

Cleistes divaricata

Spreading Pogonia

Orchidaceae



Cleistes divaricata courtesy Alan Cressler, Lady Bird Johnson Wildflower Center

***Cleistes divaricata* 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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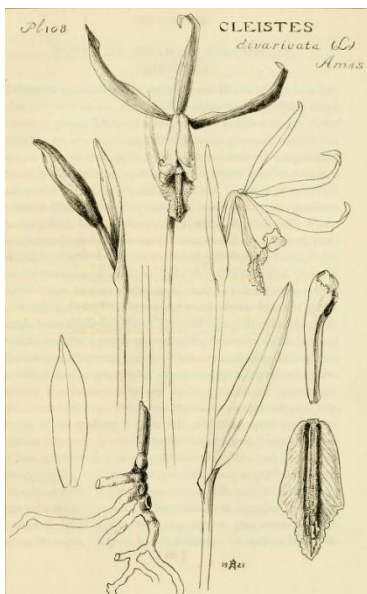
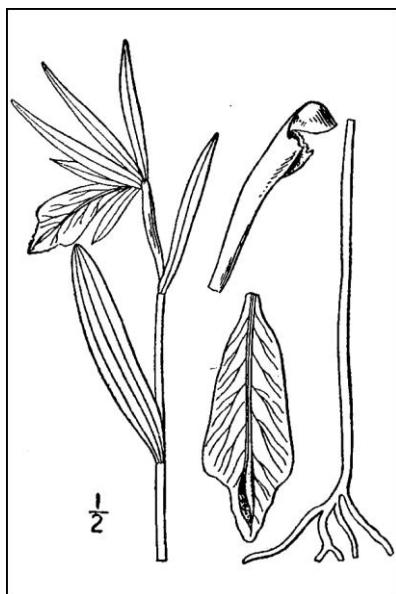
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Life History

Cleistes divaricata (Spreading Pogonia) is a striking perennial orchid that was once featured on a 20¢ postage stamp designed by Manabu Saito, a noted botanical artist from Stillwater, New Jersey (SNPM 2023). Within the Orchidaceae, *Cleistes* has been placed in Tribe Vanilleae, Subtribe Pogoniinae. Other local genera in the subtribe include *Isotria* and *Pogonia* (Dressler 1981). Three North American species of *Cleistes* have been described: They are all morphologically similar and were identified as distinct rather recently (see Synonyms and Taxonomy section). *C. divaricata* is the only one that occurs in New Jersey.

It is easiest to find *Cleistes divaricata* when the plants are in flower (Kéry and Gregg 2003). Reproductive stems are 2.5–7.5 dm high. A long-petioled leaf may be present at the base. There is a sessile narrow leaf that is 6–15 cm long at the midpoint of the stem and a similarly-shaped but smaller leaf-like bract near the base of the flower. Most plants are single-flowered but occasionally two flowers are produced. *C. divaricata* flowers have three long (3–6.5 cm), narrow, maroon-purple sepals that are upright to spreading. Portions of the lip and lateral petals are fused, forming a tube. The pink lateral petals curl up at the tips. The protruding (3.4–5.5 cm long) lip is ragged-edged, elevated near the center, and pink to white with darker veins and markings. (See Britton and Brown 1913, Gray 1950, Gleason and Cronquist 1991, Fowler 2005, Gregg and Catling 2020).



Left: Britton and Brown 1913, courtesy USDA NRCS 2024a. Center: Blanche Ames, 1922. Right: Courtesy Alan Cressler, Lady Bird Johnson Wildflower Center.

Flowering time appears to vary with latitude (Gregg and Catling 2020). *Cleistes divaricata* can start to bloom during May in the southern states (Fowler 2005, LeGrand et al. 2022, Weakley et al. 2024). In New Jersey, the orchid has been found in flower from mid-June through early July (Stone 1911, Chrysler 1932, Hough 1983, NJNHP 2024). The fruits develop soon after the flowers have finished blooming (LeGrand et al. 2022).

The roots of *Cleistes* species are about 1–2 mm wide but they often have thicker sections (nodules) that can serve as storage organs (Dressler 1981, Gregg and Catling 2020). The plants are capable of reproducing asexually by developing new stem shoots at the tips of horizontal roots (Gregg 1989, 2007). However, Fernald (1950) noted that *C. divaricata* engaged in clonal reproduction "only sparingly" and Fowler (2005) observed that the species "seems to prefer a rather solitary existence". *Cleistes* plants typically produce large overwintering buds and those that don't develop can recycle their nutrients to other buds (Gregg 2011).

Mature *Cleistes* plants do not always flower. Nonflowering plants may consist of a stem with 1–3 leaves or they may lack aboveground parts altogether (Kéry and Gregg 2003). Hough (1983) noted that *C. divaricata* only appeared sporadically in the places where it was known to occur. Kéry et al. (2005) found that 16–47% of the plants in a *Cleistes* population were likely to be dormant during any given year and that dormancy episodes could last for 1–4 years. Some root growth may continue to occur during that time (Shefferson et al. 2020). Periods of dormancy might be initiated by the loss of perennating buds, although the causes of bud failure are unknown (Gregg 2011). In some orchids dormancy can be triggered when fungal partners are in short supply (McCormick et al. 2018). Plants that are capable of persisting in a dormant state are often long-lived (Shefferson 2007). In many terrestrial orchid species the smaller individuals in a population are more susceptible to mortality but *Cleistes divaricata* appears to be among the exceptions (Shefferson et al. 2020).

Pollinator Dynamics

The manner in which *Cleistes* pollen is dispersed is fairly unusual among orchids. The pollen develops in units of four attached grains (tetrads) and the tetrads are dispensed in clusters that are held together by an unknown mechanism (Pacini and Hesse 2002). *Cleistes divaricata* is pollinated by bumblebee workers (*Bombus* spp.). Studies of a population in North Carolina suggested that *Bombus pensylvanicus* was the most frequent pollinator although several other bumblebee species were also observed carrying *Cleistes* pollen. A visiting bee first lands on the orchid's lip, and as it enters a flower the stigma smears a sticky fluid on its back. *Cleistes* flowers are nectarless—when the bee realizes that and backs out of the flower it moves a hinged anther cap and triggers the release of pollen which adheres to the stigmatic fluid. After the bee exits, the anther cap returns to its original position and the deposited pollen is likely to come into contact with the stigma of the next flower that the bee visits. The strategy allows multiple bees to be dusted with pollen from a single flower (Gregg 1989 & 1991a, Catling and Catling 1991, Fowler 2005, Argue 2012).

Cleistes was originally thought to exemplify deceptive pollination, offering a promise of food but providing no reward. Such species are known as bee food mimics (Jersáková et al. 2006, Pansarin et al. 2012). However, studies by Gregg (1989, 1991a, 1991b) revealed regional differences in the way *Cleistes* flowers interacted with pollinators that subsequently became the basis for the designation of two new species (see Synonyms and Taxonomy section). *Cleistes bifaria* flowers are odorless but a crest of bright yellow hairs on the lip appears to advertise pollen. In *Cleistes divaricata* and *C. oricamporum* yellow coloration is muted or absent but the flowers are fragrant: Those of *C. divaricata* have a daffodil-like scent while those of *C.*

oricamporum smell like vanilla. Bumblebees obtain a pollen reward from both of the scented species but not from *C. bifaria* (Gregg 1991b, Catling and Gregg 1992).

Fruit set in orchids is generally higher when pollinators are able to obtain a reward (Neiland and Wilcock 1998). The extra investment required to produce a fragrance or additional pollen may be offset by the benefits of increased pollinator visitation (Smith et al. 2004, Argue 2012). Gregg (1991b) suggested that the strategies of the *Cleistes* species may have diverged in response to competition because *C. divaricata* and *C. oricamporum* typically share habitat with an assortment of similar-looking orchids while few comparable flowers were seen growing with *C. bifaria*. The ranges of *C. divaricata* and *C. oricamporum* overlap but for the most part the range of *C. bifaria* does not intersect with those of the other two species (Kartesz 2015, LeGrand et al. 2022). It has been suggested that the exploitation of *Cleistes* flowers for pollen might be a learned behavior by bees in areas where those two species occur (Proctor and Harder 1995). In places where *Cleistes divaricata* and *C. oricamporum* co-occur they do not appear to hybridize. The blooming periods of the two species peak about a week apart, and the scent preferences of individual bees may also limit opportunities for gene flow between *C. divaricata* and *C. oricamporum* (Catling and Gregg 1992, Smith et al. 2004).

Both the pistils and stamens of *Cleistes* flowers are mature at anthesis but the anther cap reduces the probability of self-fertilization (Gregg 1989, Catling and Catling 1991). Spreading Pogonias cannot set seed without a pollen transfer, making them dependent on the bees. *Cleistes* plants can produce viable seeds if they are fertilized with their own pollen, although a higher percentage of viable seeds develop in cross-pollinated flowers. The amount of pollen deposited during a bumblebee visit can vary and the flowers typically remain fresh-looking for 10–12 days unless they receive enough pollen to produce a full capsule of seeds. Once a flower is well-pollinated the sepals begin to fade and bend forward. Even partially pollinated flowers will usually develop capsules, although they are generally smaller in size (Gregg 1989, 1991a, 2007).

Seed Dispersal and Establishment

The seeds of orchids lack endosperm and consist mainly of an embryo surrounded by a loose, papery coating (Dressler 1981). Individual plants produce numerous tiny propagules that are often referred to as dust seeds. Some orchids produce hundreds of thousands, or even millions, of seeds but seed production in *Cleistes* is relatively low in comparison (Argue 2012). Gregg (1989) reported an average of 5,069 seeds per capsule (range 120–11,000) in open-pollinated flowers of *C. bifaria* and a maximum of about 20,000 in those that had been hand pollinated.

The minute seeds are wind-dispersed and most have relatively large internal air spaces that allow them to float in the air for long periods. Many orchid seeds also have a water-resistant outer surface that—together with the internal air space—permits flotation, allowing some movement of seeds via surface water after a rain. The seeds of *Cleistes divaricata* have been reported to float when wet (Arditti and Ghani 2000). Arditti and Ghani further noted that the general characteristics of orchid seeds also allow their transport by adherence to land animals and birds.

Gregg (1989) reported a 68% viability rate in *Cleistes bifaria* seeds that had developed in naturally pollinated capsules. Most of the terrestrial orchid seeds that germinate do not survive long enough to develop aboveground structures, and mortality is also high in juvenile plants. However, those that reach maturity may be relatively long-lived (Shefferson et al. 2020). Dormancy in orchid seeds varies between species, ranging from 0–7 years (Eriksson and Kainulainen 2011). Dressler (1981) noted that the seeds of orchids may survive for long periods if they are cool and dry. When the seeds become hydrated, limited metabolic activity is initiated but germination requires appropriate physical conditions and, in nature, the right kind of fungi (Dressler 1981, Arditti and Ghani 2000). Some species are able to germinate even when a suitable fungus is not present but a mycorrhizal association is required for further development (Rasmussen and Whigham 1993, Rasmussen 2002).

When an orchid seed germinates the embryo swells into a mass of cells called a protocorm, and the lower portions initiate root hairs while the cells on the upper surface may eventually develop into a leafy shoot. Prior to leaf development the seedlings are completely dependent on their fungal associate for nutrients (Dressler 1981). Juvenile orchids, which frequently look like smaller versions of the mature plants, may continue to rely on their fungal partners and certain species require them throughout their lives (Whigham and Willems 2003, Eriksson and Kainulainen 2011, Shefferson et al. 2020). Fungal hyphae found in the roots of mature *Cleistes bifaria* plants were assumed to be mycorrhizal (Gregg 1989). Some orchids utilize different fungal associates during their germination and establishment phases, some can maintain associations with multiple types of fungi simultaneously, and some typically associate with a single fungus but are able to switch to another species during periods of stress (Whigham and Willems 2003, McCormick et al. 2006 & 2021). Bell et al. (2024) recently demonstrated that plants have a mechanism for preferentially allocating resources to the fungi that benefit them most, although the process has not yet been studied in orchids.

Habitat

Cleistes divaricata can be found at elevations of 0–200 meters above sea level in savannas and seepage bogs on the coastal plain (Gregg and Catling 2020, Weakley et al. 2024). Szakacs et al. (2022) indicated that the species had a strong preference for open habitats and it was characterized as a "sun obligate" by Weakley et al. (2024).

In New Jersey, *Cleistes divaricata* has typically been found in open or shrubby riverside savanna habitat, although it is often situated along the dryer edges where it may be partially shaded (Stone 1911, Fairbrothers and Hough 1973, Hough 1983, Johnson and Walz 2013). At one location a few plants were growing at the base of a *Chamaecyparis thyoides* (Atlantic White Cedar) tree (NJNHP 2024).

In the southern part of its range *Cleistes divaricata* is also found in savannas, although those are generally associated with Longleaf Pine (*Pinus palustris*) and Wiregrass (*Aristida stricta*) is often the dominant herb. *Cleistes divaricata* and *C. oricamporum* may co-occur in southern sites, also sharing the habitat with assorted ferns and species such as *Aletris farinosa*, *Pogonia ophioglossoides*, and *Calopogon* spp. (Gregg 1991b, Fowler 2005, Thornhill 2013). Other

habitats that are sometimes utilized by *C. divaricata* include damp pine barrens, seepage areas, wet prairies, and powerline right-of-ways (Sheridan et al. 1997, FNAI 2010, LeGrand et al. 2022, VADCR undated). Fire has historically maintained the relatively open nature of the habitats utilized by *C. divaricata* (Pridgeon 1996, Orchid Conservation Coalition 2005, VADCR undated).

Wetland Indicator Status

Cleistes divaricata 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 2024b)

CLDI

Coefficient of Conservancy (Walz et al. 2020)

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

Distribution and Range

The global range of *Cleistes divaricata* is restricted to the eastern United States (POWO 2024). The map in Figure 1 depicts the extent of the species in North America.

The USDA PLANTS Database (2024b) shows records of *Cleistes divaricata* in two New Jersey counties: Burlington and Cape May (Figure 2). Two early reports of occurrences in Atlantic and Middlesex actually referred to sites that were located in Burlington County (Britton 1881, Taylor 1915, Mid-Atlantic Herbaria 2024, NJNHP 2024). The data include historic observations and do not reflect the current distribution of the species.

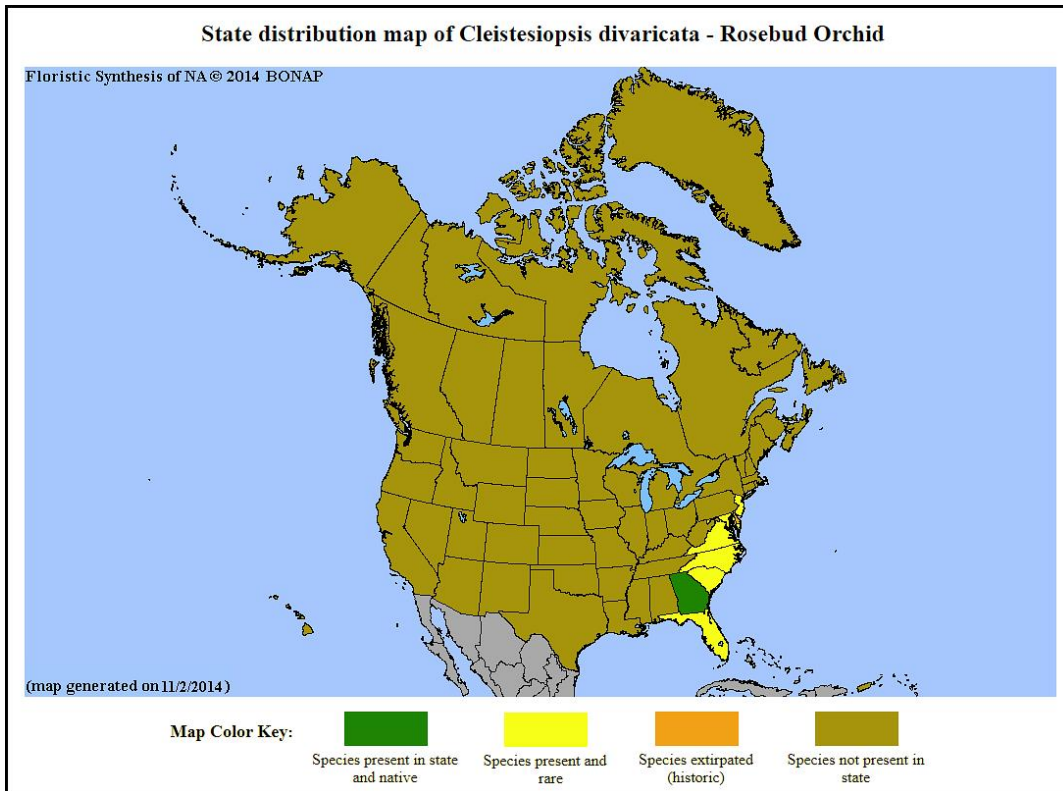


Figure 1. Distribution of *C. divaricata* in North America, adapted from BONAP (Kartesz 2015).

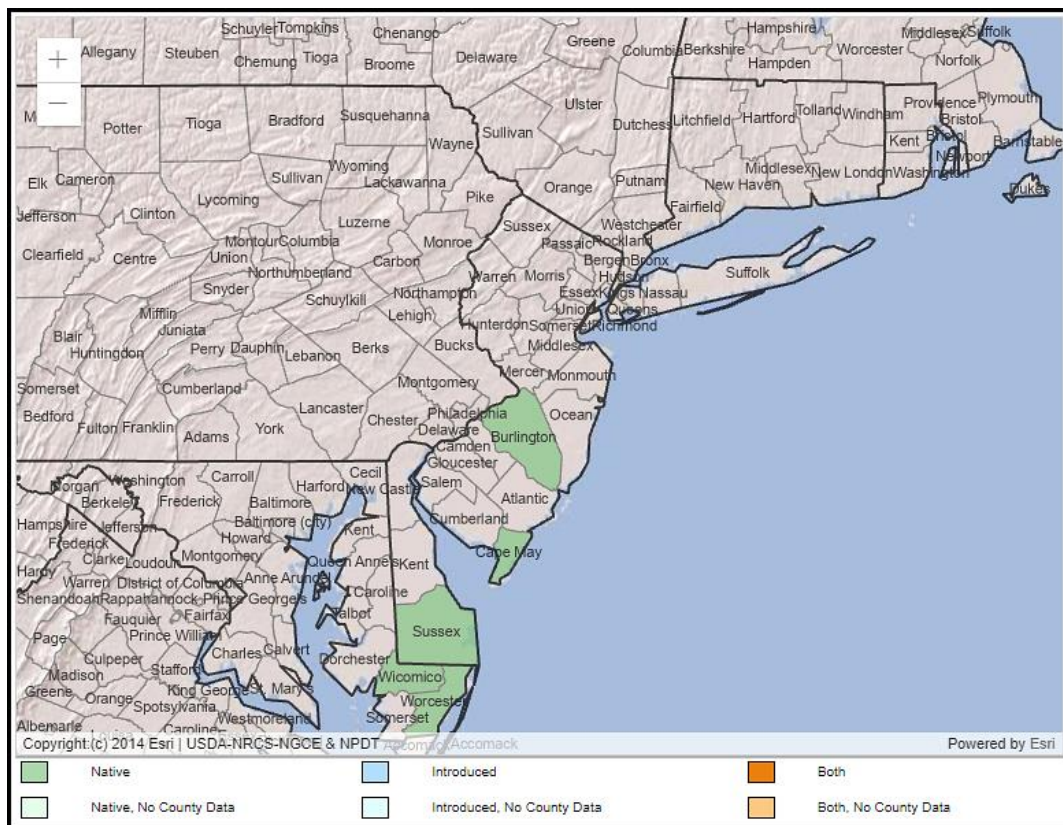


Figure 2. County records of *C. divaricata* in New Jersey and vicinity (USDA NRCS 2024b).

Conservation Status

Cleistes divaricata is apparently secure at a global scale. The G4 rank means the species is at fairly low risk of extinction or collapse due to an extensive range and/or many populations or occurrences, although there is some cause for concern as a result of recent local declines, threats, or other factors (NatureServe 2024). The map below (Figure 3) illustrates the conservation status of *C. divaricata* throughout its range. The orchid is vulnerable (moderate risk of extinction) in one state, imperiled (high risk of extinction) in one state, critically imperiled (very high risk of extinction) in four states, and presumed extirpated in Delaware. *C. divaricata* is unranked in South Carolina.

Cleistes divaricata has also been identified as a plant species of highest conservation priority for the North Atlantic region, which includes four Canadian provinces and twelve U. S. states. The species has a rank of R1 (critically imperiled), signifying a very high risk of regional extinction (Frances 2017).

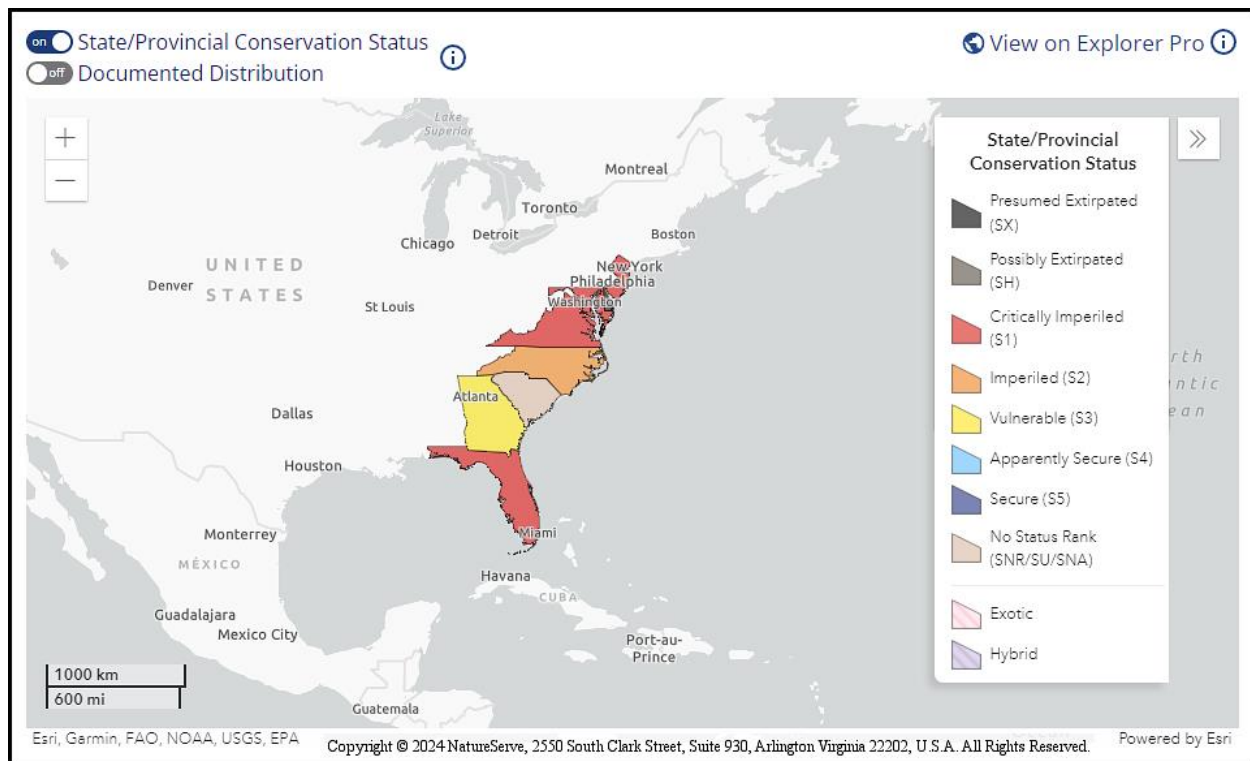


Figure 3. Conservation status of *C. divaricata* in North America (NatureServe 2024).

Cleistes divaricata 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. *C. divaricata* 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 orchid 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).

Cleistes divaricata has always been rare in New Jersey. Wherry (1928) described occurrences in the state as being beyond the species' normal range. Only two sites were known during the 1880s (Willis 1877, Britton 1881) and a third was discovered in 1909 by Stone (1911). Fables (1957) indicated that *C. divaricata* was on the verge of extinction in New Jersey. The orchid was listed as endangered by Fairbrothers and Hough (1973), who remarked that it had formerly been more abundant in the state, and by Calazza and Fairbrothers (1980), who noted that most of the sites where it occurred had been destroyed and that it had not been seen for more than two decades. The population discovered by Stone in 1909—the sole documented occurrence from Cape May County—was adjacent to an agricultural field and in 1910 it "narrowly escaped being transformed into hay" (Stone 1911). That luck did not hold: The population was apparently long gone by the middle of the century (Fairbrothers and Hough 1973) and is now considered extirpated. Five Burlington County occurrences are ranked as historical and only one tiny population is extant (NJNHP 2024).

Threats

Orchids in the northeastern United States face an assortment of threats that can include habitat loss or alteration, disruption of disturbance regimes or symbiotic relationships, an overabundance of deer, and poaching by collectors (Pace 2020). Historically, loss of coastal plain savanna habitat often resulted from the conversion of land for agriculture or resource extraction. Current losses are frequently attributable to altered hydrology, degraded water quality, or successional changes in community composition (Johnson and Walz 2013, VADCR undated).

One of New Jersey's former populations of *Cleistes divaricata* was reportedly destroyed by flooding and another was apparently lost to succession (Fairbrothers and Hough 1973, NJNHP 2024). Fire suppression was identified as the primary threat to *C. divaricata* populations in Virginia (VADCR undated), and at a North Carolina site the Spreading Pogonia decreased over time when fire frequency was reduced (Palmquist 2014, Palmquist et al. 2014).

Herbivory by White-tailed Deer (*Odocoileus virginianus*) is likely to threaten *Cleistes divaricata* in New Jersey. The overabundance of deer in the state is well-documented (NJDSR 2019) and orchids are often preferentially grazed (Miller et al. 1992). Gregg (1989) observed that browsing damage to a West Virginia population of *C. bifaria* was sporadic but took a significant toll when it occurred because the upper part of many flowering stems was removed prior to fruit set. *Cleistes* plants might also be susceptible to belowground herbivory, which was identified as one of several possible reasons for the loss of some perennating buds in the same population (Gregg 2011).

A growing worry for *Cleistes divaricata* is the disappearance of bumblebees. As previously discussed, seed set in *Cleistes* is pollinator limited and it appears that *C. divaricata* relies primarily on *Bombus pensylvanicus* and secondarily on a few other *Bombus* species for fertilization. Dramatic range-wide population declines in *B. pensylvanicus*, along with a number

of other bumblebees, have been documented in recent years (Colla and Packer 2008, Cameron et al. 2011, Gamillo 2021). *Bombus pensylvanicus* has been assessed as Vulnerable on the IUCN Red List of Threatened Species (Hatfield et al. 2015) and the insect is presently under review for listing at the federal level (USFWS 2024).

Climate Change Vulnerability

An assessment of potential climate change impacts on selected New Jersey plants by Ring et al. (2013) ranked *Cleistes divaricata* as Presumed Stable because the authors found little evidence that its abundance or range would substantially change by 2050. Pine Barren savannas appear likely to remain relatively stable as the climate changes, although they are susceptible to changes in hydrologic conditions and may be dependent on active management to control succession (Johnson and Walz 2013, Ring et al. 2013).

In New Jersey, the impacts of climate change include both elevated temperatures and an increase in extreme conditions such as droughts and floods (Hill et al. 2020). *Cleistes divaricata* is at the northern end of its range in New Jersey so it is possible that the species could benefit from higher temperatures. Gregg (2011) speculated that frost damage may have been responsible for a recorded bud loss in *C. bifaria*, and if that is the case warmer winters might allow *C. divaricata* to expand its range northward. However, the potential advantages of higher temperatures could be counteracted by more frequent or lengthier droughts since dry periods typically trigger dormancy in *Cleistes* (Kéry et al. 2005). Another significant concern for *C. divaricata* is that the decline in bumblebees is likely to be exacerbated by climate change (Soroye et al. 2020).

Management Summary and Recommendations

Although New Jersey's only known extant population of *Cleistes divaricata* is small it is situated in high quality habitat and a large fire that took place in 2022 may have created favorable conditions for it to expand (NJNHP 2024). If site conditions permit, it would be advisable to protect the remaining plants from deer browse. It might also be worthwhile to check on the plants during their fruiting period to determine whether a sufficient number of pollinators are available or if manual pollination should be considered in order to maintain the population.

It is possible that additional occurrences of *Cleistes divaricata* could be found in the state. There are a few historic collection sites that have not been searched and suitable habitat might still exist in the vicinity (NJNHP 2024). The species may also have been overlooked at some locations, as the orchids are sometimes concealed among the many graminoid species that typically share their habitat in New Jersey (Stone 1910, Calazza and Fairbrothers 1980). During a survey to evaluate the effects of life-state on detectability, Kéry and Gregg (2003) found that *Cleistes bifaria* was not easy to perceive—even in plots where the species was known to be present only about 80% of the vegetative plants were found and the more conspicuous flowering individuals could also be missed if they were growing beneath ferns or shrubby plants.

Synonyms and Taxonomy

The accepted botanical name of the species is *Cleistes divaricata* (L.) Ames. Orthographic variants, synonyms, and common names are listed below (ITIS 2024, POWO 2024, USDA NRCS 2024b).

Botanical Synonyms

Cleistesiodopsis divaricata (L.) Pansarin & F. Barros
Pogonia divaricata (L.) R. Br.
Arethusa divaricata L.

Common Names

Spreading Pogonia
Rosebud Orchis
Large Dragonmouth Pogonia

"Conservative systematists view with justifiable horror and distress the multiplication of synonyms that has attended recent activities in species making, and in their opinion the likelihood of an increase in this real evil is intensified by the difficulties that usually arise when critical species, owing to uncertainties as to their final resting-place, are passed from one genus to another." So said Oakes Ames (1922) as he moved *C. divaricata* from the genus *Pogonia* into *Cleistes*. Near the end of the 20th century, molecular studies indicated that *Cleistes* was paraphyletic (Cameron et al. 1999, Cameron and Molina 2006, Pansarin et al. 2008) so Pansarin and de Barros (2008) transferred North American *Cleistes* into *Cleistesiodopsis*. There is strong support for *Cleistesiodopsis* as a monophyletic genus (Pansarin et al. 2012) and the subject of this profile is recognized as *Cleistesiodopsis divaricata* by many current sources (eg. Kartesz 2015, ITIS 2024, NatureServe 2024, POWO 2024, Weakley et al. 2024).

Three species of *Cleistes/Cleistesiodopsis* are presently known in the eastern United States but for about two centuries all North American *Cleistes* plants were referred to *C. divaricata*. Fernald (1946) first divided *C. divaricata* into what he described as "two rather strongly defined varieties"—the typical var. *divaricata* and the smaller var. *bifaria*. Further change resulted from research on the reproductive biology of *C. divaricata* by Katharine Gregg (1989, 1991a, 1991b). Gregg's findings supported the elevation of Fernald's var. *bifaria* to specific rank (Catling and Gregg 1992). Gregg (1991b) had also noted regional differences in floral morphology within the variety that became *C. bifaria*, and a subsequent study by Smith et al. (2004) found that *C. bifaria* included two genetically distinct groups that corresponded with the morphological disparities that Gregg had observed. Consequently, southeastern populations in the coastal plain and piedmont regions were transferred to *C. oricamporum* (Pansarin and Brown 2009).

Older references to *C. divaricata* may apply to a different *Cleistes* species or to more than one species (eg. Carr 1940). Franz et al. (2016) used *Cleistes divaricata* as an example of how a complex taxonomic history can cause confusion, and they included a figure that neatly illustrates the way that changes in the species' nomenclature have unfolded over time. LeGrand et al. (2022) suggested that Spreading Pogonia is no longer a suitable common name for this orchid since its use predates the division of *C. divaricata* into three species: They have proposed Large Spreading Pogonia as an alternative.

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