Crepidomanes intricatum

Weft Fern

Hymenophyllaceae

Crepidomanes intricatum courtesy Alan Cressler, Lady Bird Johnson Wildflower Center

***Crepidomanes intricatum* 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

February, 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. *Crepidomanes intricatum* 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. 15 pp.

Probably the most surprising discovery involving North American ferns has been the realization that several species of Hymenophyllaceae and Vittariaceae in the eastern United States exist primarily as gemmiferous gametophytes, either growing north of the range of the sporophytes or, in a couple of cases, with sporophytes produced rarely if ever. (Barbara Ertter, 2000)

Life History

Crepidomanes intricatum (Weft Fern) is an unusual fern in the Hymenophyllaceae (filmy fern family) that is only known as a gametophyte. In a typical fern gametophytes are tiny—often only one cell layer thick—but green and nutritionally independent. Normal gametophytes produce both male and female reproductive organs and the sperm swim to the eggs and fertilize them. The fertilized eggs develop into the leafy sporophytes that we recognize as ferns. Mature sporophytes produce spores, which are dispersed and develop into gametophytes under favorable conditions. (Raven et al. 1986). Unlike conventional ferns, *Crepidomanes intricatum* does not produce sex organs or a sporophyte generation. Instead, the gametophytes persist and reproduce vegetatively (Montgomery and Fairbrothers 1992, Farrar 2020). The threadlike branches are a single cell wide and they grow in dense, tangled clusters that resemble green mats (Farrar 1992, Duffy 2014). The mat-like colonies can range in size from less than 10 mm^2 up to 20 m^2 (Junxia et al. 1994).


Left: Courtesy Alan Cressler, Lady Bird Johnson Wildflower Center. Right: G. Glynn, 2022.

A colony of *Crepidomanes intricatum* could be mistaken for a patch of algae or a developing moss. In fact, the first description of a free-living filmy fern gametophyte in the United States was published in a nineteenth century book about fresh water algae, although the author noted that the plant was likely to be the prothallus of a fern based on the presence of abundant chloroplasts, rhizoids, and reproductive buds known as gemmae (Farrar 1992). Some of the distinguishing structures of *C. intricatum* can be observed in the field with a 20x hand lens, including the brownish rhizoids, gemmiferous cells, and gemmae (Charpentier and Green 2019). The gemmae are small clusters of cells located at the branch tips, and the gemmifers are single, flask-shaped cells that remain attached after the gemmae have been released (Yatskievych et al.

1986). No other species of Hymenophyllaceae are presently known to occur in New Jersey (Montgomery and Fairbrothers 1992, Kartesz 2015), but in places where they do the difference between *C. intricatum* and the gametophytes of other filmy ferns cannot be determined visually (Hill 2003, Weakley et al. 2022).

According to Spencer (2013), Weft Fern gametophytes are best seen from early March through November. However, the gametophytes are perennial (Farrar 2020) so they are likely to be present year round but may be less conspicuous during the winter months. *Trichomanes speciosum*, another fern that can sustain gametophytic populations, is green when well-hydrated but changes color upon drying (Rumsey et al. 1998).

Crepidomanes intricatum was first described as *Trichomanes intricatum* (Farrar 1992), and the original name is still widely used (see Synonyms section). A molecular study by Ebihara et al. (2008) found that the fern shared a chloroplast genome with an east Asian species, *Crepidomanes schmidtianum*, and was more closely aligned with *Crepidomanes* than with *Trichomanes*. Consequently, the species has only recently been transferred to *Crepidomanes* (Weakley et al. 2011). *Crepidomanes schmidtianum* ranges from the Himalayan region east to Korea, where it grows as an independent gametophyte (Lee et al. 2020), and Japan where it is a sterile triploid species (Ebihara et al. 2008). The close relationship between the two widely separated ferns has raised some interesting questions regarding the origin and distribution of the species complex (see Ebihara et al. 2008, Duffy 2014, Pinson et al. 2017).

Pollinator Dynamics

Pollination does not occur in any ferns, and *Crepidomanes intricatum* does not reproduce sexually. Although the gametophytes may occasionally develop gametangia (gamete-producing organs) no sporophytes have ever been observed. Instead, the species persists via perennial growth and branching and by the production of gemmae (Farrar 1992, 2020). Filmy ferns develop gemmae at the tips of their branches. A gemma usually grows perpendicular to the stem axis, developing 3–4 cells before it is released. Once detached, a brown scar at the separation site remains visible for some time (Stokely 1948). Subsequent stem growth can push old gemmiferous cells into lateral positions (Farrar 1992).

The absence of sexual reproduction in *Crepidomanes intricatum* results in colonies that are genetically uniform (Morse 1994). Although the evolutionary history of *C. intricatum* is unclear, it is possible that the fern has persisted in the gametophyte state for tens of thousands of years (Farrar 1990) so there is little evidence that the species has been hindered by a lack of genetic diversity. Kuo et al. (2017) suggested that either genetic adaptations or microhabitat conditions could inhibit the production of gametangia in *C. intricatum* and similar ferns. The fact that *C. intricatum* gametophytes have not been coaxed to produce sporophytes, even in controlled conditions that would promote sporophyte development in related species, supports the former hypothesis (Farrar 1990). Nevertheless, the possibility that a cryptic population of *C. intricatum* still produces sporophytes somewhere in North America has not been completely ruled out (Farrar 1992).

Seed Dispersal

Most ferns are distributed by spores rather than seeds, but since *Crepidomanes intricatum* does not produce spores the gemmae are its primary means of dispersal. Detached gemmae that reach suitable substrates can develop rhizoids and establish as independent plants (Stokely 1948). An advantage of gemmae is that they are able to develop into new gametophytes more rapidly than spores (Raine and Sheffield 1997), although they are produced in much lower quantities and their large size may inhibit some types of dispersal (Duffy 2014).

Wind was initially proposed as a mechanism for the movement of gemmae (Farrar 1967), but the relatively large size of the propagules and the fact that *Crepidomanes intricatum* often grows in sheltered locations led to the conclusion that transport by water or animals was more likely (Farrar et al. 1983, Yatskievych et al. 1986, Farrar 1998). Wind may still play a role, particularly in local dispersal (Dassler and Farrar 2001, Farrar 2003), although Charpentier and Green (2019) cited unpublished research demonstrating that gemmae are too large to be wind dispersed.

Some Weft Fern gemmae are simply dispersed by gravity, which probably contributes to the densely tangled growth in established colonies. Water can facilitate movement over short distances, and some gemmae are likely to be carried to new locations by insects or other animals that forage near the plants. When animals that reside in rockhouses move to new shelters they may also serve as dispersal agents. Adherence to slugs has proven to be an effective means of dispersing the asexual propagules of some mosses, and gemmae might also adhere to the feet or feathers of birds. The fine strands of *Crepidomanes intricatum* gametophytes could additionally be utilized by some birds as nesting material. (See Farrar 1998, Dassler and Farrar 2001, Farrar 2003, Pinson et al. 2017).

The absence of *Crepidomanes intricatum* from suitable habitats in proximity to occupied sites suggests that successful colonization does not occur frequently (Farrar 1992), and the majority of dispersal takes place over relatively short distances (Dassler and Farrar 2001, Farrar 2003). However, there is evidence that long distance dispersal has occurred in the past since *C. intricatum* has managed to establish at a number of locations that were glaciated during the Pleistocene era (McAlpin and Farrar 1978, Yatskievych et al. 1986, Parks 1989). It is not clear whether that movement was achieved by vegetative propagules or if it was facilitated by a sporophyte-producing ancestor that no longer exists (Farrar 1990).

Habitat

Crepidomanes intricatum is most likely to be found growing on rocks in microsites that are cool, moist, and sheltered. The species has been reported at elevations from 150–1,800 meters above sea level, and the colonies are often located in regions with steep, canyonlike topography and mature forests. Typical habitats are rockhouses, caves, and crevices or ledges that are sheltered by overhanging rock. Sometimes the fern is found on boulders, and occasionally even on the bases of trees. The substrate is usually sandstone, shale, or other non-calcareous rock; in New Jersey the gametophytes were situated beneath outcrops of red shale. The microsites favored by *C. intricatum* are deeply shaded and moist. The primary sources of moisture may be wind-blown

rain, splashback from waterfalls, ceiling flow after a rainfall, or groundwater seepage (McAlpin and Farrar 1978, Farrar et al. 1983, Parks 1989, Montgomery and Fairbrothers 1992, Morse 1994, Walck et al. 1996, Farrar 1998, Spaulding et al. 2001, Gaddy 2002, Rhoads and Block 2007, Peck 2011a, Spencer 2013, Farrar 2020, NJNHP 2022, Weakley et al. 2022).

Sheltered areas like caves and rockhouses can reduce exposure to both seasonal and daily temperature variations, keeping conditions inside the sites more moderate than those outside during both winter and summer (Walck et al. 1996, Farrar 1998, Pinson et al. 2017). Some of the sites where *Crepidomanes intricatum* occurs remain moist year-round, but others may become dry periodically (Farrar et al. 1983). *C. intricatum* can tolerate drying or freezing from time to time but grows best at sites where desiccation or sub-zero temperatures are rare (Parks 1989, Farrar 1998). Walck et al. (1996) noted that fern gametophytes and gemmae are generally more tolerant of drying or freezing than the sporophytes. The site conditions that favor *C. intricatum* gametophytes may have been less well suited to sporophyte survival and thus contributed to the loss of an alternate generation in the species (Sheffield 1994, Kreig and Chambers 2021).

The majority of plants that occur in association with *Crepidomanes intricatum* are bryophytes or other ferns (Farrar 1998). *Vittaria appalachiana*, another fern that lives as an independent gametophyte, has similar ecological requirements and the two species may be found together where their ranges overlap (Parks 1989). Parks observed that when they co-occurred the *C. intricatum* gametophytes were usually hanging down in tufts from the upper surface of the rock crevice or on a vertical wall in a narrow crack while those of *V. appalachiana* were most often at the very back of a crevice or on the lower surface. A number of herbaceous flowering plants endemic to sandstone rockhouses are discussed by Walck et al. (1996), but none of the species occur in New Jersey.

Farrar et al. (1983) pointed out that *Crepidomanes intricatum* had not been found in constructed sites such as road cuts, railroad tunnels, bridges, or quarries even when there were available spots that appeared to be comparable to natural places utilized by the species. It was not clear whether that was due to undetected differences in microsite characteristics or if it was attributable to dispersal patterns or limitations.

Wetland Indicator Status

Crepidomanes intricatum is not included on the National Wetlands Plant List (NWPL). Any species not on the NWPL is usually considered to be an upland plant (U. S. Army Corps of Engineers 2020).

USDA Plants Code (USDA, NRCS 2023)

TRIN13. The USDA lists the species as *Trichomanes intricatum* and does not presently provide an alternate code for *Crepidomanes intricatum*.

Coefficient of Conservatism (Walz et al. 2018)

CoC = 10. 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 *Crepidomanes intricatum* is restricted to eastern North America (POWO 2023, NatureServe 2023). The map in Figure 1 depicts the extent of the species in the United States. Peck (2011a, 2011b) has also reported it in Arkansas. Farrar et al. (1983) predicted that the fern would reach its northern limit in the mountainous region of southern Quebec, and NatureServe (2023) shows the species as present in that province.

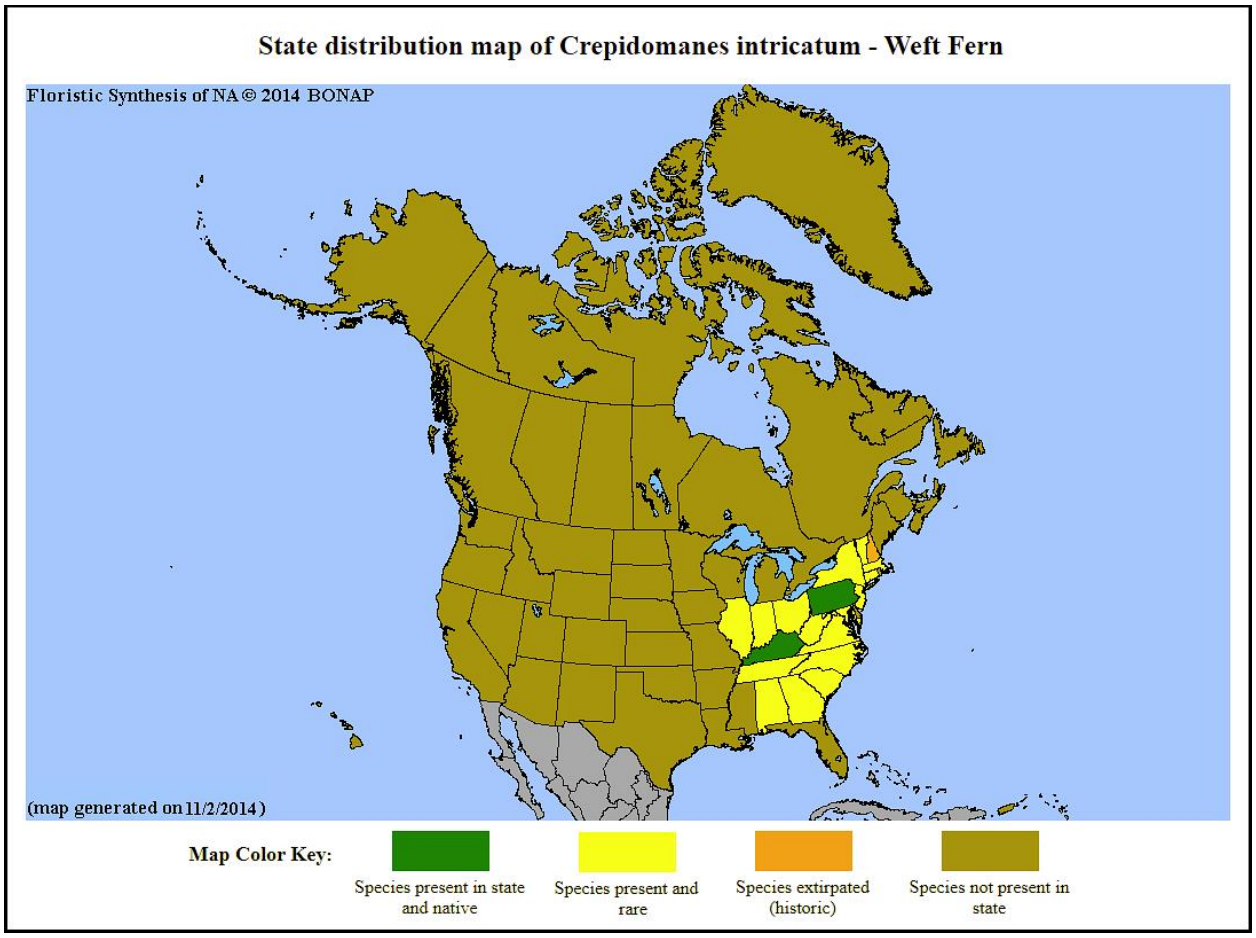

Figure 1. Distribution of C. intricatum in North America, adapted from BONAP (Kartesz 2015).

The USDA PLANTS Database (2023) shows records of *Crepidomanes intricatum* in one New Jersey county: Warren (Figure 2 below). The map reflects the current known distribution of the species in the state.

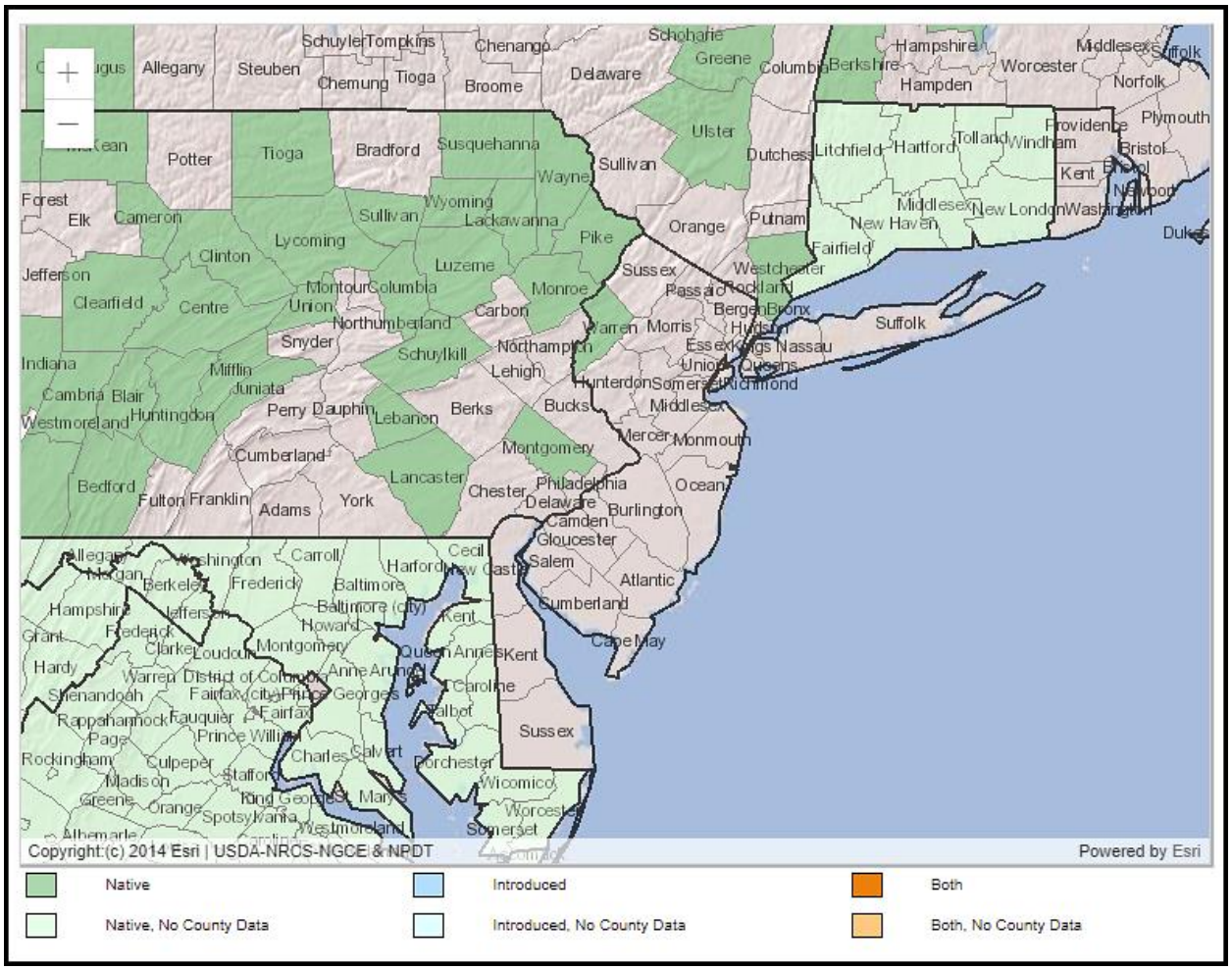

Figure 2. County records of C. intricatum in New Jersey and vicinity (USDA NRCS 2023).

Conservation Status

Crepidomanes intricatum has a global rank of G4G5, meaning there is some uncertainty as to whether it should be considered apparently secure or secure. A G4 species has a 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 local recent declines, threats, or other factors. A G5 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 *Crepidomanes intricatum* throughout its range. The species is vulnerable (moderate risk of extinction) in two states, imperiled (high risk of extinction) in one state, critically imperiled (very high risk of extinction) in four states, and possibly extirpated in New Hampshire and West Virginia. *C. intricatum* is unranked in other districts where it has been reported.

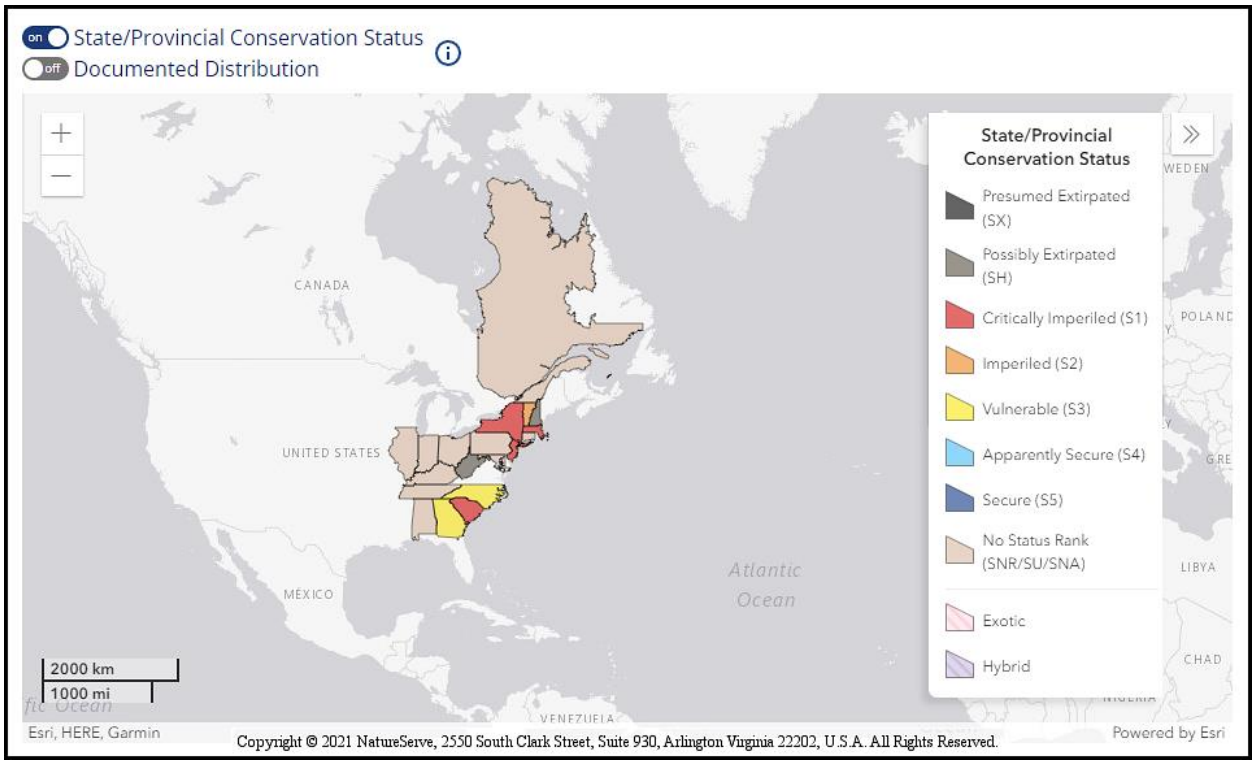

Figure 3. Conservation status of C. intricatum in North America (NatureServe 2023).

Crepidomanes intricatum is ranked S1.1 in New Jersey (NJNHP 2022), meaning that it is critically imperiled due to extreme rarity. A species with an S1.1 rank has only ever been documented at a single location in the state. *C. intricatum* 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 plant 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).

New Jersey's only known occurrence of *Crepidomanes intricatum* was documented by Donald Farrar in 1981 during a study of independent gametophytes in the eastern United States that resulted in the initial description of the species (Farrar et al. 1983, Farrar 1992). Another collection was made at the site in 1988, but subsequent searches of nearby habitat have not turned up any additional occurrences (NJNHP 2022).

Threats

The sites where *Crepidomanes intricatum* grows are often relatively secluded and inaccessible so the gametophytes face few local threats from disturbance or human activity (Farrar 1998). No specific threats were noted for the New Jersey occurrence of *Crepidomanes intricatum*, although it has been 35 years since the colony was last observed (NJNHP 2022).

Some other populations, particularly at lower elevations, could be extirpated if the downstream damming of a canyon river inundated the site where the Weft Fern was growing. Canopy removal in the vicinity of *Crepidomanes intricatum* colonies could result in reduced temperature moderation, greater exposure to the elements, and disturbance of the natural moisture regime (Farrar 1998).

In intact sites, *C. intricatum* populations in rockhouses and caves that are somewhat protected from the elements may be less vulnerable to extreme conditions resulting from climate change than plant species which grow in more open habitats. However, in places that are experiencing more frequent or longer droughts in combination with higher temperatures, changes in moisture availability could make some locations unsuitable for the gametophytes. Climate-driven impacts to canopy trees in the forests that shelter *C. intricatum* sites could have similar results. The loss of suitable habitat would probably increase the species' risk of extirpation due to its limited capacity for dispersal to favorable locations.

Management Summary and Recommendations

A site visit to New Jersey's only extant population of *Crepidomanes intricatum* is recommended in order to assess the current status of the species in the state. There is also some potential for the discovery of new occurrences via careful searches of suitable habitat, as it has often been noted that the gametophyte is inconspicuous and can easily be overlooked or mistaken for a bryophyte (Morse 1994, Mehrhoff 1995, Spencer 2013).

There are many aspects of *Crepidomanes intricatum* that beg for research. For example, additional investigations of the population genetics of *C. intricatum* and its near relatives could provide more insight into the origin, evolution, and current distribution of the fern. According to Pinson et al. (2017), "virtually no studies have been undertaken that attempt to determine the underlying factors inhibiting sporophyte production in ferns." From a management perspective, explaining how Weft Fern is dispersed to new locations might be the most important area of focus for potential research (Farrar 1998). While working with a related species, Raine and Sheffield (1997) demonstrated that gemmae can be used to grow new gametophytes ex situ. Kreig and Chambers (2021) have suggested that gametophytic ferns be introduced to new sites to determine whether any given species could establish outside of its current geographic range. Cultured gemmae could also be utilized to evaluate the ability of *C. intricatum* to establish on different substrates within its current range, which might provide some additional insights regarding its dispersal, local distribution, and adaptability.

Synonyms

The accepted botanical name of the species is *Crepidomanes intricatum* (Farrar) Ebihara & Weakley. Orthographic variants, synonyms, and common names are listed below. The species has only recently been transferred to the genus *Crepidomanes* (Weakley et al. 2011) and the synonym show below is still widely applied (eg. ITIS 2023, NatureServe 2023, POWO2023, USDA NRCS 2023).

Botanical Synonyms	Common Names
Trichomanes intricatum Farrar	Weft Fern Grotto-felt

References

Charpentier, Matthew and Laura Green. 2019. Habitat characterization and assessment of the northern range limit of the regionally rare *Crepidomanes intricatum* in Northeast North America. 2019 Les Mehrhoff Botanical Research Award Final Report. Available at http://www.rhodora.org/awards/mehrhoff/Mehrhoff-Report-Charpentier-Green-2019.pdf

Cressler, Alan. 2012. Cover photo of *Crepidomanes intricatum*. Courtesy of the Lady Bird Johnson Wildflower Center, https://www.wildflower.org/. Used with permission.

Cressler, Alan. 2015. Photo of *Crepidomanes intricatum* from Georgia. Courtesy of the Lady Bird Johnson Wildflower Center, https://www.wildflower.org/. Used with permission.

Dassler, Cynthia L. and Donald R. Farrar. 2001. Significance of gametophyte form in long-distance colonization by tropical, epiphytic ferns. Brittonia 53(2): 359–359.

Duffy, Aaron M. 2014. Synthesizing research and education: Ecology and genetics of independent fern gametophytes and teaching science inquiry and content through simulations. Ph.D. dissertation, Utah State University, Logan, UT. 128 pp.

Ebihara, Atushi, Donald R. Farrar, and Motomi Ito. 2008. The sporophyte-less filmy fern of eastern North America *Trichomanes intricatum* (Hymenophyllaceae) has the chloroplast genome of an Asian species. American Journal of Botany 95: 1645–1651.

Ertter, Barbara. 2000. Floristic surprises in North American north of Mexico. Annals of the Missouri Botanical Garden 87(1): 81–109.

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

Farrar, Donald R. 1967. Gametophytes of four tropical fern genera reproducing independently of their sporophytes in the southern Appalachians. Science 155: 1266–1267.

Farrar, Donald R. 1990. Species and evolution in asexually reproducing independent fern gametophytes. Systematic Botany 15(1): 98–111.

Farrar, Donald R. 1992. *Trichomanes intricatum*: the independent *Trichomanes* gametophyte in the eastern United States. American Fern Journal 82: 68–74.

Farrar, Donald R. 1998. The tropical flora of rockhouse cliff formations in the eastern United States. Journal of the Torrey Botanical Society 125(2): 91–108.

Farrar, Donald Ray. 2003. Gametophyte morphology and breeding systems in ferns. In Subhash Chandra and Mrittunjai Srivastava (eds.). Pteridology in the New Millennium. NBRA Golden Jubilee Volume. Kluwer Academic Publishers, Boston, MA. 542 pp.

Farrar, Donald R. Page updated November 5, 2020. *Trichomanes intricatum* Farrar. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico [Online]. 22+ vols. New York and Oxford. Accessed January 31, 2023 at http://floranorthamerica.org/Trichomanes_intricatum

Farrar, Donald R., J. C. Parks, and B. W. McAlpin. 1983. The fern genera *Vittaria* and *Trichomanes* in the northeastern United States. Rhodora 85: 83–92.

Gaddy, L. L. 2002. A Biological Survey for Plant Communities, Wetlands, and Rare Plants Associated with the Duke Power - Nantahala Area Relicensing Project Area, Macon, Jackson, and Swain Counties, North Carolina. Prepared for Duke Power company, Charlotte, NC. 35 pp.

Glynn, G. 2022. Photo of *Crepidomanes intricatum* from Vermont. Shared via iNaturalist at https://inaturalist.ca/observations/118459006, licensed by https://creativecommons.org/licenses/by-nc/4.0/

Hill, Steven R. 2003. Conservation assessment for Appalachian Bristle Fern (*Trichomanes boschianum* Sturm). Hill Center for Biodiversity Technical Report 2003 (5) Illinois Natural History Survey, Champaign, IL. 34 pp.

ITIS (Integrated Taxonomic Information System). Accessed January 31, 2023 at http://www.itis.gov

Junxia, Ji, Stephen J. Russell, Mary Gibby, and Johannes C. Vogel. 1994. A technique for the investigation of genetic variation in filamentous gametophytes of *Trichomanes* (Hymenophyllaceae). American Fern Journal 84(4): 126–130.

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)].

Kreig, Christopher P. and Sally M. Chambers. 2021. The ecology and physiology of fern gametophytes: A methodological synthesis. Applications in Plant Sciences 10(2): e11464. https://doi.org/10.1002/aps3.11464

Kuo, Li-Yaung, Cheng-Wei Chen, Wataru Shinohara, Atsushi Ebihara, Hiroshi Kudoh, Hirotoshi Sato, Yao-Moan Huang, and Wen-Liang Chiou. 2017. Not only in the temperate zone:

Independent gametophytes of two vittarioid ferns (Pteridaceae, Polypodiales) in East Asian subtropics. Journal of Plant Research 130(2): 255–262.

Lee, Chang Shook, Kanghyup Lee, and Youngsim Hwang. 2020. Identification of three independent fern gametophytes and *Hymenophyllum wrightii* f. *serratum* from Korea based on molecular data. Korean Journal of Plant Taxonomy 50(4): 403−412.

McAlpin, Bruce and Donald R. Farrar. 1978. *Trichomanes* gametophytes in Massachusetts. American Fern Journal 68(4): 97–98.

Mehrhoff, Leslie J. 1995. Additions to the primary checklist of vascular flora of Connecticut. Rhodora 97(889): 9–38.

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

Morse, Larry E. 1994. *Trichomanes intricatum* conservation status factors. NatureServe, Arlington, VA. Accessed January 31, 2023 at https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.154804/Trichomanes_intricatum

NatureServe. 2023. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed January 31, 2023 at https://explorer.natureserve.org/

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.

Parks, James C. 1989. Distribution of gametophytic populations of *Vittaria* and *Trichomanes* in Pennsylvania. Rhodora 91(866): 201–206.

Peck, James H. 2011a. New and noteworthy additions to the Arkansas fern flora. Phytoneuron 30: 1–33.

Peck, James H. 2011b. History of Arkansas pteridophyte studies with a new annotated checklist and floristic analysis. Phytoneuron 38: 1–39.

Pinson, Jerald B., Sally M. Chambers, Joel H. Nitta, Li-Yaung Kuo, and Emily B. Sessa. 2017. The separation of generations: Biology and biogeography of long-lived sporophyteless fern gametophytes. International Journal of Plant Science 178(1): 1–18.

POWO. 2023. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Accessed January 31, 2023 at http://www.plantsoftheworldonline.org/

Raine, C. A. and E. Sheffield. 1997. Establishment and maintenance of aseptic culture of *Trichomanes speciosum* gametophytes from gemmae. American Fern Journal 87(3): 87–92.

Raven, Peter H., Ray F. Evert and Susan E. Eichhorn. 1986. Biology of Plants. Worth Publishers, New York, NY. 775 pp.

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

Rumsey, F. J., A. C. Jermy, and E. Sheffield. 1998. The independent gametophytic stage of *Trichomanes speciosum* Willd. (Hymenophyllaceae), the Killarney Fern and its distribution in the British Isles. Watsonia 22: 1–19.

Sheffield, E. 1994. Alternation of generations in ferns: Mechanisms and significance. Biological Reviews of the Cambridge Philosophical Society 69(3): 331–343.

Spaulding, Daniel D., J. Mark Ballard, and R. David Whetstone. 2001. Pteridophytes of Northeast Alabama and adjacent highlands IV: Polypodiales (Dryopteridaceae to Osmundaceae). Journal of the Alabama Academy of Science 72(4): 230–252.

Spencer, Elizabeth. 2013. New York Natural Heritage Program online conservation guide for *Crepidomanes intricatum*. Accessed December 17, 2021 at https://guides.nynhp.org/appalachian-bristle-fern/

Stokely, Alma G. 1948. Reproductive structures of the gametophytes of *Hymenophyllum* and *Trichomanes*. Botanical Gazette 109(4): 363–380.

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). 2023. PLANTS profile for *Trichomanes intricatum* (Weft Fern). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed January 31, 2023 at http://plants.usda.gov

Walck, Jeffrey L., Jerry M. Baskin, Carol C. Baskin, and S. Wilson Francis. 1996. Sandstone rockhouses of the eastern United States, with particular reference to the ecology and evolution of the endemic plant taxa. The Botanical Review 62(4): 311–362.

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, Alan S., Richard J. LeBlond, Bruce A. Sorrie, C. Theo Witsell, L. Dwayne Estes, Kanchi Gandhi, Katherine Gould Mathews and Atsushi Ebihara. 2011. New combinations, rank changes, and nomenclatural and taxonomic comments in the vascular flora of the southeastern United States. Journal of the Botanical Research Institute of Texas 5(2): 437–455.

Weakley, A. S. and Southeastern Flora Team. 2022. Flora of the Southeastern United States. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC. 2022 pp.

Yatskievych, George, Michael A. Homoya, and Donald R. Farrar. 1986. The fern genera *Vittaria* and *Trichomanes* in Indiana. Proceedings of the Indiana Academy of Science 96: 429–434.