Obolaria virginica

Virginia Pennywort

Gentianaceae

Obolaria virginica courtesy Alan Cressler (2018), Lady Bird Johnson Wildflower Center

***Obolaria virginica* 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

July, 2022

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. 2022. *Obolaria virginica* 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

Obolaria is a monospecific genus in the Gentianaceae, a family that displays a broad array of morphological and life history traits (Zomlefer 1994). Even within such a diverse group *Obolaria* is unique and in the past it has been included in other families, set apart as its own family, or identified as a separate subfamily or tribe within the Gentianaceae (Reveal 2011). Current classification systems place *Obolaria* in tribe Gentianeae, subtribe Swertiinae, so the most closely related genera in New Jersey are *Bartonia*, *Gentianella*, and *Gentianopsis* (Struwe et al. 2002, Kartesz 2015).

Obolaria virginica is a thief. In other words, *O. virginica* (Virginia Pennywort) is largely mycoheterotrophic, deriving a substantial amount of its nutrition from other plants by connecting to local fungal networks. Even the earliest accounts of the species made note of its roots, which Linnaeus characterized as coralloid (Linnæi 1753). A detailed description of the pennywort's subterranean structures indicated that they were relatively few in number and divisions, fleshy, irregularly thickened, wrinkled, light brown in color, and lacking in root hairs (Holm 1897). Holm dissected the roots and found that their odd shapes were due to the presence of mycorrhizae. Nearly all members of the Gentianaceae, including *Obolaria*, have a specific kind of arbuscular mycorrhizae known as the Paris type which is characterized by two different forms of hyphae (arbuscules and coils). Under normal circumstances mycorrhizal relationships are mutually beneficial—the fungus obtains carbon from the host plant and in turn offers a variety of benefits that may include increasing availability of water and certain nutrients, boosting resistance to pathogens and herbivores, or moderating the effects of environmental stresses (Sýkorová 2014). Cameron and Bolin (2010) found that *Obolaria virginica* was significantly enriched in carbon compared to other plant species growing in its vicinity, signifying that the pennywort is removing carbon from the network rather than providing it, so the plant's relationship with the fungus is more parasitic than mutualistic. However, unlike a few members of the gentian family which are completely heterotrophic, *O. virginica* does contain some chlorophyll in its leaves (Cameron and Bolin 2010).

The aboveground portion of *Obolaria virginica* is small and inconspicuous, although the plants tend to be distributed in clumps throughout their habitats. The perennial herb typically appears at the surface during late winter or early spring and the plants begin senescing within 15–16 weeks of emergence, completing their reproductive cycle prior to full canopy closure (Wood and Bornstein 2011). The appearance of *O. virginica* has been described as erratic (Fairbrothers and Hough 1973) so it is possible that the rootstock does not produce shoots every year. Sometimes the plants develop small shoots that fail to emerge from the litter layer (Wood and Bornstein 2011).

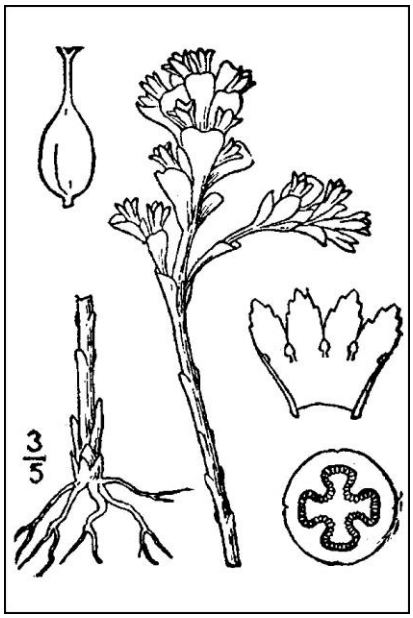
The stems of *O. virginica* are usually 8–15 cm tall and may be solitary or sparsely branched (Gleason and Cronquist 1991). A mean stem height of 9.2 cm was reported for a population in Missouri (Wood and Bornstein 2011). The leaves are in pairs, and those on the lower part of the stem are scale-like while those near the top are stalkless, somewhat fan-shaped, and purplish in color (Gillett 1959, Rhoads and Block 2007). The purple color of the leaves is due to anthocyanins in the epidermal cells, the production of which is thought to be initiated by light (Leake 1994). Some plants that are adapted to shady environments can experience damage to

their photosynthetic apparatus when exposed to high levels of light and anthocyanins play a protective role, dissipating the excess energy by diverting it from the chloroplasts to other pigments which then release it as heat (Gould 2004, Trafton 2020).

Left: Plant in bud, J. S. Dodds, 2018. Right: Flower closeup, courtesy Alan Cressler (2017), Lady Bird Johnson Wildflower Center.

Flowers of *Obolaria virginica* are 1–1.5 cm long with four whitish or sometimes purplish petals that are joined in a tube up to about the middle then divide and end in slightly flared lobes (Britton and Brown 1913, Fernald 1950). Occasionally a flower may have a five-lobed corolla (Holm 1897). Pennywort blooms occur singly or in groups of three (Struwe et al. 2002). Larger plants may produce up to 21 flowers (Holm 1897) but an average of 14 per plant was reported by Wood and Bornstein (2011). At the base of each flower is a pair of appendages which may be either sepals or bracts that function as a calyx (Struwe et al. 2002, Rhoads and Block 2007). The correct term for the organs has long been subject to debate (Gray 1848, Holm 1897, Nicolson 2000) but in any case they are similar to the upper stem leaves in appearance.

In New Jersey, the expected flowering period for *Obolaria virginica* ranges from late April through late May or June (Stone 1911, Hough 1983). Flowering occurs earlier further south. Dates reported for the start of blooming in Washington, D. C. between 1970 and 1983 ranged from April 12 to April 30 (Shetler and Wiser 1987), but early March or even late February are within the normal range of expectation throughout the species' range (Gillet 1959, Weakley 2015). Gaddy et al. (1984) found that temperature cues play a significant role in the initiation of flowering. They studied colonies of *O. virginica* that occupied different habitat niches in the same South Carolina cove, reporting that plants in warmer, sheltered areas reached peak bloom by mid-January while the flowering of those at cooler sites peaked nearly two months later.



Left: Britton and Brown 1913, courtesy USDA NRCS 2022a. Right: Floral cutaway with the leaflike calyx or bracts, Link M. Davis, 2021.

Pollinator Dynamics

The pollinators of *Obolaria virginica* have not been documented. Fertilization of flowers in the Gentianaceae is typically fauna-mediated but includes an assortment of insects, birds, and bats (Albert and Struwe 2002). *Obolaria* flowers have nectaries at the base of the ovaries (von Hagen and Katereit 2002), although Wood and Weaver (1982) observed that they are small and not well-developed. In addition to nectaries, *O. virginica* flowers have fingerlike scales in the lower part of the corolla tube which may function as a nectar guide for pollinators (Struwe et al. 2002, Meszaros et al. 2002). Hawkmoths often pollinate flowers in the Gentianaceae that have long, light-colored corolla tubes while bumblebees are typical pollinators of flowers with flared lobes (Albert and Struwe 2002). Bees were noted as the most common pollinator group in the gentian family (Meszaros et al. 2002), and it seems likely that some type of insect pollinates *O. virginica*. Unfortunately, the only bee activity reported for Virginia Pennywort was nectar robbery by insects that pierced the corollas for easy access to the reward (Harshberger 1808).

The anthers of *O. virginica* mature before the stigmas (Wood and Weaver 1982), which is likely to promote outcrossing. However, no information was found regarding the species' capacity for self-fertility.

Seed Dispersal

The ovoid fruits of *Obolaria virginica* contain numerous tiny seeds: Gillett (1959) estimated the number at 1600 per capsule. The seeds are elliptic and 260 x 155 μm in size with smooth, irregular ridges on the surface (Bouman et al. 2002). Such seeds are commonly known as dust seeds, and they are primarily dispersed by wind. The light weight of the seeds allows them to be

distributed widely (Eriksson and Kainulainen 2011) and the ridges on the seed coat may improve buoyancy in the air (Leake 1994). The low stature of *O. virginica* plants could limit dispersal distance, particularly when the vegetative cover is dense (Leake 1994), but that might benefit the species by keeping many of the propagules in a favorable environment.

Leake (1994) suggested that a capacity for dormancy may be critical for mycoheterotrophs, and a number of orchid species with dust seeds are known to remain dormant until the following growing season. However, this has not been studied in *Obolaria virginica* so it is also possible that germination takes place quickly when seeds land in a suitable site. When dust seeds germinate they develop a subterranean seedling stage that may last for up to four years (Eriksson and Kainulainen 2011). During the seedling phase *O. virginica* plants are completely dependent on their fungal network (Cameron and Bolin 2010). Most species in the Gentianaceae are fairly flexible about their host fungi, but achlorophyllous members of the family show strong host specificity and the requirements of partial mycoheterotrophs like *Obolaria* are not clear (Sýkorová 2014). Eriksson and Kainulainen (2011) postulated that partially mycoheterotrophic species were likely to be generalists. As previously noted, mature *O. virginica* plants continue to rely on their fungal associates throughout their lives for at least a portion of their carbon needs (Cameron and Bolin 2010). Generally speaking, plant species with dust seeds are not dominant in natural communities because the probability of successful establishment is low even for seeds that land at favorable germination sites (Eriksson and Kainulainen 2011), but copious seed production can improve their odds.

Habitat

Most mycoheterotrophic plants are found in habitats with a dense overstory and deep shade (Leake 1994), and *Obolaria virginica* is nearly always associated with mature deciduous woods. Many of New Jersey's populations are situated on sloping hillsides where the dominant trees are likely to include *Liriodendron tulipifera*, *Fagus grandifolia*, *Fraxinus americana*, *Acer saccharum*, *Quercus spp*. and *Carya spp*. (NJNHP 2022). *O. virginica* habitats are frequently described as nutrient-rich, but moisture levels are highly variable and the sites may be wet, moist, well-drained, or dry (Taylor 1915, Gillett 1959, Fairbrothers and Hough 1973, Hough 1983, Walker 1998, Rhoads and Block 2007, Poster et al. 2015, Weakley 2015). Although there is usually intense competition for light on the forest floor, Virginia Pennywort is able utilize the fungal network to exploit species that would otherwise outcompete it (Eriksson and Kainulainen 2011). *O. virginica* has also adapted to the challenges of its woodland habitat by completing the above ground portion of its life cycle before the trees have fully leafed out.

The local distribution of *Obolaria virginica* may be influenced by the depth of leaf litter at various locations on the forest floor. A greater accumulation of leaves in hollows can deter the establishment and growth of many herbaceous species (Sydes and Grime 1981). Wood and Bornstein (2011) observed that *O. virginica* plants at microsites where the litter layer was heavy were required to invest more in stem growth, which had a negative impact on both emergence and flower production. They suggested that a heavy litter cover could also inhibit seedling establishment in the species.

Wetland Indicator Status

Obolaria virginica 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)

OBVI

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 *Obolaria virginica* is limited to the eastern and central United States (POWO 2022). The map in Figure 1 depicts the extent of Virginia Pennywort in North America.

The USDA PLANTS Database (2022b) shows records of *Obolaria virginica* in thirteen New Jersey counties: Camden, Cumberland, Essex, Gloucester, Hunterdon, Mercer, Morris, Ocean, Passaic, Salem, Somerset, Sussex, and Union (Figure 2). The data include historic observations and do not reflect the current distribution of the species. There is also a specimen in the Pennsylvania State University Herbarium that originated in Warren County (Mid-Atlantic Herbaria 2022).

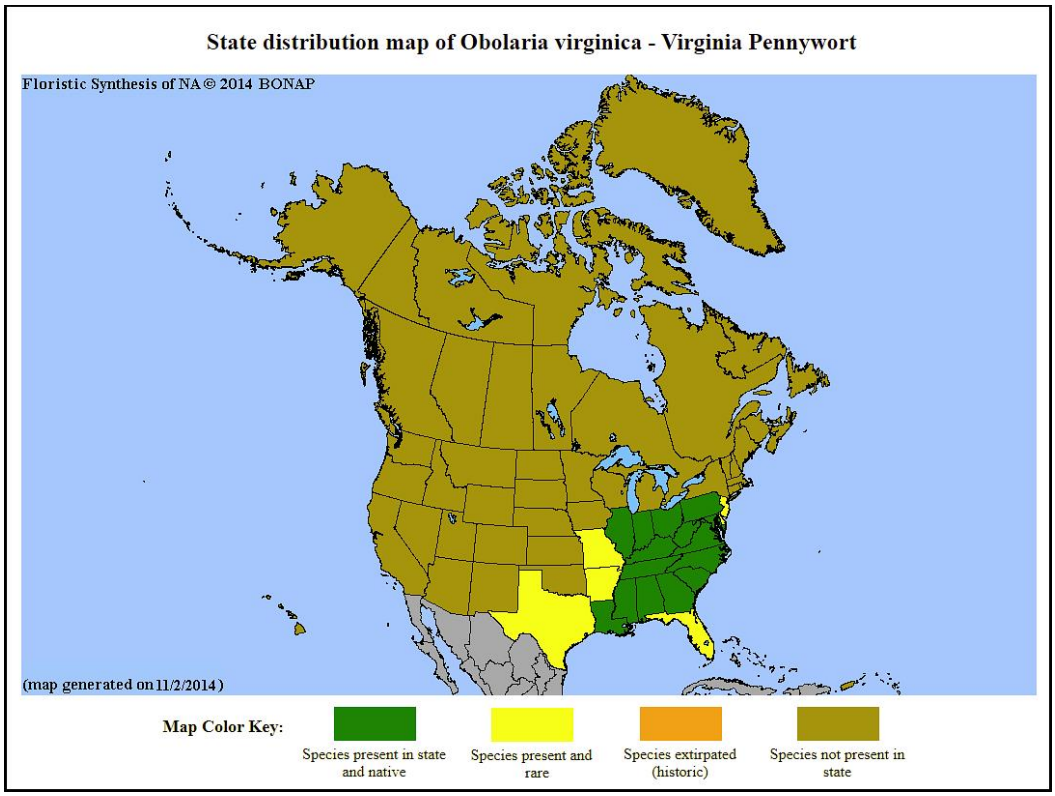


Figure 1. Distribution of O. virginica in North America, adapted from BONAP (Kartesz 2015).

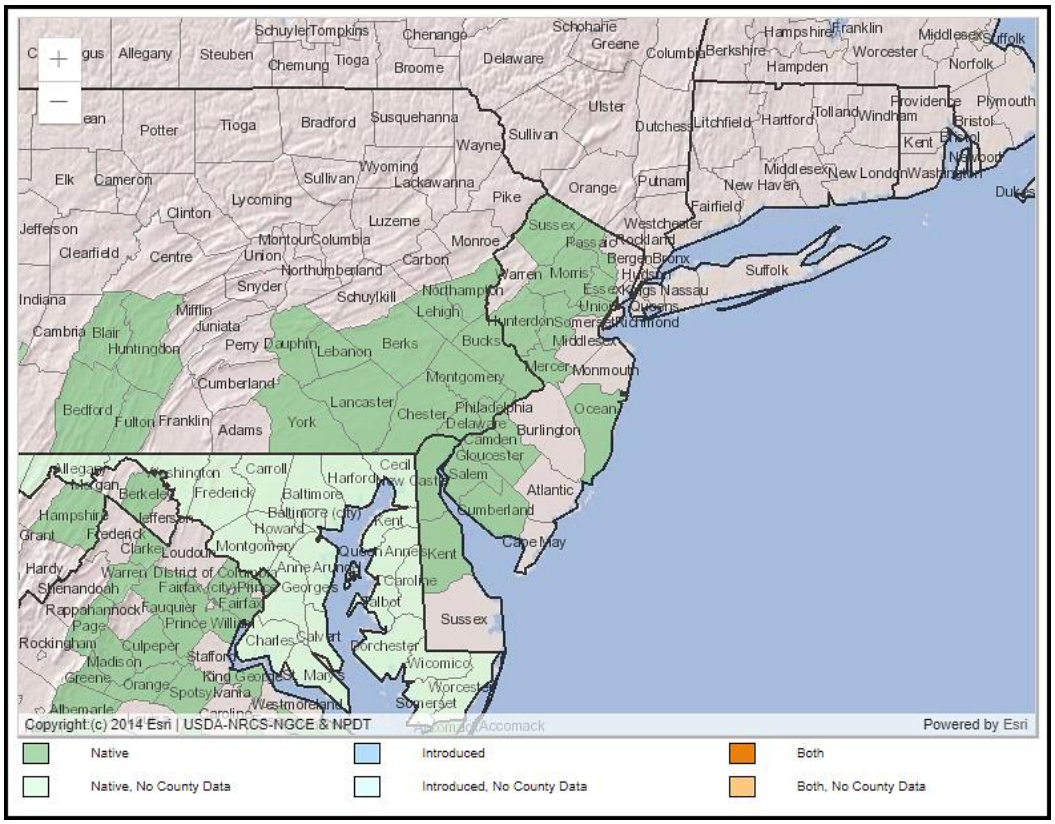


Figure 2. County records of O. virginica in New Jersey and vicinity (USDA NRCS 2022b).

Conservation Status

Obolaria virginica 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 2022). The map below (Figure 3) illustrates the conservation status of *O. virginica* throughout its range. Virginia Pennywort is imperiled (high risk of extinction) in three states and vulnerable (moderate risk of extinction) in two states. It has been ranked as secure or apparently so in five states, and has not been ranked in the remaining states where it occurs. *Obolaria virginica* was reported as eligible for listing in Texas due to rarity (Walker 1998) but it is not included on the state list of rare species (Texas Parks and Wildlife 2020). However, Virginia Pennywort is considered common throughout the most of the southeastern United States (Kondo 1970).

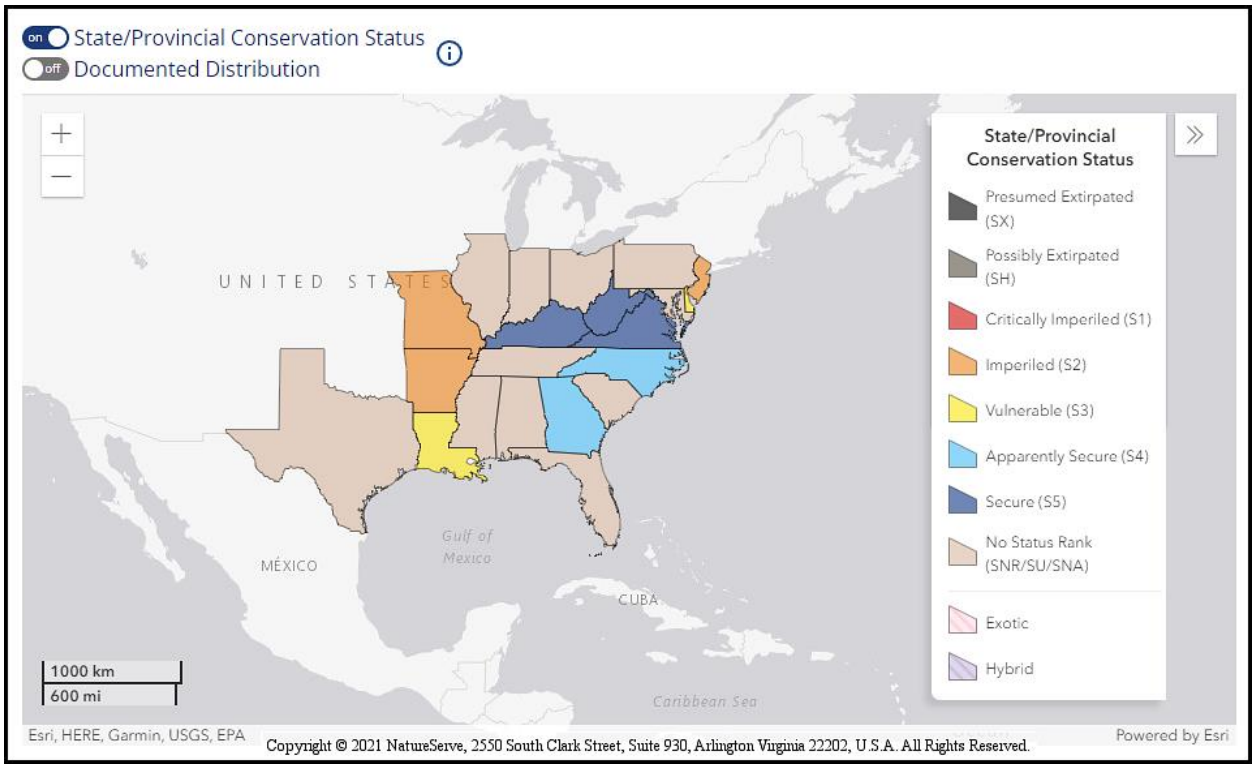


Figure 3. Conservation status of O. virginica in North America (NatureServe 2022).

New Jersey is one of the states where *Obolaria virginica* is imperiled (NJNHP 2022). The S2 rank indicates that the species is very rare in the state, with 6 to 20 occurrences. Species with an S2 rank may have once been more abundant in the state but now persist in only a few of their former locations. A regional status code of HL has also been assigned to *O. virginica*, signifying that the species is eligible for protection within the jurisdiction of the Highlands Preservation Area (NJNHP 2010).

Obolaria virginica has always been somewhat scarce in New Jersey. Willis (1874) remarked that Virginia Pennywort was "a very curious and interesting plant," noting that it was not common, and Britton (1881) reported the species as rare and local in the state. It was included on one of the state's earliest lists of rare plants (Fairbrothers and Hough 1973). The highest

concentration of *O. virginica* has always been centered in Hunterdon and Mercer Counties, while records from the southern and northern ends of New Jersey have been sparse (Britton 1889, Keller and Brown 1905, Stone 1911, Mid-Atlantic Herbaria 2022). Fifteen of the 19 extant occurrences are located in one of those two counties and the four remaining populations are also situated in the north-central part of the state (NJNHP 2022).

Threats

Although *Obolaria virginica* has developed strategies that allow it to co-occur with other native plants in a highly competitive environment, those tools may be less effective with non-indigenous species. Exotic plants are a significant problem for rare native flora in New Jersey (NJ Division of Science and Research 2021), and invasive species have been noted as imminent or potential threats to nearly two-thirds of New Jersey's extant occurrences of *O. virginica* (NJNHP 2022). The species most frequently cited as a problem for Virginia Pennywort populations in the state is Japanese Barberry (*Berberis thunbergii*), which not only forms dense thickets that crowd out other plants but also alters soil characteristics (Kaufman and Kaufman 2007). Changes in soil chemistry may disrupt the fungal community, making a site less hospitable for *O. virginica*. Other species that have been observed establishing in the immediate vicinity of *Obolaria virginica* colonies include *Rosa multiflora*, *Alliaria petiolata*, *Cardamine impatiens*, *Celastrus orbiculatus*, *Euonymus alatus*, *Lonicera japonica*, *L. morrowii*, *Polygonum perfoliatum*, and *Rhodotypos scandens* (NJNHP 2022). All of those species are considered highly threatening to native communities in the state (Van Clef 2009, FoHVOS 2022).

The exotic plant problem in New Jersey's forests is becoming further exacerbated by an introduced insect. The Emerald Ash Borer (*Agrilus planipennis*) has been rapidly spreading throughout the state, and infested ash trees usually die within 3–4 years (NJ Department of Agriculture 2019). Ash (*Fraxinus*) is a significant component of the state's northwestern woodlands, and the beetle has the potential to kill as many as 99% of the ash trees in the region (Yoo 2018). Death of the trees results in higher light levels on the forest floor, making the communities more accessible to a host of non-indigenous plants.

High levels of deer herbivory were noted in the vicinity of several *Obolaria virginica* populations in New Jersey but direct damage to pennywort plants was not reported (NJNHP 2022). There are some indications that browsing might not be a major threat to *O. virginica*. The plants may be overlooked because they are small and the purplish leaves blend in with the leaf litter (Wood and Bornstein 2011). Leake (1994) suggested that plant pigments could play an important role in preventing grazing and Gould (2004) cited anthocyanins as a possible deterrent to herbivory. Virginia Pennywort has been described as having a bitter taste (Gray 1848, Gillett 1959), which may be an additional disincentive for herbivores.

It is difficult to project how *Obolaria virginica* will be affected by climate change. Higher temperatures will probably cause the plants to emerge and bloom earlier in the season, but without an understanding of the species' pollination dynamics it is impossible to say whether that response will be adaptive or problematic. Because the species spends most of the year below ground it may be somewhat shielded from other climactic changes predicted for New Jersey such

as more frequent and intense storms or extended periods of drought (Hill et al. 2020). At some locations, increased erosion from storm events may result in changes to the habitat or community composition.

Management Summary and Recommendations

Management of invasive species is a high priority for many of New Jersey's *Obolaria virginica* populations. Where *Berberis thunbergii* and other exotic plants have been noted as a threat, site specific plans should be developed to control the spread of invasives without harming *O. virginica* or other rare species that may be present.

Nearly three quarters (74%) of the state's extant occurrences have been discovered within the past 16 years (NJNHP 2022) and surveys of suitable habitat in New Jersey could result in the documentation of additional populations. Many observers have noted that *O. virginica* tends to be inconspicuous in its habitat (e.g. Nicolson 2000) and the plants are only above ground for a limited time so they may have been overlooked at some sites.

Documentation of the species' pollination strategies is a critical research need for *Obolaria virginica*. Additional information is called for regarding both the timing of and requirements for seed germination and development. It would also be useful to know whether *O. virginica* is able to form associations with a broad range of mycorrhizal fungi or if it is narrowly host-specific.

Synonyms

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

Botanical Synonyms	Common Names
Schultesia obolarioides Raf.	Virginia Pennywort
Schultzia virginica (L.) Kuntze	

References

Albert, V. A. and L. Struwe. 2002. Gentianaceae in context. In Lena Struwe and Victor A. Albert (eds.). Gentianaceae: Systematics and Natural History. Cambridge University Press, New York, NY.

Bouman, F., L. Cobb, N. Devente, V. Goethals, P. J. M. Maas, and E. Smets. 2002. The seeds of Gentianaceae. . In Lena Struwe and Victor A. Albert (eds.). Gentianaceae: Systematics and Natural History. Cambridge University Press, New York, NY.

Britton, N. L. 1881. A preliminary catalogue of the flora of New Jersey. Geological Survey of New Jersey, Office of the Survey, Rutgers College, New Brunswick, NJ. 233 pp.
Britton, N. L. 1889. Catalog of plants found in New Jersey. Geological Survey of New Jersey, Final report of the State Geologist 2: 27–642.

Britton, N. L. and A. Brown. 1913. An Illustrated Flora of the Northern United States and Canada in three volumes: Volume III (Gentian to Thistle). Second Edition. Reissued (unabridged and unaltered) in 1970 by Dover Publications, New York, NY. 637 pp.

Cameron, Duncan D., and Jay F. Bolin. 2010. Isotopic evidence of partial mycoheterotrophy in the Gentianaceae: *Bartonia virginica* and *Obolaria virgini*ca as case studies. American Journal of Botany 97: 1272–1277.

Cressler, Alan. 2017. Flowers of *Obolaria virginica*. Courtesy of the Lady Bird Johnson Wildflower Center, https://www.wildflower.org/. Used with permission.

Cressler, Alan. 2018. Cover photo of *Obolaria virginica*. Courtesy of the Lady Bird Johnson Wildflower Center, https://www.wildflower.org/. Used with permission.

Davis, Link M. 2021. Cutaway view photo of *Obolaria virginica* flower. Shared via iNaturalist at https://www.inaturalist.org/observations/74766011, licensed by https://creativecommons.org/licenses/by-nc/4.0/

Eriksson, Ove and Kent Kainulainen. 2011. The evolutionary ecology of dust seeds. Perspectives in Plant Ecology, Evolution and Systematics 13(2): 73–87.

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.

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

FoHVOS (Friends of Hopewell Valley Open Space). 2022. New Jersey Invasive Species Strike Team. Invasive species list with control recommendations. Available online at https://www.fohvos.info/invasive-species-strike-team/info-center/

Gaddy, L. L., Ph. W. Suckling, and V. Meentermeyer. 1984. The relationship between winter minimum temperatures and spring phenology in a Southern Appalachian Cove. Archives for Meteorology, Geophysics, and Bioclimatology, Series B 34: 155–162.

Gillett, J. M. 1959. A revision of *Bartonia* and *Obolaria* (Gentianaceae). Rhodora 61: 43–63.

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.

Gould, Kevin S. 2004. Nature's Swiss army knife: The diverse protective roles of anthocyanins in leaves. Journal of Biomedicine and Technology 5: 314–320.

Gray, Asa. 1848. Chloris Boreali-Americana: Illustrations of new, rare, or otherwise interesting North American plants, selected chiefly from those recently brought into cultivation at the botanic garden of Harvard University, Cambridge. Memoirs of the American Academy of Arts and Sciences 3: 1–56.

Harshberger, John W. 1898. A few ecological notes. The Asa Gray Bulletin 6(2): 37–39.

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.

Holm, Theo. 1897. *Obolaria virginica* L.: A morphological and anatomical study. Annals of Botany 11(43): 369–383.

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)].

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.

Keller, Ida A. and Stewardson Brown. 1905. Handbook of the Flora of Philadelphia and Vicinity. Philadelphia Botanical Club, Philadelphia, PA. 360 pp.

Kondo, K. 1970. The chromosome number of *Obolaria virginica* L. (Gentianaceae). Rhodora 72: 551–553.

Leake, J. R. 1994. The biology of myco-heterotrophic ('saprophytic') plants. New Phytologist 127: 171–216.

Linnæi, Caroli. 1753. Species Plantarum, Tomus II (page 632). Salvii, Stockholm.

Meszaros, S., J. de Laet, V. Goethals, E. Smets, and S. Nilsson. 2002. Cladistics of Gentianaceae: A morphological approach. In Lena Struwe and Victor A. Albert (eds.). Gentianaceae: Systematics and Natural History. Cambridge University Press, New York, NY.

Mid-Atlantic Herbaria. 2022. https://midatlanticherbaria.org/portal/index.php. Accessed on July 20, 2022.

NatureServe. 2022. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed July 20, 2022 at https://explorer.natureserve.org/

Nicolson, D. H. 2000. *Obolaria*: A study of imponderables. The Plant Press 3(4): 5.

NJ Department of Agriculture. 2019. Emerald Ash Borer. Accessed July 23, 2022 at https://www.nj.gov/agriculture/divisions/pi/prog/emeraldashborer.html and https://www.nj.gov/agriculture/divisions/pi/prog/whatiseab.html

NJ Division of Science and Research. 2021. Endangered Plants. From Environmental Trends: Plants and Wildlife, N. J. Department of Environmental Protection, available at https://www.nj.gov/dep/dsr/trends/

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.

Poster, Lauren S., James S. Pringle, and Lena Struwe. 2015. Identification and descriptions of the Gentianaceae in New Jersey. Bartonia 67: 1–34.

POWO. 2022. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Retrieved January 5 2022 from http://www.plantsoftheworldonline.org/

Reveal, James L. 2011. Indices Nominum Supragenericorum Plantarum Vascularium – O. Family names website accessed July 21, 2022 at http://www.plantsystematics.org/reveal/pbio/fam/allspgfileO.html

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

Shetler, Stanwyn G. and Susan K. Wiser. 1987. First flowering dates for spring-blooming plants of the Washington, D. C. area for the years 1970 to 1983. Proceedings of the Biological Society of Washington 100(4): 993–1017.

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

Struwe, L., K. W. Kadereit, J. Klackenberg, S. Nilsson, M. Thiv, K. B. von Hagen, and V. A. Albert. 2002. Systematics, character evolution, and biogeography of Gentianaceae, including new tribal and subtribal classification. In Lena Struwe and Victor A. Albert (eds.). Gentianaceae: Systematics and Natural History. Cambridge University Press, New York, NY.

Sydes, C. and J. P. Grime. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland: I. Field investigations. Journal of Ecology 69(1): 237–248.

Sýkorová, Zuzana. 2014. The role of arbuscular mycorrhiza in the growth and development of plants in the family Gentianaceae. In J. J. Rybczyński et al. (eds.), The Gentianaceae - Volume 1: Characterization and Ecology. Springer-Verlag, Berlin, Germany.

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.

Texas Parks and Wildlife. 2020. Species of greatest conservation need. State status list of rare species accessed July 20, 2022 at https://tpwd.texas.gov/landwater/land/tcap/sgcn.phtml

Trafton, Anne. 2020. How plants protect themselves from sun damage. MIT News, March 10 2020, Massachusetts Institute of Technology, available at https://news.mit.edu/2020/how-plants-protect-sun-damage-0310

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. *Obolaria virginica* 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 *Obolaria virginica* (Virginia Pennywort). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed July 20, 2022 at http://plants.usda.gov

Van Clef, M. 2009. New Jersey Strategic Management Plan for Invasive Species: The Recommendations of the New Jersey Invasive Species Council to Governor Jon S. Corzine, Pursuant to New Jersey Executive Order #97. Appendix II, Prioritized Listing of New Jersey's Nonindigenous Plant Species, prepared by David Snyder. Available at http://www.nj.gov/dep/njisc/docs/Final%20NJ%20Strategic%20Management%20Plan%20for%20Invasive%20Species%2011.09.pdf

von Hagen, K. Bernhard and Joachim W. Kadereit. 2002. Phylogeny and flower evolution of the Swertiinae (Gentianaceae-Gentianeae): Homoplasy and the principle of variable proportions. Systematic Botany 27(3): 548–572.

Walker, Suzanne Birmingham. 1998. The status of *Obolaria virginica* L. (Gentianaceae) in Texas and surrounding states. Phytologia 84(2): 64–68.

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.

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.

Willis, O. 1874. Catalogue of Plants Growing in the State of New Jersey. J. W. Schermerhorn, New York, NY. 92 pp.

Wood, Diane L. and Allan J. Bornstein. 2011. Notes on the biology of *Obolaria virginica* (Gentianaceae) in southeast Missouri, and the effects of leaf litter on emergence and flower production. Castanea 76(2): 157–163.

Wood, Carroll E. Jr. and Richard E. Weaver Jr. 1982. The genera of Gentianaceae in the southeastern United States. Journal of the Arnold Arboretum 63(4): 441–487.

Yoo, Rosa. 2018. Remove or treat ash trees today. NJ Municipalities, January 2018: 28–29.

Zomlefer, Wendy B. 1994. Guide to Flowering Plant Families. University of North Carolina Press, Chapel Hill, North Carolina. 430 pp.