November 5, 2020. *Diplazium pycnocarpon* (Sprengel) M. Broun. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico [Online]. 22+ vols. New York and Oxford. Accessed April 2, 2023 at http://floranorthamerica.org/Diplazium_pycnocarpon

Kato, Masahiro and Dedy Darnaedi. 1988. Taxonomic and phytogeographic relationships of *Diplazium flavoviride*, *D. pycnocarpon*, and *Diplaziopsis*. American Fern Journal 78(3): 77–85.

Kaufman, Sylvan Ramsey and Wallace Kaufman. 2007. Invasive Plants: Guide to the Impacts and Control of Common North American Species. Stackpole Books, Mechanicsburg, PA. 458 pp.

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

LADWF (Louisiana Department of Wildlife and Fisheries). 2009. Rare plant species fact sheet for Glade Fern. Available at https://www.wlf.louisiana.gov/resources/category/plants-and-natural-communities/rare-plant-species-fact-sheets

Leopold, Donald J. 2005. Native Plants of the Northeast: A Guide for Gardening and Conservation. Timber Press, Portland, OR. 308 pp.

Markham, Kevin, Tanya Chalk, and C. Neal Stewart Jr. 2006. Evaluation of fern and moss protein-based defenses against phytophagous insects. International Journal of Plant Sciences 167(1): 111–117.

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.

NatureServe. 2023. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed April 2, 2023 at https://explorer.natureserve.org/

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

NCCE (North Carolina Cooperative Extension). 2023. *Homalosorus pycnocarpos*. North Carolina Extension Gardener Plant Toolbox, accessed April 8, 2023 at https://plants.ces.ncsu.edu/plants/homalosorus-pycnocarpos/

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.

Oliver, Jeanette C. 1968. A study of spore characteristics of the ferns of Indiana. American Fern Journal 58(1): 5–12.

Pichi Sermolli, Rodolfo E. G. 1977. Fragmenta Pteridologiae—VI. Webbia 31(1): 237–259.

POWO. 2023. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Accessed April 2, 2023 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.

Reese, William D. and John W. Thieret. 1966. Botanical study of the five islands of Louisiana. Castanea 31(4): 251–277.

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

Schneller, J. J., C. H. Haufler, and T. A. Ranker. 1990. Antheridiogen and natural gametophyte populations. American Fern Journal 80(4): 143–152.

Small, John Kunkel. 1935. Ferns of the Vicinity of New York. Science Press, Lancaster, PA. 285 pp.

Smith, Welby R. 2021. *Homalosorus pycnocarpos*. Species profile prepared for Minnesota Department of Natural Resources. Accessed April 8, 2023 at https://www.dnr.state.mn.us/rsg/profile.html?action=elementDetail&selectedElement=PPDRY090C0

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.

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). 2023a. *Diplazium pycnocarpon* 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). 2023b. PLANTS profile for *Diplazium pycnocarpon* (Glade Fern). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed April 2, 2023 at http://plants.usda.gov

Vasco, Alejandra, Robbin C. Moran, and Barbara A. Ambrose. 2013. The evolution, morphology, and development of fern leaves. Frontiers in Plant Science 4: https://doi.org/10.3389/fpls.2013.00345

Wade, Gary, Elaine Nash, Ed McDowell, Tom Goforth, Brenda Beckham, and Sharlys Crisafulli. 2009. Native Plants for Georgia. Part II: Ferns. The University of Georgia Cooperative Extension Bulletin 987-2. 52 pp.

Wagner, Warren H. Jr. 1955. Cytotaxonomic observations on North American ferns. Rhodora 57(680): 219–240.

Wagner, W. H. Jr. and D. M. Johnson. 1983. Trophopod, a commonly overlooked storage structure of potential systematic value in ferns. Taxon 32(2): 268–269.

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.

Ware, Donna M. E. and Stewart Ware. 1992. An *Acer barbatum*-rich ravine forest community in the Virginia coastal plain. Castanea 57(2): 110–122.

Weatherby, C. A. 1936. Small's "Ferns of the Vicinity of New York". Rhodora 38: 163–164.