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FLORA OF NORTHERN ALABAMA, PART 1.
FERNS AND LYCOPHYTES

DANIEL D. SPAULDING
Senior Curator
Anniston Museum of Natural History
800 Museum Drive
Anniston, Alabama 36206
dspaulding@annistonal.gov

JOHN W. SHORT
Senior Project Scientist
Weston Solutions, Inc.
1625 Pumphrey Avenue
Auburn, Alabama 36832
johnshor@gmail.com

T. WAYNE BARGER
Biology Professor
Southern Union State Community College
301 Lake Condy Road
Opelika, Alabama 36801
wayne_barger@yahoo.com

JOHN T. KARTESZ
BONAP Director
9319 Bracken Lane
Chapel Hill, North Carolina 27516
john_kartesz@yahoo.com

NOAH D. YAWN
Ecologist
Pennsylvania Natural Heritage Program
Western Pennsylvania Conservancy
800 Waterfront Drive
Pittsburgh, Pennsylvania 15222

ABSTRACT

This paper is a floristic guide to native and naturalized ferns and lycophytes found in northern Alabama. It includes identification keys, photographs, illustrations, maps, habitats, distributional data, pertinent synonymy, and comments for each taxon. The study area encompasses four of the state's five physiographic provinces, excluding plants that occur exclusively in the Coastal Plain.

Ferns and lycophytes are considered ancient plants with a long evolutionary history dating back over 400 million years. They were among the earliest land plants and became especially abundant during the Carboniferous period (358.9–298.9 million years ago), when vast coal-forming swamps dominated the landscape. These swamps gave rise to the extensive coal deposits that humans continue to exploit today. Over time, evolutionary advances in seed plants, combined with environmental changes, increased competition, and growing habitat specialization, contributed to the decline in dominance of ferns and lycophytes (Soltis et al. 2008).

Although unrelated, ferns and lycophytes share similar ecological and reproductive traits, leading to their frequent study together. Traditionally, botanists have grouped them under the term *pteridophytes* (meaning "feather-plants") or referred to them as ferns and fern allies (Clute 1905; Dean 1969; FNA 1993; Lellinger 1985; Small 1938; Thieret 1980). Because these plants lack flowers and seeds, pteridologists (fern specialists) often classified them as cryptogams ("hidden reproduction") alongside mosses, fungi, and algae (Smith 1938). Christenhusz and Chase (2014) noted that "fern allies have previously been loosely defined as vascular spore-bearing plants that are not ferns." Many of these so-called allies differ markedly from typical ferns, resembling rushes, mosses, tiny trees, tufts of grass, or exhibiting unique growth forms.

Historically, the term "fern allies" referred to a diverse assemblage of plants, often including clubmosses (*Lycopodiaceae*), firmosses (*Huperziaceae*), spikemosses (*Selaginellaceae*), quillworts (*Isoetaceae*), horsetails (*Equisetaceae*), whisk ferns (*Psilotaceae*), grape ferns and adder's-tongues (*Ophioglossaceae*), and water ferns (*Marsileaceae* and *Salviniaceae*). However, these families do not share a common ancestor, rendering them a paraphyletic group (Smith et al. 2006). Advances in molecular systematics have since clarified these relationships, reshaping fern classification. DNA-based phylogenies show that only the lycophytes—clubmosses, firmosses, spikemosses, and quillworts—form a monophyletic clade. The remaining "allied" families fall within the fern clade (Fig. 1), which is more closely related to seed plants than to lycophytes (Christenhusz & Chase 2014). Although pteridologists no longer recognize pteridophytes as a formal taxonomic group, the word remains informally used to describe all spore-bearing vascular plants.

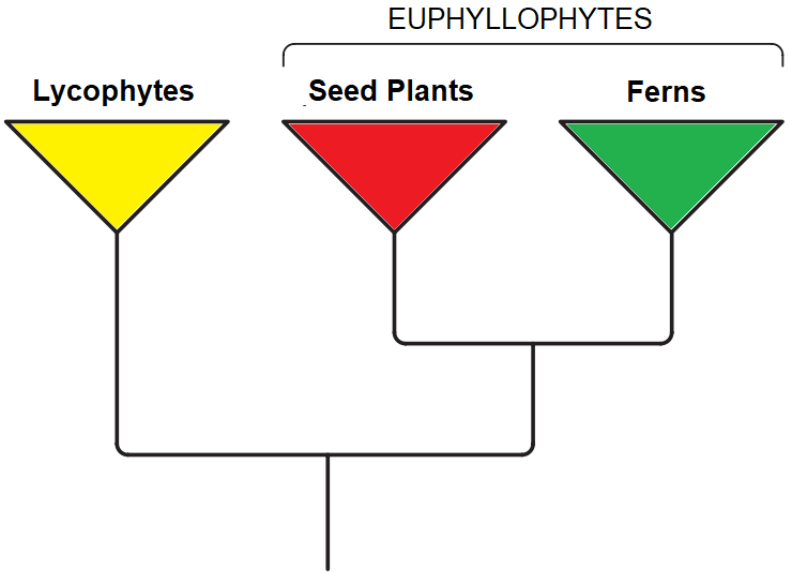


Figure 1. Phylogeny depicting relationships of vascular plant lineages (adapted from Smith et al. 2006).

Ferns and lycophytes are vascular plants that reproduce by spores and undergo a life cycle known as alternation of generations (Fig. 2). This cycle has two distinct phases: a sexual gametophyte stage and an asexual sporophyte stage. The familiar, conspicuous plant seen in nature—the sporophyte—is typically diploid (2n) and produces spores through meiosis, each with half the chromosome number of the parent. Specialized structures called *sporangia* (singular: *sporangium*) release these spores into the environment, where they develop into small haploid (n) gametophytes. These, in turn, produce gametes for sexual reproduction, completing the cycle.

Spore dispersal mechanisms vary between passive and active strategies. Lycophytes and some ferns rely on passive dispersal, where sporangia gradually open or break down, allowing wind or water to transport the spores. Conversely, most ferns—particularly those in Polypodiales (Table 4)—use an active dispersal mechanism. Their sporangia feature a ring of specialized thick-walled cells called the *annulus*, which resembles a segmented worm crawling on top of the spore case. As the sporangium dries, the annulus contracts, then snaps forward suddenly, ejecting spores in a catapult-like motion. This explosive dehiscence creates a fine "spore dust" of individual spores that can travel great distances, thus facilitating colonization across diverse environments (Moran 2004). If a spore lands in a suitable habitat, it germinates into the gametophyte called a *prothallus*. Gametophytes are often cordate (heart-shaped), though in some species they may be ribbon-like, strap-shaped, or even filamentous (Fig. 3). While most gametophytes are terrestrial, some grow underground (subterranean), on plants (epiphytic), on rocks (epipetric), or in aquatic habitats, where they may be submerged or floating.

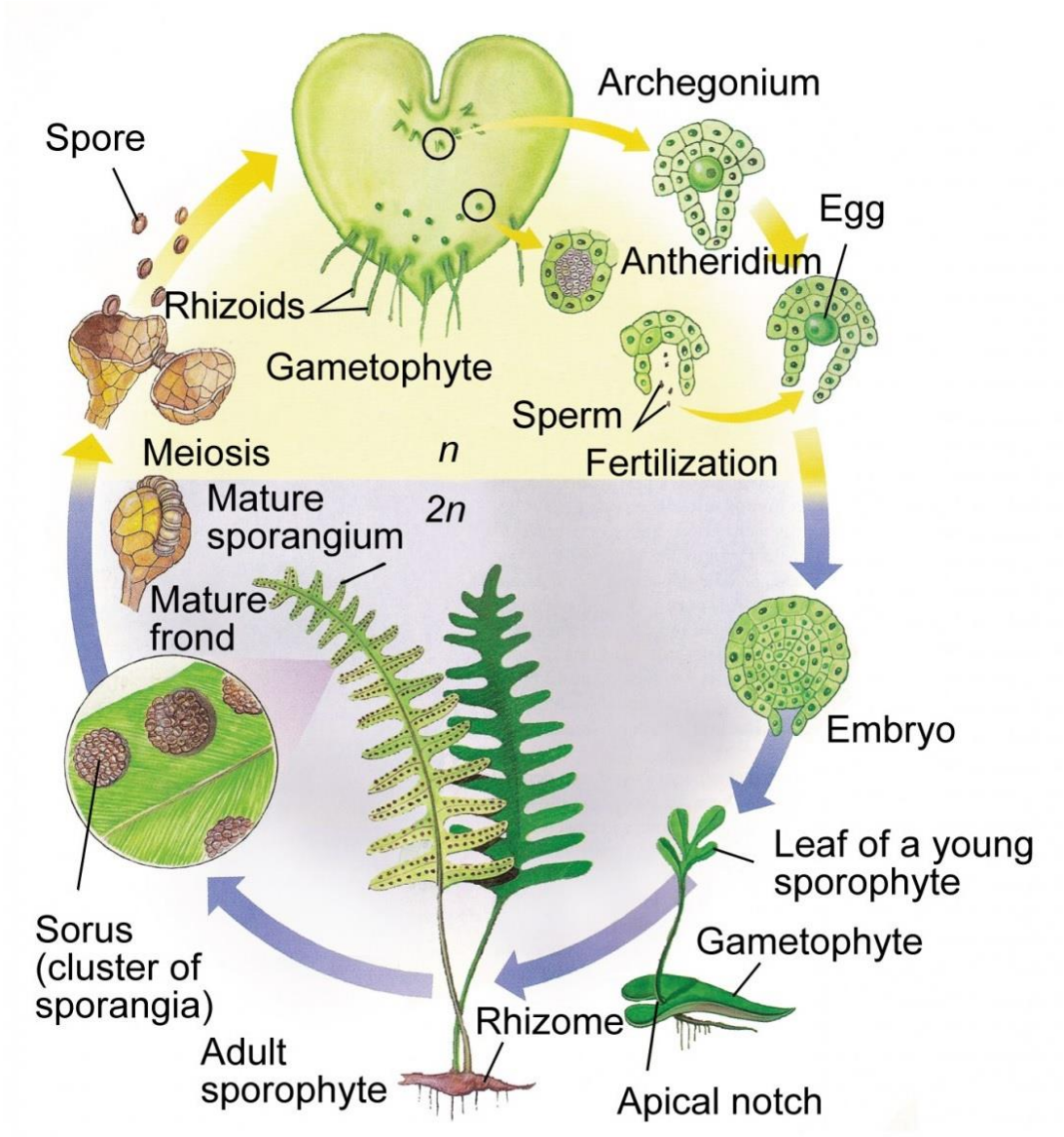


Figure 2. Illustration of alternation of generations (<www.gotalktogetherdotcom.wordpress.com/?s=Ferns>).

The gametophyte is an independent generation capable of photosynthesis but occasionally relies upon mycorrhizal fungi for nutrition. Slender, root-like *rhizoids* typically anchor it to the substrate. Since it is haploid, the gametophyte produces gametes through mitosis rather than meiosis. On the undersurface of the prothallus, specialized reproductive structures called *antheridia* generate male gametes (sperm), while *archegonia* produce female gametes (eggs). The sperm, equipped with flagella, swim through water to reach and fertilize an egg, forming a *zygote* that develops into a new sporophyte. However, in some fern species, the sporophyte stage is absent, and the gametophyte reproduces exclusively through asexual budding from structures called gemmae (Christenhusz & Chase 2014).

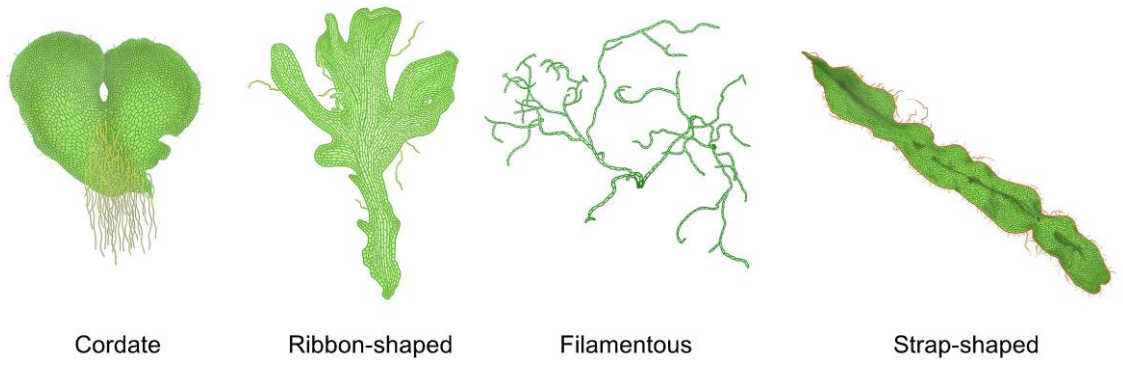


Figure 3. Various morphologies of fern gametophytes, illustrated by Simon Parsons (Pinson et al. 2017).

While ferns and lycophytes share a similar life cycle, they differ significantly in their vascular systems and leaf morphology. The stems of ferns possess a *siphonostele*, a complex vascular system with distinct *xylem* and *phloem* tissues that efficiently transport water and nutrients. In contrast, lycophyte stems have a *protostele* (Fig. 4a), a simpler vascular strand, which often limits their growth potential (Foster & Gifford 1974). Most ferns have *megaphylls*—leaves with multiple branching veins and leaf stalks (petioles). However, some groups deviate from this pattern: whisk ferns (*Psilotum*) bear tiny, veinless scales called *enations*, while horsetails (*Equisetum*) have highly modified leaves fused into sheaths. Lycophytes, by comparison, have *microphylls*—leaves with a single, unbranched vein and no petiole (Fig. 4b). The microphylls of clubmosses and spikemosses are usually less than 1 cm long, whereas, in quillworts (*Isoetes*), they are grass-like and significantly longer.

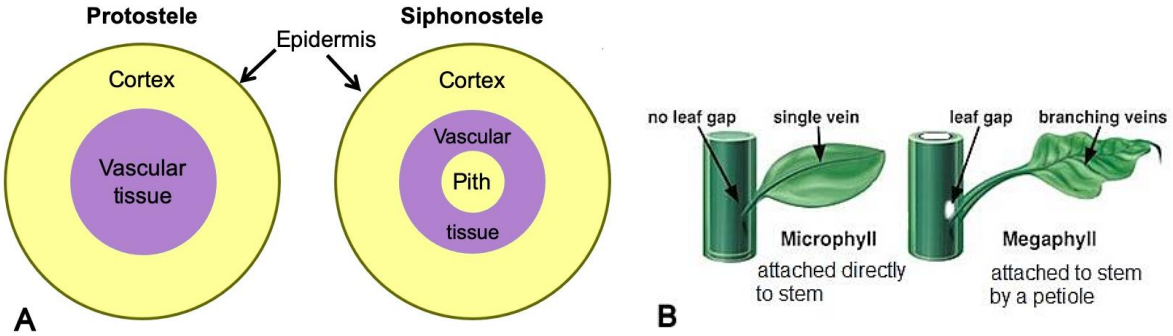


Figure 4. Distinguishing characteristics of lycophytes and ferns. **A.** Lycophyte protostele and fern siphonostele (<www.digitalatlasofancientlife.org/>). **B.** Lycophyte and fern leaves: microphylls versus megaphylls (<www.slideserve.com/dympna/plant-evolution#google_vignette>).

Most ferns produce sporangia on the undersides of leaves, typically arranged in clusters called *sori* (singular: *sorus*) along the veins or near the edges of the leaf segments (Fig. 5a). The shape, position, arrangement, and covering of these sori vary widely among species. In many ferns, a thin, protective membrane known as the *indusium* (plural: *indusia*) covers each sorus (Fig. 5c–e). This scale-like structure may appear circular, crescent-shaped, linear, kidney-shaped, or irregular, depending on the species. The indusium shields the developing spores from environmental stress and usually persists until the spores reach maturity. At maturity, the indusium dries or withers, allowing for the release of the spores. Some ferns lack indusia (Fig. 5b), while others possess a false indusium—a flap formed when the leaf margin folds over the sori (Fig. 5f).

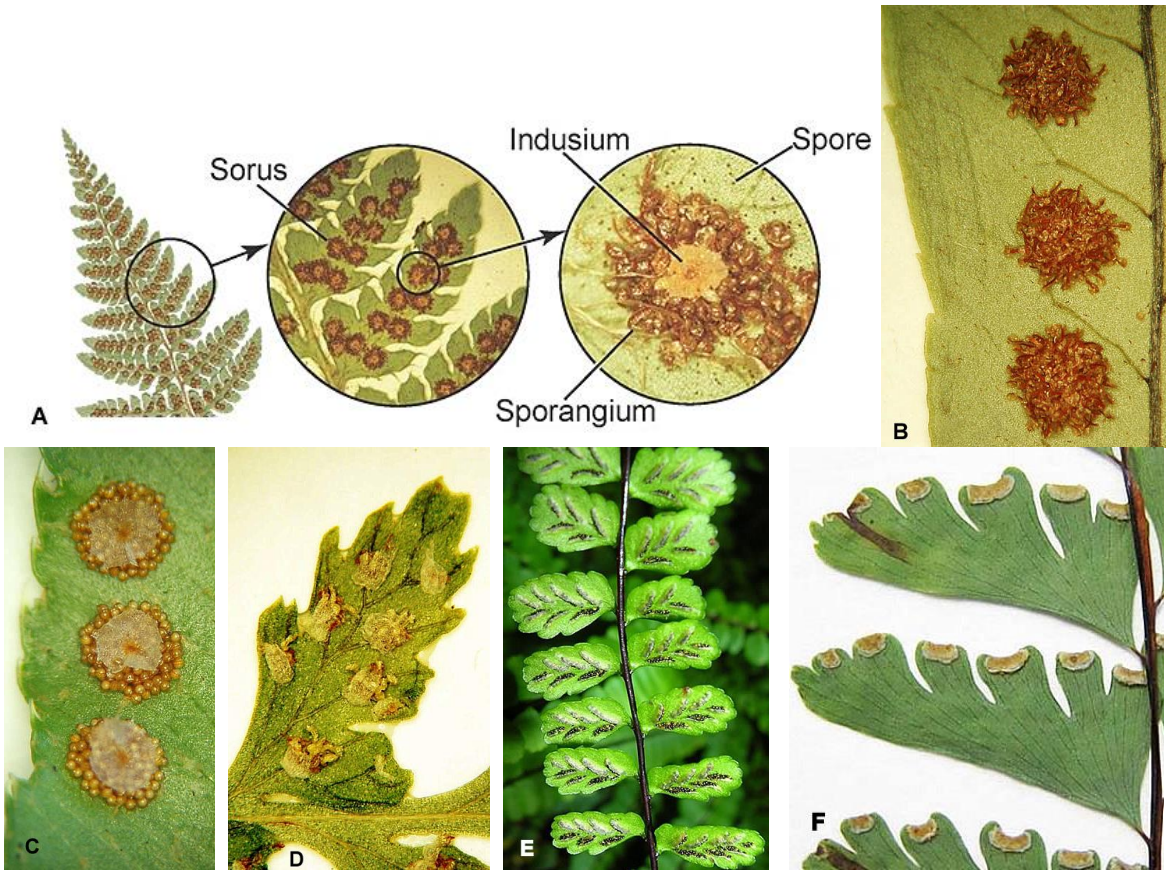


Figure 5. A. Anatomy of a typical fern sori. **B.** Sori lacking indusia. **C.** Sori with umbrella-like indusia. **D.** Sori with hood-like indusia. **E.** Sori with linear indusia. **F.** Sori covered by a false indusia (rolled-under segment margin). <www.fs.usda.gov/wildflowers/beauty/ferns/structure.shtml.>

Unconventional ferns, once treated as fern allies, employ different reproductive strategies. Horsetails produce cone-like *strobili* (singular: *strobilus*) borne at stem tips (Fig. 6a). Each strobilus consists of an axis with whorls of umbrella-shaped *sporangiophores*. In contrast, whisk ferns bear fused clusters of sporangia that form cylindrical or slightly elongated synangia (Fig. 6b). Members of the adder's-tongue family develop fronds divided into a sterile, photosynthetic *trophophore* and a fertile *sporophore* bearing sporangia (Fig. 6c). By comparison, water ferns enclose their sporangia in hard, pill-like *sporocarps* (Fig. 7). These compact, durable structures not only shield the spores from desiccation and other environmental threats but also enhance dispersal, particularly in aquatic habitats where they may float or remain viable in the substrate until conditions are favorable for germination.

Figure 6. Illustrations of non-typical fern reproductive structures. **A.** *Equisetum* strobili, Helen Sharp, 1892. **B.** *Psilotum* synangia, Walter Hood Fitch, 1838. **C.** *Ophioglossum* frond, Giuseppe Bonelli, 1773.

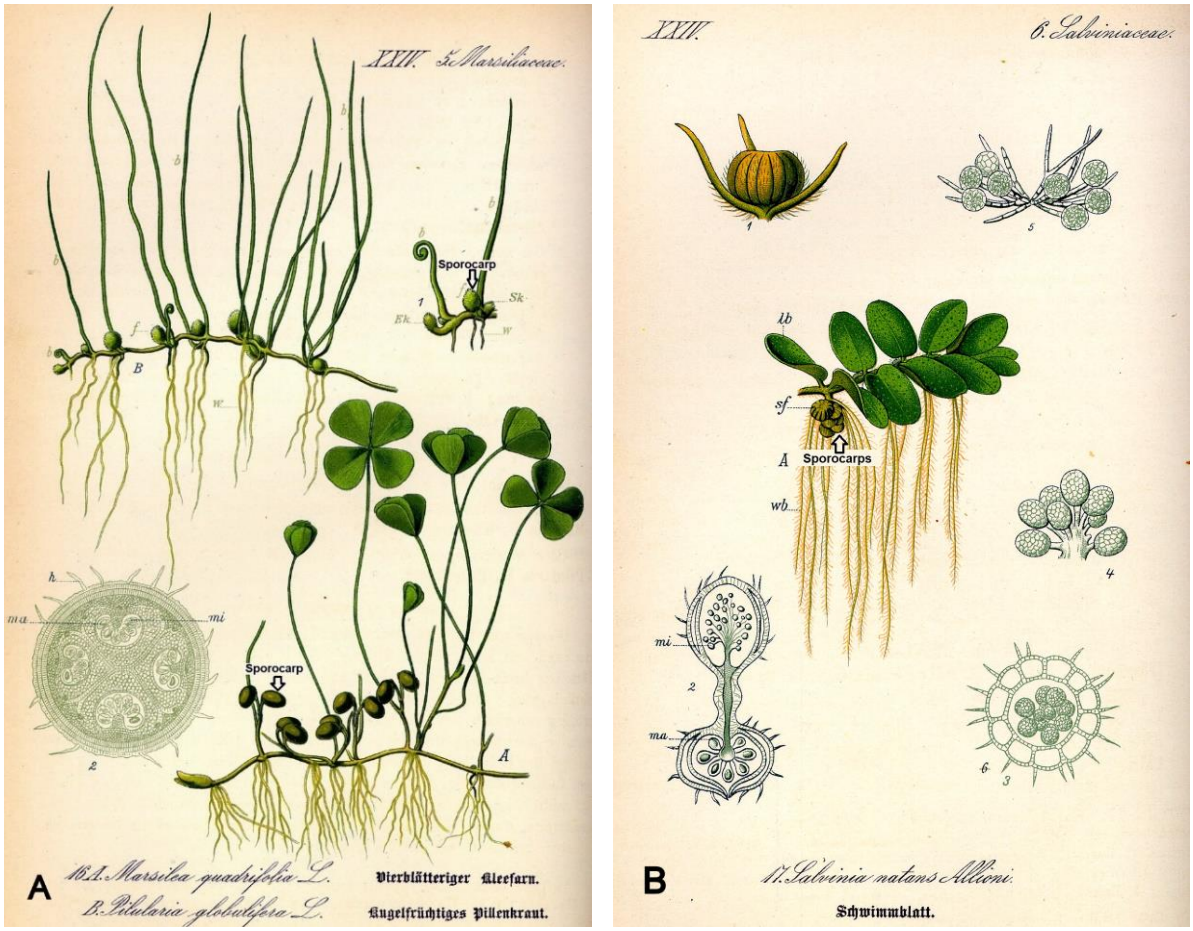


Figure 7. Sporocarps in Marsileaceae and Salviniaceae, illustrations by Otto Wilhelm Thomé, 1885.

Lycophytes have specialized leaves called *sporophylls*, which bear a single sporangium on the upper surface of the leaf next to the stem. Unlike ferns, which typically produce many sporangia per leaf, lycophytes produce only one per sporophyll. In clubmosses (Fig. 8a) and spikemosses (Fig. 8b), sporophylls cluster at branch tips to form cone-like structures known as *strobili*. Whereas, firmosses (Fig. 8c) and quillworts (Fig. 8d) do not produce strobili; their sporophylls resemble the sterile leaves.

Figure 8. Illustrations of species in lycophyte families. **A.** Lycopodiaceae (Clubmoss family), *Lycopodium clavatum* by Édouard Maubert, 1872. **B.** Selaginellaceae (Spikemoss family), *Selaginella willdenowii* by William Jackson Hooker, 1831. **C.** Huperziaceae (Firmoss family), *Huperzia selago* by James Sowerby, 1807. **D.** Isoetaceae (Quillwort family), *Isoetes echinospora* by Walter Hood Fitch, 1863.

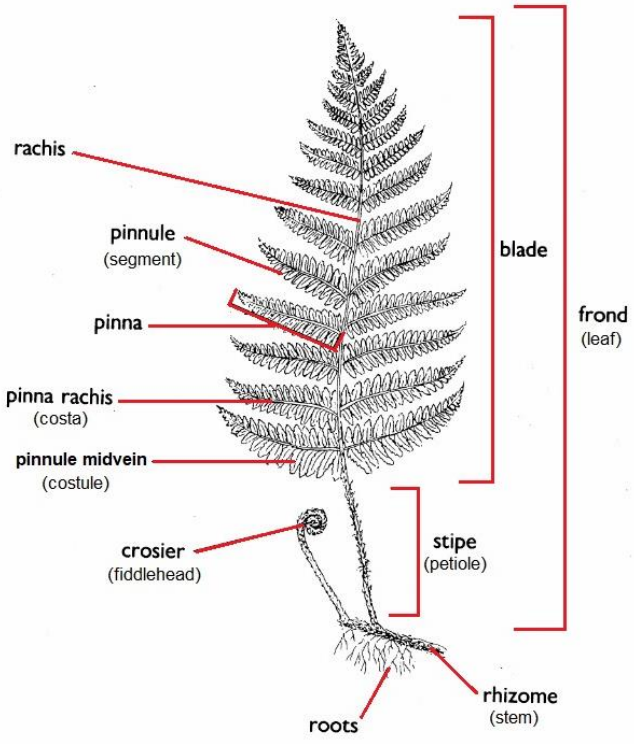


Figure 9. Anatomy of a typical fern, Illustration: Edgar M. Paulton (Mickel 1994).

Classic ferns have distinctive leaves called *fronds*, which arise from a root-like stem known as a *rhizome*. Each frond has two main parts: the blade and the petiole (or *stipe*). Young fronds first emerge as tightly coiled fiddleheads, or *crosiers*, which gradually uncurl as they expand. In undivided fronds, the blade's central axis is the midrib; in divided fronds, it is called the *rachis*. In many species, the blade divides into primary leaflets called *pinnae* (singular: *pinna*), each with its own midrib, the *costa* (plural: *costae*). These may subdivide into *pinnules*, which bear a central vein, the *costule* (plural: *costules*). Pinnules can divide again into still finer units, sometimes termed *pinnulets*. The smallest divisions of the frond are the *ultimate segments*, representing its final level of dissection (Fig. 9).

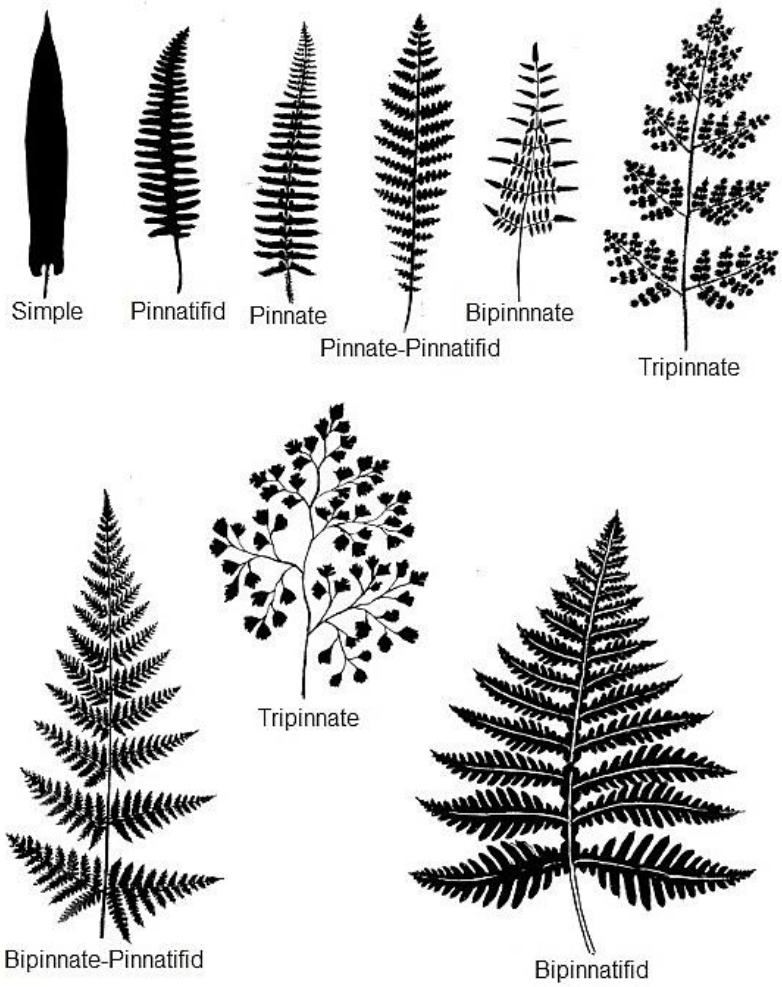


Figure 10. Frond dissection of ferns, Illustration: Edgar M. Paulton (Mickel 1994).

Fronds display a wide range of divisions, from entire, undivided blades to highly intricate forms with multiple levels of segmentation (Fig. 10). These patterns often produce the characteristic feathery appearance seen in many fern species. A frond may be *simple*, with a continuous blade, or *pinnatifid*, with shallow cuts that nearly reach the midrib, giving the rachis a winged appearance. *Pinnate* fronds divide once into distinct leaf segments; *bipinnate* (2-pinnate) fronds divide twice; and *tripinnate* (3-pinnate) fronds divide three times. In some instances, the secondary divisions stop short of the midvein (costa or costule) of the pinna or ultimate segment. Botanists describe this intermediate condition as *pinnatifid* dissection (e.g., pinnate-pinnatifid). Occasionally, fronds are palmately compound or lobed, with segments radiating from a central point like the fingers of a hand.

Fern leaves typically serve two functions: photosynthesis for food production and spore generation for reproduction. Although fertile fronds may appear slightly narrower or taller than vegetative fronds, they often resemble sterile fronds. Since these leaves are similar in shape and size, they are usually called *monomorphic* fronds. However, some fern species display *dimorphic* fronds, with a single plant producing two distinct leaf types (Fig. 11). In some species, only part of the frond exhibits modifications, such as seen in the Royal Fern (*Osmunda spectabilis*) and Christmas Fern (*Polystichum acrostichoides*). In others, like the Sensitive Fern (*Onoclea sensibilis*) and Netted Chain Fern (*Lorinseria areolata*), the fertile fronds differ morphologically in a substantial way from sterile ones. The difference is so extreme in the Cinnamon Fern (*Osmundastrum cinnamomeum*) that fertile fronds lack blade tissue, consisting only of veins and sporangia.

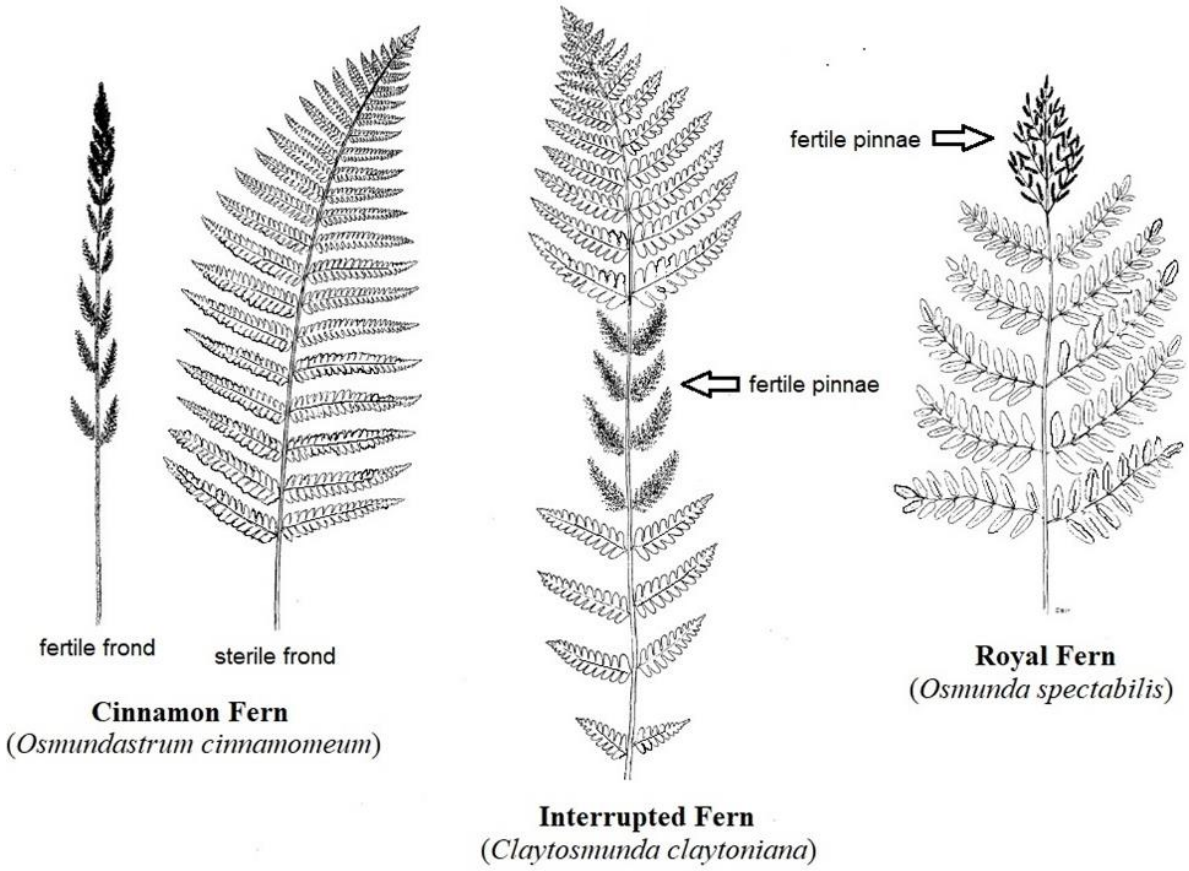


Figure 11. Three expressions of frond dimorphism among closely related species in the Osmundaceae. Illustrated by Edgar M. Paulton (Mickel 1994).

In this publication, we provide a historical overview and detailed analysis of 111 fern and lycophyte taxa documented from northern Alabama, comprising 104 species and 7 hybrids. Of these, 91 are native and 20 are introduced. Within the study area, 36 taxa are of conservation concern (Tables 1–3). Two species are of particular significance, both federally listed as threatened (LT): *Asplenium scolopendrium* var. *americanum* (American Hart's-Tongue Fern) and *Leptogramma burksiorum* (Alabama Streak-Sorus Fern). Overall, this treatment accounts for roughly 80% of the state's pteridophyte flora, which totals 145 taxa—134 species and 11 hybrids—of which 118 are native and 27 are exotic (Kartesz 2025).

Table 1. Lycophytes and ferns of conservation concern in northern Alabama.

Scientific Name	Vernacular Name	State Rank [/Federal Rank]	Global Rank
Asplenium abscissum	Cutleaf Spleenwort	S1	G3
Asplenium bradleyi	Bradley's Spleenwort	S2	G4
Asplenium ×ebenoides	Scott's Spleenwort	S1	GNR
Asplenium ×gravesii	Graves' Spleenwort	S1	GNR
Asplenium ×kentuckiense	Kentucky Spleenwort	S1	GNR
Asplenium monanthes	Single-Sorus Spleenwort	S1	G4
Asplenium ×reverterum	Reverted Spleenwort	S1	GNR
Asplenium ruta-muraria var. *cryptolepis*	American Wall-Rue	S1	G5T5 (variety secure)
Asplenium scolopendrium var. *americanum*	American Hart's-Tongue Fern	S1/LT*	G5T3 (variety vulnerable)
Asplenium ×trudellii	Trudell's Spleenwort	S1	GNR
Astrolepis integerrima	Southwestern Cloak Fern	S1	G5
Bryodesma corallinum	Sandstone Bluff Spikemoss	S2	G4
Bryodesma rupestre	Ledge Spikemoss	S2S3	G5
Claytosmunda claytoniana	Interrupted Fern	S1	G5
Cystopteris tennesseensis	Tennessee Bladder Fern	S2	G5
Dendrolycopodium obscurum	Princess-Pine	S1	G5
Didymoglossum petersii	Dwarf Filmy Fern	S2	G4
Dryopteris australis	Dixie Wood Fern	S1	GNR
Dryopteris celsa	Log Fern	S2	G4
Dryopteris ×cressleri	Cressler's Wood Fern	S1	GNR
Equisetum arvense	Field Horsetail	S2	G5
Huperzia ×bartleyi	Bartley's Firmoss	S1	GNR
Huperzia lucidula	Shining Firmoss	S1	G5
Huperzia porophila	Rock Firmoss	S1	G4
Hymenophyllum tayloriae	Taylor's Filmy Fern	S1	G2
Isoetes appalachiana	Appalachian Quillwort	S2	G4
Isoetes butleri	Limestone Quillwort	S2S3	G4
Isoetes graniticola	Flat Rock Quillwort	S1	G2
Isoetes melanopoda subsp. *melanopoda*	Black Foot Quillwort	S1	G5T5 (variety secure)
Isoetes piedmontana	Piedmont Quillwort	S2	G3
Leptogramma burksiorum	Alabama Streak-Sorus Fern	S1/LT*	G1
Lycopodium clavatum	Running Clubmoss	S1	G5
Lygodium palmatum	American Climbing Fern	S1	G4
Pellaea glabella	Smooth Cliffbrake	S1	G5
Pilularia americana	American Pillwort	S1	G5
Sceptridium jenmanii	Dixie Grape Fern	S1	G3

*LT= Federally listed threatened species

Table 2. Definition of state ranks.

Code	Designation	State Rank Definition
S1	Critically Imperiled	At high risk of extirpation because of extreme rarity (5 or fewer occurrences of very few remaining individuals or acres) or because of some factor(s) making it especially vulnerable to extirpation from Alabama.
S2	Imperiled	At risk of extirpation because of rarity – very restricted range, very few populations, steep declines, or other factors making it very vulnerable to extirpation from Alabama.
S3	Vulnerable	Rare or uncommon in Alabama – at moderate risk of extirpation due to a restricted range, relatively few populations, recent and widespread declines, or other factors.
S4	Apparently Secure	May be uncommon, but not rare. May have some cause for long-term concern due to declines or other factors.
S5	Secure	Demonstrably secure in Alabama; common, widespread, and abundant in the state.
SX	Presumed Extirpated	Species or community is believed to be extirpated from Alabama. Not located despite intensive searches of historical sites and other appropriate habitat, and virtually no likelihood that it will be rediscovered.
SH	Historical	Species or communities occurred historically in Alabama, and there is some possibility that they may be rediscovered. Its presence may not have been verified in the past 20–40 years.

Table 3. Definition of global ranks.

Code	Designation	Global Rank Definition
G1	Critically Imperiled	At very high risk of extinction due to extreme rarity (often 5 or fewer populations), very steep declines, or other factors.
G2	Imperiled	At high risk of extinction due to very restricted range, very few populations (often 20 or fewer), steep declines, or other factors.
G3	Vulnerable	At moderate risk of extinction due to a restricted range, relatively few populations (often 80 or fewer), recent and widespread declines, or other factors.
G4	Apparently Secure	Uncommon but not rare; some cause for long-term concern due to declines or other factors.
G5	Secure	Common; widespread and abundant.
GX	Presumed Extinct	Not located despite intensive searches and virtually no likelihood of rediscovery.
GH	Historical	Possibly Extinct. Known from only historical occurrences but still some hope of rediscovery.
GNR	Globally not ranked	Taxa not ranked to date. In reference to hybrids, the complex nature of hybridization, combined with their variability and context dependency, makes it challenging to create a global ranking system that accurately reflects their status.

Table 4. Classification of pteridophytes of northern Alabama.

CLADE	CLASS	ORDER	FAMILY	GENUS
LYCOPHYTES	Lycopodiopsida	Lycopodiales	Huperziaceae	*Huperzia*
			Lycopodiaceae	*Dendrolycopodium* *Diphasiastrum* *Lycopodiella* *Lycopodium* *Pseudolycopodiella*
		Isoetales	Isoetaceae	*Isoetes*
		Selaginellales	Selaginellaceae	*Bryodesma* *Didiclis* *Selaginella*
FERNS	Equisetopsida	Equisetales	Equisetaceae	*Equisetum*
	Psilotopsida	Psilotales	Psilotaceae	*Psilotum*
		Ophioglossales	Ophioglossaceae	*Botrypus* *Ophioglossum* *Sceptridium*
	Polypodiopsida	Osmundales	Osmundaceae	*Claytosmunda* *Osmunda* *Osmundastrum*
		Hymenophyllales	Hymenophyllaceae	*Crepidomanes* *Didymoglossum* *Hymenophyllum* *Vandenboschia*
		Schizaeales	Lygodiaceae	*Lygodium*
		Salviniales	Salviniaceae	*Azolla* *Salvinia*
			Marsileaceae	*Marsilea* *Pilularia*
		Polypodiales	Pteridaceae	*Adiantum* *Astrolepis* *Myriopteris* *Pellaea* *Pteris* *Vittaria*
			Dennstaedtiaceae	*Hypolepis* *Pteridium* *Sitobolium*
			Cystopteridaceae	*Cystopteris*
			Diplaziopsidaceae	*Homalosorus*
			Aspleniaceae	*Asplenium*
			Woodsiaceae	*Woodsia*
			Onocleaceae	*Onoclea*
			Blechnaceae	*Anchistea* *Lorinseria*
			Athyriaceae	*Anisocampium* *Athyrium* *Deparia*
			Thelypteridaceae	*Amauropelta* *Christella* *Leptogramma* *Macrothelypteris* *Pelazoneuron* *Phegopteris* *Thelypteris*
			Dryopteridaceae	*Arachniodes* *Cyrtomium* *Dryopteris* *Polystichum*
			Polypodiaceae	*Pleopeltis* *Polypodium*

METHODS AND FORMAT OF THE FLORA

The study area in northern Alabama extends across two major physiographic divisions: the Interior Plains and the Appalachian Highlands (Fig. 12). Following the framework of Fenneman (1938), the Interior Plains are represented in Alabama by the Interior Low Plateaus Province (Highland Rim Section), while the Appalachian Highlands include three provinces—the Appalachian Plateaus (Cumberland Plateau Section), the Ridge and Valley (Southern Section), and the Piedmont Plateau (Piedmont Upland Section). Our flora does not treat vascular plants restricted to the Coastal Plain. For further discussion of Alabama's geologic and phytogeographic regions, see page 301.

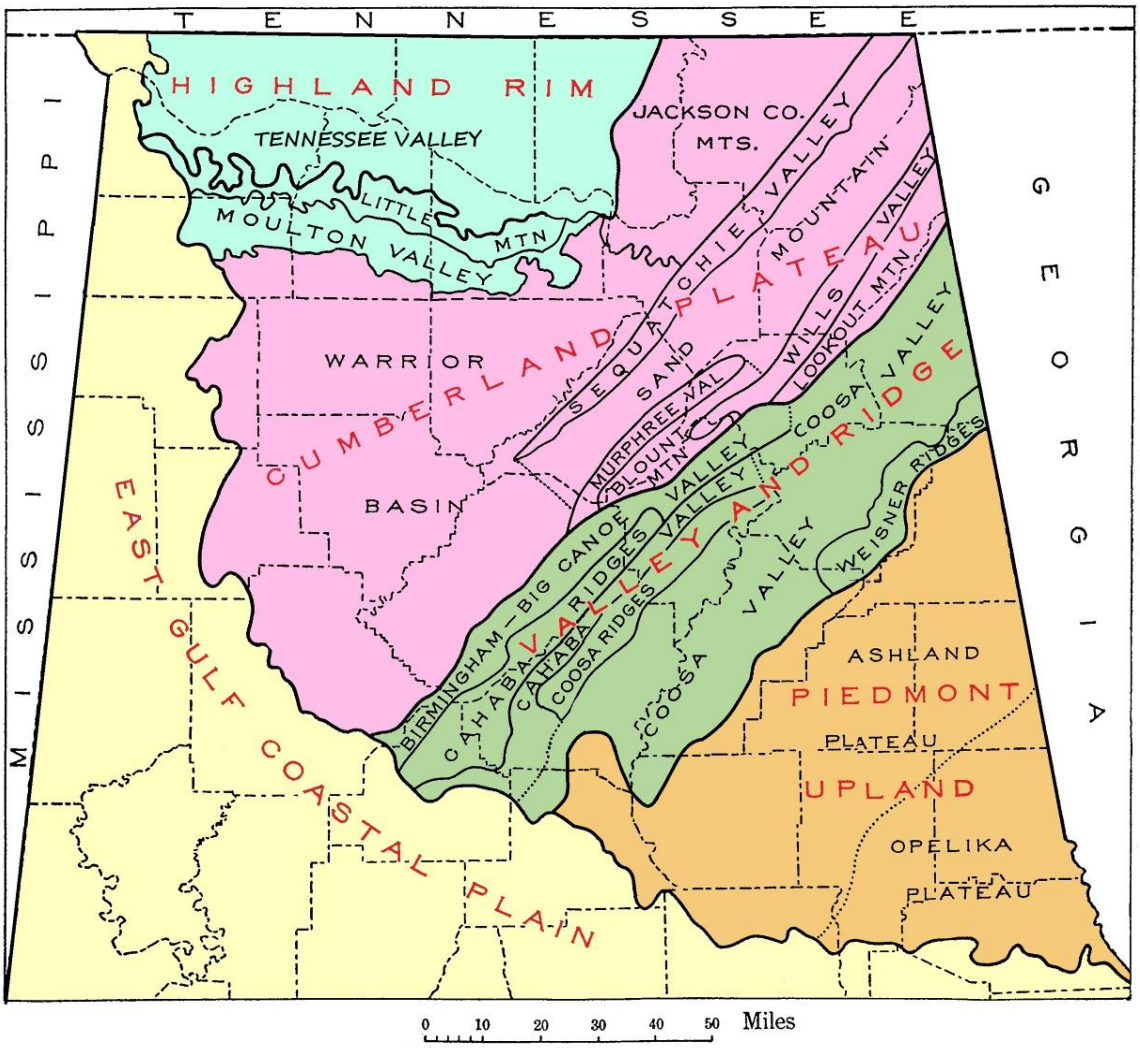


Figure 12. Map of northern Alabama's physical divisions (adapted and modified from Johnston 1930).

According to Johnson's (1930) physiographic map, the study area includes 34 counties within the Highland Rim, Cumberland Plateau, Ridge and Valley (also called Valley and Ridge), and Piedmont Upland (Fig. 13a–b). The Warrior Basin District of the Cumberland Plateau extends into northeastern Lamar County along the Buttahatchee River and its tributaries, and the Piedmont reaches the northeast corner of Russell County along Mill Creek and Holland Creek (Adams et al. 1926). Because both counties contain only minor portions of the Appalachian Highlands, we exclude them from the study.

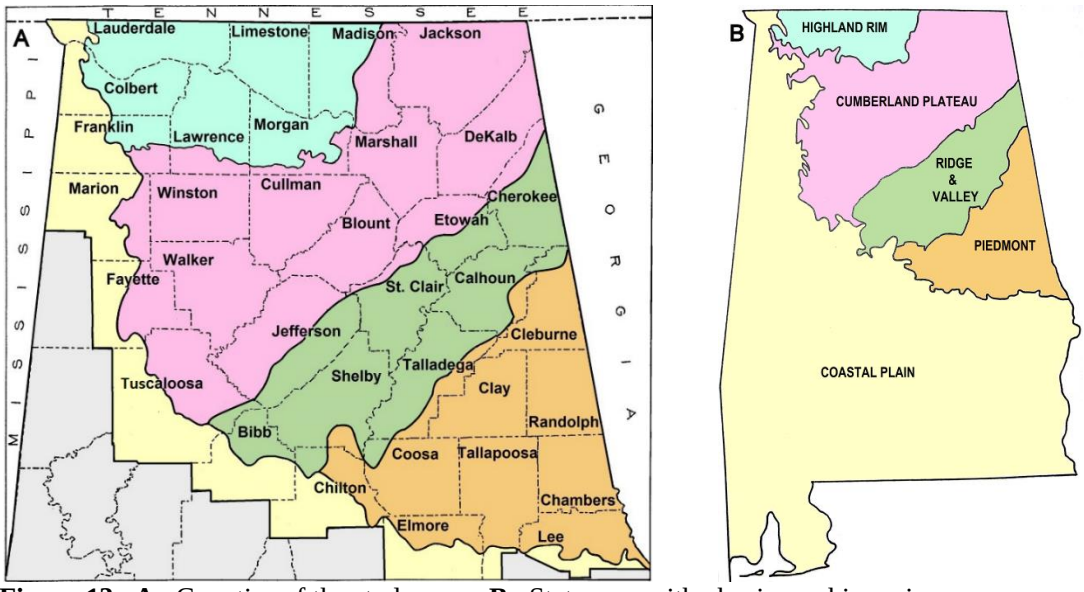


Figure 13. A. Counties of the study area. **B.** State map with physiographic regions.

County distribution maps with physiographic regions are provided for each species within the study area. Symbols indicate county-level occurrences within specific physiographic provinces (Table 5). Counties with multiple sections may display more than one symbol. Specimens were examined from various herbaria, and searches for online collections were conducted using the following resources: Alabama Plant Atlas (Keener et al. 2025), Floristic Synthesis of North America (Kartesz 2025), iNaturalist (2025), Southeast Regional Network of Expertise and Collections Data Portal (SERNEC 2024), and Southwestern Environmental Information Network (SEINet 2024). Vouchered specimens accessed for this study were obtained from the following herbaria: ALNHS, AMAL, APSC, AUA, AUM, BRIT, CATU, CM, DSC, DUKE, FLAS, FSU, GA, GH, JSU, KSP, LSU, MICH, MISS, MO, MSC, NCSC, NCU, NLU, NY, PH, SAMF, SIM, SMU, TENN, TROY, UNA, UNAF, UNCC, USF, UWAL, WCUH, WIS, WS, VDB, and VT. Herbarium acronyms follow the *Index Herbariorum* (Thiers 2016), and author name abbreviations adhere to Brummitt and Powell (1992).

Table 5. Map key to the symbols.

MAP KEY	
●	Native taxon, present in a physiographic area of the county
✪	Sensitive species, listed as imperiled or rare in Alabama
⭘	Introduced in the region but native to the southeastern USA
▼	Exotic taxon, adventive or naturalized in Alabama
✱	Waif: cultivated escape, likely not persisting in the wild

The phylogenetic arrangement of families and genera follows Weakley et al. (2025), while species are listed alphabetically. Generic names include the author and date of publication. Common names generally adhere to the formats outlined by Kartesz (2025) and Kartesz and Thieret (1991). Each taxon description follows a consistent sequence: scientific name and authority citation for specific and infraspecific taxa, including their etymology; vernacular name(s); synonyms; habit/duration; sporulation dates and frequency of occurrence in Alabama provinces; overall range and distribution; and additional comments. The derivation of scientific names is sourced primarily from Coombes

(1987), Diggs et al. (2006), Fernald (1950), the Flora of North America Committee (1993), Gledhill (1989), Neal (1992), Stearn (1983, 2002), and Stewart et al. (1983). For each genus, we also provide a suggested pronunciation (Jaeger 1960).

Frequency of occurrence is categorized as follows: **common**—abundant and widespread across a province; **frequent**—occurs throughout a province but not in large numbers; **uncommon**—restricted to scattered localities; **rare**—limited to 6–20 populations, often confined to specific habitats or regions; and **very rare**—restricted to five or fewer populations, typically narrow endemics, disjuncts, or peripheral taxa at the edge of their ranges.

The following publications were instrumental in developing the taxonomic keys: Brunton (2015); Clewell (1985); Diggs et al. (2006); Fernald (1950); Flora of North America Committee (1993); Gleason (1952); Gleason & Cronquist (1963); Haines (2011); Jones (2005); Lellinger (1985); Mohlenbrock (1967, 1975); Morton (1957); Nelson (2000); Radford et al. (1968); Rhoads & Block (2007); Sessa (2024); Short & Spaulding (2012); Small (1938); Smith (1994); Spaulding et al. (2000b, 2001a–c); Strausbaugh & Core (1997); Tennessee Flora Committee (2015); Thieret (1980); Wagner & Darling (1957); Weakley et al. (2025); Wherry (1961, 1964); Wofford (1989); and Yatskievych (1999). Specimens from Alabama herbaria and the Botanical Research Institute of Texas (BRIT) were also examined to aid in constructing the keys.

KEY TO FAMILIES

1. Gametophyte generation dominant, reproducing by gemmae (asexual buds), sporophytes absent or sterile; plants filamentous (forming felt-like mats) or ribbon-like (resembling liverworts); plants usually epipetric, often growing in moist rock crevices.

    2. Plant filamentous; sporophyte absent..... **Hymenophyllaceae** (*Crepidomanes*)
    2. Plant ribbon-like, resembling a liverwort; sporophyte absent, abortive, or occasionally present.

        3. Gemmae linear, arranged in single-celled rows (uniseriate); sporophytes linear and hairless.....**Pteridaceae** (*Vittaria*)
        3. Gemmae spatulate, with 2 or more cells near the apex; sporophytes ribbon-like with stellate (star-shaped) hairs .....**Hymenophyllaceae** (*Hymenophyllum*)

1. Sporophyte generation dominant, reproducing by spores, plant not filamentous or ribbon-like; plants epipetric, epiphytic, terrestrial, or aquatic.

    4. Leaves resembling a four-leaf clover (blade with 4 leaflets) ..... **Marsileaceae** (*Marsilea*)
    4. Leaves not clover-like.

        5. Plants grass-like.

            6. Plants epipetric on vertical bedrock or epiphytic .....**Pteridaceae** (*Vittaria*)
            6. Plants aquatic, amphibious, or terrestrial, occasionally in thin soil on flatrocks.

                7. Leaves tufted, tightly clustered on thick corm-like stems; sporangia enclosed in cavities at the leaf bases ..... **Isoetaceae**
                7. Leaves scattered on creeping stems; sporangia enclosed in sporocarps (hardened, bean-like structures) attached to the stem by short stalks ..... **Marsileaceae** (*Pilularia*)

5. Plants not grass-like.

    8. Plants floating on water or stranded on moist substrates, not rooted in soil ....**Salviniaceae**
    8. Plants rooted in soil, terrestrial or aquatic, or growing on rocks or trees.

        9. Plants resembling mosses, liverworts, or miniature coniferous trees; leaves reduced, simple, veinless or with a single midvein; sporangia borne singly in axils of leaves or within a cone-like strobili consisting of spirally-arranged modified leaves.

            10. Horizontal stems absent, all stems erect or pendant; sporangia borne on sporophylls similar to the sterile leaves; strobili absent..... **Huperziaceae**
            10. Horizontal stems present, with some stems erect or ascending; sporangia borne in strobili terminating the branches, with sporophylls dissimilar to the sterile leaves.

                11. Strobili usually quadrangular (four-sided), sessile at branch tips; plants heterosporous, producing spores of two sizes ..... **Selaginellaceae**
                11. Strobili cylindric, sessile at branch tips or borne on conspicuous stalks; plants homosporous, producing spores all of one size..... **Lycopodiaceae**

        9. Plants not resembling mosses, liverworts, or miniature coniferous trees; leaves various; sporangia three or more per leaf and variously arranged.

            12. Leaves inconspicuous, forming sheaths at the nodes or reduced to scale-like appendages; veins absent or solitary and unbranched; erect stems dominant.

                13. Stems ridged and hollow; nodes jointed; branches whorled at nodes or absent; leaves basally fused into sheaths, each with a single unbranched vein; sporangia in terminal, cone-like strobili; true roots present .....**Equisetaceae**
                13. Stems smooth and solid; nodes not jointed; branches dichotomous (Y-forked); leaves reduced to veinless, needle-like appendages; sporangia fused into 3-lobed synangia, each enclosed by a 2-lobed, bract-like structure along branches; true roots absent .....**Psilotaceae**

            12. Leaves conspicuous, with expanded blades; veins numerous and branched; erect stems present or absent.

                14. Plants vine-like, climbing on shrubs, trees, or fences; fronds with indeterminate growth (the frond itself forming an ever-growing 'vine,' with the rachis serving as the 'stem') ..... **Lygodiaceae**
                14. Plants not vine-like; fronds with determinate growth (ceases growing once mature).....**Key A**

Key A

1. Leaves simple, entire, not lobed or divided (though basal lobes may be present).

    2. Sporangia borne on a spike-like fertile branch (sporophore) arising from a common stalk with a photosynthetic leaf blade (trophophore); plants usually producing one leaf (rarely two) per growing season.....**Ophioglossaceae** (*Ophioglossum*)

2. Sporangia borne on the undersurfaces or margins of leaves, never on a separate fertile branch; plants producing many leaves throughout the growing season.

    3. Leaves less than 3 cm long; blades very thin between veins, nearly transparent, only one cell thick; sori solitary at leaf tips, each surrounded by a tubular cup-like structure with an exserted bristle; rhizomes thread-like, long-creeping and intertwined; plants usually growing on acidic rock ..... **Hymenophyllaceae** (*Didymoglossum*)
    3. Leaves more than 3 cm long; blades thicker, opaque, several cells thick; sori linear, borne on undersides of leaflets; rhizomes thicker, erect to ascending, not long-creeping; plants growing on calcareous rock..... **Aspleniaceae** (in part)

1. Leaves pinnatifid (deeply lobed but not cut to the midrib) or compound (dissected into distinct segments).

    4. Leaf blades 1–2-pinnatifid (at least on the sterile fronds), lobes not cut to the rachis (midrib), except sometimes near the base.

        5. Fronds strongly dimorphic, fertile (spore-bearing) leaves significantly dissimilar to sterile ones; leaves deciduous; plants terrestrial, rooted in soil.

            6. Sterile leaves mostly with opposite leaf segments; margins undulating to lobed; fertile leaves contracted into bead-like clusters ..... **Onocleaceae**
            6. Sterile leaves mostly with alternate leaf segments; margins serrulate; fertile leaves pinnate with linear sporangia lined in rows, not bead-like..... **Blechnaceae** (*Lorinseria*)

        5. Fronds monomorphic, sterile and fertile leaves similar; leaves deciduous or evergreen; plants terrestrial (in soil), epipetric (on rocks), or epiphytic (on trees).

            7. Leaf blades with transparent, needle-like hairs; leaf segments shallowly or deeply lobed; fronds deciduous..... **Thelypteridaceae** (*Phegopteris*)
            7. Leaf blades glabrous, scaly, or pubescent with brownish hairs; leaf segments unlobed or only slightly lobed (usually in lower pinnae); fronds evergreen.

                8. Sori round, indusia absent; petiole (leaf stalk) green or straw-colored; rhizomes long-creeping ..... **Polypodiaceae**
                8. Sori elongate, indusia present; petiole brown, at least near the base; rhizomes short-creeping, ascending, or erect .....**Aspleniaceae** (in part)

    4. Leaf blades pinnate, bipinnate, tripinnate, or more finely divided.

        9. Sporangia borne on a specialized fertile branch (sporophore) arising from a common stalk with a photosynthetic leaf blade (trophophore); plant usually producing one leaf (rarely two) per growing season.....**Ophioglossaceae** (in part)
        9. Sporangia borne on the undersurface or along the margin of a leaf, never on a separate fertile branch; plant producing many leaves through the growing season.

            10. Leaves very thin, nearly transparent, only one cell thick between veins; sporangia borne along margins of leaves in a tubular cup-like structure (involucre) with an exserted bristle; plant growing on acidic rock ..... **Hymenophyllaceae** (*Vandenboschia*)

10. Leaves thicker, blade tissue several cells thick and not transparent; sporangia borne on the underside or margins of leaflets (not in an involucre with an exserted bristle); plants growing in soil, on plants, or various types of rock..... **Key B**

Key B

1. Leaves 1-pinnate (pinnae toothed or unlobed) or 1-pinnate-pinnatifid.

2. Leaflets densely clothed with fringed or stellate (star-shaped) scales; sori covered by revolute (rolled-under) leaflet margin; plants on calcareous rock..... **Pteridaceae** (*Astrolepis*)
2. Leaflets smooth, hairy, or scaly but lacking fringed or stellate scales; sori not covered by a revolute margin of leaf segment; plants growing in soil, on trees, or on various rock types.

3. Leaves 1-pinnate, pinnae toothed, slightly lobed or entire, occasionally with a basal ear or lobe.

4. Petiole densely scaly; sori round ..... **Dryopteridaceae** (in part)
4. Petiole smooth, hairy, or with scattered scales, not densely scaly; sori elongate.

5. Leaves large, more than 30 cm long and 10 cm wide, deciduous; petiole and rachis grooved..... **Diplaziopsidaceae**
5. Leaves smaller, less than 30 cm long and 10 cm wide, evergreen; petiole and rachis not grooved.....**Aspleniaceae** (in part)

3. Leaves 1-pinnate-pinnatifid, pinnae deeply lobed.

6. Fronds dimorphic (leaves of two distinct forms), fertile segments lacking blade tissue, with sporangia borne on naked veins; young leaves clothed in woolly, cinnamon-colored hairs; rhizomes short-creeping, tips often erect, with large clustered leaves; sporangia lacking a well-defined annulus (row of thick-walled cells) .....**Osmundaceae** (in part)
6. Fronds monomorphic (leaves all similar), fertile leaf segments with blade tissue, sporangia borne on undersides of leaf segments; young leaves glabrous, scaly, or pubescent but never with woolly, brown hairs; rhizome short- or long-creeping with large or small leaves; sporangia with a well-defined annulus.

7. Veins partially netted, forming a series of chain-like loops along the midveins of leaflets; sori linear, arranged in chain-like rows parallel to the midveins; rhizomes long-creeping..... **Blechnaceae** (*Anchistea*)
7. Veins free, forked, or variously netted, never forming chain-like loops along the midveins; sori round or elongate, not aligned parallel with midveins; rhizome short- or long-creeping.

8. Leaf blades with transparent, needle-like hairs; sori with or without indusia; petiole bases smooth or with a few scales ..... **Thelypteridaceae** (in part)
8. Leaf blades glabrous or pubescent, lacking transparent, needle-like hairs; sori with indusia; petiole bases smooth to densely scaly.

9. Leaf blades narrow, usually less than 7 cm wide; sori elongate; petioles wiry, not grooved, brown to black at least near the base; leaves evergreen; plants epipetric (growing on rock).....**Aspleniaceae** (in part)
9. Leaf blades broader, usually more than 8 cm wide; sori round or elongate; petioles stout, grooved, blackish or straw-colored; leaves evergreen or deciduous; plants terrestrial (growing in soil) or epipetric.

10. Sori elongate; costae (leaflet midveins) and rachis hairy; vascular bundles 2 (appearing as thread-like strands) ..... **Athyriaceae** (*Deparia*)
10. Sori round; costae and rachis hairless, occasionally with scales; vascular bundles 3–5 ..... **Dryopteridaceae** (in part)

1. Leaves 2-pinnate or more divided (leaf blades cut at least twice near the base).

11. Fronds strongly dimorphic (fertile leaves smaller than sterile and greatly reduced at the apex); fertile segments lacking blade tissue, sporangia borne on naked veins; leaves usually robust (0.75–1 m long), clustered on short-creeping rhizomes, often with erect tips; stipules (flat, bract-like scales) present at leaf bases; sporangia without a well-defined annulus (row of thick-walled cells).....**Osmundaceae** (*Osmunda*)
11. Fronds monomorphic or only slightly dimorphic; fertile segments with blade tissue, sporangia borne on undersides of leaf segments; leaves robust or small, on short- or long-creeping rhizomes; stipules absent at leaf bases; sporangia with a well-defined annulus.

12. Sori continuous, forming linear clusters along leaflet margins, at least partially covered by revolute (rolled-under) edges.

13. Rachis (leaf axis) 3-branched, the petiole dividing into three main branches; leaf blades (three pinnae) broadly triangular; rhizome hairy, long-creeping, and deeply buried .....**Dennstaedtiaceae** (*Pteridium*)
13. Rachis unbranched; leaf blades not broadly triangular; rhizome scaly, short-creeping to erect, often exposed above ground surface.....**Pteridaceae**

12. Sori distinct, neither continuous nor covered by revolute leaflet margins.

14. Sori elongate.

15. Sori crescent-shaped, usually partly covering veins; leaves large (blade length > 12 cm long), deciduous (dying back in winter); petioles stout, with two vascular bundles (appearing as thread-like strands) ..... **Athyriaceae** (in part)
15. Sori straight, usually bordering veins only along one side; leaves small (blade length < 12 cm long); leaves evergreen (persisting through winter); petioles wiry, with a single vascular bundle .....**Aspleniaceae** (in part)

14. Sori round.

16. Leaf blades pubescent with clear, whitish, or silvery-gray hairs; glands present on leaves.

17. Hairs jointed with dark bands; glands long- or short-stalked; sori located along segment margins within a cup- or pouch-like indusia; rhizomes hairy, long-creeping, and deeply buried ..... **Dennstaedtiaceae** (in part)
17. Hairs transparent, needle-like, not jointed with dark bands; glands nearly sessile; sori scattered on the underside of the leaf blade, with tiny, round, and inconspicuous indusia; rhizomes scaly, short-creeping, and shallowly buried..... **Thelypteridaceae** (*Macrothelypteris*)

16. Leaf blades smooth, scaly, or with unicellular brownish hairs; glands present or absent on leaves.

18. Leaves evergreen (at least the sterile fronds); indusia round or kidney-shaped, attached on top of sorus; petiole densely covered with scales; vascular bundles more than 3..... **Dryopteridaceae** (in part)
18. Leaves deciduous; indusia hood- or cup-like and attached underneath the sori; petiole smooth or scaly; vascular bundles 2.

19. Petioles smooth or with a few scattered scales; veins reaching the leaf margins; old leaf stalks not persisting through winter; indusium hood-like or pocket-like, attached along one side of the sorus and arching over the sporangia..... **Cystopteridaceae**
19. Petioles distinctly scaly; veins ending before reaching the leaf margins; old leaf stalks persisting through winter; indusium not hood-like, but fully attached beneath the sorus, covering the sides and, at maturity, splitting into flaps that often form a star-shaped cup (these scale-like structures are deciduous and eventually fall off).....**Woodsiaceae**

1. HUPERZIACEAE (Firmoss Family) – in Lycopodiales

1. HUPERZIA Bernhardi 1801 {hyoo-PER-zee-uh}

[For Johann Peter Huperz (1771–1816), German botanist and fern horticulturist]

A distinctive reproductive feature of *Huperzia* is the production of specialized vegetative propagules known as *gemmae* (singular, *gemma*). These flattened and fan-shaped structures feature three main leaves and two smaller ones (Fig. 14a). Gemmae develop in the leaf axils of the current year's growth, typically in a whorl near the tip of the stem. These buds detach from the parent plant and give rise to new individuals, facilitating rapid and efficient colonization in suitable environments. The shape, size, and morphology of gemmae assist in identifying firmosses (Gilman & Testo 2015).

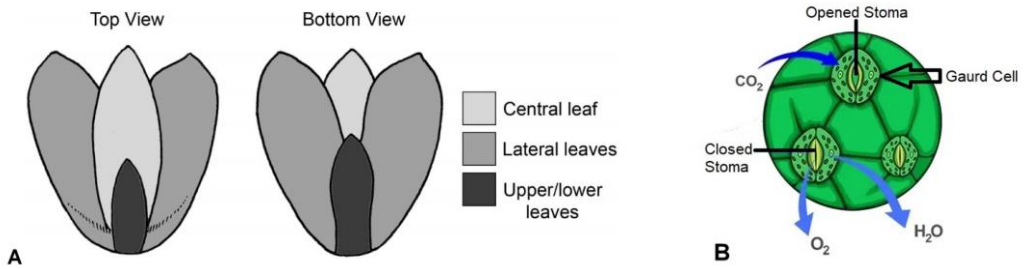


Figure 14. A. Diagram of the structure of a *Huperzia* gemma (Gilman & Testo 2015). **B.** Diagram of stomata on leaf undersurface. < https://www.geeksforgeeks.org/diagram-of-stomata-and-its-types>

The pattern and distribution of stomata on leaf surfaces provide valuable characters for distinguishing taxa. Stomata are microscopic pores, each bordered by a pair of kidney-shaped guard cells that regulate opening and closing (Fig. 14b). Stomatal density—defined as the number per unit area—can vary markedly among species, and differences between the upper and lower leaf surfaces often serve as valuable traits for taxonomic identification.

1. Plants growing in moist forest soil; erect stems in loose clusters; sporophylls (fertile leaves), distinctly shorter than vegetative leaves; stomata confined to lower leaf surfaces; vegetative leaves oblanceolate (widest above middle), upper margins serrate with irregular teeth; gemmae nearly as wide as long, lateral and central leaves broadly obtuse .....***Huperzia lucidula***
1. Plants growing on shaded sandstone ledges beneath cliffs or on boulders in rock shelters; erect stems usually in dense tufts; sporophylls similar in size or only slightly shorter than vegetative leaves; stomata present on both leaf surfaces, sometimes sparse above; leaves linear-lanceolate with roughly parallel sides (sometimes broadest near middle or base); upper margins of leaves entire (toothless) or sparsely denticulate with tiny teeth; gemmae usually longer than wide, lateral and central leaves acute to narrowly obtuse.

    2. Prostrate portion of stems short, plants mostly erect; sporophylls and vegetative leaves nearly equal in length; stomata frequent on upper leaf surface; spores normal, tetrahedral with three concave faces and one rounded..... ***Huperzia porophila***
    2. Prostrate portion of stems long-creeping, plants partially decumbent (stems lying flat at base with upper portion erect); sporophylls slightly shorter than vegetative leaves; stomata scarce on the upper surface of leaves; spores aborted, shrunken, and deformed .....***Huperzia ×bartleyi***

1. Huperzia ×bartleyi (Cusick) Kartesz & Gandhi {for Floyd Bartley, 1888–1974, Ohio botanist} — BARTLEY'S FIRMOSS; BARTLEY'S CLUBMOSS (Fig. 15). [*Lycopodium ×bartleyi* Cusick]

Figure 15. *Huperzia ×bartleyi*, Winston Co., Alabama, 13 Jun 2024. Photo: Dan Spaulding.

Plants epipetric or terrestrial in thin soil over rock; evergreen. Ledges of shaded sandstone cliffs or on boulders in rock shelters. Sterile hybrid reproducing readily by vegetative gemmae; very rare in the Warrior Basin District of the Cumberland Plateau (Fig. 16). Occurs throughout the geographic range of its parents in the eastern USA, mainly from northern Alabama to Wisconsin, Michigan, and Ohio, south to South Carolina (Kartesz 2025). The Alabama Natural Heritage program does not track *Huperzia ×bartleyi*, but we consider it critically imperiled (S1) in Alabama due to its rarity.

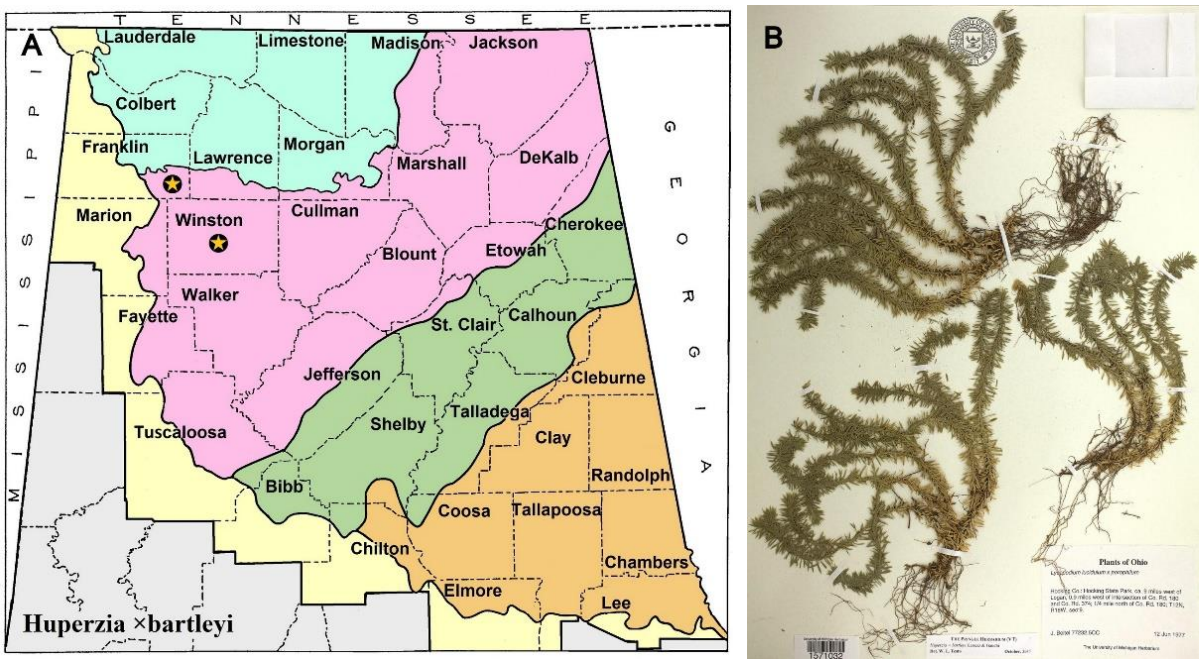


Figure 16. *Huperzia ×bartleyi.* **A.** Distribution map. **B.** Herbarium specimen (MICH), *Beitel 77232.5cc*, Hocking Co., Ohio, 12 Jun 1977.

Huperzia ×bartleyi is a sterile hybrid resulting from the cross between *Huperzia lucidula* and *H. porophila*. Bartley's Firmoss exhibits a blend of traits from its parents. It resembles *H. porophila* with its linear-lanceolate leaves and stomata on both surfaces. This hybrid also inherits its tufted upright stems and preference for sandstone cliff ledges from *H. porophila*. However, it tends to favor moist to wet habitats with some soil accumulation (Fig. 17) and has longer prostrate stems (Fig. 18a), traits derived from *H. lucidula*. In contrast, *H. porophila* has very short prostrate stems and grows on damp to dry ledges with little soil, but often grows within moss like *H. ×bartleyi*. Cusick (1987) stated, "The hybrid plants usurp the space on the cliffs and ledges which is available to *Lycopodium porophilum* [=*H. porophila*]. This preemption of its habitat is apparently a significant factor in the present rarity of *L. porophilum* in Ohio." We do not know if this is the case in Alabama, though some populations previously thought to be *H. porophila* have turned out to be *H. ×bartleyi*.

The identification of *Huperzia ×bartleyi* often requires a microscopic examination of the plant. The gemmae (vegetative propagules) of this hybrid (Fig. 18b) are intermediate between its parents but shaped more like those of *H. lucidula* (Fig. 19a). The upper surface of its leaves has stomata like *H. porophila*, though in much fewer numbers (Fig. 19b–d), whereas *H. lucidula* has none on the upper side of its leaves. Unlike its fertile parents, which have normal tetrahedral spores (Fig. 20), the sporangia (spore sacs) of *H. ×bartleyi* contain non-viable, shrunken spores.

Figure 17. *Huperzia ×bartleyi*, Winston Co., Alabama, 19 Jun 2024. Photo: Dan Spaulding.

Figure 18. *Huperzia ×bartleyi*, Winston Co., Alabama, 13 Jun 2024. **A.** Prostrate portion of the stems. **B.** Whorl of gemmae near the tip of the stem. Photos: Dan Spaulding.

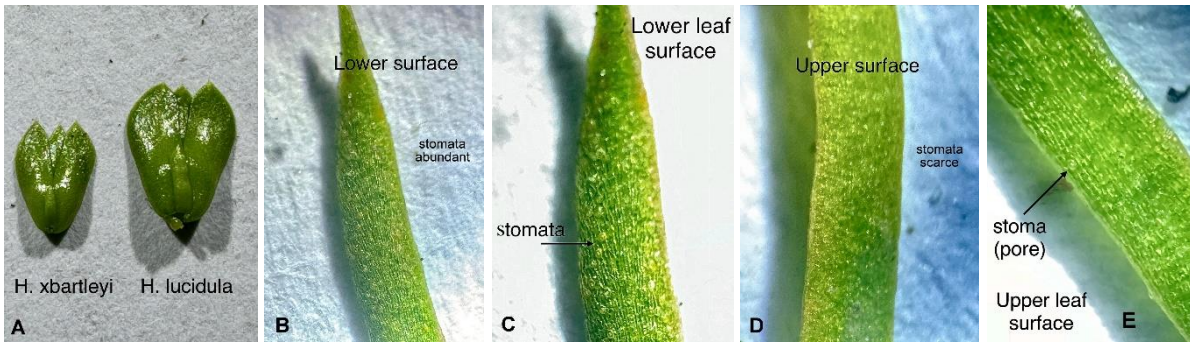


Figure 19. A. Gemmae of *Huperzia* ×*bartleyi* and *H. lucidula*. **B–E.** Stomata on *Huperzia* ×*bartleyi* leaf surfaces. B. Underside of leaf. C. Stomata on lower leaf surface. D. Upper surface of leaf. E. Stoma on upper surface of leaf. Plants collected from Winston Co., Alabama, 13 Jun 2024. Photos: Dan Spaulding.

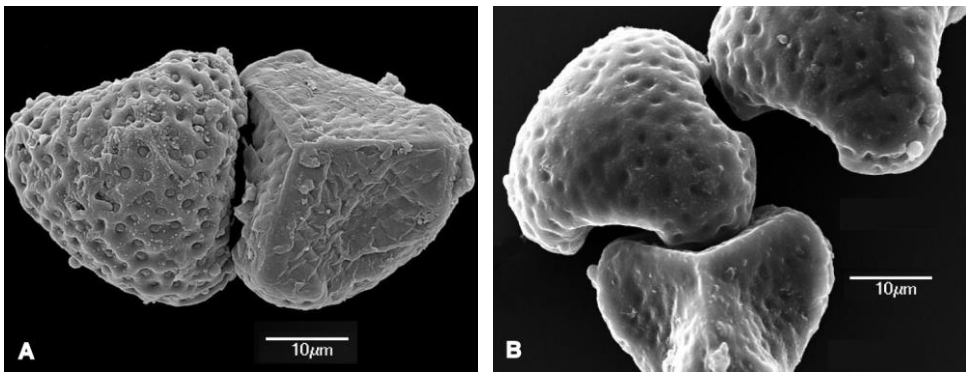


Figure 20. Normal spores from the parents of *Huperzia* ×*bartleyi*. **A.** *Huperzia porophila*. **B.** *Huperzia lucidula*. SEM images by Judith Garrison Hanks and Robbin Moran. <www.plantsystematics.org>

2. Huperzia lucidula (Michx.) Trevis. {somewhat shining; leaves} — SHINING FIRMOSS, SHINING CLUBMOSS; MOONFRUIT-PINE (Fig. 21). [*Lycopodium lucidulum* Michx.]

Figure 21. *Huperzia lucidula*, Winston Co., Alabama, 13 Jun 2024. Photos: Dan Spaulding.

Plants terrestrial; evergreen. In Alabama, it is restricted to moist to wet, often rocky soil in deep shade, often near sandstone cliffs. Sporulates June–September; very rare in the Warrior Basin and Lookout Mountain districts of the Cumberland Plateau (Fig. 22). Common in the northeastern USA and southeastern Canada, west to the upper Mississippi Valley and south to the mountains of Tennessee, North Carolina, Georgia, and northwestern Alabama (Wagner & Beitel 1993b). Disjunct in northern Arkansas, the Rocky Mountains (Kartesz 2025), and northeastern China (Shan 2013). The Alabama Natural Heritage Program (2023) lists this species as imperiled (S2) in the state.

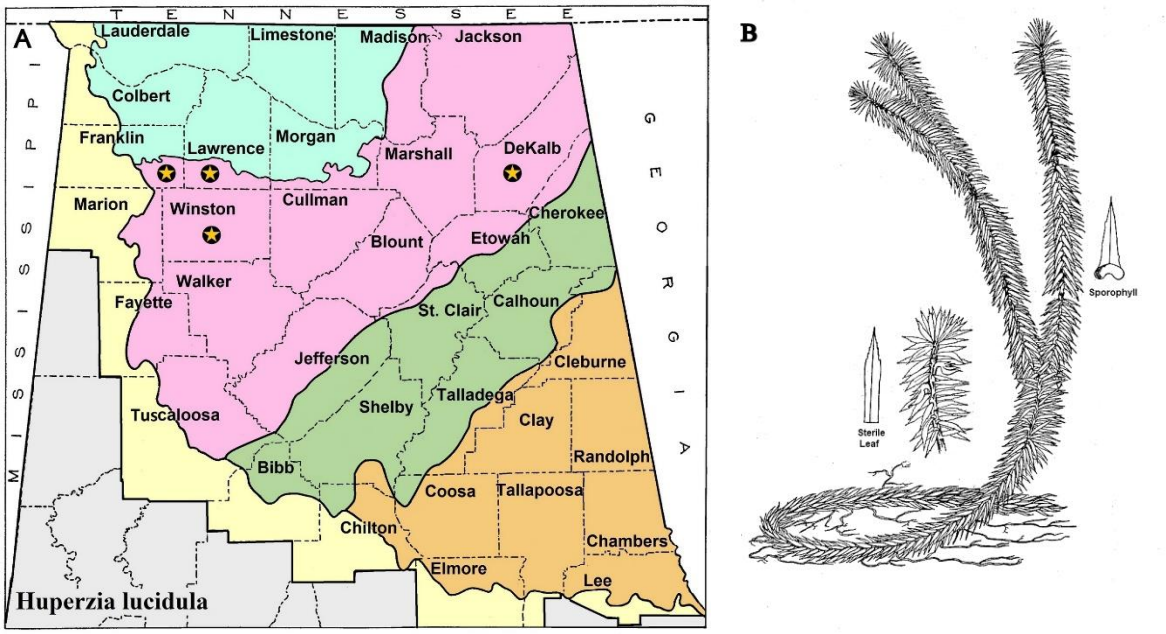


Figure 22. *Huperzia lucidula*. **A.** Distribution map. **B.** Illustration: Ruth Sinclair George, 1938.

Although rare in Alabama, this species is more common farther north, where it thrives in shaded habitats such as rocky stream banks, swamp margins, and moist hillsides. Weakley et al. (2025) note that Shining Firmoss is the largest *Huperzia* species in the eastern United States and the only one that typically grows in forest soils rather than exclusively on rock outcrops.

Figure 23. *Huperzia lucidula*, Winston Co., Alabama, 13 Jun 2024. **A.** Sporangia. **B.** Upright portion of the stem with shorter sporophylls. **C.** Vegetative leaves oblanceolate and toothed. Photos: Dan Spaulding.

Huperzia lucidula can be identified by its sprawling growth habit and frequently forking branches. As the plant ages, fallen leaves accumulate on the lower prostrate stems, pressing them to the ground, while the upper portions continue to grow upright and branch, often forming large colonies (Waterway 1986). Each year, the plant produces a zone of sporophylls, with sporangia nestled within the axils of these specialized leaves (Fig. 23a). The sporophylls are typically shorter and lance-shaped, contrasting with the larger, somewhat spoon-shaped sterile leaves. This alternation of short and long leaves creates a distinctive wave-like pattern along the branches, giving the plant a knobby appearance (Fig. 23b). The vegetative leaves of *H. lucidula* differ from those of *H. porophila* and *H.* ×*bartleyi* by being widest above the middle, having serrate tips (Fig. 23c), and possessing stomata (pores) only on the lower surfaces (Fig. 24). Shining Firmoss gemmae are nearly as wide as long, with the central and lateral leaves being broadly obtuse (Fig. 25).

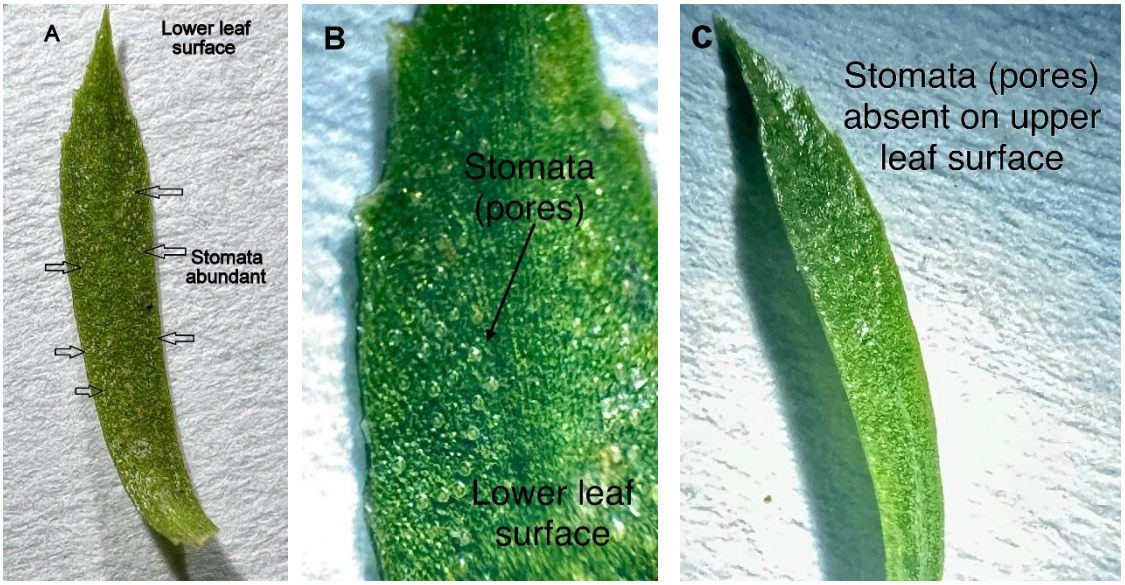


Figure 24. *Huperzia lucidula*, Winston Co., Alabama, 13 Jun 2024. **A.** Lower leaf surface. **B.** Stomata on the underside of a leaf. **C.** Upper surface of a leaf. Photos: Dan Spaulding.

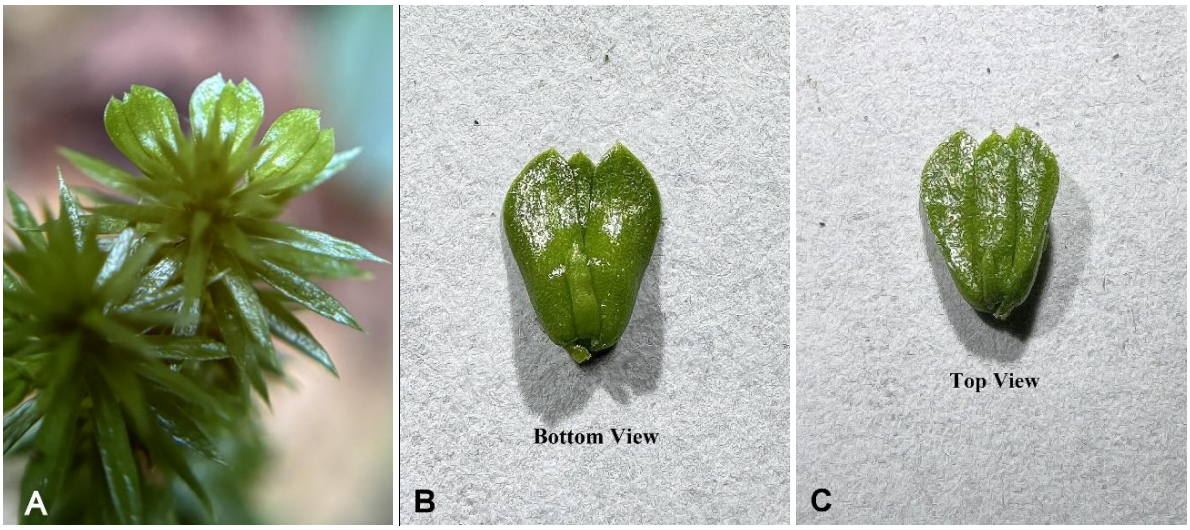


Figure 25. *Huperzia lucidula*, Winston Co., Alabama, 13 Jun 2024. **A.** Whorl of gemmae on new growth. **B.** Bottom view of a gemma. **C.** Top view of a gemma. Photos: Dan Spaulding.

Historically, the Iroquois used *Huperzia lucidula* for its purported medicinal properties, employing it to treat colds, "purify bad blood," and heal neck sores (Moerman 1998). The plant's common name and its specific epithet both refer to the characteristically glossy sheen of its leaves. The older name "moon-fruit pine" likely arose from its superficial resemblance to a miniature pine tree and the crescent-moon shape of its sporangia—spore-producing structures sometimes mistaken for fruit.

3. Huperzia porophila (F.E. Lloyd & Underw.) Holub {stone lover} — ROCK FIRMOSS, ROCK CLUBMOSS; CLIFF CLUBMOSS (Fig. 26). [*Lycopodium lucidulum* Michx. var. *occidentale* (Clute) L.R. Wilson; *Lycopodium lucidulum* var. *porophilum* (Lloyd & Underw.) Clute; *Lycopodium porophilum* F.E Lloyd & Underw.]

Figure 26. *Huperzia porophila* on a boulder, Winston Co., Alabama, 3 Jul 2024. Photo: Dan Spaulding.

Plants epipetric; evergreen. Ledges and cracks of shaded sandstone cliffs or boulders in rock shelters. Sporulates June–September; very rare in the Warrior Basin District of the Cumberland Plateau (Fig. 27). Native to eastern North America with scattered populations from eastern Pennsylvania west to the upper Mississippi Valley and south to the Central Appalachians (Weakley et al. 2025). The Alabama Natural Heritage Program (2023) lists this species as critically imperiled (S1) in the state.

Rock Firmoss (*Huperzia porophila*) is distinct from Shining Firmoss (*H. lucidula*) in its growth pattern, smaller size, and habitat preference. *Huperzia porophila* grows on rock ledges (Fig. 28) or boulders on the floor of rock shelters (Fig. 29a), has very short prostrate stems, and tends to branch two or three times early in its growth, with rare branching in subsequent years. This trait results in smaller, tufted plants with branched bases and several upright stems. Occasionally, accumulated leaf litter may cause the plants to bend outward or hang over cliff ledges rather than stand erect (Waterway 1986).

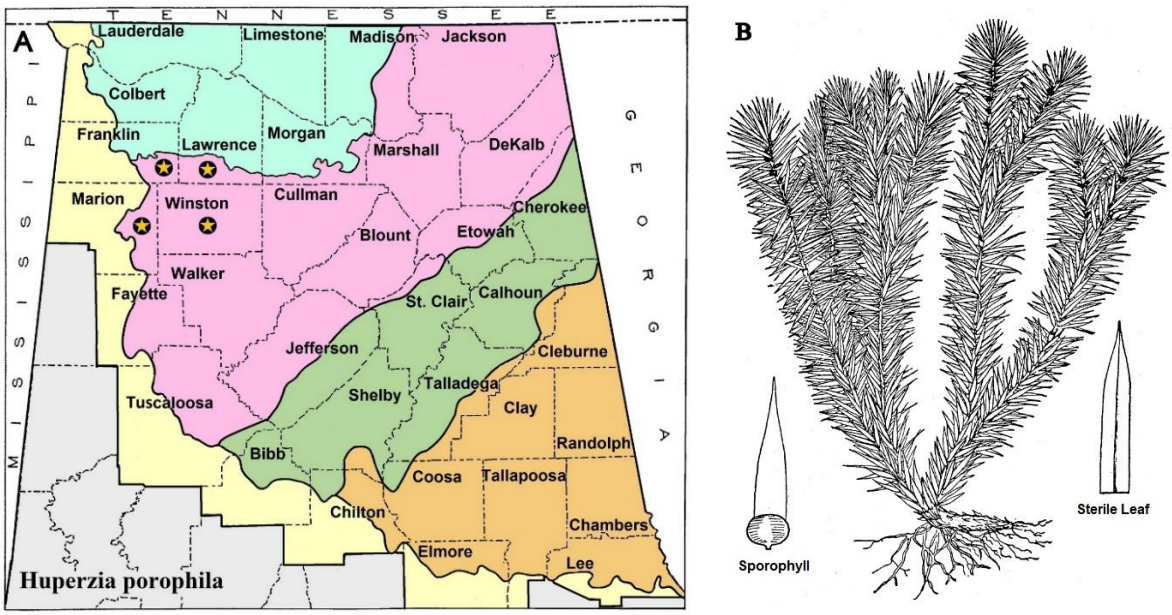


Figure 27. *Huperzia porophila*. **A.** Distribution map. **B.** Illustration: Ruth Sinclair George, 1938.

Figure 28. *Huperzia porophila* habitat, Winston Co., Alabama, 19 Jun 2024. Photo: Dan Spaulding.

Another distinguishing feature between these two Alabama firmosses is the relative length of their sporophylls and the shape of their gemmae (vegetative propagules). In *Huperzia porophila*, the sporophylls are approximately equal in length to the sterile leaves. Its gemmae are longer than broad (Fig. 29c), with acute lateral and central leaves (Fig. 30a). In contrast, the sporophylls of *H. lucidula* are distinctly shorter than the sterile leaves, and its gemmae are nearly as wide as long, with broadly obtuse lateral and central leaves. However, the most reliable way to distinguish the two is by examining the distribution of stomata (microscopic pores): in *H. porophila*, stomata occur on both leaf surfaces (Fig. 30b–c), whereas in *H. lucidula*, they are restricted to the undersides of its leaves.

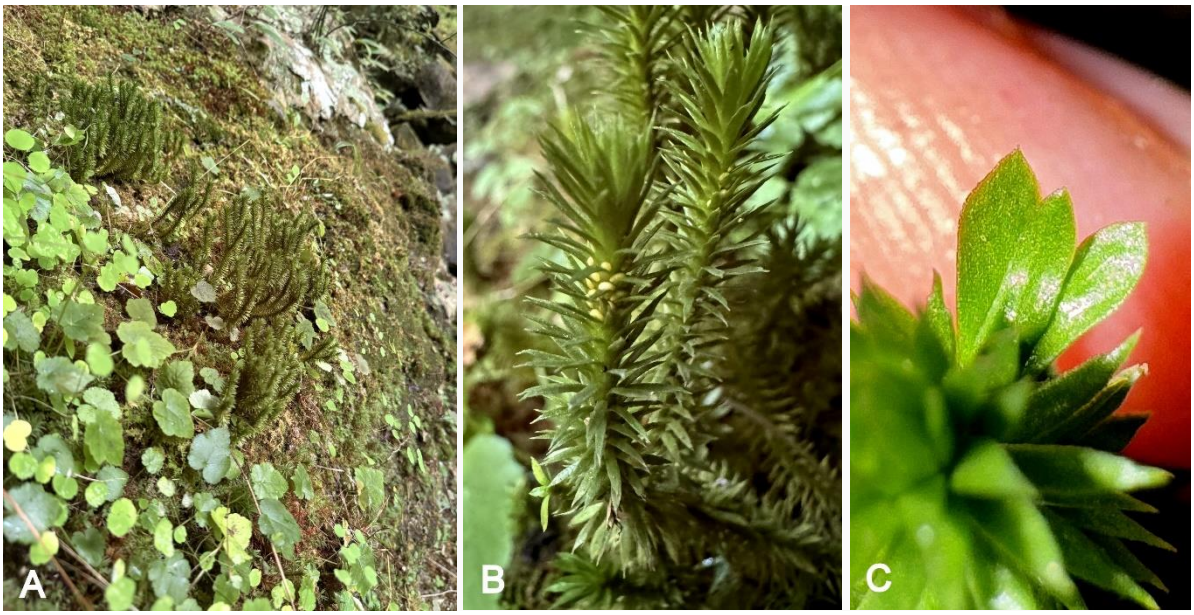


Figure 29. *Huperzia porophila*, Winston Co., Alabama, 3 Jul 2024. **A.** On a boulder within a rock shelter. **B.** Sporophylls are about the same size as sterile leaves. **C.** Acute leaves of gemma. Photos: Dan Spaulding.

Huperzia ×*bartleyi* resembles *H. porophila*, with both species sharing tufted, erect stems and leaves with roughly parallel margins. Additionally, they both inhabit sheltered cliff ledges. However, the hybrid has longer decumbent stems, sporophylls slightly shorter than its vegetative leaves, fewer stomata on the upper leaf surfaces, and abortive, shrunken spores.

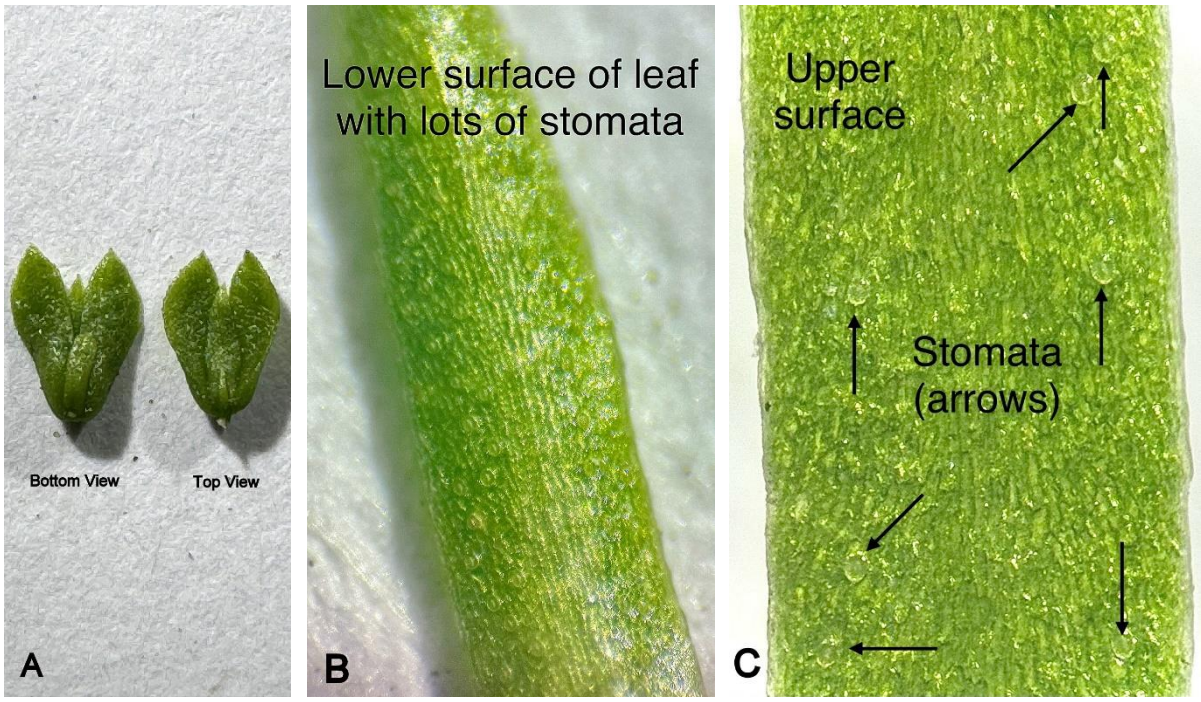


Figure 30. *Huperzia porophila*, Winston Co., Alabama, 19 Jun 2024. **A.** Gemma, bottom and top view. **B.** Lower leaf surface with numerous stomata. **C.** Upper surface of the leaf. Photos: Dan Spaulding.

2. **LYCOPODIACEAE** (Clubmoss Family) – in Lycopodiales

1. Leaves flaccid, pale or yellow-green, dull; plants of wetlands, rooting in mud or wet sands, dying back in winter, except for evergreen buds.

    2. Leaves of horizontal stems similar in size or slightly larger than those of upright stems; erect stems densely leafy, with numerous overlapping leaves that obscure the stem; sporophylls (leaves of strobilus) narrowly lance-linear, resembling vegetative leaves; horizontal stem leaves with or without marginal teeth .....***Lycopodiella***
    2. Leaves of horizontal stems much broader than the scale-like leaves of upright stems; erect stems sparsely leafy, stem clearly visible; sporophylls broadly ovate with long acuminate tips; horizontal stem leaves lacking marginal teeth .....***Pseudolycopodiella***

1. Leaves rigid, bright to dark green, shiny; plants primarily of uplands, rooting mainly in drier soils, persistent and green through winter.

    3. Branches appearing fan-like, 1–3 mm wide; leaves appressed, in four rows on stem and fused basally; branches usually 3 mm or less wide; strobili borne on long, dichotomously branched (Y-forked) peduncles ..... ***Diphasiastrum***
    3. Branches appearing shaggy, 5–12 mm wide; leaves widely spreading or ascending, spirally arranged in six rows with distinctly separate bases; strobili sessile at tips of upper branches or borne on long, alternately branched peduncles.

        4. Plant tree-like, resembling a miniature pine; upright stems with numerous branches; horizontal stems subterranean and deeply buried; leaves acuminate to acute, lacking terminal bristles; strobili sessile at the tips of branches ..... ***Dendrolycopodium***
        4. Plant not tree-like, upright stems with few branches; horizontal stems creeping along the soil surface; leaves attenuate (sharply tapered), tipped with hair-like bristles; strobili borne on elongate peduncles at the tips of branches ..... ***Lycopodium***

1. **DENDROLYCOPODIUM** A. Haines 2003 {DEN-droh-ly-koh-POH-dee-um}
[Greek *dendron*, tree, and *Lycopodium*; a tree-like clubmoss]

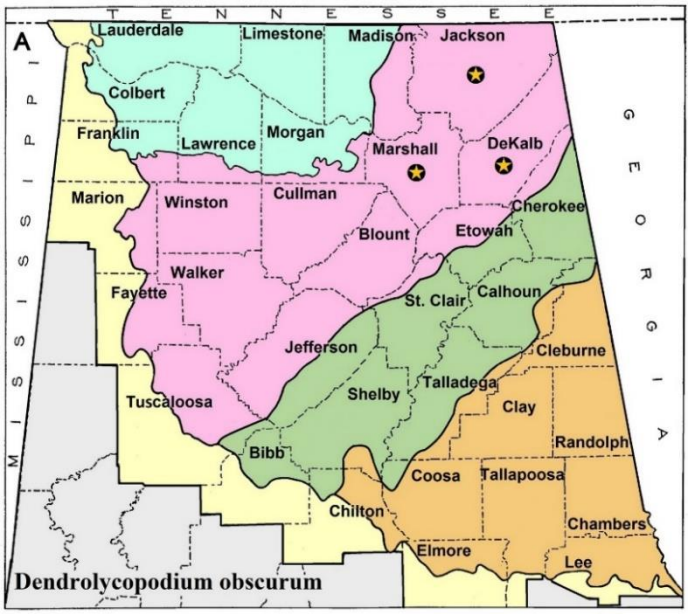
1. Dendrolycopodium obscurum (L.) A. Haines {obscure; hidden, deep rhizome} — PRINCESS-PINE; FLAT-BRANCHED TREE-CLUBMOSS; COMMON GROUNDPINE (Fig. 31). [*Lycopodium obscurum* L.]

Plants terrestrial; evergreen. Acidic hardwood and coniferous forests, often in thin, moist soil over sandstone. Sporulates July–September; very rare in the Cumberland Plateau of northeast Alabama (Fig. 32). Widespread in the northeastern USA and southeastern Canada, extending west to the Great Lakes and south through the Appalachian Mountains to northeastern Alabama (Kartesz 2025). Also found in East Asia, including Japan, Taiwan, Korea, the Russian Far East, and northeastern China. In the state, it is listed as critically imperiled (S1) by the Alabama Natural Heritage Program (2023).

Dendrolycopodium obscurum has been documented in Heard and Carroll counties in the Piedmont region of western Georgia (Kartesz 2025). Given the proximity of these counties to the Alabama state line, it is plausible that this clubmoss also occurs in Alabama's Piedmont. The species derives its common names from its striking resemblance to miniature coniferous trees, with colonies forming dense, forest-like mats reminiscent of tiny pines or spruces (Fig. 33). Historically, “Princess-Pine” was harvested extensively for Christmas decorations (Dean 1969), a practice that led to

population declines in many areas. Due to its rarity in Alabama, collection is strongly discouraged. Notably, *D. obscurum* contains bioactive alkaloids and has been used in traditional Chinese medicine (Zhang et al. 2013) and by certain Native American tribes to treat rheumatism, blood disorders, and gynecological issues (Moerman 1998).

Figure 31. *Dendrolycopodium obscurum*, Jackson Co., Alabama, 13 Apr 2011. Photo: Wayne Barger.



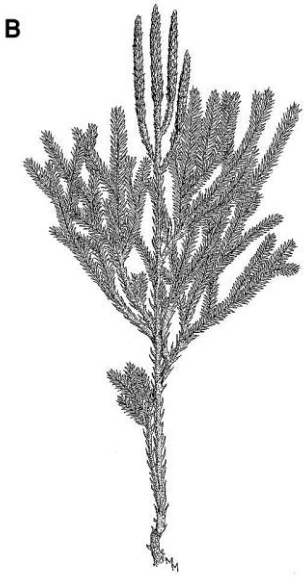


Figure 32. *Dendrolycopodium obscurum.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 33. *Dendrolycopodium obscurum*, Jackson Co., North Carolina, 22 Jun 2021. Photo: Alan Cressler.

2. DIPHASIASTRUM Holub 1975 {dye-phase-ee-ASS-trum}
[*Diphasium*, a lycophyte generic name, and *astrum*, an incomplete resemblance]

1. Diphasiastrum digitatum (Dill. ex A. Braun) Holub {finger-like; the branches} — SOUTHERN GROUND-CEDAR; FAN CLUBMOSS; SOUTHERN RUNNING-CEDAR; FAN GROUND-PINE; CROWFOOT CLUBMOSS; FAN CREEPING-CEDAR; TURKEY-FOOT; BEAR'S-PAW (Fig. 34). [*Lycopodium digitatum* Dill. ex A. Braun; *Lycopodium flabelliforme* (Fernald) Blanch.]

Figure 34. *Diphasiastrum digitatum*, Cleburne Co., Alabama, 12 Jun 2024. Photo: Eric Soehren.

Plants terrestrial; evergreen. Dry to moist acidic mixed woods, pine forests, roadsides, powerline rights-of-way, and other open areas. Sporulates June–September (strobili persistent through winter); uncommon in the Highland Rim and Ridge & Valley; frequent in the Cumberland Plateau and Piedmont; rare in the Coastal Plain (Fig. 35). Ranges from southeastern Canada and northeastern USA west to Minnesota, south to Arkansas, Mississippi, Alabama, and Georgia (Kartesz 2025). Freeman et al. (1979) initially designated *Diphasiastrum digitatum* as a Species of Special Concern in the state; however, this clubmoss is more abundant than previously thought.

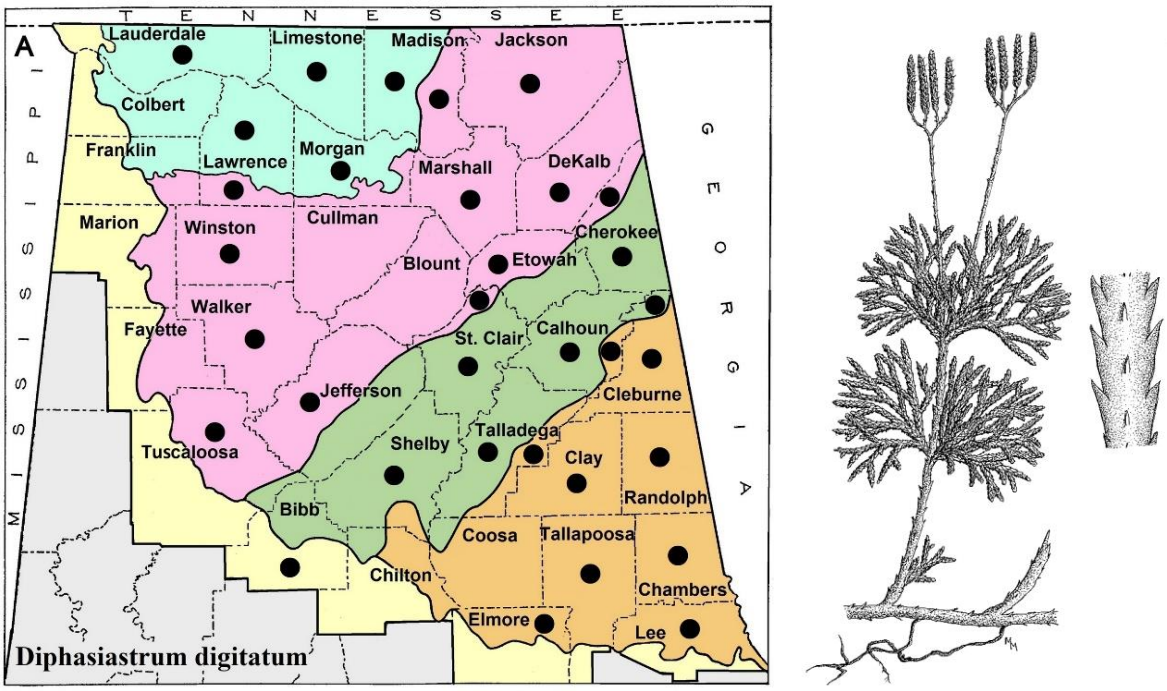


Figure 35. *Diphasiastrum digitatum.* **A**. Distribution map. **B**. Illustration: Marion Montgomery, 1999.

Figure 36. *Diphasiastrum digitatum*, Cleburne Co., Alabama, 13 Mar 2023. Photos: Dan Spaulding.

Southern Ground-Cedar is North America's most abundant *Diphasiastrum* species (Wagner & Beitel 1993a). Its rhizomes spread across the surface, forming an extensive ground cover (Fig. 36a). Artisans, florists, and hobbyists frequently harvest this plant to make decorative wreaths, particularly for the Christmas season. This clubmoss has garnered numerous common names, many of which reference its fan-shaped branchlets and resemblance to miniature cedar or pine trees (Fig. 36b).

Figure 37. *Diphasiastrum tristachyum* and *Diphasiastrum digitatum* growing together, Jackson Co., North Carolina, 25 Sep 2021. Photo: Noah Yawn.

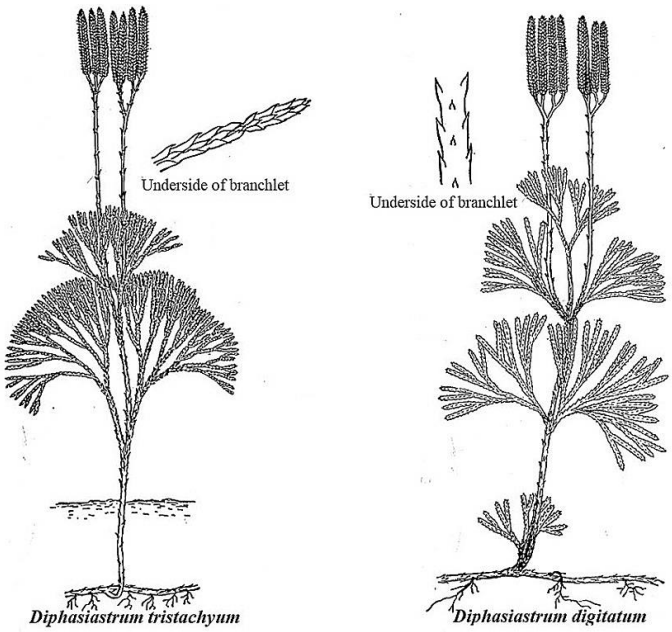


Figure 38. Comparison of two running-cedars, illustrated by James C.W. Chen (Wherry 1961).

Spaulding et al. (2000b) and Short and Spaulding (2012) reported *Diphasiastrum tristachyum* (Pursh) Holub [Blue Running-Cedar] from Jackson County, Alabama. We exclude the species here based on a reevaluation of the material: the JSU specimen (*Whetstone 13017*) is *D. digitatum*, and the US collection (*E.W. Graves s.n.*) remains unverified. Although the two species share several traits, *D. tristachyum* stands out by its bluish hue (Fig. 37) and deeply buried rhizomes (Fig. 38). In addition, its leaves are uniform in size throughout, whereas in *D. digitatum*, the middle row of leaves on the lower side of each branch is noticeably shorter than those above (Fig. 38).

3. LYCOPODIELLA Holub 1964 {ly-koh-poh-dee-EL-uh}

[The genus *Lycopodium*, and Latin *-ella*, diminutive suffix; translates to "tiny wolf's-paw"]

1. Horizontal stems arching above ground, rooting only at the tips (arches lack roots), leaves monomorphic (uniform in size); upright stems with strongly spreading leaves; strobili (cones) with spreading sporophylls (fertile leaves) .....***Lycopodiella alopecuroides***
1. Horizontal stems creeping flat on the ground, rooting continuously along the lower surface, leaves monomorphic or dimorphic (of two different sizes); upright stems with spreading to appressed leaves; strobili with spreading or appressed sporophylls.

   2. Strobili 1.5–2 cm in diameter, distinctly broader than the adjacent upright stem by 3–6 mm; sporophylls spreading to somewhat ascending; horizontal stem leaves dimorphic, with smaller dorsal leaves and larger lateral leaves spreading outward in two rows.....***Lycopodiella prostrata***
   2. Strobili less than 1 cm in diameter, only slightly broader than adjacent upright stem by 0–2 mm; sporophylls appressed; horizontal stem leaves monomorphic, uniform in size and shape, arranged in multiple rows and spreading in all directions..... ***Lycopodiella appressa***

1. Lycopodiella alopecuroides (L.) Cranfill {resembling the genus *Alopecurus*; foxtail grass} — FOXTAIL BOG CLUBMOSS; FOXTAIL CLUBMOSS (Fig. 39). [*Lycopodium alopecuroides* L.]

Figure 39. *Lycopodiella alopecuroides*, Baldwin Co., Alabama, 13 Jul 2011. Photo: Wayne Barger.

Plants terrestrial; deciduous with evergreen buds. Bogs, seepages, wet ditches, pine savannas, and wet pine flatwoods. Sporulates July–September; very rare in northern Alabama; frequent in the lower Coastal Plain, increasingly rare toward the Fall Line (Fig. 40). This species primarily occurs in the Southeastern Coastal Plain. It ranges from New England, south along the East Coast to Florida, and west to eastern Texas, along the Gulf Coast (Wagner & Beitel 1993c). *Lycopodiella alopecuroides* is widespread in tropical Americas from Cuba and Mexico south through Central America to northern South America (Weakley et al. 2025).

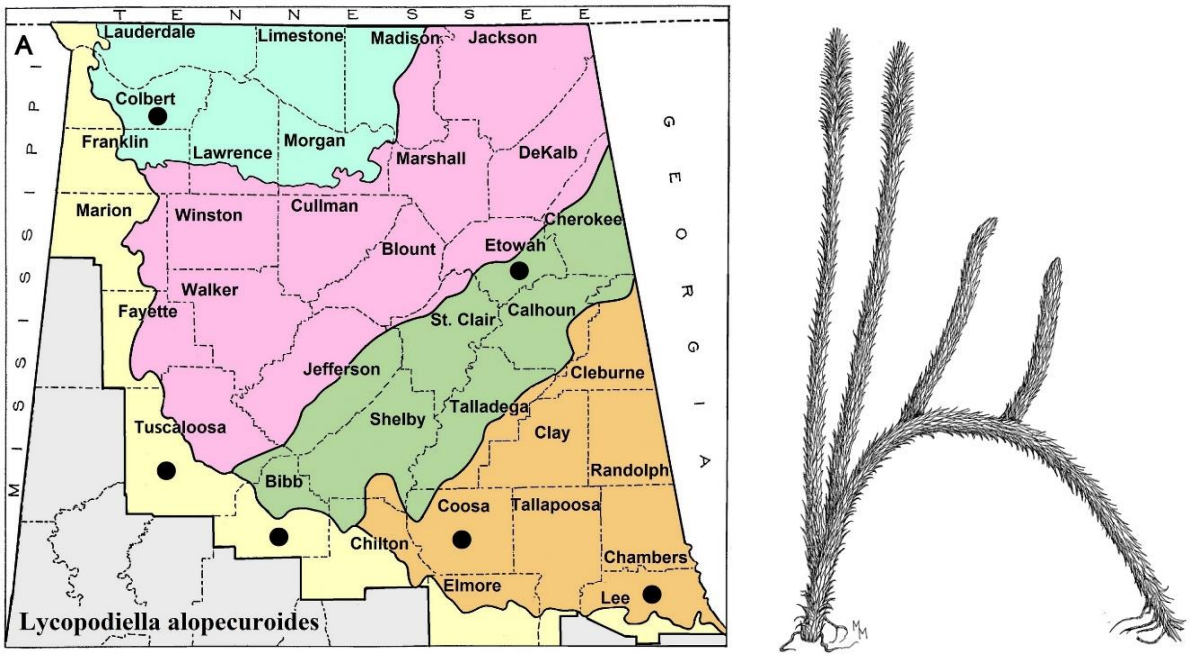
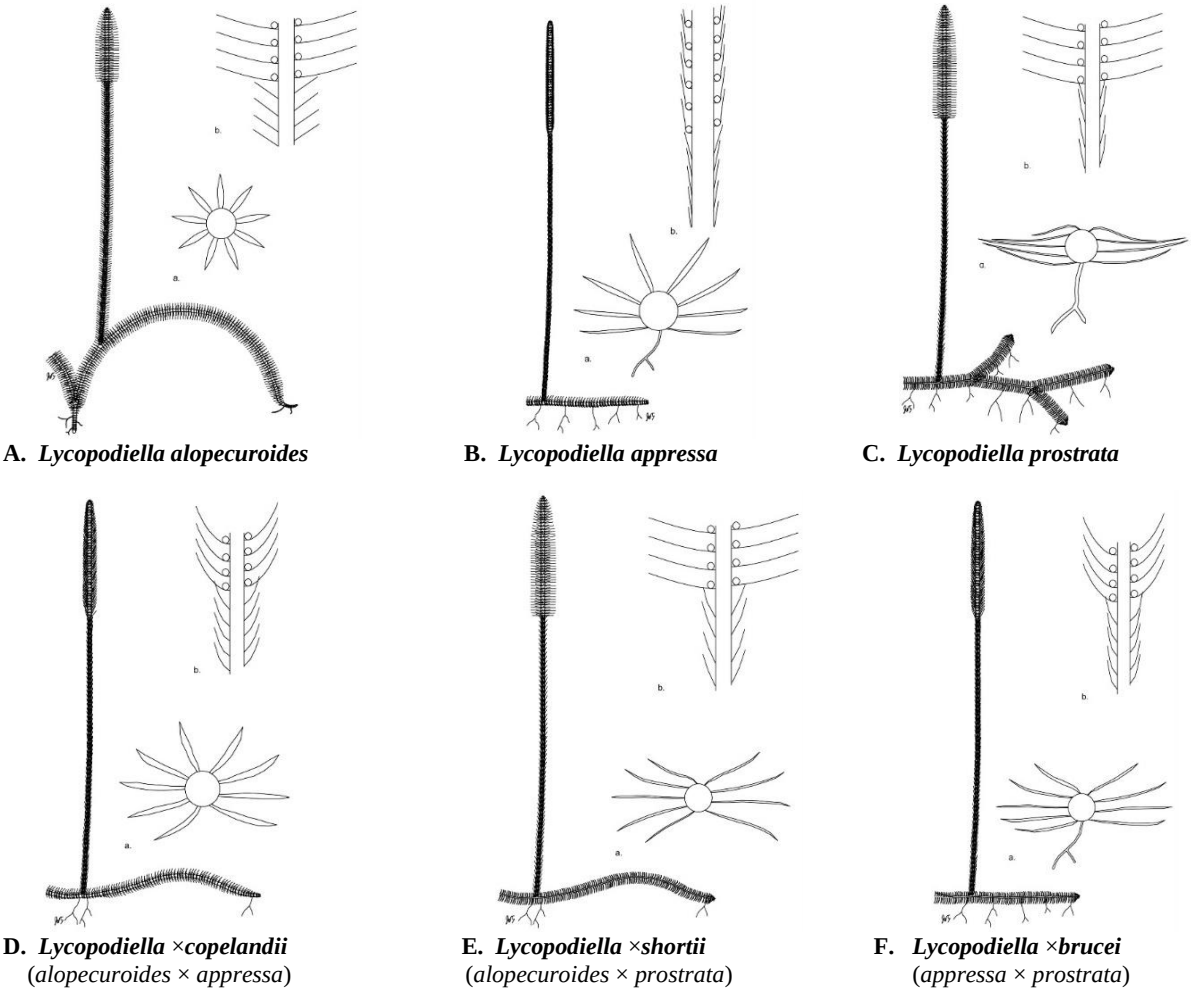


Figure 40. *Lycopodiella alopecuroides.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 41. *Lycopodiella alopecuroides.* **A.** Wet pine flatwoods in Liberty Co., Florida, 6 Nov 2022. Photo: Noah Yawn. **B.** Strobili, Taylor Co., Georgia, 16 Sep 2018. Photo: Alan Cressler.

Finnish-Swedish naturalist Peter Kalm encountered *Lycopodiella alopecuroides* in the New Jersey Pine Barrens during his travels in North America (1748–1751). Linnaeus later examined and named Kalm's specimen, making it one of the earliest documented examples of bog clubmoss (Thieret 1980). Commonly known as Foxtail Bog-Clubmoss, this species stands out as the largest *Lycopodiella* in Alabama. Despite its size, it often goes unnoticed among the dense herbaceous vegetation in its wetland habitat. This species is easily recognized by its strongly arching, horizontal stems (Fig. 41a) and spreading sporophylls (Fig. 41b). Its bushy strobilus is the inspiration for its common name.



A. *Lycopodiella alopecuroides* **B. *Lycopodiella appressa*** **C. *Lycopodiella prostrata***

D. *Lycopodiella* ×*copelandii* (*alopecuroides* × *appressa*) **E. *Lycopodiella* ×*shortii*** (*alopecuroides* × *prostrata*) **F. *Lycopodiella* ×*brucei*** (*appressa* × *prostrata*)

Figure 42. *Lycopodiella* species and their hybrids, drawings by John W. Short (Short & Spaulding 2012).

Lycopodiella alopecuroides (Fig. 42a), *L. prostrata* (Fig. 42b), and *L. appressa* (Fig. 42c) frequently cross in Alabama, producing three distinctive sterile hybrids. (1) *Lycopodiella* ×*copelandii* (Eiger) Cranfill (*alopecuroides* × *appressa*, Fig. 42d) has weakly arching stems and ascending sporophylls—traits intermediate between the strongly arching stems with widely spreading sporophylls of *L. alopecuroides* and the tightly appressed sporophylls of *L. appressa*. (2) *Lycopodiella* ×*shortii* Spaulding (*alopecuroides* × *prostrata*, Fig. 42e), named in honor of our coauthor John Short (Spaulding 2025), closely resembles *L. prostrata* but differs in its briefly arching, less feathery horizontal stems. (3) *Lycopodiella* ×*brucei* Cranfill (*appressum* × *prostrata*, Fig. 42f) bears strobili narrower than those of *L. prostrata* yet broader than those of *L. appressa*; its horizontal stems are somewhat feathery, though less so than in *L. prostrata*, and its sporophylls are more loosely arranged than in *L. appressa*. Within Alabama, these hybrids are so far known only from the Coastal Plain.

2. Lycopodiella appressa (Chapm.) Cranfill {appressed; upright stem leaves and sporophylls} — APPRESSED BOG CLUBMOSS; SOUTHERN BOG CLUBMOSS; TIGHT-LEAF CLUBMOSS (Fig. 43). [*Lycopodium adpressum* (Chapm.) F.E. Lloyd & Underw.; *Lycopodium inundatum* L. var. *bigelovii* Tuck.]

Figure 43. *Lycopodiella appressa*, Baldwin Co., Alabama, 5 Apr 2023. Photo: Craig Martin. (Red plant is the Spoonleaf Sundew, *Drosera intermedia* Hayne).

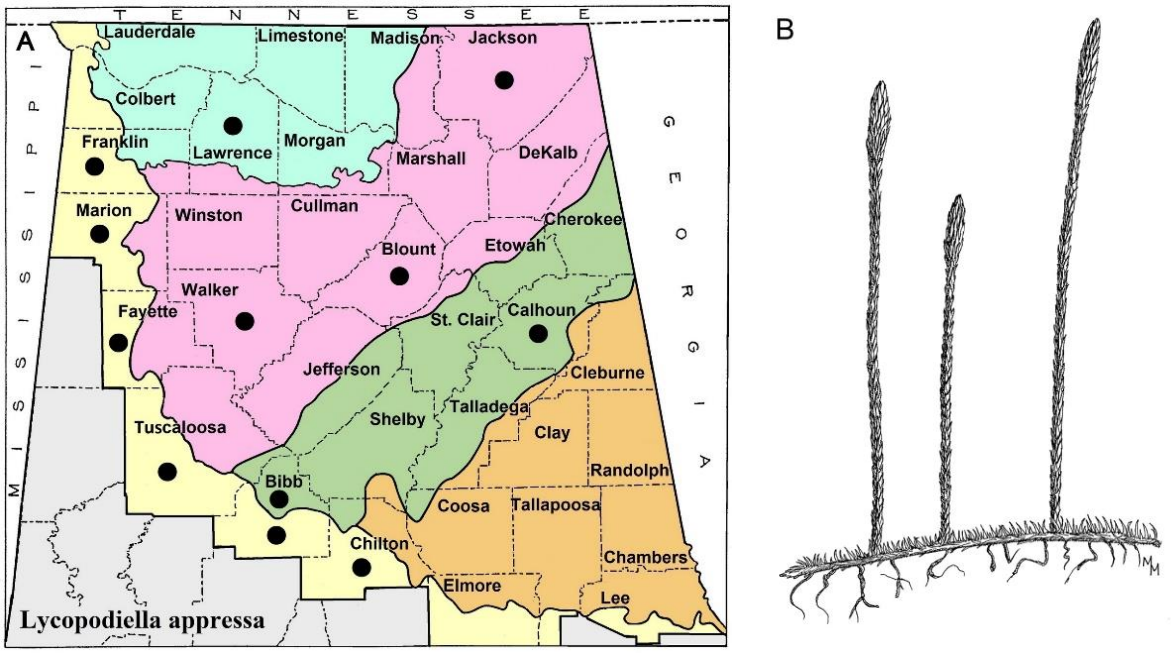


Figure 44. *Lycopodiella appressa.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Plants terrestrial; deciduous with evergreen buds. Bogs, seepages, wet ditches, pond margins, pine savannas, wet pine flatwoods, and wet meadows. Sporulates July–September; rare in northern Alabama; frequent in the Coastal Plain, uncommon near the Fall Line (Fig. 44). The species primarily inhabits the Southeastern Coastal Plain and occurs only in eastern North America, Cuba, and the West Indies. In North America, it ranges from Newfoundland south along the Coastal Plain to Florida and west along the Gulf and Atlantic coasts to eastern Texas. Inland, it extends from the Gulf Coast to southeastern Oklahoma, southern Arkansas, and western Kentucky, and appears rarely and sporadically in the Appalachian Mountains (Wagner & Beitel 1993c).

Figure 45. *Lycopodiella appressa*. **A.** Bog in Rabun Co., Georgia, 11 Jul 2008. Photo: Alan Cressler. **B.** Prostrate stem, Covington Co., Alabama, 23 Aug 2024. Photo: Steven A. Lovelace.

The distinguishing characteristics of the Appressed Bog Clubmoss (*Lycopodiella appressa*) are its prostrate horizontal stems and slender strobili with appressed sporophylls, which inspired its common name (Fig. 45a). This species frequently hybridizes with *L. alopecuroides* and *L. prostrata*. The hybrid between *L. appressa* and *L. alopecuroides* (*L.* ×*copelandii*, Fig. 42d) exhibits intermediate characteristics, such as slightly arching stems and slender strobili with ascending sporophylls. In contrast, the hybrid between *L. appressa* and *L. prostrata* (*L.* ×*brucei*, Fig. 42f) produces strobili that are narrower and more compact than the bushy strobili of *L. prostrata* but broader and looser than those of *L. appressa*. The horizontal stems of *L.* ×*brucei* bear mildly dimorphic leaves that appear feathery, though less so than in *L. prostrata*. In comparison, the leaves of *L. appressa* are uniform in size and shape (Fig. 45b).

3. Lycopodiella prostrata (R.M. Harper) Cranfill {prostrate; horizontal stems creeping} — FEATHER-STEM CLUBMOSS, PROSTRATE BOG CLUBMOSS (Fig. 46). [*Lycopodium inundatum* L. var. *pinnatum* Chapm.; *Lycopodium prostratum* R.M. Harper]

Figure 46. *Lycopodiella prostrata*. **A.** Georgetown Co., South Carolina, 7 Jul 2023. Photo: Eric Ungberg. **B.** Strobili, Glynn Co., Georgia, 24 Oct 2009. Photo: Alan Cressler.

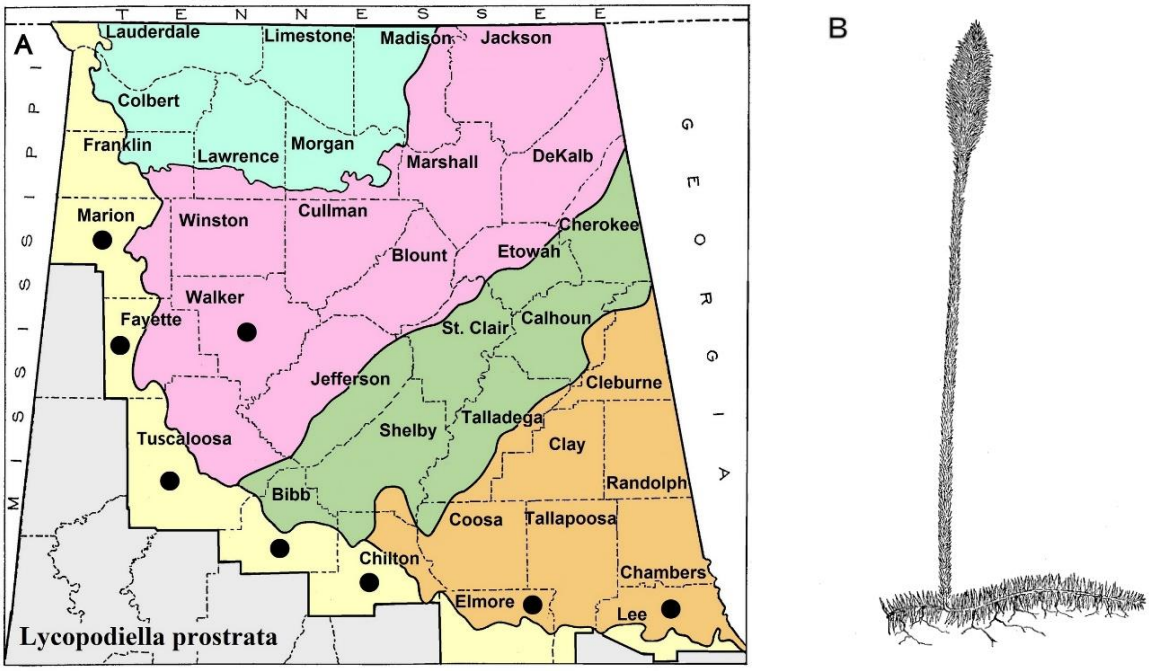


Figure 47. *Lycopodiella prostrata*. **A.** Distribution map. **B.** Illustration: James C.W. Chen, 1961.

Plants terrestrial; deciduous with evergreen buds. Bogs, wet ditches, seepages, wet meadows, pine savannas, and wet pine flatwoods. Sporulates July–September; very rare in northern Alabama; frequent in the Coastal Plain, increasingly rare toward the Fall Line (Fig. 47). This species is nearly endemic to the Southeastern Coastal Plain, ranging from North Carolina south to Florida and west to Arkansas and eastern Texas, with scattered inland disjunct occurrences (Kartesz 2025).

Lycopodiella prostrata resembles *L. alopecuroides* in having strobili (spore-bearing cones) with spreading sporophylls, but the two differ markedly in growth habit and leaf arrangement. The main stems of *L. prostrata* creep along the soil surface and root continuously, while those of *L. alopecuroides* arch upward and root only at their tips. In *L. prostrata*, the leaves along horizontal stems vary in size—shorter dorsal leaves contrast with larger lateral leaves that spread outward, giving the plant a feather-like appearance and inspiring its common name (Fig. 48). By contrast, *L. alopecuroides* bears uniformly sized leaves arranged in multiple rows radiating around the stem.

Figure 48. *Lycopodiella prostrata*, Emmanuel Co., Georgia, 27 Nov 2020. Photo: Daniel Folds.

Alabama state botanist Roland M. Harper (1906) was the first to correctly identify Feather-Stem Clubmoss as *Lycopodium prostratum* [= *Lycopodiella prostrata*]. At the time, botanists referred to the taxon as *Lycopodium pinnatum* (Chapman) Lloyd & Underwood, but Harper rejected this name, noting that Lamarck had already used it in 1789 for a species growing in trees in the West Indies. Despite this, Edward W. Graves reported in *The Fern Flora of Alabama* (1920) that both *L. prostratum* and *L. pinnatum* occurred in Alabama. Graves observed that *L. prostratum* was abundant in southern Alabama, while *L. pinnatum* was rare. However, because *Lycopodium pinnatum* (now treated as a synonym of *Plagiochila aerea* Taylor) does not occur in North America, Graves likely misapplied the name to one of the hybrids involving *Lycopodiella prostrata* (Short & Spaulding 2012).

3. LYCOPODIUM Linnaeus 1753 {ly-koh-POH-dee-um}
[Greek *lykos*, wolf, and *podes*, foot; resemblance of branch tips to a wolf's paw]

1. Lycopodium clavatum L. {club-shaped; the strobili} — RUNNING CLUBMOSS; STAGHORN CLUBMOSS; RUNNING GROUNDPINE; COMMON CLUBMOSS: CORAL-EVERGREEN; WOLF'S-CLAWS; (Fig. 49).

Figure 49. *Lycopodium clavatum*, Clay Co., Alabama. **A.** Growth habit, 14 Nov 2021. Photo: Alan Cressler. **B.** Strobili, 23 May 2019. Photo: Alvin Diamond.

Plants terrestrial; evergreen. Wooded roadbanks and woodlands. Sporulates July–September (strobili persistent through winter); very rare in the Ashland Plateau District of the Piedmont (Fig. 51). Circumboreal species; in eastern North America south along the Appalachians to North Carolina, north Georgia, and northeast Alabama; also occurring in the West Indies, Mexico, Central America, South America, Europe; Asia, Africa, and Pacific Islands (Wagner & Beitel 1993d). The Alabama Natural Heritage Program (2023) lists this species as critically imperiled (S1) in the state.

Figure 50. *Lycopodium clavatum* habitat, Clay Co., Alabama, 13 Nov 2023. Photo: Melanie Spaulding.

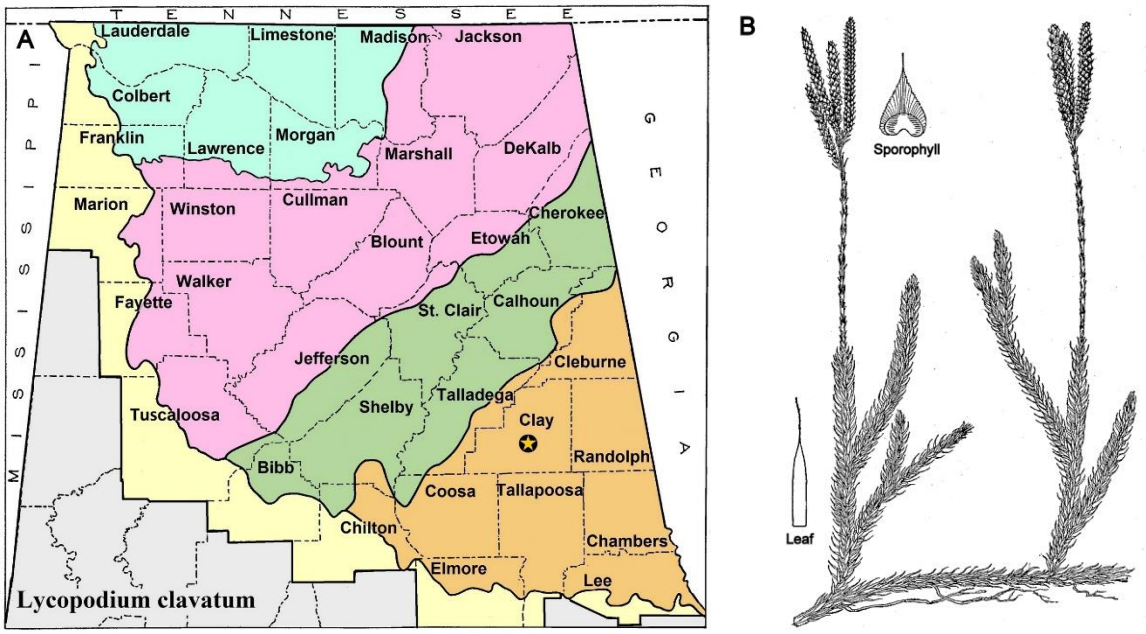


Figure 51. *Lycopodium clavatum*. **A.** Distribution map. **B.** Illustration: Ruth Sinclair George, 1938.

In 2019, Alvin Diamond (2020) documented *Lycopodium clavatum* in Clay County, Alabama, where he found a population growing on a dry roadbank within the Talladega National Forest (Fig. 50). The nearest known population occurs in the mountains of northeastern Georgia (Kartesz 2025). This evergreen lycophyte features strobili on elongated peduncles (Fig. 52a), leaves tipped with hair-like bristles (Fig. 52b), and sprawling horizontal stems that blanket the ground (Fig. 51b). Its many common names reflect both its wide geographic range and the imaginative ways people have described its creeping, branched growth and resemblance to other plants. Notably, the Nodding Clubmoss, *Palhinhaea cernua* (L.) Franco & Vasc. (Fig. 52c), a species native to the Coastal Plain, also bears the common name "staghorn clubmoss," shared with *Lycopodium clavatum*. Early observers thought the fertile branches of *P. cernua* and the erect strobili of *L. clavatum* both resembled the antlers of a stag.

Figure 52. A. *Lycopodium clavatum* strobili, Watauga Co., North Carolina, 11 Jul 2023. Photo: Kristin Wyatt. **B.** *Lycopodium clavatum* with hair-like bristles on leaf tips, Garrett Co., Maryland, 10 Jun 2023. Photo: Clara Thiel. **C.** *Palhinhaea cernua*, Liberty Co., Florida, 1 Jan 2022. Photo: Noah Yawn.

Historically, druggists marketed the spores of *Lycopodium clavatum* as "lycopodium powder," valued for its absorbent and styptic properties, which made it ideal for halting bleeding by absorbing fluids when applied to wounds. The U.S. Pharmacopoeia once recommended its use as a dusting powder for surgical gloves, suppositories, pills, and even condoms. However, medical professionals now discourage many of these applications due to potential allergic reactions and inflammatory effects. Notably, the high oil content of the spores makes them highly flammable, igniting with a bright flash of light. This property made them valuable for early flash photography and fireworks (Whitebread 1941, Balick & Beitel 1989). In Europe, the powder earned the nickname "witch's-flour" due to its tendency to ignite explosively (Abbe 1981).

4. PSEUDOLYCOPODIELLA Holub 1983 {soo-doh-lye-koh-poh-dee-EL-uh}
[Green *pseudo*, false, and the genus *Lycopodiella*, alluding to its resemblance to the genus]

1. Pseudolycopodiella caroliniana (L.) Holub {of Carolina} — SLENDER CLUBMOSS; CAROLINA BOG CLUBMOSS (Fig. 53). [*Lycopodiella caroliniana* (L.) Pichi Sermolli; *Lycopodium carolinianum* L.]

Figure 53. *Pseudolycopodiella caroliniana*, Baldwin Co., Alabama, 24 Jul 2012. Photo: Wayne Barger.

Plants terrestrial; deciduous with evergreen buds. Bogs, seepages, and pine savannas in the Coastal Plain. Sporulates July–September; very rare in the Weisner Ridge District of the Ridge & Valley; uncommon in the Coastal Plain (Fig. 54). Primarily occurring in the eastern USA on the Coastal Plain from New Jersey to East Texas with scattered populations further north; also in Mexico, Central America, South America, Asia, and Africa (Wagner & Beitel 1993e).

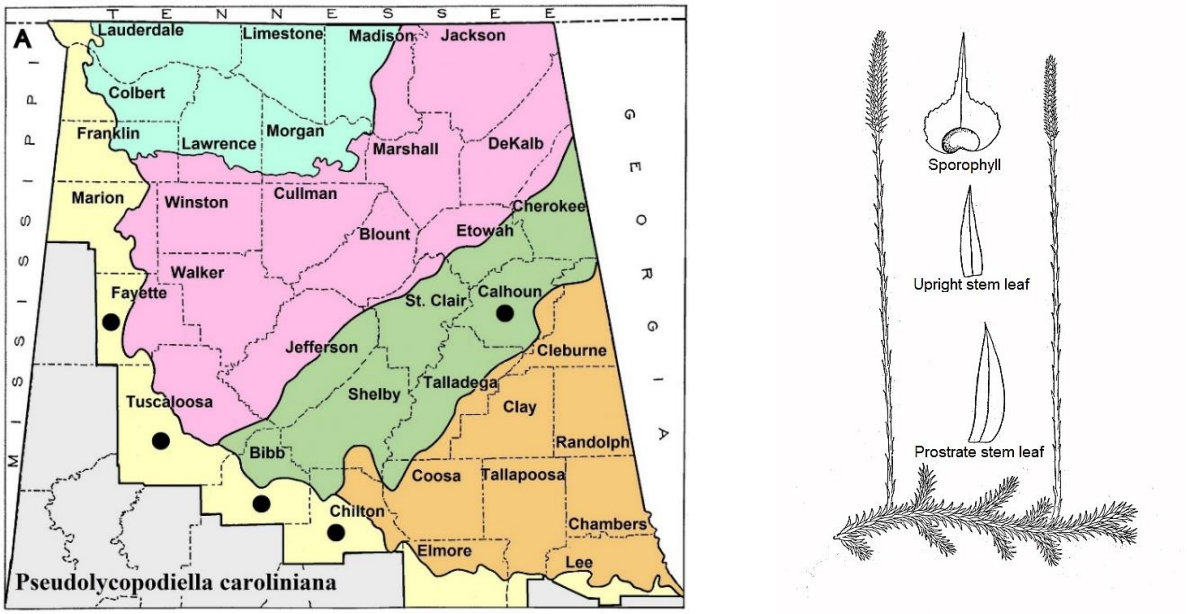


Figure 54. *Pseudolycopodiella caroliniana*. **A.** Distribution map. **B.** Illustration: Ruth Sinclair George, 1938.

The Slender Clubmoss (*Pseudolycopodiella caroliniana*) typically grows close to the ground, often blending into its surroundings among taller grasses and other vegetation, which can obscure its upright, strobili-bearing stalks. This inconspicuous growth habit may explain why collectors frequently overlook it, suggesting the species could be more widespread than current records indicate. Although common in the bogs of the southeastern United States, this lycophyte is winter-hardy and extends its range as far north as New England. Notably, in 1993, Chris Oberholster—then Director of the Nature Conservancy in Alabama—collected it from a boggy seep in Calhoun County, marking the only record of this species from above the Fall Line in the state.

Figure 55. *Pseudolycopodiella caroliniana*, Tattnall Co., Georgia, 23 Oct 2009. Photo: Alan Cressler.

Pseudolycopodiella differs from *Lycopodiella* by its prostrate shoots with laterally flattened leaves that give the plant a distinctive two-ranked appearance (Fig. 55). The leaves are noticeably broader, ranging from 1.3–2.1 mm wide, compared to the narrower 0.5–1.2 mm leaves of *Lycopodiella*. Unlike *Lycopodiella*, the leaves of *Pseudolycopodiella* are widest near the midpoint and have smooth, untoothed margins (Weakley et al. 2025). Other distinguishing traits include upright stems with visible stalks, produced by scattered, non-overlapping leaves, and broadly ovate sporophylls that narrow into long, acuminate tips (Fig. 56).

Figure 56. *Pseudolycopodiella caroliniana*, Ware Co., Georgia, 10 Jun 2024. Photos: Matthew Gobbi.

3. ISOETACEAE (Quillwort Family) – in Isoetales

1. ISOETES Linnaeus 1753 {eye-soh-EE-teez}

[Greek *isos*, equal, and *etos*, year; referring to the evergreen habit of some species]

Quillworts produce tufts of grass-like leaves arranged in a circular pattern around a short, fleshy, corm-like rootstock. The common name "quillwort" refers to the quill-like shape of their leaves. Due to their appearance, they are often mistaken for immature wild onions (*Allium*), rushes (*Juncus*), spikerushes (*Eleocharis*), or other graminoids. However, the leaves of *Isoetes* are uniquely three-dimensional, with a distinctly flatter upper surface and a more rounded underside. They also contain air chambers crossed by thin diaphragms, which appear externally as pale striations. Quillworts are *heterosporous*, producing both megaspores and microspores that develop into separate female and male gametophytes. Their sporangia, which house the spores, are located on the spoon-shaped basal inner surface of the leaves (Fig. 57).

Experts frequently struggle to identify *Isoetes* species due to their morphological similarities. To distinguish species of quillworts, they commonly rely on geographic distribution, habitat, sporangial wall markings, velum coverage, and megaspore surfaces (Taylor et al. 1993). In 1882, George Engelmann noted that many botanists overlooked the genus, dismissing the plants as insignificant or sterile. This perception led to limited collections and hindered early taxonomic studies. Norma Etta Pfeiffer (1922) later emphasized the value of megaspore ornamentation for species identification in her *Monograph of the Isoetaceae*, and this method remains a cornerstone of *Isoetes* taxonomy today.

Identifying *Isoetes* species can be difficult. Researchers often rely on the size and surface texture of mature, dry megaspores (Taylor et al. 1975). These spores are typically white or gray, spherical, and marked by an equatorial ridge with three radial ridges extending to the apex. Their surfaces vary widely, with bumpy, spiny, crested, or net-like ornamentation formed by raised structures called muri (Fig. 58a). Another useful characteristic is the percent of velum coverage. This thin membrane partially or fully covers the upper part of the sporangium (Fig. 58b & 59). Velum length is measured from the base of the ligule downward toward the center of the sporangium (Kott & Britton 1985). The ligule is a tiny, tongue-like structure located above the sporangium (Fig. 57).

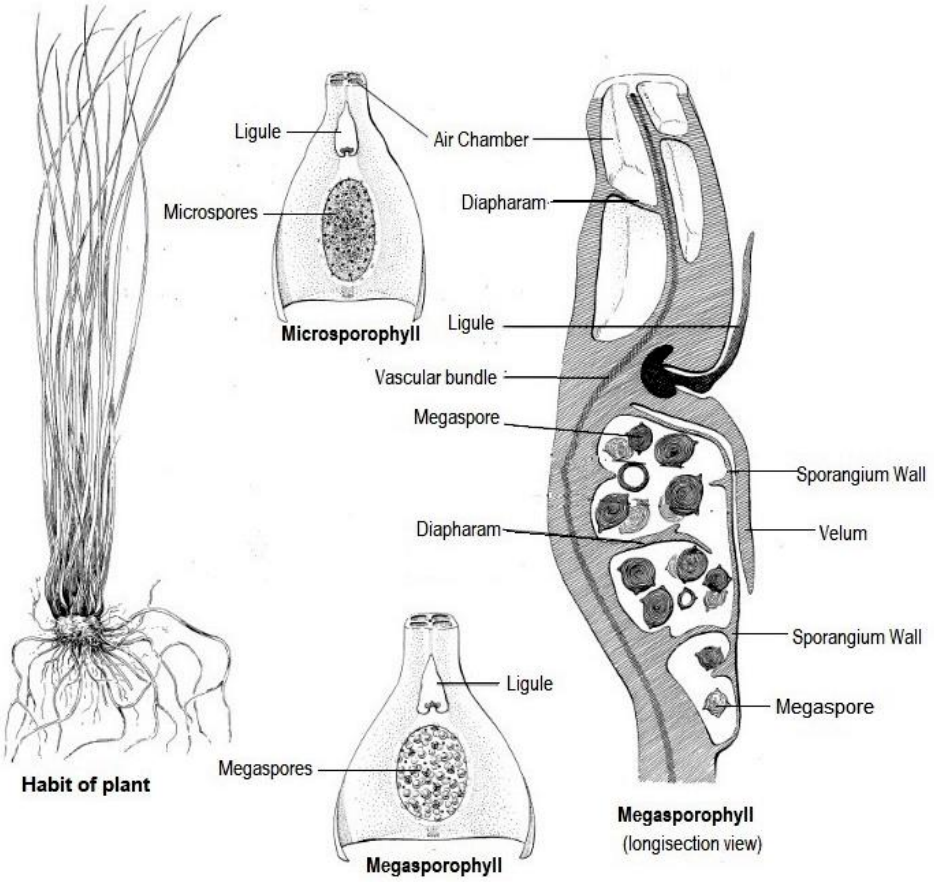


Figure 57. Illustration of *Isoetes* sporophyte and details of the sporophylls (Foster & Gifford 1974).

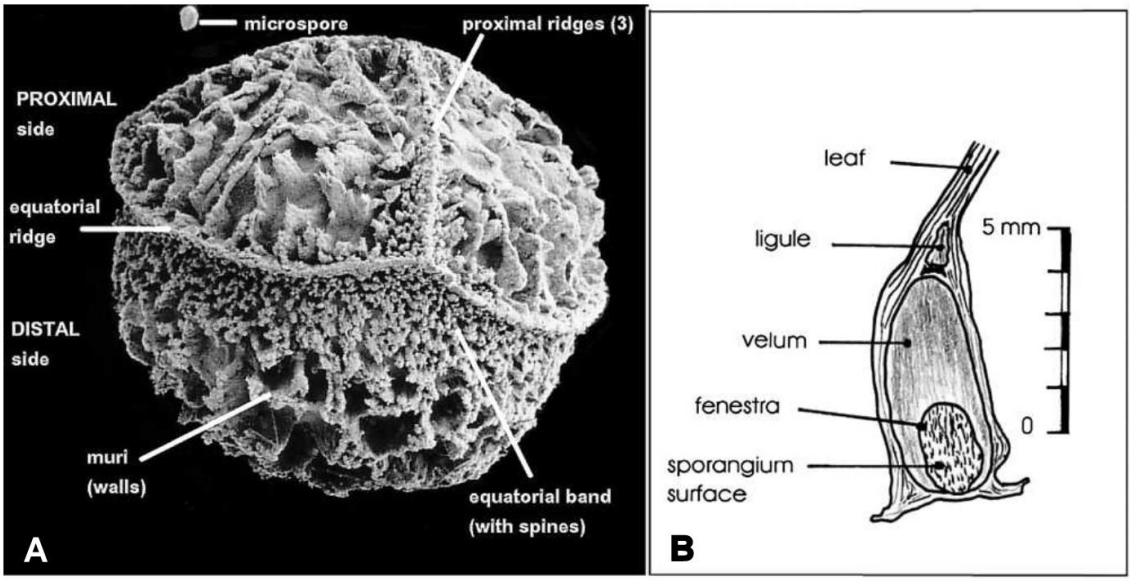


Figure 58. A. SEM image of megaspore and single microspore of *Isoetes tuckermanii* A. Br. (Guysborough Co., Nova Scotia, *Smith et al. 6780-* ACAD). SEM: Daniel F. Brunton & Donald F. Britton. **B.** Features of the basal inner leaf (*I. georgiana* N. Luebke, note extensive velum coverage). Illustration: Dan Brunton.

Figure 59. Base of *Isoetes* sporophylls with sporangia (velum highlighted in red). Photos by Peter Schafran. <www.isoetes.org/identification.html?utm_source>

Hybrids arise in habitats where two or more species coexist, often exhibiting hybrid vigor that enables them to grow larger than either of their parent species. Botanists recognize these hybrids by their aborted megaspores, which show marked polymorphism—variation in size, shape, and surface ornamentation. In contrast, the megaspores of the parent species are uniform and consistent in these traits. Although hybridization plays a significant role in shaping the diversity and evolution of quillworts, this paper focuses solely on the species-level taxonomy of *Isoetes*.

Excluding hybrids, Alabama is home to 12 quillwort taxa, with four species restricted to the Coastal Plain. The following taxonomic key is adapted from Dan Brunton's (2015) work on southeastern quillworts and an unpublished treatment he prepared for *Isoetes* species in northern Alabama (pers. comm., Dan Spaulding, 8 August 2023). Accurate identification requires mature specimens, as immature plants are notoriously difficult and often impossible to classify. Young or underdeveloped megaspores lack the distinctive surface patterns and structural features characteristic of mature spores (Kott & Britton 1983). Dan Brunton generously provided the scanning electron microscope (SEM) photomicrographs in this work.

1. Leaves stiff, 0.5–1.0 mm wide, 3–20 cm long, deciduous (usually withering by July); plants initially amphibious early in the season, becoming terrestrial as the water recedes; growing in ephemeral pools and seeps on exposed bedrock outcrops.

    2. Plants in calcareous soil of vernal seepages on limestone or dolomitic flats; leaves grass-green; megaspores > 525 µm diam., surface typically granular with low tubercles .....***Isoetes butleri***
    2. Plants in acidic soil in wet depressions on granitic or sandstone outcrops; leaves gray-green to bright green; megaspores < 525 µm diam., surface ridged or tuberculate.

        3. Megaspore ornamentation pattern densely tuberculate, short-ridged, or occasionally pseudo-reticulate; megaspores typically < 450 µm diam.; plants in ephemeral pools on granite or sandstone outcrops .....***Isoetes piedmontana***
        3. Megaspore ornamentation pattern wrinkled with low vermiform (worm-like) ridges or low tuberculate; megaspores typically 440–510 µm diam.; plants in ephemeral pools exclusively on granite outcrops..... ***Isoetes graniticola***

1. Leaves flaccid or flexible, 1.0–2.25 mm wide, > 15 cm long, evergreen or deciduous; plants aquatic, amphibious, or terrestrial; growing in swamp channels, creeks, seepages, depressions in alluvial forests, seasonally inundated grasslands, and occasionally ephemeral pools on acidic rock. (Note: the leaves of *Isoetes melanopoda* subsp. *melanopoda* are ±1 mm wide and often stiffly erect.)

4. Megaspore surface granular, tuberculate, or rugulate (irregularly ridged or wrinkled); leaves deciduous, typically withering by July; leaf bases black, brown, or whitish; velum coverage 5–15%; spores mature April–June.

    5. Leaves > 1.3 mm wide, 25–35 cm long, light green to grass-green; megaspores > 400 µm diam., surface conspicuously ornamented with numerous low tubercles or ridges; plants typically in deciduous woodland pools .....***Isoetes melanopoda*** subsp. ***silvatica***
    5. Leaves ±1 mm wide, 15–25 cm long, gray-green; megaspores < 380 µm diam., surface granular or obscurely ornamented with scattered tubercles and ridges; plants typically in wet grasslands or unforested seeps .....***Isoetes melanopoda*** subsp. ***melanopoda***

4. Megaspore surface variably reticulate (with a net-like pattern); leaves evergreen, persisting through winter; leaf bases whitish; velum coverage 5–70%; spores mature May–October.

    6. Megaspore ornamentation pattern uniformly reticulate, ridges forming regular geometric honeycombs; velum coverage typically 5–15% .....***Isoetes engelmannii***
    6. Megaspore ornamentation pattern irregularly reticulate, ridges ragged and incomplete; velum coverage typically 20–70%.

        7. Velum coverage 45–70%; sporangium wall unmarked; leaves grass-green or yellow-green; megaspores < 500 µm diam. ..... ***Isoetes valida***
        7. Velum coverage 20–25%; sporangium wall brown-streaked; leaves dull olive-green; megaspores > 525 µm diam. .....***Isoetes appalachiana***

1. Isoetes appalachiana D.F. Brunt. & D.M. Britton {Appalachian} — APPALACHIAN QUILLWORT (Fig. 60). [*Isoetes engelmannii* A. Braun var. *georgiana* Engelm.]

Figure 60. *Isoetes appalachiana*, Cleburne Co., Alabama, 16 May 2020. Photos: Dan Spaulding.

Plants aquatic or amphibious; evergreen. Woodland streams, swamp forests, river margins, seepages, and ephemeral depressions in hardwood floodplains. Sporulates May–October; very rare in the Cumberland Plateau, Piedmont, and Coastal Plain (Fig. 61). This species is widely distributed in the eastern USA, ranging from New Jersey and Pennsylvania, south to northern Florida, Alabama, and northeastern Mississippi (Weakley et al. 2025). The Alabama Natural Heritage Program (2023) lists this species as imperiled (S2) in the state.

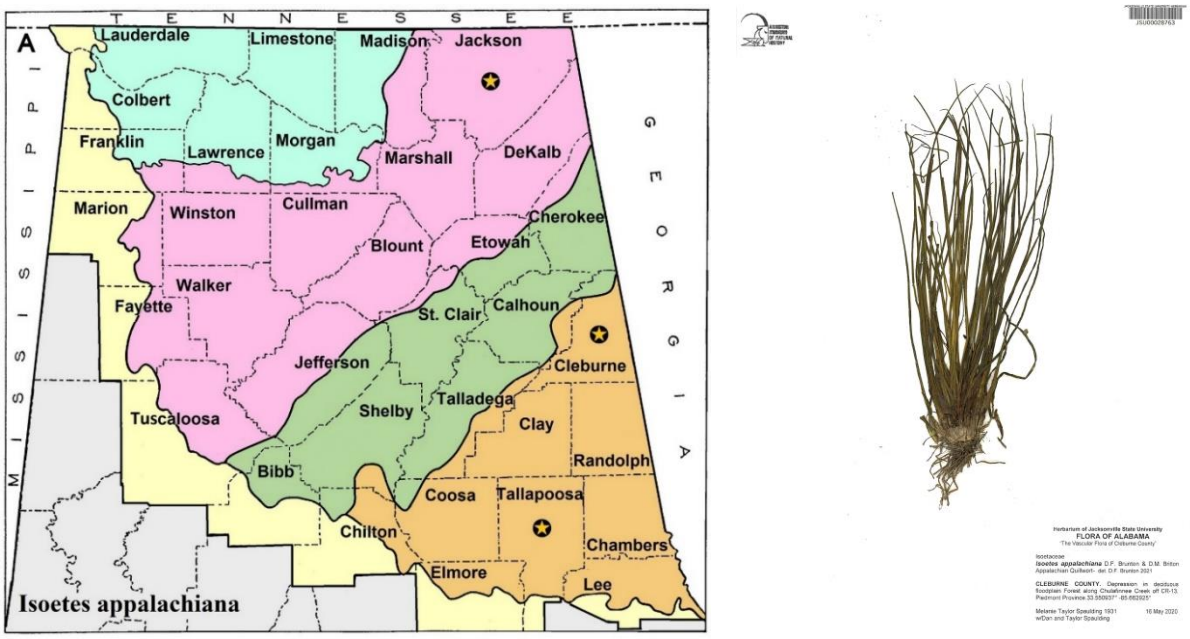


Figure 61. *Isoetes appalachiana*. **A.** Distribution map. **B.** Herbarium specimen (AMAL), *M.T. Spaulding 1931*, Cleburne Co., Alabama, 16 May 2020.

Brunton and Britton (1997) named *Isoetes appalachiana* due to its apparent prevalence in the Appalachian Mountains. They argued that the unique cytology, distribution, and morphology support its recognition as a distinct species. The authors suggest that it likely corresponds to the taxon initially described by George Engelmann over a century ago as *I. engelmannii* var. *georgiana*. Most populations of *I. appalachiana* produce megaspores with a ragged-reticulate surface (Fig. 62), in contrast to the regularly reticulate ornamentation of *I. engelmannii* (Brunton & Britton 1997). As tetraploids, *Isoetes appalachiana* plants produce larger spores (>500 µm) than the diploid *I. engelmannii* (<500 µm).

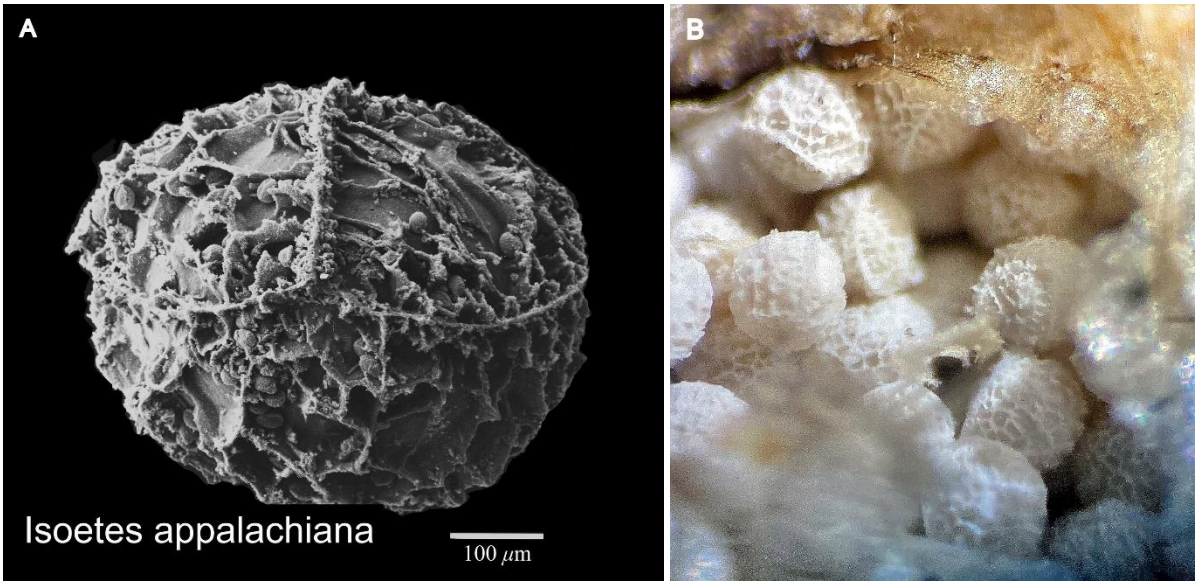


Figure 62. Megaspores of *Isoetes appalachiana*. **A.** SEM image by Donald M. Britton (*Brunton & McIntosh 11171*, Huntingdon Co., Pennsylvania, 6 Jul 1992, OAC). **B.** Herbarium specimen (AMAL), *M.T. Spaulding 1931*, Cleburne Co., Alabama, 16 May 2020. Photo: Dan Spaulding.

Isoetes appalachiana evolved as an allopolyploid through chromosome doubling of *I.* ×*altonharvillii* Musselman & R.D. Bray, the sterile hybrid between the diploid species *I. engelmannii* and *I. valida* (Brunton & Britton 1997, Schafran, 2019). Musselman et al. (1995) named the hybrid in honor of Alton M. Harvill Jr. (1916–2008), a distinguished botanist from Virginia. Initially, experts believed that Harvill's Quillwort grew in a forested creek in Jackson County, Alabama. However, Dan Brunton has questioned this record, noting that further investigations, including genetic analysis, will be needed to confirm the true identity of this population (pers. comm. Dan Spaulding, 16 January 2025).

2. Isoetes butleri Engelm. {in honor George Dexter Butler, 1850–1910} — GLADE QUILLWORT; LIMESTONE QUILLWORT; BUTLER'S QUILLWORT (Fig. 63).

Figure 63. *Isoetes butleri*, Bibb Co., Alabama, 11 Apr 2020. Photo: Alan Cressler.

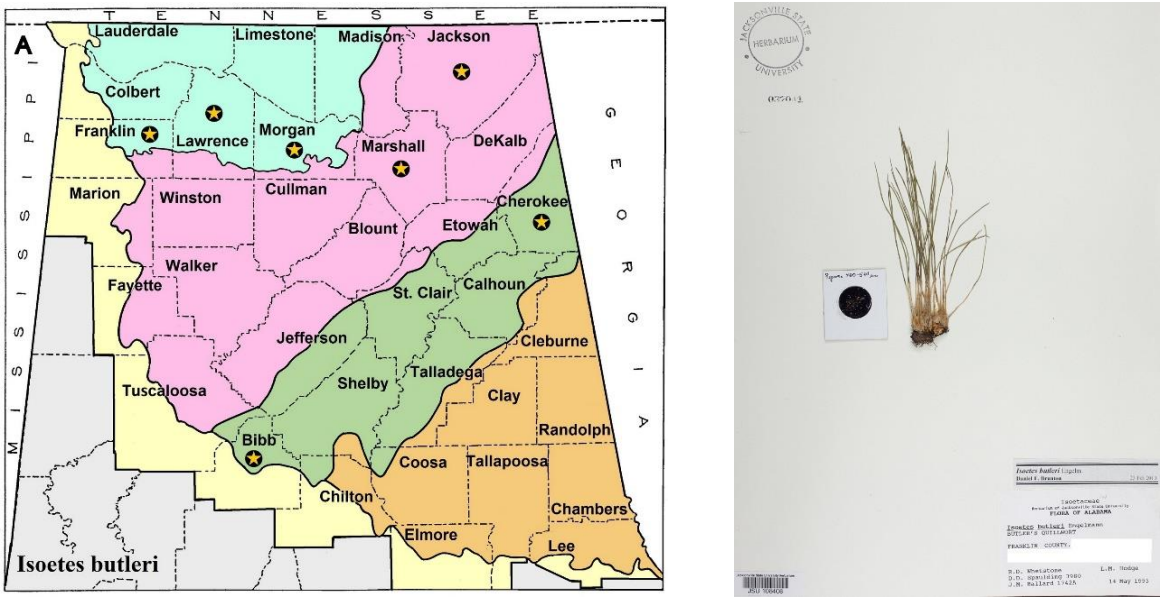


Figure 64. *Isoetes butleri.* **A.** Distribution map. **B.** Herbarium specimen (JSU), *Spaulding et al. 3980*, Franklin Co., Alabama, 14 May 1993.

Plants terrestrial (initially amphibious); deciduous. Depressions and seepages in calcareous soil of glades and barrens. Sporulates April–June; rare in the Highland Rim, very rare in Cumberland Plateau and Ridge & Valley (Fig. 64). Populations scattered from Illinois south through Oklahoma to eastern Texas and from southcentral Kentucky south to northern Alabama and west to northeastern Georgia (Taylor et al. 1993). The Alabama Natural Heritage Program (2023) lists this species as imperiled to vulnerable (S2S3) in the state.

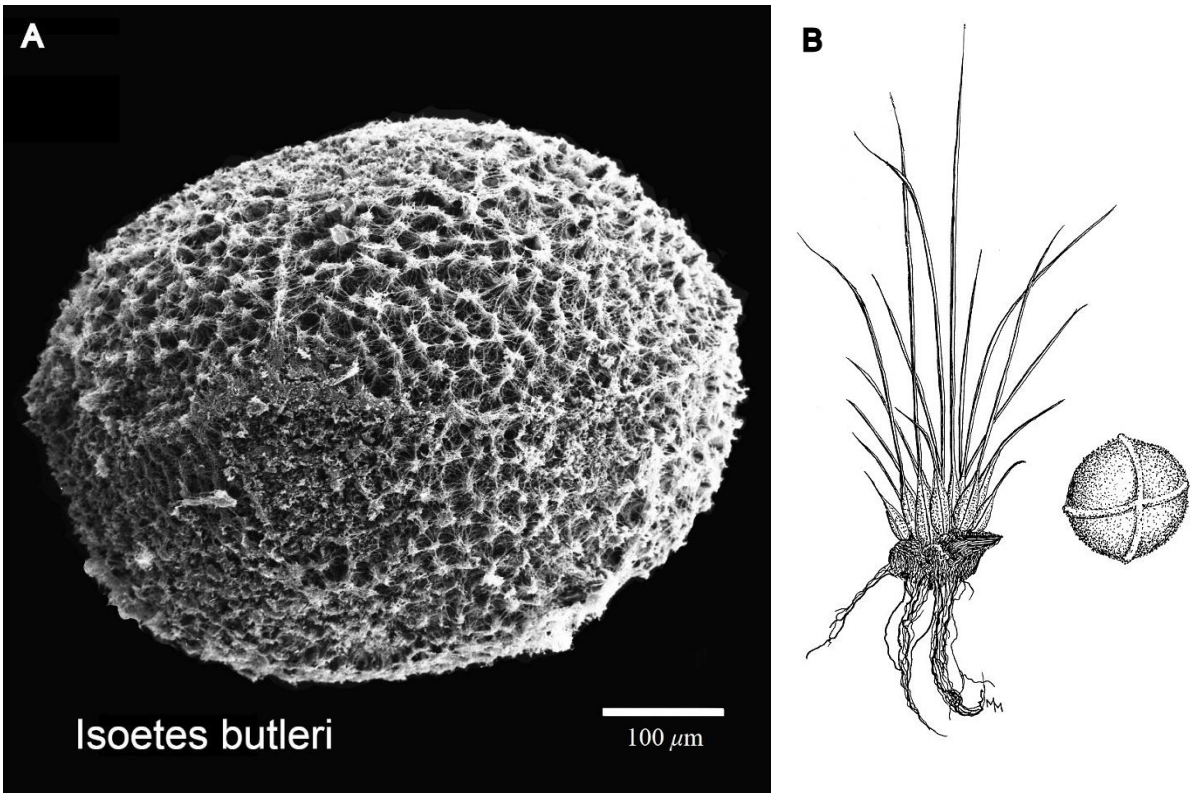


Figure 65. *Isoetes butleri.* **A.** SEM image of megaspore by Donald M. Britton (*Brunton & McIntosh 10331*, Rutherford Co., Tennessee, 22 May 1991, OAC). **B.** Illustration: Marion Montgomery, 1999.

In 1878, George Engelmann named *Isoetes butleri* in honor of George D. Butler, a lawyer, teacher, and botanist with whom he corresponded (Jepson 1928). This species thrives in open areas with thin, alkaline soils that remain water-saturated during the late winter and spring. During the dry summer months, its leaves turn yellow and die back, leaving the dormant rootstock to persist until favorable conditions return (Taylor et al. 1993). Unlike most quillworts, which are monoecious and produce both megaspores and microspores on the same plant, *I. butleri* is dioecious, with individual plants producing only one type of spore (Turner et al. 2005). The Limestone Quillwort is readily identified by its calcareous glade habitat and granular megaspores (Fig. 65).

3. Isoetes engelmannii A. Braun {George Engelmann, 1809–1884, German-American botanist} — ENGELMANN'S QUILLWORT (Fig. 66).

Plants aquatic or amphibious; evergreen. Small streams, ponds, lakes, pools, and ditches. Sporulates May–October; rare throughout Alabama (Fig. 67). This species occurs throughout the eastern USA and is disjunct in adjacent Canada (Ontario). The species ranges from New England south to Georgia and west to Oklahoma and Michigan, occurring frequently in the Appalachian highlands but only infrequently and in scattered locations elsewhere (Kartesz 2025).

Figure 66. *Isoetes engelmannii*. **A.** Upper Paint Rock River valley, Jackson Co., Alabama, 6 May 2012. **B.** Small tributary to Big Dry Creek, Floyd Co., Georgia, 3 May 2009. Photos: Alan Cressler.

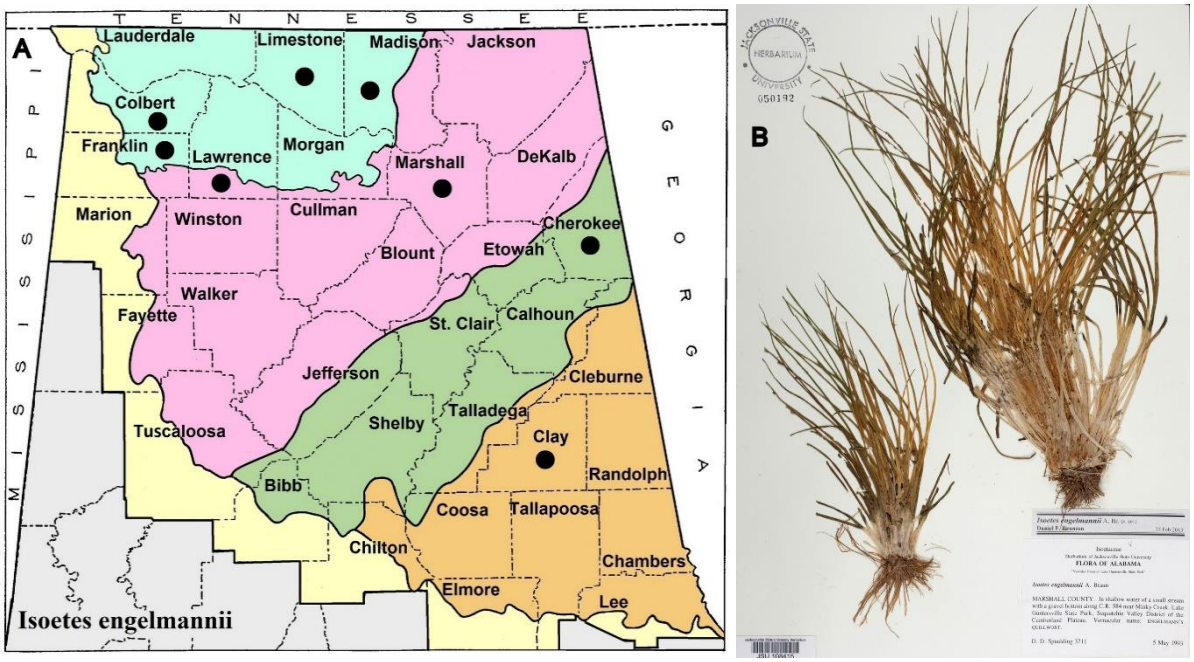


Figure 67. *Isoetes engelmannii.* **A.** Distribution map. **B.** Herbarium specimen (JSU), *Spaulding 3711*, Marshall Co., Alabama, 5 May 1993.

Isoetes engelmannii, the most widely distributed quillwort in the eastern United States, was once more common but has suffered significant population declines in recent decades due to habitat degradation (Sessa 2024). George Engelmann discovered the species in 1842 near St. Louis, Missouri, and it was later named in his honor by the German botanist Alexander Braun (Dean 1969). Engelmann's Quillwort typically thrives as an emergent plant in the shallow waters of lakes, ponds, ditches, and streams. As water levels recede, it transitions to an amphibious growth form (Fig. 68).

Figure 68. *Isoetes engelmannii*, Stanley Co., North Carolina, 3 Apr 2016. Photo: Dan Brunton.

A closely related species, *Isoetes appalachiana*, is similar in appearance but differs genetically and morphologically; *I. appalachiana* is a tetraploid, while *I. engelmannii* is a diploid. The primary distinguishing feature between the two lies in their megaspore ornamentation patterns and size: The larger (>500 µm) *I. appalachiana* megaspores exhibit a broken-reticulate pattern with ragged crests, whereas the smaller (<500 µm) megaspores of *I. engelmannii* (Fig. 69) display an unbroken reticulate pattern with generally smooth crests (Brunton & Britton 1997).

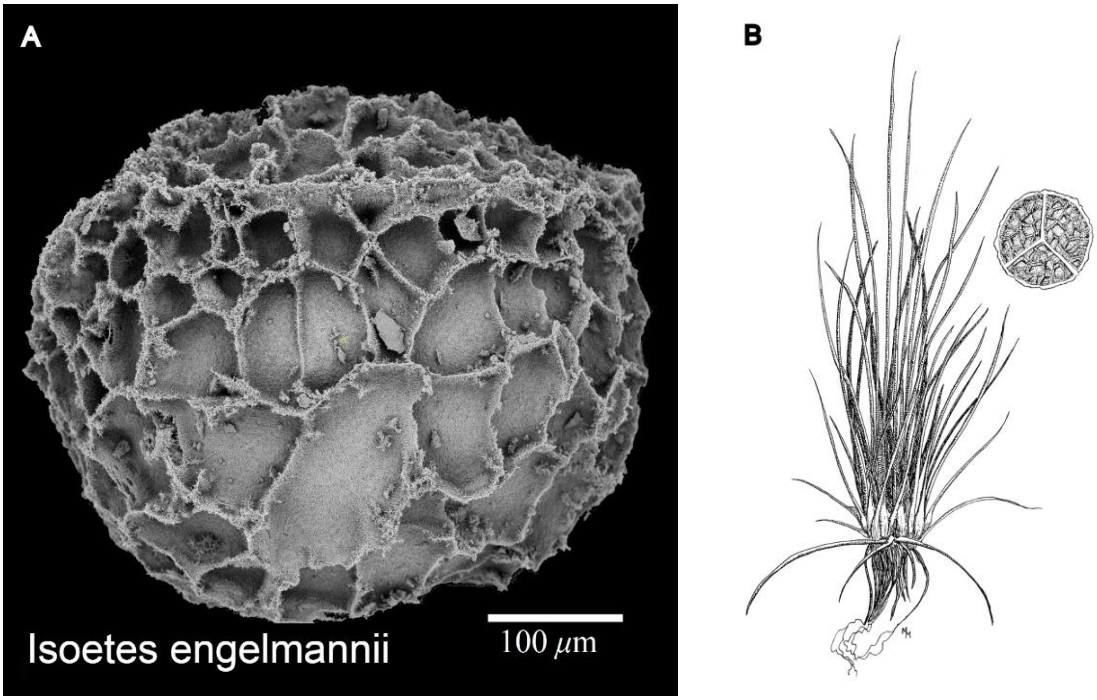


Figure 69. *Isoetes engelmannii*. **A.** SEM image of megaspore by Donald M. Britton, University of Guelph (*Engelmann s.n.*, Jefferson Co., Missouri, Sep 1842, P). **B.** Illustration: Marion Montgomery, 1999.

4. Isoetes graniticola D.F. Brunt. {granite dweller} — FLATROCK QUILLWORT; ALABAMA GRANITE QUILLWORT (Fig. 70).

Figure 70. *Isoetes graniticola*, granite outcrop (type locality), Randolph Co., Alabama. **A.** 19 May 2023. Photo: Noah Yawn. **B.** 22 Mar 2020. Photo: Dan Spaulding.

Plants terrestrial (initially amphibious); deciduous. Depressions or solution pits exclusively on granite flatrocks. Sporulates March–June; very rare in the Piedmont (Fig. 71). Endemic to the Piedmont of Alabama (Brunton 2016). The Alabama Natural Heritage Program (2023) lists this species as critically imperiled (S1) in the state.

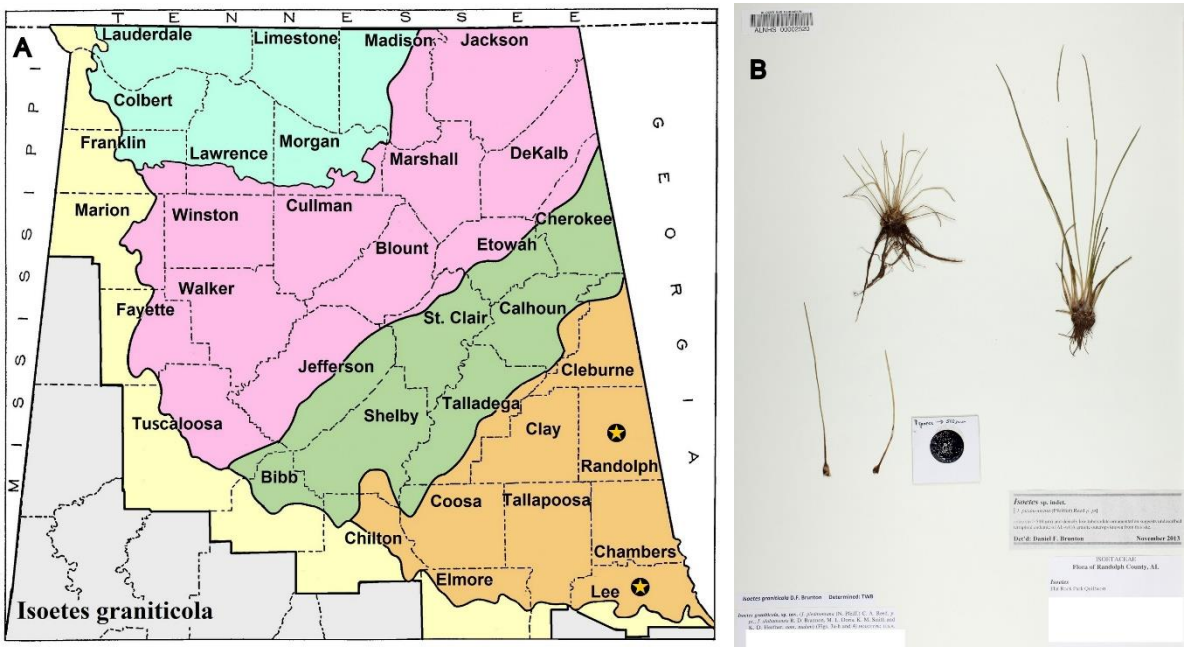


Figure 71. *Isoetes graniticola*. **A.** Distribution map. **B.** Herbarium specimen (ALNHS), *Barger & Holt SP#1189*, Randolph Co., Alabama, 10 Jun 2013.

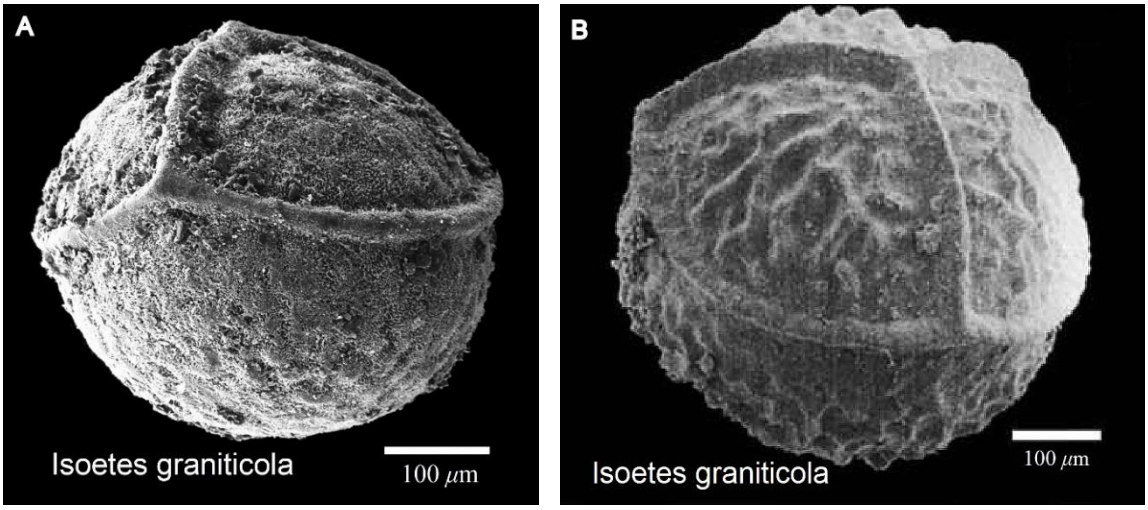


Figure 72. *Isoetes graniticola* megaspores. **A.** *Brunton &. McIntosh 11394*, Randolph Co., Alabama, 19 Mar 1993 (OAC). **B.** *Kral 63718*, Lee Co., Alabama, 24 May 1979 (VDB). SEM images: D.M. Britton, OAC, University of Guelph.

Flat Rock Quillwort (*Isoetes graniticola*) is a rare Alabama endemic restricted to ephemeral pools on granite outcrops in Randolph and Lee counties, with a possible occurrence in adjacent Heard County, Georgia. Unlike the widespread diploid Piedmont Quillwort (*I. piedmontana*, 2n = 22), *I. graniticola* is a tetraploid with 2n = 44 chromosomes. Although the two species are similar in appearance, *I. graniticola* has larger megaspores, characterized by low mounds and worm-like surface ridges (Fig. 72). The combination of its tetraploid status, restricted geographic range, and unique morphological traits supports the conclusion that *I. graniticola* is specifically distinct from the diploid *I. piedmontana* (Brunton 2016).

5. Isoetes melanopoda Gay & Durieu subsp. **melanopoda** {black-foot; dark leaf bases} — BLACKFOOT QUILLWORT; MIDLAND QUILLWORT; PRAIRIE QUILLWORT (Fig. 73).

Figure 73. *Isoetes melanopoda* subsp. *melanopoda*, wet pasture in Lawrence Co., Alabama, 2 May 2013. Photos: Wayne Barger.

Plants terrestrial (initially amphibious); deciduous. Ephemeral wet prairies, graminoid swales, seasonally flooded fields and pastures, and occasionally in seeps on sandstone outcrops. Sporulates April–June; very rare in the Moulton Valley District of the Highland Rim, Sand Mountain District of the Cumberland Plateau, and Black Prairie District of the Coastal Plain (Fig. 74). Its primary range is west of the Mississippi River, covering the midwestern USA from southwestern Minnesota and Illinois south to Louisiana and Texas. Disjunct populations east of the Mississippi River occur in Alabama, Mississippi, Tennessee, Kentucky, and southern Indiana (Kartesz 2025). The Alabama Natural Heritage Program (2017) previously classified *Isoetes melanopoda* (sensu lato) as critically imperiled (S1), and we recommend retaining this rank in the state because of its rarity.

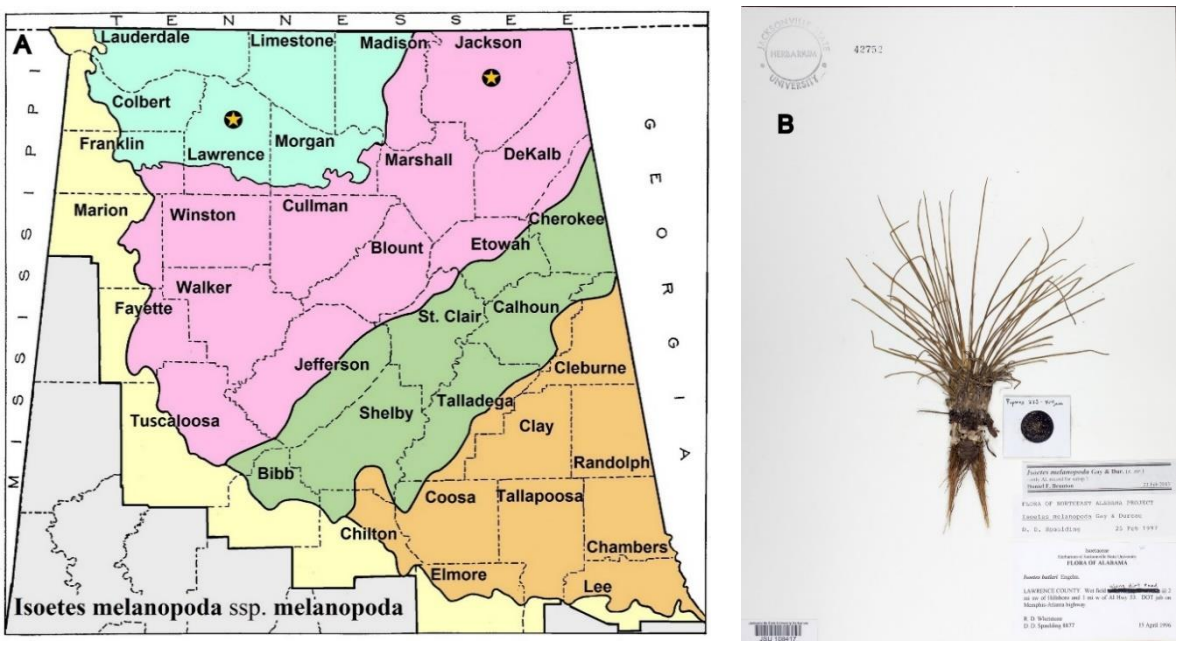


Figure 74. *Isoetes melanopoda* subsp. *melanopoda*. **A**. Distribution map. **B**. Herbarium specimen (JSU), *Spaulding & Whetstone 8877*, Lawrence Co., Alabama, 15 Apr 1996.

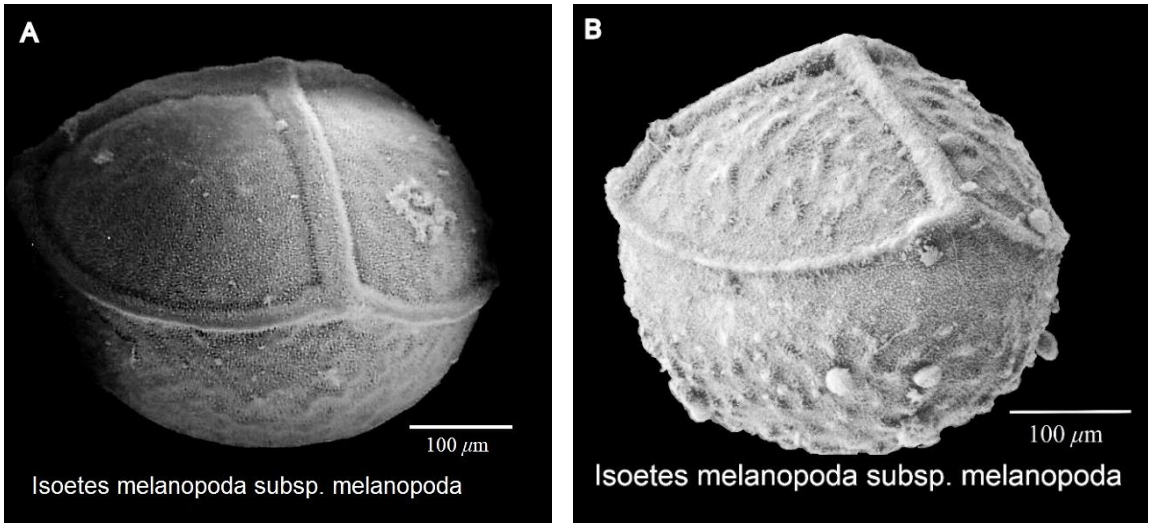


Figure 75. *Isoetes melanopoda* subsp. *melanopoda* megaspores. **A.** *Hellquist & Couch 12849*, Pushmataha Co., Oklahoma, 1 Jul 1978 (UNA). **B.** *Hall s.n. 63718*, Menard Co., Illinois, Jul 1863 (NY). SEM: Donald M. Britton, University of Guelph.

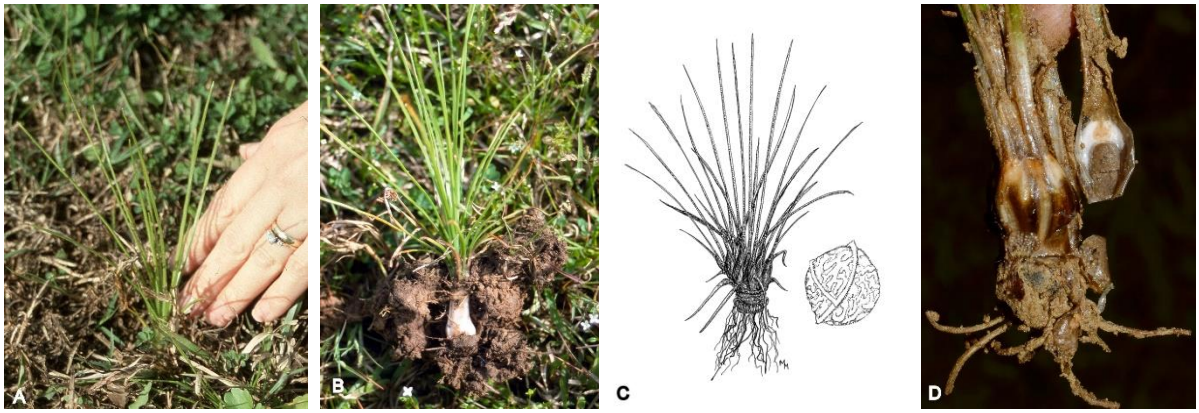


Figure 76. *Isoetes melanopoda* subsp. *melanopoda*. **A**–**B.** Whole plant, Caddo Parish, Louisiana, 15 Mar 1994. Photos: Dan Brunton. **C.** Illustration: Marion Montgomery, 1999. **D.** Plant base, Pulaski Co., Arkansas, 4 Jul 2020. Photo: Richard Abbott.

Brunton and Britton (2006) distinguish *Isoetes melanopoda* subsp. *melanopoda* from subsp. *silvatica* based on differences in megaspore ornamentation, habitat preferences, and leaf morphology. Subspecies *melanopoda* produces smaller megaspores (< 380 μm) with a plain or obscurely ornamented surface (Fig. 75). Plants are relatively small and inhabit unforested, ephemeral wet sites. Their slender, stiffly erect, grayish-green leaves (Fig. 76a–c) typically have chestnut-brown or shiny black bases (Fig. 76d). In contrast, subsp. *silvatica* produces larger megaspores (> 400 μm) with prominently tuberculate or densely short-ridged ornamentation. These more robust plants primarily occupy ephemeral woodland swamps in eastern North America. Their leaves are light green, slightly broader, and weak, with whitish bases. Both subspecies are deciduous, with leaves that wither during the summer in southern regions, and share the trait of minimal velum coverage (5–15%).

6. Isoetes melanopoda Gay & Durieu subsp. **silvatica** D.F. Brunton & D.M. Britton {of woodlands} — WOODLAND QUILLWORT; EASTERN BLACKFOOT QUILLWORT (Fig. 77).

Figure 77. *Isoetes melanopoda* subsp. *silvatica*. **A.** Cherokee Co., Alabama, 5 Apr 2015. Photo: Dan Brunton. **B.** Shelby Co., Alabama, 22 Feb 2022. Photo: Wayne Barger.

Plants amphibious; deciduous. Woodland pools, hardwood swamp edges, and ephemeral woodland swamps. Sporulates April–June; rare in the Highland Rim, Cumberland Plateau, Ridge & Valley, and Coastal Plain (Fig. 78). The subspecies is restricted to the southeastern USA east of the Mississippi River. It ranges from Virginia and Tennessee south to Mississippi, Alabama, and Georgia, and is disjunct in Southern New Jersey (Kartesz 2025).

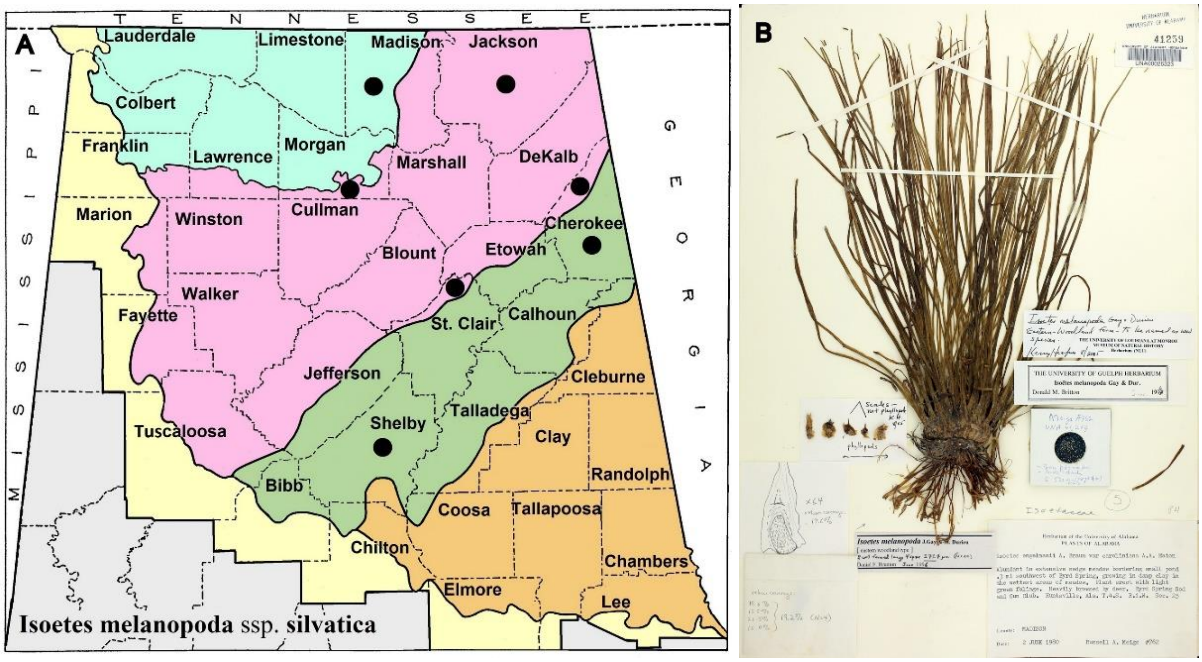


Figure 78. *Isoetes melanopoda* subsp. *silvatica.* **A**. Distribution map. **B**. Herbarium specimen (UNA), *Meigs 762*, Madison Co., Alabama, 2 Jun 1980.

Figure 79. *Isoetes melanopoda* subsp. *silvatica* in woodland pool, Eagle Point Nature Preserve, Rowan Co., North Carolina, 3 Apr 2016. Photo: Dan Brunton.

Brunton and Britton (2006) identified two subspecies of Blackfoot Quillwort, both occurring in northern Alabama. They classified *Isoetes melanopoda* (sensu lato) as a diploid species occupying two distinct ecological regions: *I. melanopoda* subsp. *melanopoda* typically inhabits ephemeral prairie wetlands in central North America, while subsp. *silvatica* is found in deciduous swamp forests in the eastern part of the continent (Fig. 79). Detailed analysis of morphological and ecological traits—including leaf width, habitat preference, leaf base color, megaspore ornamentation, and megaspore size—revealed two distinct population groups within its range. *Isoetes melanopoda* subsp. *silvatica* is a more robust plant, characterized by longer (25–35 cm) and broader (>1.3 mm) leaves with a whitish base. Its relatively larger megaspores exhibit prominently tuberculate and/or densely short-ridged ornamentation (Fig. 80).

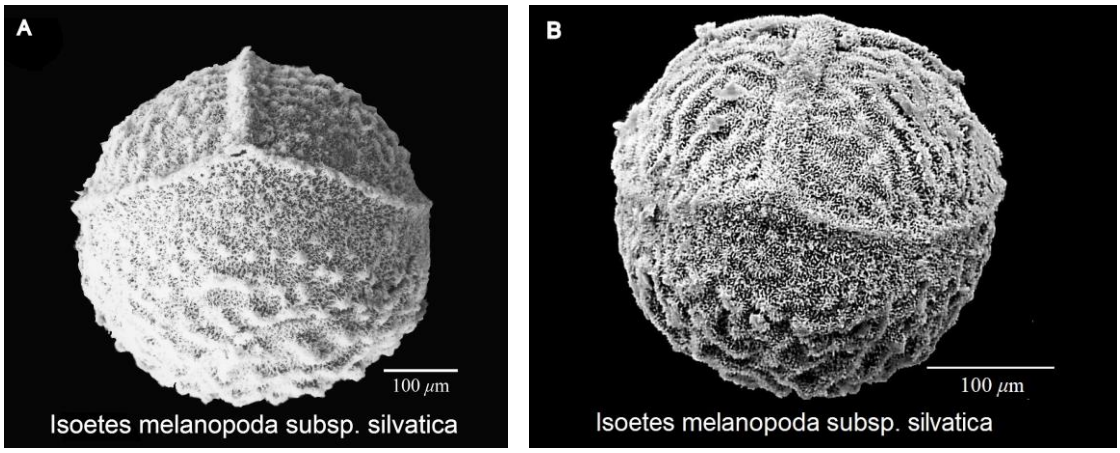


Figure 80. *Isoetes melanopoda* subsp. *silvatica* megaspores. **A.** *Matthews s.n.*, Mecklenburg Co., North Carolina, 7 May 1993 (OAC). **B.** *Brunton & McIntosh 11426*, Fauquier Co., Virginia, 21 May 1993 (OAC). SEM credit: Donald M. Britton.

Although these subspecies occupy different geographic and ecological regions and exhibit unique characteristics, intermediate populations in transitional zones suggest they should remain classified at the subspecific level rather than as distinct species (Brunton & Britton 2006). Alabama's intermediate location between the ranges of the western and eastern subspecies reflects this transitional nature, with frequent populations exhibiting traits of both taxa. The absence of sterile hybrids between the two subspecies indicates no effective genetic barrier, a key criterion for distinguishing true species. This situation exemplifies the gradual transition of subspecific populations within a single species (pers. comm. Dan Brunton, 16 January 2025).

Recent molecular studies have challenged this classification. Schafran (2019) demonstrated that the subspecies are polyphyletic and argued that molecular phylogenetic data support elevating *I. melanopoda* subsp. *silvatica* to species rank. However, Dan Brunton (pers. comm., 16 January 2025) noted that the genetic evidence also supports recognizing additional distinct taxa within the *I. melanopoda* complex.

7. Isoetes piedmontana (N. Pfeiff.) C.F. Reed {of the Piedmont} — PIEDMONT QUILLWORT (Fig. 81). [*Isoetes virginica* N. Pfeiff. var. *piedmontana* N. Pfeiff.]

Plants terrestrial (initially amphibious); deciduous. Depressions on granite flatrock, rarely on sandstone outcrops. Sporulates March–June; very rare in the Lookout Mountain District of the Cumberland Plateau, rare in the Piedmont (Fig. 82). Chiefly in the Piedmont from Virginia south to Alabama (Kartesz 2025). The Alabama Natural Heritage Program (2023) lists this species as imperiled (S2) in the state.

Figure 81. *Isoetes piedmontana.* **A.** Granite outcrop, Chambers Co., Alabama, 14 Feb 2021. Photo: Alan Cressler. **B.** Sandstone outcrop, Etowah, Co., Alabama, 12 Apr 2018. Photo: Wayne Barger.

Isoetes piedmontana is the most common of the flat rock quillworts. This lycophyte primarily grows on granite outcrops, though it occasionally appears on sandstone. It thrives in and around solution pits—shallow, temporary pools that form on the rock surface and fill with water from winter through early summer. The harsh outcrop environment presents challenges, including intense light exposure, seasonal flooding, and its thin, acidic, nutrient-poor substrates. Summer heat and drought further intensify these conditions (Brunton 2016).

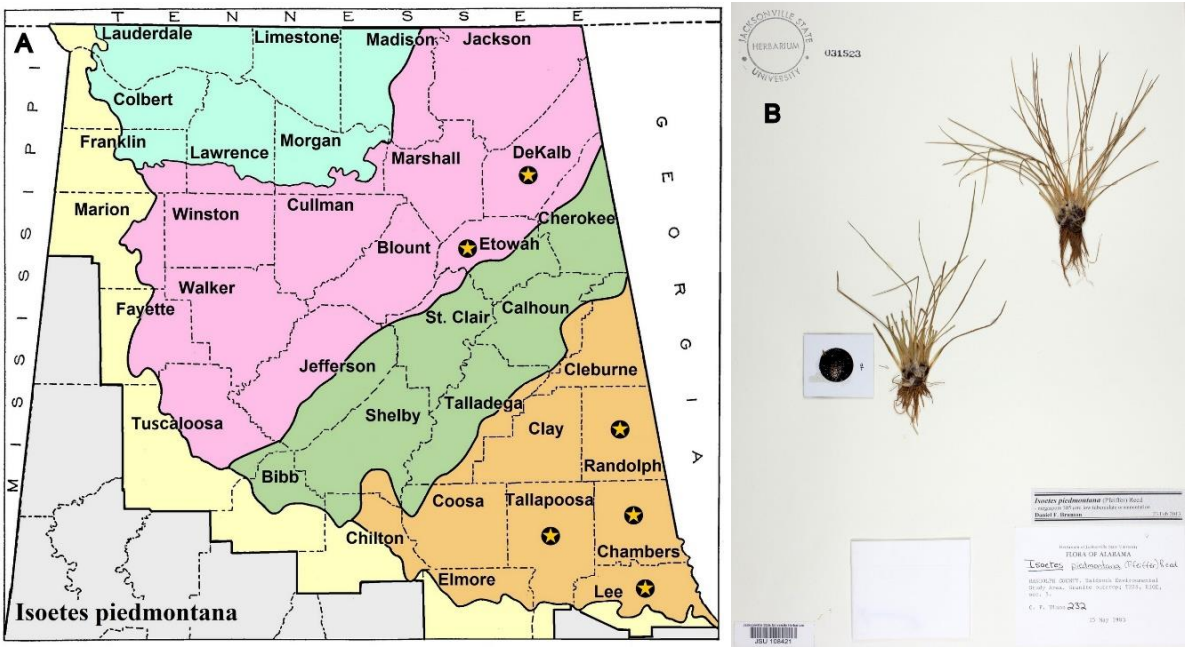


Figure 82. *Isoetes piedmontana.* **A.** Distribution map. **B.** Herbarium specimen (JSU), *Nixon 232*, Randolph Co., Alabama, 15 May 1983.

The Piedmont Quillwort (*Isoetes piedmontana*), a diploid species, closely resembles the tetraploid Flat Rock Quillwort (*I. graniticola*) in morphology and habitat preference. Both species thrive in ephemeral, water-filled solution pits on granite outcrops. However, *I. piedmontana* has a broader ecological range, inhabiting sandstone glades (Fig. 83). The most notable difference between the two species lies in their megaspores. *Isoetes piedmontana* produces smaller megaspores (<450 µm) with highly pronounced ornamentation, ranging from densely tuberculate to short-ridged forms (Fig. 84). In contrast, *I. graniticola* typically has larger megaspores (440–510 µm) with more subdued ornamentation, featuring low mounds or low vermiform (worm-like) ridges. These differences in spore size and ornamentation highlight the subtle morphological divergence between the species (Brunton 2016).

Figure 83. *Isoetes piedmontana*, sandstone outcrop habitat on Lookout Mountain, DeKalb Co., Alabama, 27 Jan 2018. Photo: Alan Cressler.

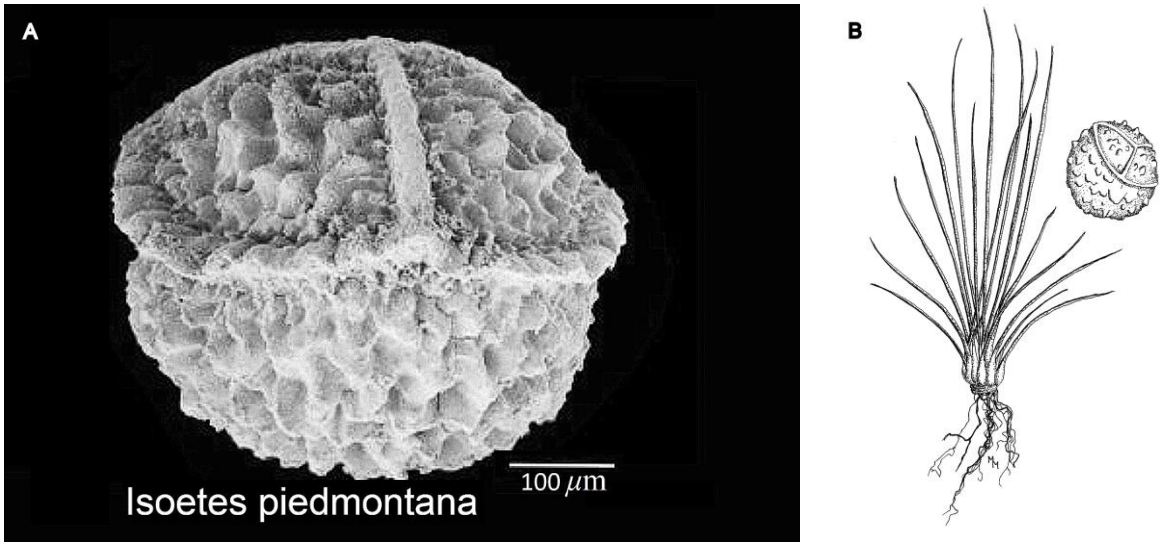


Figure 84. *Isoetes piedmontana.* **A.** Short-ridged megaspore, *Kral 57557*, Columbia Co., Georgia, 10 Apr 1976 (VDB). SEM: Donald M. Britton, OAC, University of Guelph. **B.** Illustration of plant and tuberculate megaspore by Marion Montgomery, 1999.

8. Isoetes valida (Engelm.) Clute {strong, robust; referring to large size} — STRONG QUILLWORT; TRUE QUILLWORT; MOUNTAIN QUILLWORT; CAROLINA QUILLWORT (Fig. 85). [*Isoetes caroliniana* (A.A. Eaton) N. Luebke; *Isoetes engelmannii* A. Braun var. *caroliniana* A.A. Eaton; *Isoetes engelmannii* var. *valida* Engelm.]

Figure 85. *Isoetes valida*, swamp margin, Conecuh Co., Alabama, 7 May 2013. Photos: Wayne Barger.

Plants aquatic or amphibious; evergreen. Seeps, bogs, margins of swamps, streams, and ponds. Sporulates May–October; rare in the Cumberland Plateau, Ridge & Valley, Piedmont, and Coastal Plain (Fig. 86). Native to the eastern USA from southern New York, south chiefly through the Appalachians to southern Alabama (Kartesz 2025).

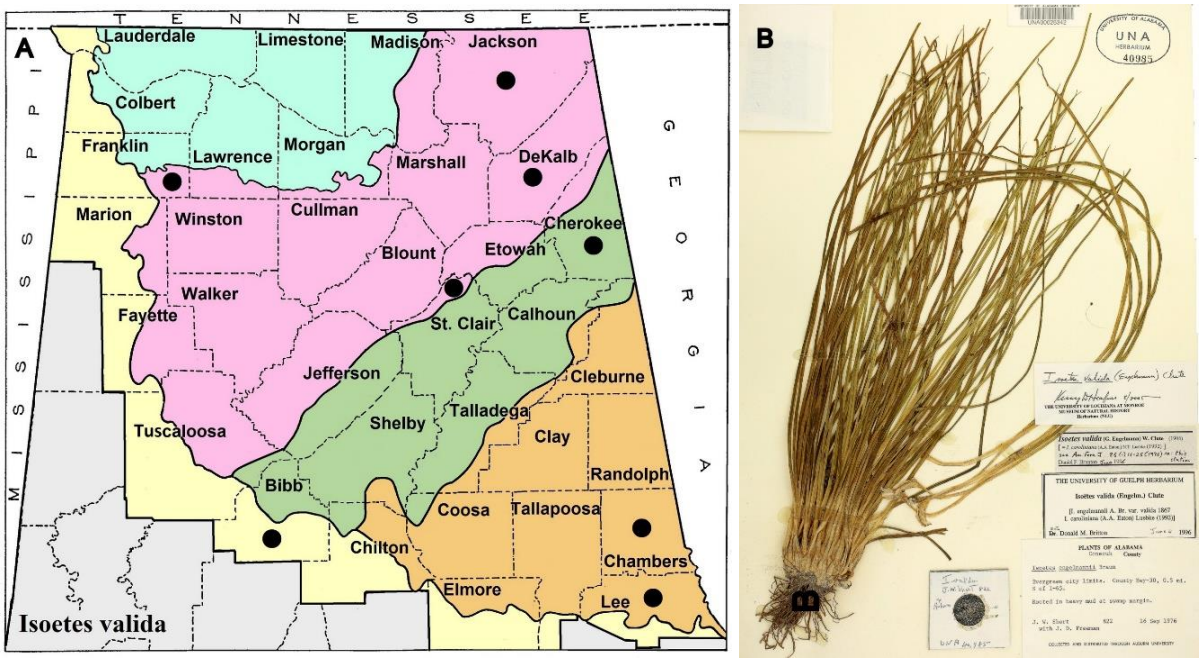


Figure 86. *Isoetes valida.* **A.** Distribution map. **B.** Herbarium specimen (UNA), *Short & Freeman 822*, Conecuh Co., Alabama, 16 Sep 1976.

In 1862, American botanist Thomas C. Porter discovered the Strong Quillwort in Lancaster, Pennsylvania. George Engelmann (1882) later described Porter's collection as *Isoetes engelmannii* var. *valida*, identifying it as the largest *Isoetes* in North America. The epithet *valida*, meaning 'strong,' highlighted its robust size and inspired its common name. In 1905, Willard Clute elevated the taxon to species rank as *I. valida* in his second book devoted to North American fern allies, citing its distinctive morphological features.

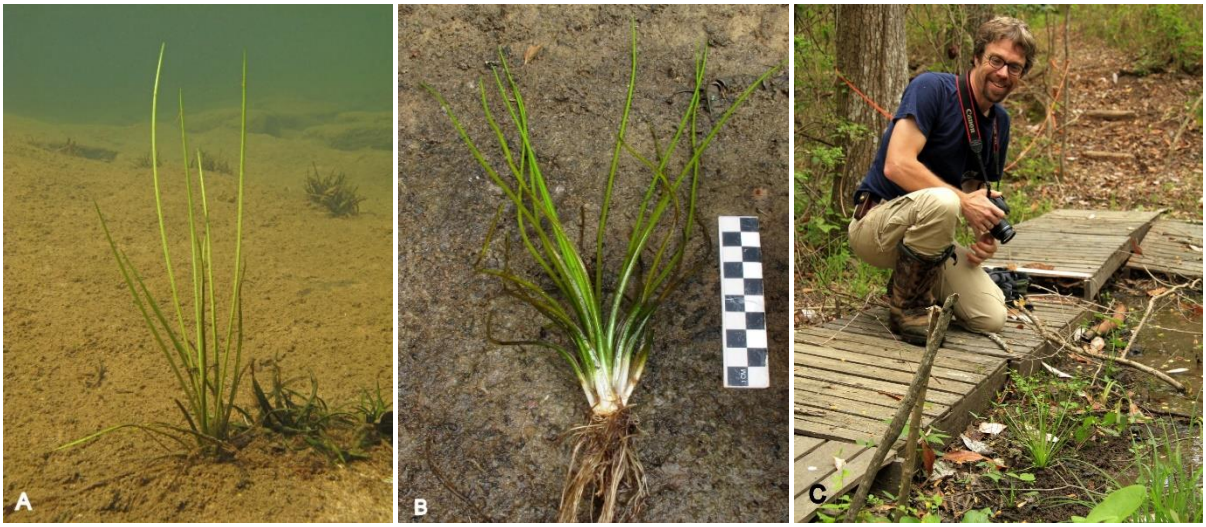


Figure 87. *Isoetes valida.* **A**–**B.** Lookout Mountain, Chattanooga Co., Tennessee, 17 Jun 2011. Photos: Alan Cressler. **C.** Wayne Barger with *I. valida*, Pike Co., Alabama, 6 Apr 2015. Photo: Dan Brunton.

Isoetes valida belongs to the *I. engelmannii* species complex, with both quillworts sharing morphological similarities and aquatic to amphibious habitats (Fig. 87). However, several distinct traits differentiate *I. valida* from *I. engelmannii*. The megaspores of *I. valida* exhibit a ragged, net-like ornamentation (Fig. 88), whereas those of *I. engelmannii* display a more regular reticulate pattern. The velum in *I. valida* covers at least half of the sporangium wall, compared to less than 25% in *I. engelmannii*. Leaf morphology also sets the two species apart: *I. valida* features wider, erect, and broadly arching leaves with a distinctly yellowish-green color, while *I. engelmannii* has narrower, darker-green leaves that are somewhat wiry to slightly flattened and tend to be loosely reflexed or sprawling. Additionally, *I. valida* emerges earlier in the year than any other aquatic or amphibious quillwort in the southeastern United States (Brunton & Britton 1996).

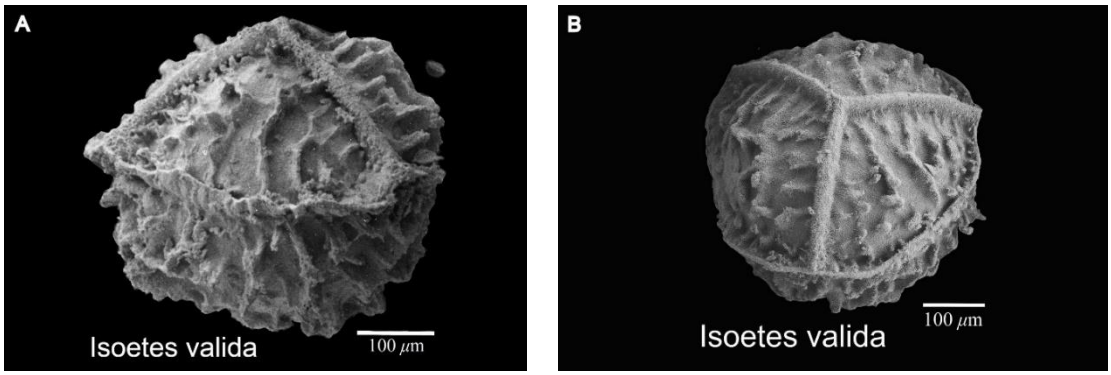


Figure 88. *Isoetes valida* megaspores. **A.** *Porter s.n.*, Lancaster Co., Pennsylvania, Oct 1866 (P). **B.** *Brunton & McIntosh 21342*, Jackson Co., Alabama, 26 Jun 2024 (DFB). SEM credit: Paul C. Sokoloff & Donald M. Britton, Canadian Museum of Nature, Ottawa.

4. SELAGINELLACEAE (Spikemoss Family) – in Selaginellales

The family Selaginellaceae has a complex taxonomic history, with botanists proposing multiple classification systems over time. Historically, they included all species in a single, broadly defined genus, *Selaginella* (Sessa 2024), but Weakley et al. (2025) now recognize several distinct genera.

1. Leaves nearly equal in size, spirally arranged, not in distinct ranks; stems and branches rounded or quadrangular; leaf tips acuminate, ending in long, hair-like extensions ..... ***Bryodesma***
1. Leaves dimorphic, arranged in four ranks (two appressed lateral and two spreading medial); stems and branches flattened; leaf tips acute, ending in a short, sharp point.

   2. Stems erect, with stiff hairs; plants bushy, fern-like ..... ***Didiclis***
   2. Stems creeping or weakly arching, hairless; plants short-branched, moss-like ..... ***Selaginella***

1. BRYODESMA Soják 1992 {bry-oh-DEZ-muh}

[Greek *bryo*, moss, and *desma*, bundle; referring to moss-like appearance]

1. Stems primarily erect or ascending, forming compact clumps; aerial roots confined to the stem base; bud-like branches present; megaspores honey-combed ..... ***Bryodesma corallinum***
1. Stems primarily creeping, often with upright tips, forming mats; aerial roots present along most of the stem; bud-like branches absent; megaspores nearly smooth ..... ***Bryodesma rupestre***

1. Bryodesma corallinum (Riddell) Weakley {coral; coral-like branching} — RIDDELL'S SPIKEMOSS SANDSTONE BLUFF SPIKEMOSS (Fig. 89). [*Bryodesma arenicola* (Underw.) Soják subsp. *riddellii* (Van Eselt.) Skoda; *Selaginella arenicola* Underw. subsp. *riddellii* (Van Eselt.) R.M. Tryon; *Selaginella corallina* (Riddell) Wilbur & Whitson; *Selaginella riddellii* Van Eselt.]

Figure 89. *Bryodesma corallinum*. **A.** Sandstone outcrop, Jefferson Co., Alabama, 13 Dec 2024. Photo: Dan Spaulding. **B.** Strobili, Shelby Co., Alabama, 22 Jan 2022. Photo: Noah Yawn.

Plants epipetric or terrestrial; evergreen. On granite and sandstone outcrops in northern Alabama, and in dry sandy soils of longleaf pine and sandhill communities in the Coastal Plain. Sporulates year-round; rare in the Cumberland Plateau, Ridge & Valley, Piedmont, and Coastal Plain (Fig. 90). Endemic to the southeastern USA. Ranging from eastern Oklahoma to Arkansas, south to Louisiana and Texas, and disjunct in Alabama, Georgia, and northwestern South Carolina (Kartesz 2025). The Alabama Natural Heritage Program (2023) lists this species as imperiled (S2) in the state.

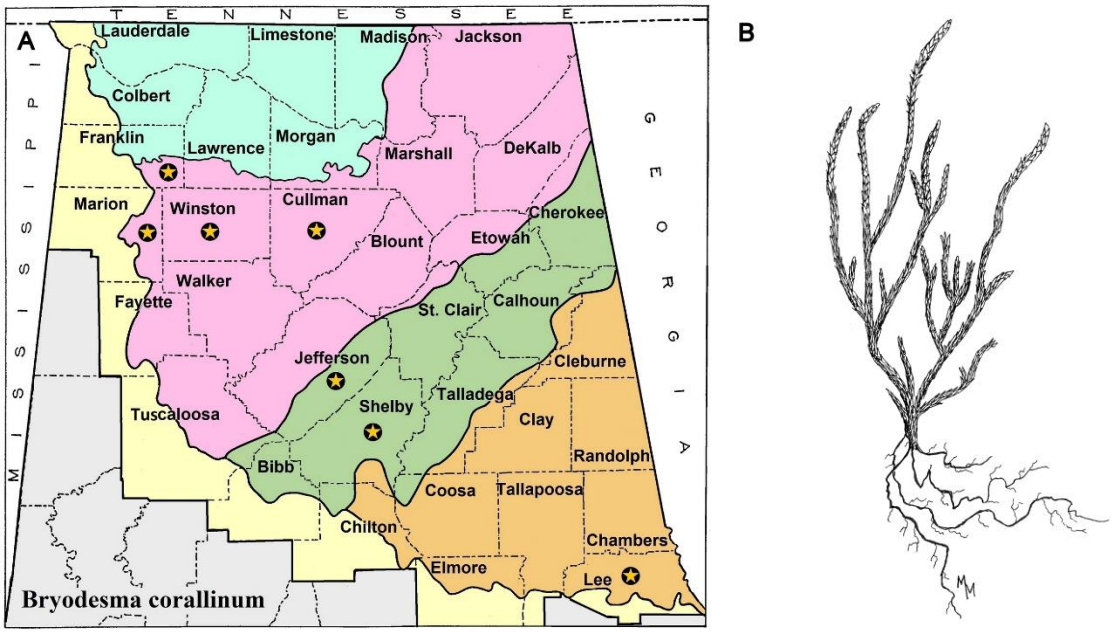


Figure 90. *Bryodesma corallinum*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 2000.

Figure 91. *Bryodesma corallinum*, rock outcrop in Shelby Co., Alabama, 22 Jan 2022. Photo: Noah Yawn.

The common name of this spikemoss honors John Leonard Riddell (1807–1865), inventor of the binocular microscope and author of an early flora of Louisiana. *Bryodesma corallinum* typically inhabits rock outcrops in northern Alabama (Fig. 91) but also thrives in sandy habitats of the Coastal Plain. In the Piedmont, a single population occurs in Lee County, where ecological succession has dramatically altered its habitat. During a 2009 visit to the granite outcrop site, John Short and Dan Spaulding found no trace of the spikemoss. Soil accumulation and the encroachment of shrubs and small trees have overtaken the formerly open rock surface where the species once flourished.

2. Bryodesma rupestre (L.) Soják {of rocks} — ROCK SPIKEMOSS; LEDGE SPIKEMOSS; DWARF SPIKEMOSS (Fig. 92). [*Selaginella rupestris* (L.) Spring]

Figure 92. *Bryodesma rupestre*, Cleburne Co., Alabama, 30 Apr 2023. Photos: Dan Spaulding.

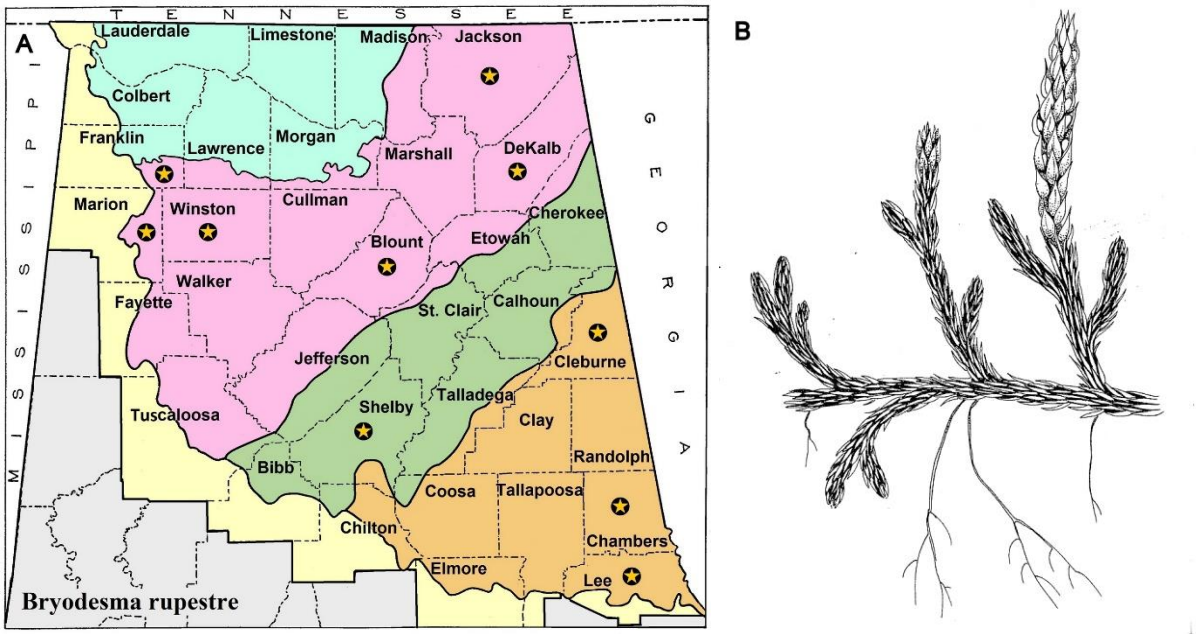


Figure 93. *Bryodesma rupestre*. **A.** Distribution map. **B.** Illustration: Miriam Wysong Meyer, 1967.

Plants epipetric; semi-evergreen. Grows in thin soil on dry sandstone, granitic, and occasionally phyllite outcrops. Sporulates May–September; rare in the Cumberland Plateau, Ridge & Valley, and Piedmont (Fig. 93). This species occurs mainly in eastern North America, ranging from Nova Scotia west to British Columbia and south to Oklahoma, Alabama, and Georgia, with a disjunct population in southern Greenland (Weakley et al. 2025). The Alabama Natural Heritage Program (2023) ranks it as imperiled to vulnerable (S2S3) within the state.

Figure 94. *Bryodesma rupestre* on phyllite, Cleburne Co., Alabama, 30 Apr 2023. Photo: Dan Spaulding.

Bryodesma rupestre often forms dense, carpet-like mats across the surface of dry, flat rocks (Fig. 94). Like many rock-dwelling species, it thrives during the cooler, wetter months of winter and spring when rainfall is plentiful. In summer, the thin soil dries under intense heat, causing the plants to appear dead; however, they quickly revive with the return of late-season rains.

2. DIDICLIS P. Beauvois ex Mirbel 1802 {dih-DIH-kliss}
[Greek *di*, double, and *diklis*, two-doored; alluding to the two valves of the sporangia]

1. **Didiclis braunii** (Baker) Li Bing Zhang & X.M. Zhou {for Emma Lucy Braun, 1889–1971, American ecologist} — ARBORVITAE-FERN; TREELET SPIKEMOSS, BRAUN'S SPIKEMOSS (Fig. 95). [*Lycopodioides braunii* (Baker) Kuntze; *Selaginella braunii* Baker]

Figure 95. *Didiclis braunii* in cultivation, Calhoun Co., Alabama, 20 Sep 2024. Photos: Dan Spaulding.

Plants terrestrial; evergreen to semi-evergreen. Moist areas around old homesites and gardens. Sporulates May–September; very rare throughout Alabama (Fig. 96). Native to China and only sparsely naturalized in the southeastern USA (Valdespino 1993).

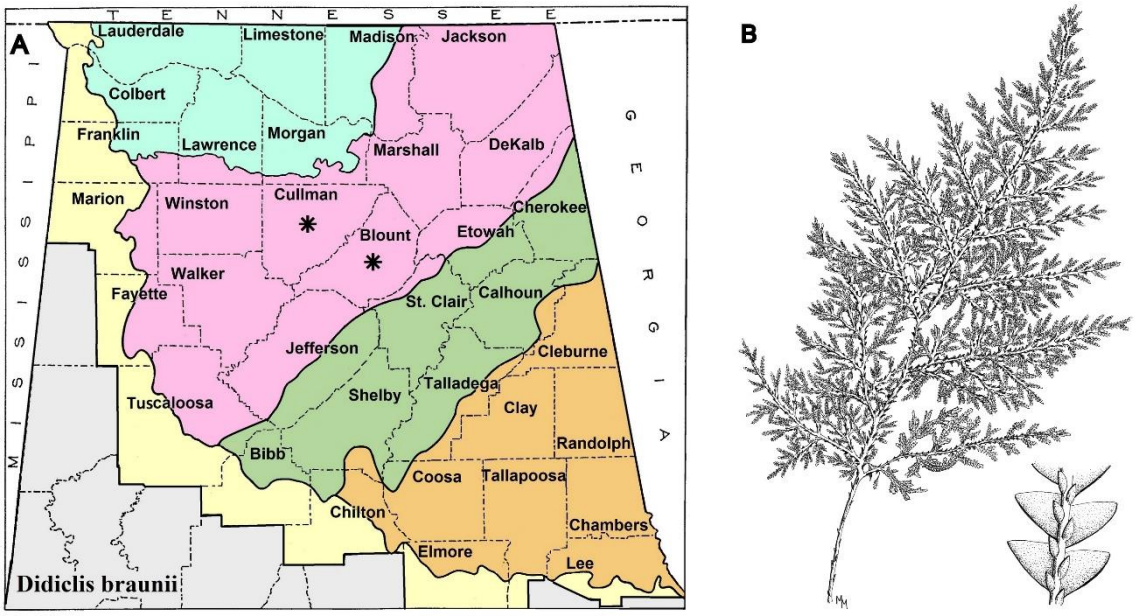


Figure 96. *Didiclis braunii.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 2000.

Gardeners often cultivate the Arborvitae-Fern (*Didiclis braunii*), particularly in southern regions of the United States. Botanists have documented it at two abandoned homesites in northern Alabama, representing the only known occurrences in that part of the state. Elsewhere, *D. braunii* occurs primarily in the Coastal Plain of the southeastern United States (Kartesz 2025). A related Chinese species, the Peacock-Moss, *D. uncinata* (Desv. ex Poir.) Li Bing Zhang & X.M. Zhou (Fig. 97), is sparingly naturalized in the Coastal Plain, with a single documented occurrence in Alabama. In 1954, University of Alabama student Jesse S. White discovered a thriving population near a cave entrance in Monroe County, far from any former homesite. *Didiclis uncinata* differs from *D. braunii* in having creeping to ascending stems and often bluish-green leaves.

Figure 97. *Didiclis uncinata*, Hamilton Co., Tennessee, 22 Jul 2022. Photo: Heather DeGaetnano.

3. SELAGINELLA Palisot de Beauvois 1804 {seh-lah-jih-NELL-uh}
[*Selago*, an old name for *Huperzia*, and Latin *-ella*, diminutive suffix; "like a small selago"]

1. Selaginella apoda (L.) Fernald {footless; referring to lack of well-developed root system} — MEADOW SPIKEMOSS (Fig. 98). [*Diplostachyum apodum* (L.) P. Beauv.; *Lycopodioides apodum* (L.) Kuntze; *Selaginella apus* (L.) Spring]

Figure 98. *Selaginella apoda*, Cleburne Co., Alabama, 6 May 2023. Photos: Dan Spaulding.

Plants terrestrial, occasionally epipetric; deciduous. Wet meadows, stream/lake margins, wet lawns, seepages, bogs, damp rocks, moist ledges, and bases of spray cliffs. Sporulates May–October; frequent throughout Alabama (Fig. 99). Native to eastern USA, ranging from southern Maine to Ohio, south to East Texas, and central Florida; disjunct in central and southern Mexico (Valdespino 1993).

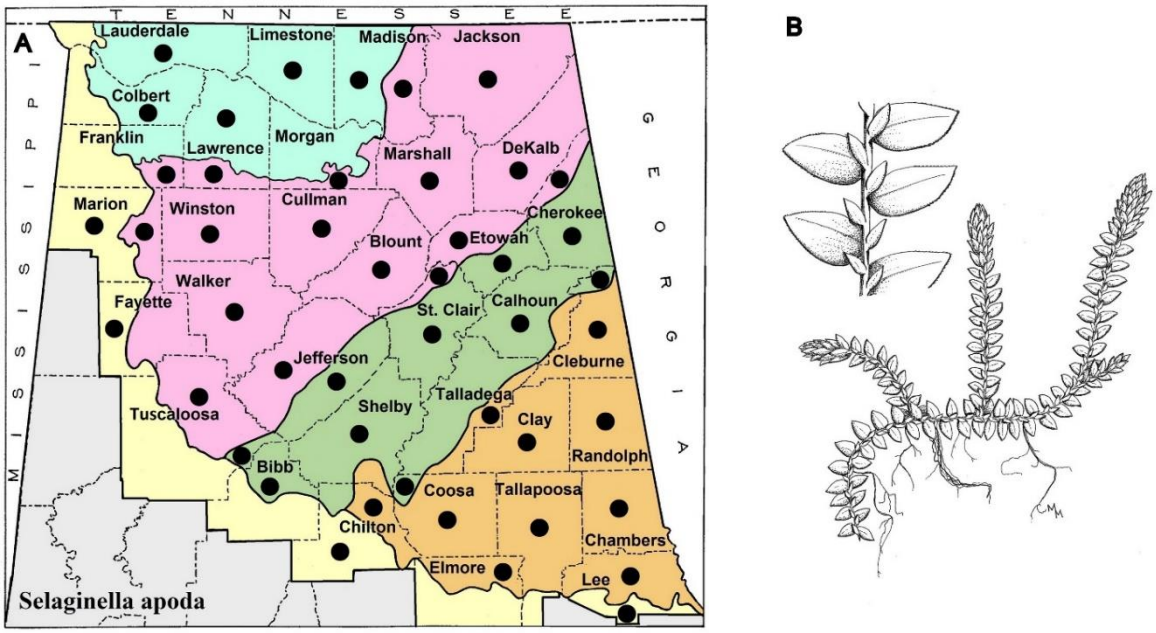


Figure 99. *Selaginella apoda*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 100. *Selaginella apoda*, Upper Jigger Creek Falls, Chattahoochee National Forest, Murray Co, Georgia, 6 Nov 2024. Photo: Alan Cressler.

Selaginella apoda is an inconspicuous species often overlooked due to its resemblance to liverworts or mosses. Like many bryophytes, it commonly grows on rocks and mimics their growth habits (Fig. 100). Its branching stems creep across the substrate, rooting at multiple points along their length, with only the tips remaining unrooted. The leaves are arranged in four rows and vary in size—some spreading outward, others pressed tightly against the stem. The Gulf Spikemoss, *S. ludoviciana* A. Braun (Fig. 101), a similar species confined to the Coastal Plain, shares this leaf arrangement but differs in its arching stems, erect lateral branches, and leaves edged with glassy, translucent cells.

Figure 101. *Selaginella ludoviciana*, Gadsden Co., Florida, 2 Jan 2022. Photo: Alan Cressler.

5. EQUISETACEAE (Horsetail Family) – in Equisetales

1. EQUISETUM Linnaeus 1753 {eh-kwuh-SEE-tuhm}

[Latin *equus*, horse, and *seta*, bristle; branching in some species somewhat resembles a horse's tail]

1. Stems monomorphic (similar in form), 100 cm or taller; fertile and sterile stems, green and unbranched; nodal sheaths with dark bands (present above and/or below sheath); strobili 0.5–1.5 cm long, sessile to subsessile, apex mucronate, maturing in late spring through summer; aerial stems evergreen, rigid ..... ***Equisetum praealtum***
1. Stems dimorphic (of two forms), less than 50 cm tall; sterile stems green with whorls of branches at nodes, fertile stems brownish and unbranched; nodal sheaths lacking dark bands; strobili 1–3 cm long, stalks 2–5 cm long, apex rounded, maturing in early spring before sterile stems; aerial stems deciduous, flexuous..... ***Equisetum arvense***

1. Equisetum arvense L. {of fields} — FIELD HORSETAIL, BOTTLE-BRUSH HORSETAIL; COMMON HORSETAIL (Fig. 102).

Figure 102. *Equisetum arvense*. **A.** Hughes Spring, Morgan Co., Alabama, 30 Aug 2010. Photo: Alan Cressler. **B–D.** Greene Co., Pennsylvania, 27 Apr 2024. Photos: Noah Yawn.

Plants terrestrial; deciduous. Damp woodlands, seepage areas, streambanks, and moist bases of cliffs. Sporulates March–May; very rare in the Cumberland Plateau, Ridge & Valley, and the Blackbelt of the Coastal Plain (Fig. 103). A circumboreal species that occurs throughout most of North America; also in Eurasia south to the Himalayas, central China, Korea, and Japan (Hauke 1993). The Alabama Natural Heritage Program (2023) lists this species as imperiled (S2) statewide.

Although abundant and often weedy in the northern and western United States, *Equisetum arvense* is rare in Alabama and neighboring states. Alabama state botanist Roland M. Harper first documented the species in 1908 on the banks of the Tombigbee River in Marengo County near Demopolis (Harper 1910). The species went unobserved in the state for over six decades until David Whetstone discovered a population in 1974 near Hughes Spring in Morgan County, in the Jackson County Mountains district of the Cumberland Plateau. In 1978, John Short located another population in Greene County, thriving at the base of a high chalk bluff along the Black Warrior River, covering an extensive sandy area on the riverbank (Short 1981). In subsequent decades, botanists have documented additional populations in northeast Alabama.

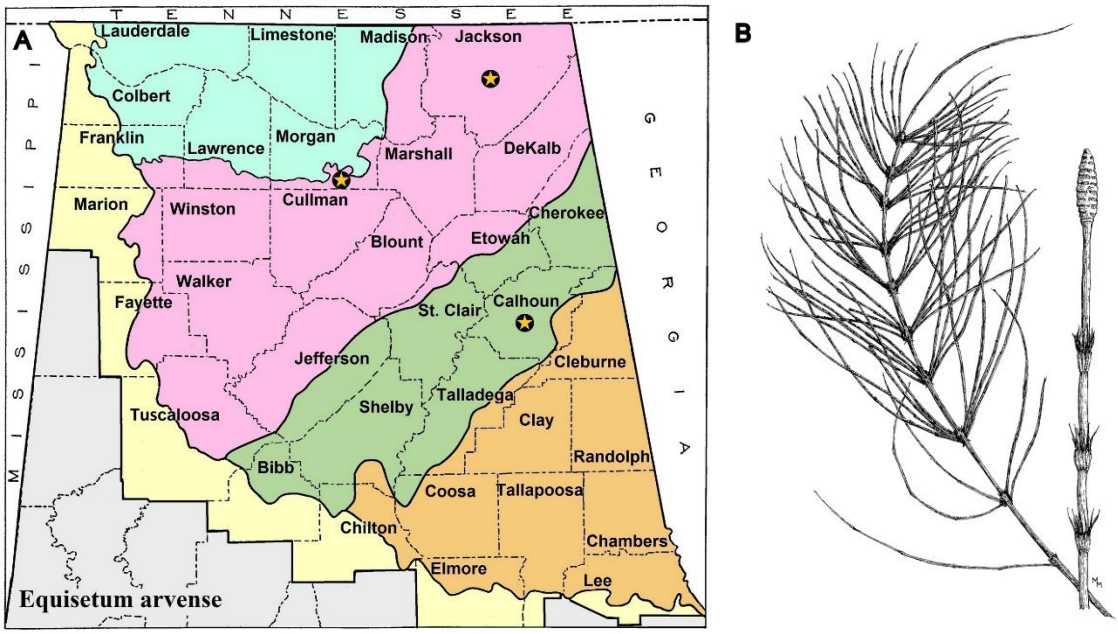


Figure 103. *Equisetum arvense*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Practitioners of European medicine have long valued *Equisetum arvense* for its medicinal properties. A traditional remedy involved mixing its juice with vinegar to treat ulcers and dropsy, a condition characterized by fluid retention and swelling (Abbe 1981). Herbalists also used dried, powdered forms of the plant, including its ash, as astringents to relieve stomach ailments. Due to its high silica content, they recommended *E. arvense* for strengthening nails, hair, and connective tissue. Folk healers have attributed diuretic, anti-inflammatory, and wound-healing properties to the species, often incorporating it into herbal teas or topical preparations for skin and urinary tract conditions (Crellin & Philpott 2000). The common name "horsetail" refers to the plant's appearance: its erect, jointed sterile stems, with whorled, brush-like branches, resemble a horse's tail (Fig. 104).

Figure 104. *Equisetum arvense*, Camas Creek, Lemhi Co., Idaho, 15 Jul 2024. Photos: Dan Spaulding.

2. Equisetum praealtum Raf. {very tall} — TALL SCOURING-RUSH; RIVER SCOURING-RUSH (Fig. 105). [*Equisetum hyemale* L. subsp. *affine* (Engelm.) Calder & R.L. Taylor; *Equisetum hyemale* var. *elatum* (Engelm.) Morton; *Equisetum hyemale* var. *robustum* (A. Braun) A.A. Eaton]

Figure 105. *Equisetum praealtum*. **A.** Shelby Co., Alabama, 9 Jun 2024. Photo: Vitaly Charny. **B.** Franklin Co., Alabama, 2 Aug 2023. Photo: Dan Spaulding. **C.** Morgan Co., Alabama, 30 Aug 2024. Photo: Alan Cressler.

Plants terrestrial; evergreen. Streambanks, riverbanks, pond shores, seepages, alluvial floodplains, and roadside ditches. Sporulates May–September; uncommon in the Highland Rim, Cumberland Plateau, Ridge & Valley, and Coastal Plain; rare in the Piedmont (Fig. 106). Widespread throughout Canada and the USA, south through Mexico to El Salvador (Weakley et al. 2025).

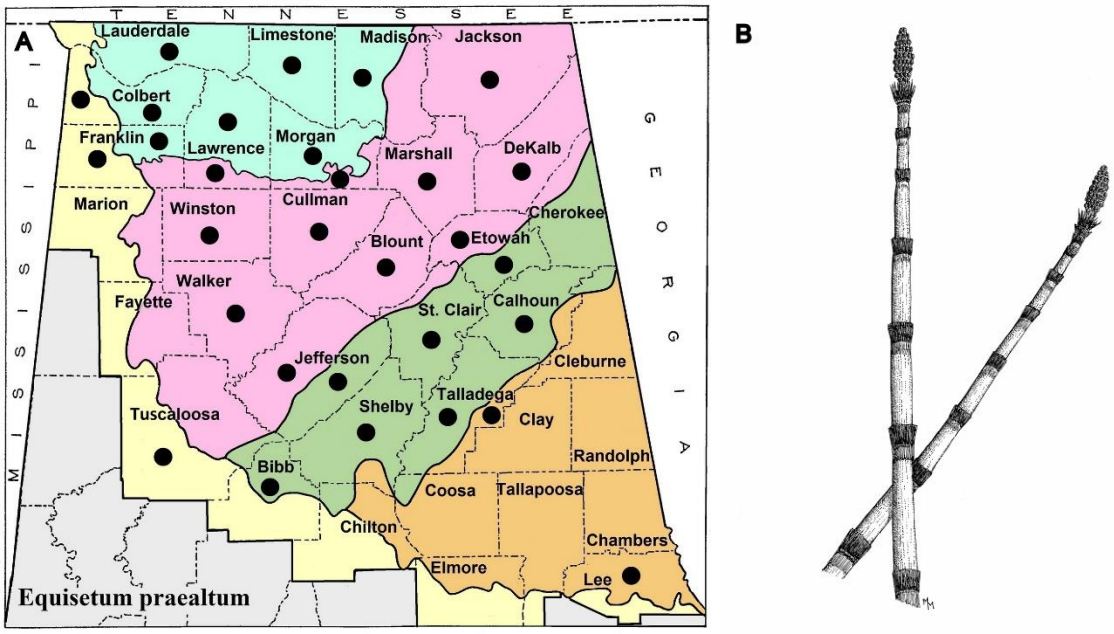


Figure 106. *Equisetum praealtum.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

The cells of *Equisetum praealtum* and many related species contain minute silica crystals, a hard, sand-like substance that gives the stems their distinctive rough texture. This abrasive quality led people to use the plant for polishing pewter, scrubbing floors, and scouring pots, pans, and other utensils—hence the common name "scouring-rush" (Abbe 1981). Although people in developed countries rarely employ the plant for cleaning today, artisans and musicians still use scouring-rush stems as a fine "sandpaper" for specialized tasks. For example, musicians crafting double reeds for oboes, bassoons, and similar instruments rely on the stems, known as the "Dutch rush," to perform the final smoothing and tuning of the reeds (Short & Spaulding 2012).

Figure 107. *Equisetum praealtum*, Talladega Co., Alabama, 15 Mar 2021. Photo: Dan Spaulding.

Tall Scouring-Rush (*Equisetum praealtum*) has strong weedy tendencies due to its aggressive growth and ability to spread rapidly through extensive underground rhizomes (Fig. 107). This resilient perennial thrives across diverse conditions, including wet soils, disturbed habitats, and riparian zones, making it particularly challenging to control. The plant's deep, interconnected rhizomes allow it to outcompete other vegetation, resist herbicides, and regenerate even after mechanical removal (Blanchon et al. 2012). While some gardeners and landscapers value *E. praealtum* as an ornamental plant or for erosion control, it frequently invades gardens and agricultural landscapes, creating significant management problems due to its tenacious growth (Olsen 2007). Furthermore, species of *Equisetum* can poison horses and other livestock when consumed with hay (Pohl 1955).

A related taxon, Ferriss' Scouring-Rush (*Equisetum* ×*ferrissii* Clute), is known in Alabama from two historical collections—one from Bibb County near the Fall Line and another from the Coastal Plain in Sumter County (Keener et al. 2025). The name honors James H. Ferriss, a prolific fern collector of the late 19th and early 20th centuries (Short & Spaulding 2012). It is a hybrid of *E. praealtum* and *E. laevigatum* A. Braun (Smooth Scouring-Rush), a species not documented in Alabama and rare in the southeastern United States. *Equisetum laevigatum* ranges from Canada south through the Midwest and western United States into Mexico (Kartesz 2025). According to Weakley et al. (2025), *E.* ×*ferrissii*, which spreads vegetatively, often behaves as a distinct species, occurring independently of one or both parents. Though similar to *E. praealtum*, it differs in several traits: the upper stems die back in winter; stems are smoother and less gritty; and spores, if present, are pale and shrunken rather than dark and round. This hybrid typically grows in disturbed soils along stream banks, lake shores, and roadsides.

6. **PSILOTACEAE** (Whiskfern Family) – in Psilotales

1. **PSILOTUM** Swartz 1800 {sigh-LOH-tum}
[Latin *psilos*, naked; referring to the plant's leafless stems]

1. Psilotum nudum (L.) P. Beauv. {naked; leafless stems} — WHISK FERN; SKELETON FORK FERN; WHISK-PLANT (Fig. 108).

Figure 108. *Psilotum nudum*, Baldwin Co., Alabama, 22 Feb 2012. Photo: Wayne Barger.

Plants terrestrial, epipetric, or epiphytic; evergreen. In northern Alabama, this species has become naturalized, growing terrestrially in mixed pine-hardwood forests, among pine straw mulch, and epipetrically on sheltered masonry. In the Coastal Plain of the southeastern United States, it occurs in bottomland forests, strand swamps, and wet hammocks—either terrestrially or epiphytically on trees, stumps, and exposed roots. Sporulates April–September; rare throughout Alabama (Fig. 109). In North America, it is native primarily to the lower southeastern Coastal Plain, with disjunct occurrences in the southwestern United States. Globally, it has a broad distribution across tropical regions (Thieret 1993). The Alabama Natural Heritage Program (2023) lists it as critically imperiled (S1) within the state. However, Weakley et al. (2025) consider populations outside the Lower Coastal Plain to be adventive.

Educational institutions have long used *Psilotum* to illustrate early land plants and primitive ferns. Among extant vascular plants, it most closely resembles ancient vascular plant fossils. Its unique features—such as the absence of roots and leaves and the placement of sporangia at branch tips—reflect characteristics found in extinct genera like *Rhynia* (Fig. 110a), which thrived around 400 million years ago during the Devonian Period (Kenrick & Crane 1997). Botanists historically considered *Psilotum* a "living fossil," a term for organisms that show minimal evolutionary divergence from their ancient ancestors (Thieret 1980). However, molecular evidence from plastid 16S ribosomal DNA sequences revealed that *Psilotum* and its close relative *Tmesipteris* (Psilotaceae) form a well-supported sister group to *Ophioglossaceae* (Manhart 1995). Although this finding initially surprised researchers, subsequent morphological studies confirmed the relationship (Christenhusz & Chase 2014).

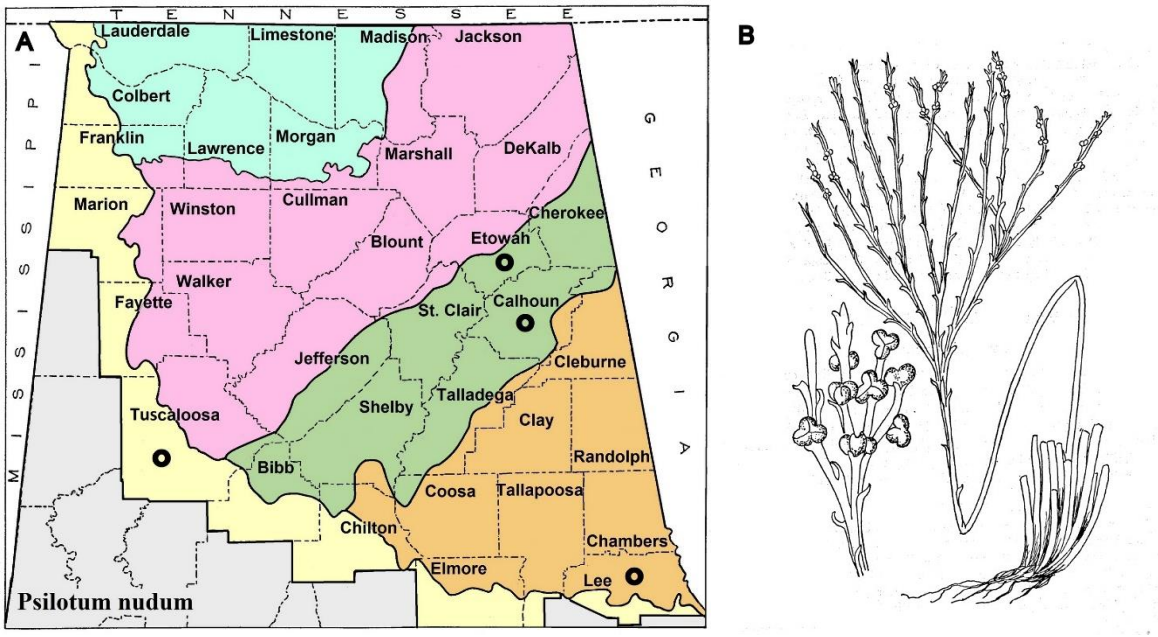


Figure 109. *Psilotum nudum.* **A.** Distribution map. **B.** Illustration: Ruth Sinclair George, 1938.

In 1986, John D. Freeman, a professor at Auburn University, documented the first occurrence of *Psilotum nudum* in Alabama when he discovered it in the Piedmont region of Lee County (Freeman 1987). This finding marked the first recorded instance of *Psilotum* growing above the Fall Line in the United States. Although the species typically grows epiphytically on trees (Fig. 110b), stumps, rotting logs, and other organic substrates, Freeman observed the Lee County population growing terrestrially. Its rhizomes were anchored in soil beneath the leaf litter of a young, mixed pine-hardwood forest. Subsequent discoveries have expanded the known range of *Psilotum nudum* in Alabama. In 2008, Hayes Jackson found it growing along the north-facing wall of an old building in Calhoun County (Fig. 110c). More recently, in late 2021, Wayne Barger documented the fern in a landscaped bed mulched with pine straw in Etowah County. The common name "whisk fern" refers to the plant's resemblance to a small broom or whisk.

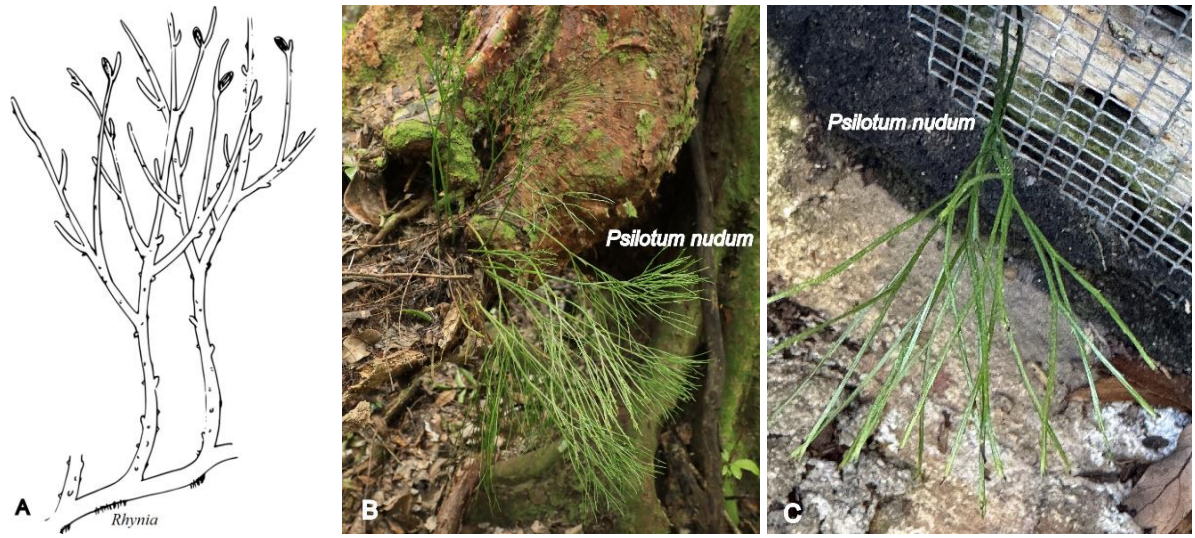


Figure 110. A. Drawing of *Rhynia gwynne-vaughanii* (Kenrick & Crane 1997). **B.** Dade Co., Florida, 26 Dec 2022. Photo: Alan Cressler. **C.** Calhoun Co., Alabama, 14 Mar 2024. Photo: Dan Spaulding.

7. **OPHIOGLOSSACEAE** (Adder's-Tongue Family) – in Ophioglossales

1. Leaves simple, blades ovate to lanceolate, spoon-like, veins anastomosing (forming a net); fertile spike unbranched, resembling a rattlesnake's tail ..... ***Ophioglossum***
1. Leaves compound or deeply lobed, blades triangular, veins free; fertile spike branched, resembling a tiny cluster of grapes.

   2. Fertile stalk (sporophore) arising from the base of sterile leaf blade; common stalk elevated well above the ground surface; leaf blades thin, absent in winter..... ***Botrypus***
   2. Fertile stalk arising below the base of sterile leaf blade; common stalk at or near ground level; leaf blades papery to leathery, present at least through winter ..... ***Sceptridium***

1. **BOTRYPUS** Richard 1801 {bo-TRIH-puhs}

[Greek *botrys*, cluster, and *pous*, foot; referring to the clustered arrangement of sporangia]

1. Botrypus virginianus (L.) Michx. {of Virginia; first discovered} — RATTLESNAKE FERN; VIRGINIA GRAPE FERN (Fig. 111). [*Botrychium virginianum* (L.) Sw.; *Osmundopteris virginiana* (L.) Small]

Figure 111. *Botrypus virginianus*, Jackson Co., Alabama, 26 Apr 2023. Photos: Wayne Barger.

Plants terrestrial; deciduous. Moist hardwood, pine, or mixed forests, thickets, and meadows. Sporulates April–June; frequent throughout Alabama (Fig. 112). Widespread throughout most of North America except northern Canada and the southwestern deserts; it also occurs in Mexico, Central America, South America, and Eurasia (Wagner & Wagner 1993a).

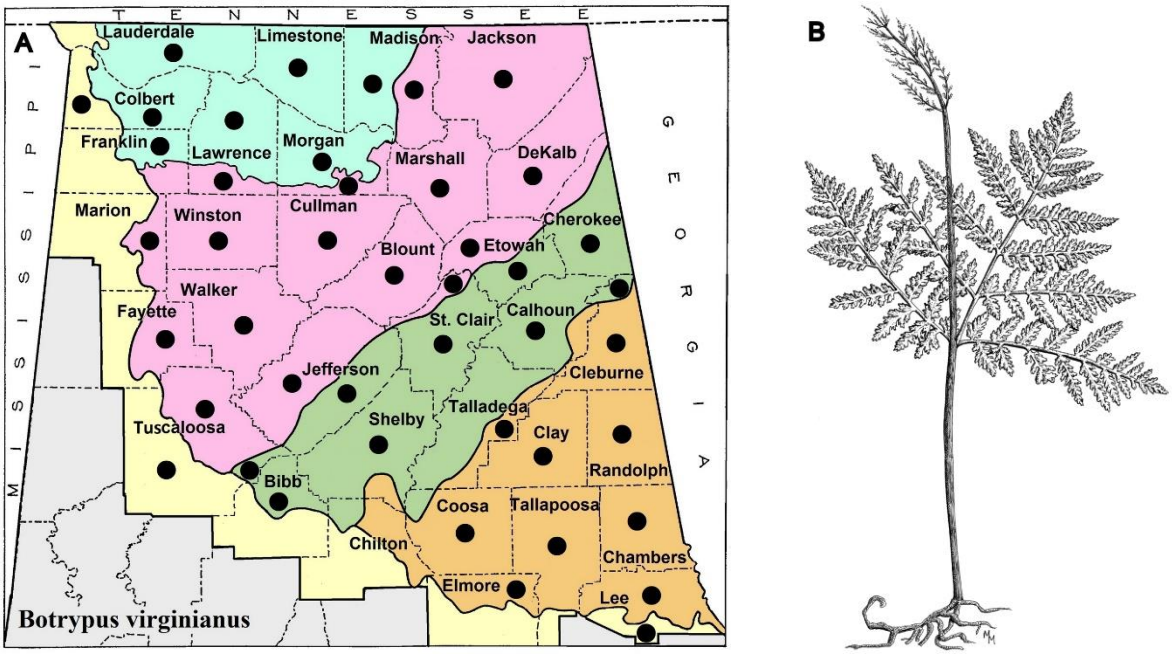


Figure 112. *Botrypus virginianus.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Botrypus virginianus differs from other grape ferns (*Sceptridium*) by its thin, delicate sterile blades called trophophores, which emerge in spring and die back by fall. In contrast, *Sceptridium* species typically have thicker, leathery blades and produce new growth in fall or winter, with most remaining evergreen year-round—except *S. lunarioides*, which dies back in summer and reemerges later in the season. *Botrypus* also differs in the position of the fertile stalk, known as a sporophore, which arises from the base of the sterile blade, while in *Sceptridium* it attaches well below the base.

The origin of the common name "rattlesnake fern" is unclear. However, it likely stems from the resemblance of the fertile stalk to a rattlesnake's tail and the plant's broader association with snakes in folklore and traditional botany (Clute 1901). Native Americans actively incorporated *Botrypus virginianus* into their medicinal and cultural practices. Healers applied poultices made from the rhizome to treat snakebites, believing the plant's symbolic link to snakes enhanced its healing power. These poultices were also used on wounds, such as bruises, cuts, and sores, to reduce inflammation and promote recovery (Foster & Duke 1990). Beyond medicine, Native American women boiled the roots to make a decoction that they sprinkled around their wigwams as a deterrent against snakes (Abbe 1981).

2. **OPHIOGLOSSUM** L. 1753 {oh-fee-oh-GLOSS-um}

[Greek *ophis*, snake, and *glossa*, tongue; alluding to the spike-like sporophore]

The genus *Ophioglossum*, commonly known as adder's-tongues, is easily distinguished from typical ferns by its unusual morphology. Each plant produces a single, elliptical to ovate leaf blade known as a trophophore. The sterile frond exhibits a complex, reticulate venation pattern—an intricate network of interconnected, anastomosing veins that is most visible when viewed against strong backlighting. Arising near the base of the trophophore is a narrow, fertile segment called the sporophore, which lacks blade tissue and bears only sporangia. The genus name and common name both allude to the supposed resemblance of this fertile structure to a serpent's tongue (Thieret 1980). However, it more closely resembles a rattlesnake's tail with its rows of prominent sporangia. Historically, herbalists prescribed its fronds as a folk remedy for snake bites (Frankel 1981).

1. Underground stem globose-bulbous, 3–11 mm in diameter; leaf blades deltate to cordate and borne almost flat on the ground ..... ***Ophioglossum crotalophoroides***
1. Underground stem narrowly cylindrical, 2–4 mm in diameter; leaves ovate to elliptical and usually upright.

    2. Apex of sterile leaf blade apiculate (ending abruptly in a small, slender point); leaves commonly folded lengthwise; venation netted, with large, heavy veins enclosing more numerous finer veins; fresh specimens malodorous; plants of limestone outcroppings or thin soil over calcareous rock..... ***Ophioglossum engelmannii***
    2. Apex of sterile leaf blade rounded or obtuse; leaves typically flat; venation netted but lacking secondary areoles, though some free veinlets may be present; fresh specimens not ill-scented; plants usually of moist forests..... ***Ophioglossum pycnostichum***

1. Ophioglossum crotalophoroides Walter {resembling a rattle-bearer; referring to its sporangial clusters} — BULBOUS ADDER'S-TONGUE (Fig. 113). [*Haukia crotalophoroides* (Walter) Li Bing Zhang & Liang Zhang; *Ophioglossum bulbosum* Michx.; *Ophioglossum crotalophoroides* var. *nanum* Osten ex J.S. Licht.]

Figure 113. *Ophioglossum crotalophoroides*, Baldwin Co., Alabama, 23 Feb 2012. Photos: Wayne Barger.

Plants terrestrial; deciduous. Open grassy areas that are frequently mowed, including lawns, fields, and cemeteries. Sporulates February–September; rare in northern Alabama; frequent in the Coastal Plain (Fig. 114). This species occurs chiefly in the southeastern USA along the Gulf Coast from eastern Texas to Florida and northward to North Carolina; it also occurs in Mexico, the West Indies, Central America, and South America (Wagner & Wagner 1993b). The Alabama Natural Heritage Program (1994) initially classified this species as vulnerable (S3) in the state, but has stopped monitoring it after discovering it is more common than previously thought.

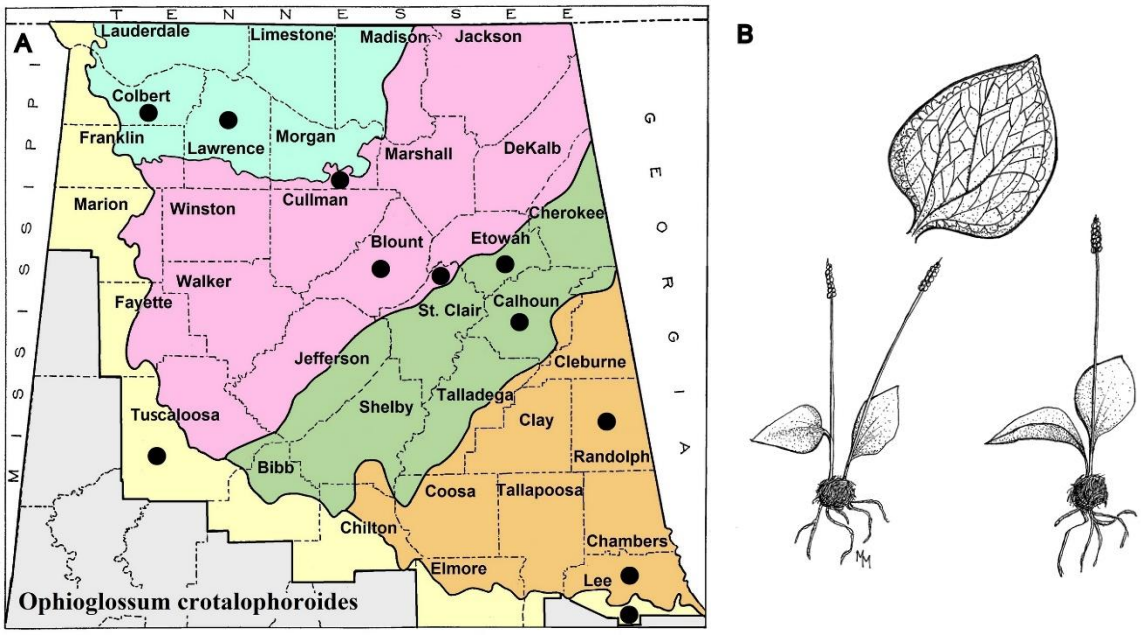


Figure 114. *Ophioglossum crotalophoroides*. **A.** Distribution map. **B.** Illustration, Marion Montgomery, 1999.

Bulbous Adder's-Tongue (*Ophioglossum crotalophoroides*) was first described in 1788 by Thomas Walter in his *Flora Caroliniana* (Dean 1969). This diminutive fern often goes unnoticed, frequently inhabiting mowed grassy areas such as rural cemeteries—sites that botanists seldom survey. Spotting individual plants typically requires kneeling and bringing one's head close to the ground, as they are easily overlooked.

Figure 115. A. *Ophioglossum nudicaule*, Baldwin Co., Alabama, 22 Jan 2008. Photo: Wayne Barger. **B.** *Ophioglossum petiolatum*, Collier Co., Florida, 28 Dec 2022. Photo: Noah Yawn.

Dr. Warren H. Wagner (pers. comm., 1999) noted in a letter to Dan Spaulding that two Coastal Plain species—the Least Adder's-Tongue (*Ophioglossum nudicaule* L. f.) and Stalked Adder's-Tongue (*O. petiolatum* Hook.)—possibly inhabit northern Alabama, thriving in habitats similar to those of *O. crotalophoroides*. In April 1994, Dr. R. Dale Thomas and his son, Scott D. Thomas, collected *O. nudicaule* from the Coastal Plain region of Lee County. This adder's-tongue grows low to the ground like *O. crotalophoroides* but differs from it by lacking bulbous, corm-like rhizomes and by having leaves that are not cordate-deltate.

Ophioglossum nudicaule (Fig. 115a) can be distinguished from *O. petiolatum* (Fig. 115b) by differences in size and leaf blade position. *Ophioglossum nudicaule* is less than 6 cm tall, with its leaf blades emerging near the base of the plant. In contrast, *O. petiolatum* is slightly taller, with its leaf blades positioned higher on the stem. While *O. nudicaule* is native to the region, researchers suspect that *O. petiolatum* is introduced, possibly arriving through the nursery trade (Nelson 2000).

2. Ophioglossum engelmannii Prantl {George Engelmann, 1809–1884, American botanist} — LIMESTONE ADDER'S-TONGUE; ENGELMANN'S ADDER'S-TONGUE (Fig. 116). [*Whittieria engelmannii* (Prantl) Li Bing Zhang & Liang Zhang]

Figure 116. *Ophioglossum engelmannii*, Bibb Co., Alabama, 11 Apr 2020. Photos: Alan Cressler.

Plants terrestrial; deciduous. Limestone barrens, cedar glades, prairies, clay barrens, open grassy woodlands, rarely over metamorphic rock. Sporulates March–June; rare throughout Alabama (Fig. 117). This species ranges from northern Florida to western Virginia, westward through the Ohio Valley to eastern Kansas and southeastern Arizona, and also occurs in Mexico and Central America (Wagner & Wagner 1993b). The Alabama Natural Heritage Program (2016) previously classified this species as imperiled to vulnerable (S2S3) in the state. However, by 2019, they ceased tracking it after discovering that its presence was more common than previously thought.

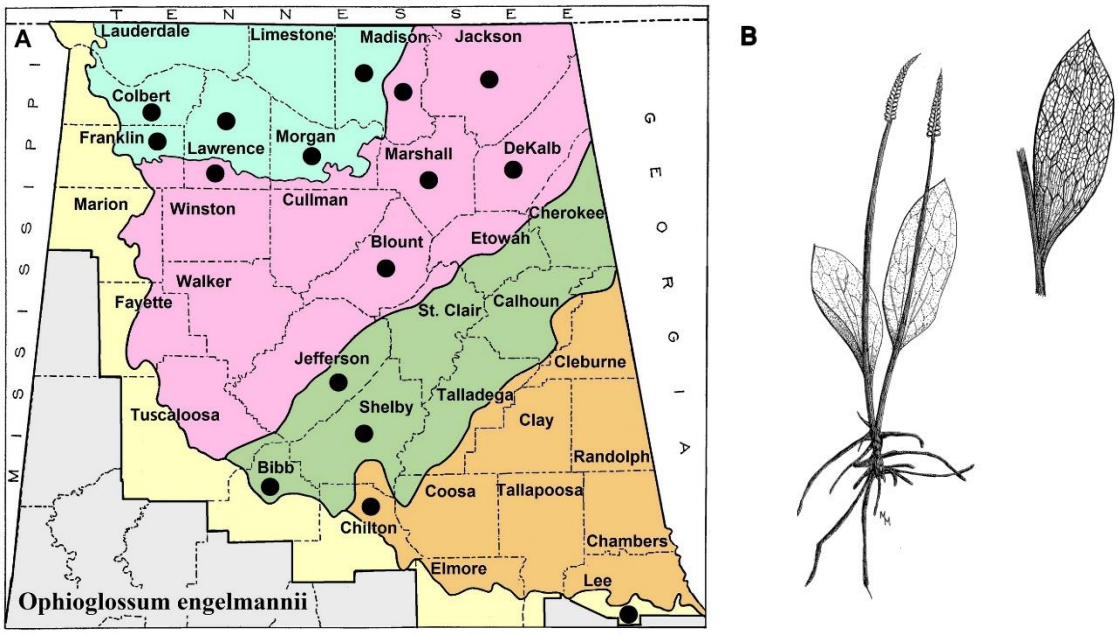


Figure 117. *Ophioglossum engelmannii*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Limestone Adder's-Tongue also reproduces vegetatively, forming dense colonies in favorable habitats (Fig. 118). These populations—sometimes numbering in the hundreds or thousands—can spread across several square meters and may resemble a thick mat of grass (Palmer 1932). Leaves typically emerge in early spring and begin to yellow by late May or early June as moisture declines, triggering dormancy. Occasionally, a few new leaves appear in late summer or fall, though few are fertile (Baskin & Baskin 1974).

Figure 118. *Ophioglossum engelmannii*, Washita Co., Oklahoma, 22 Apr 2024. Photo: Canaan Sutton.

Fresh specimens of *Ophioglossum engelmannii* emit a distinct, unpleasant odor, and their leaves often fold lengthwise. The species can be recognized by its sharply pointed leaf tips and by a fine secondary network of veinlets enclosed within larger, netted veins (Fig. 117b). It typically grows in limestone-rich soils throughout its range, prompting Earnest Palmer (1932) to describe it as a strict calciphile. Wherry (1926) further observed that it generally thrives in soils with a neutral to slightly alkaline pH, reinforcing its affinity for calcareous habitats.

3. Ophioglossum pycnostichum (Fernald) Á. Löve & D. Löve {with crowded rows; sporangia} — SOUTHERN ADDER'S-TONGUE; COMMON ADDER'S-TONGUE (Fig. 119). [*Ophioglossum vulgatum* L. var. *pycnostichum* Fernald]

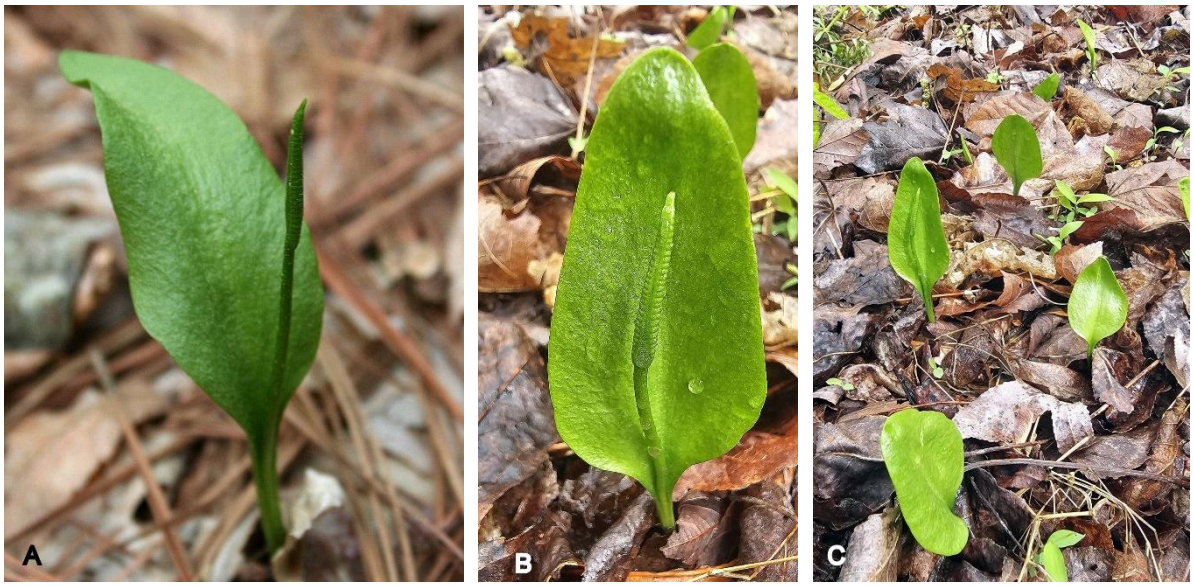


Figure 119. *Ophioglossum pycnostichum*. **A.** Cherokee Co., Alabama, 11 Apr 2008. Photo: Wayne Barger. **B**–**C.** Limestone Co., Alabama, 8 Apr 2024. Photos: Tabatha Fiacco.

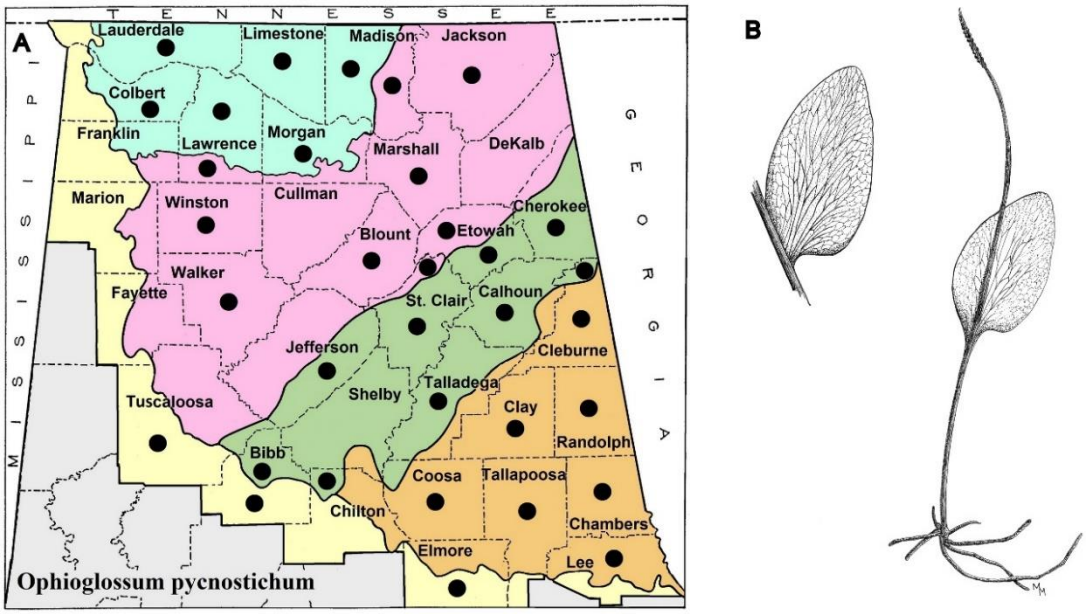


Figure 120. *Ophioglossum pycnostichum.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Plants terrestrial; deciduous. Bottomland forests, alluvial woods, damp meadows, swamp margins, moist successional forests, and low fields bordering woods. Sporulates March–July; uncommon throughout Alabama (Fig. 120). Native to the eastern United States south of the Wisconsin glacial boundary, this species ranges from New Jersey west to Illinois and south to East Texas and the Florida Panhandle, with a disjunct population in Arizona (Wagner & Wagner 1993b).

Ophioglossum pycnostichum closely resembles *O. engelmannii*, but its leaf blades, which lack a secondary network of veins and have rounded tips, provide a clear distinction. Additionally, while *O. engelmannii* can form large colonies, *O. pycnostichum* typically occurs in small populations, often consisting of just a few plants or even a single specimen. This trait inspired Palmer (1932) to write, "In most parts of the country, it is sufficient of a rarity to give a thrill of pleasure to the botanical explorer who has the good fortune to come upon it."

The taxonomic status of *Ophioglossum pycnostichum* remains unresolved. Some authors consider the North American species indistinguishable from the Eurasian *O. vulgatum* and treat it as synonymous, while others recognize it as a distinct variety of *O. vulgatum*. Weakley et al. (2025) state that *O. vulgatum*, when narrowly defined, is confined to Eurasia. Fernald (1939) identifies several distinguishing characteristics that separate *O. pycnostichum* from its Eurasian counterpart, while Wagner & Wagner (1993b) combine the two species. Determining the most accurate classification of this group remains unresolved and will require further research.

3. **SCEPTRIDIUM** L. Lyon 1905 {sehp-TRID-ee-um}

[Latin *Sceptrum*, scepter or wand, and *idium*, little; referring to the elongated fertile frond]

The common name for species in this genus originates from the distinctive appearance of their fertile branches, known as sporophores. These separate stalks rise above the sterile blades, called trophophores, and bear clusters of sporangia. These spore-bearing structures form dense, rounded groups that closely resemble small bunches of grapes. This unique grape-like appearance of the sporophores inspired the vernacular name "grape fern."

1. Leaf segments fan-shaped, mostly as long as or slightly longer than wide, with broadly obtuse apices; venation nearly fan-like, midrib absent or poorly developed.

    2. Leaves sessile or short-stalked; blades prostrate, lying flat on the ground; leaflets lacking a midrib; roots smooth; spores produced in late winter to early spring (January–April); new leaves emerge in late fall and wither before summer ..... ***Sceptridium lunarioides***
    2. Leaves distinctly stalked; blades ascending, held well above the ground; leaflets with a weak midrib; roots ribbed; spores produced in summer or fall (July–October); new leaves appear in spring or summer and persist through the year ..... ***Sceptridium jenmanii***

1. Leaf segments not fan-shaped, distinctly longer than wide, with acute or subacute apices; venation pinnate (feather-like), midrib distinct.

    3. Leaf blade typically bipinnate (occasionally 1–3 pinnate), flaccid with a papery texture; margins finely serrate; pinnae and larger pinnules mostly oblong with nearly parallel sides and relatively blunt tips, smaller pinnules somewhat rounded .....***Sceptridium biternatum***
    3. Leaf blade typically tripinnate (occasionally 2–4 pinnate), firm with a leathery texture; margins serrate, coarsely cut, or lacerate; pinnae and pinnules mostly obliquely angular, ovate, or trowel-shaped (sides not parallel) with relatively pointed tips.....***Sceptridium dissectum***

1. Sceptridium biternatum (Savigny) Lyon {twice ternate; leaves} — SOUTHERN GRAPE FERN; SPARSE-LOBED GRAPE FERN (Fig. 121). [*Botrychium biternatum* (Savigny) Underw.; *Botrychium dissectum* Spreng. var. *tenuifolium* (Underw.) Farw.]

Figure 121. *Sceptridium biternatum*, Cleburne Co., Alabama, 8 Dec 2024. Photos: Dan Spaulding.

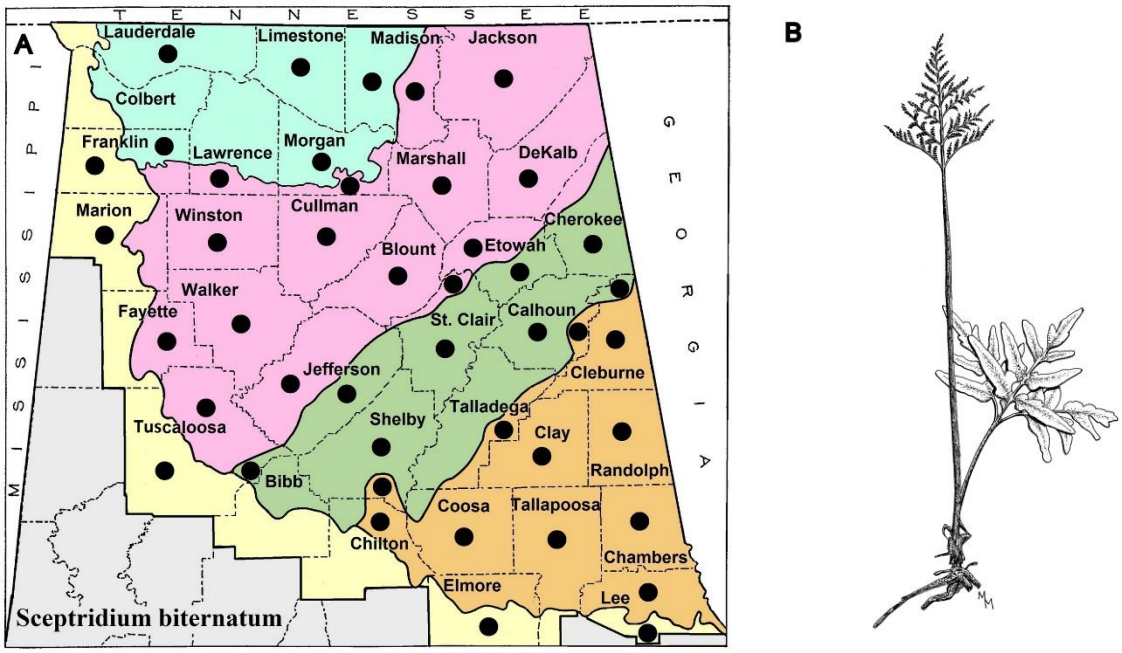


Figure 122. *Sceptridium biternatum.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Plants terrestrial; evergreen. Moist forests, bottomlands, mesic slopes, rich woods, floodplains, swamps, shaded roadsides, forested drainages, and other low habitats. Sporulates August–October; frequent throughout Alabama (Fig. 122). Ranging chiefly in the southeastern USA, from Florida west to eastern Texas, north to Maryland and southern Illinois (Wagner & Wagner 1993a).

Figure 123. *Sceptridium biternatum*. **A.** Lawrence Co., Alabama, 9 Oct 2018. Photo: Helen A. Czech. **B.** Cleburne Co., Alabama, 10 Feb 2024. **C.** McDuffie Co., Georgia, 4 Dec 2023. Photos: Dan Spaulding.

Distinguishing *Sceptridium biternatum* from the less dissected leaf form of *S. dissectum* (forma *obliquum*) can be challenging and often requires close examination of subtle morphological traits. Although leaf blade division in *S. biternatum* varies (Fig. 123), the fronds typically appear blunter and less finely dissected than those of *S. dissectum*. The blades of *S. biternatum* are more sparsely lobed, with rounded or blunt tips, whereas *S. dissectum* displays more angular lobes with distinctly straight outer margins. In addition, *S. dissectum* tends to have thicker, leathery blade tissue, while *S. biternatum* exhibits slightly thinner blades. These subtle differences are essential for accurately identifying these closely related ferns.

2. Sceptridium dissectum (Spreng.) Lyon {dissected} — CUT-LEAF GRAPE FERN; DISSECTED GRAPE FERN; BRONZE FERN (Fig. 124). [*Botrychium dissectum* Spreng.; *Botrychium dissectum*. var. *obliquum* (Muhl. ex Willd.) Clute; *Botrychium obliquum* Muhl. ex Willd.; *Sceptridium dissectum* (Spreng.) Lyon var. *obliquum* (Muhl. ex Willd.) Mohlenbr.]

Plants terrestrial; evergreen. Moist forests, alluvial woods, wooded drainages, bottomland hardwoods, and partially shaded roadsides. Sporulates August–October; frequent throughout Alabama (Fig. 125). Native to the eastern USA and adjacent Canada, from Nova Scotia to southern Ontario, south to East Texas, and northern Florida (Wagner & Wagner 1993a).

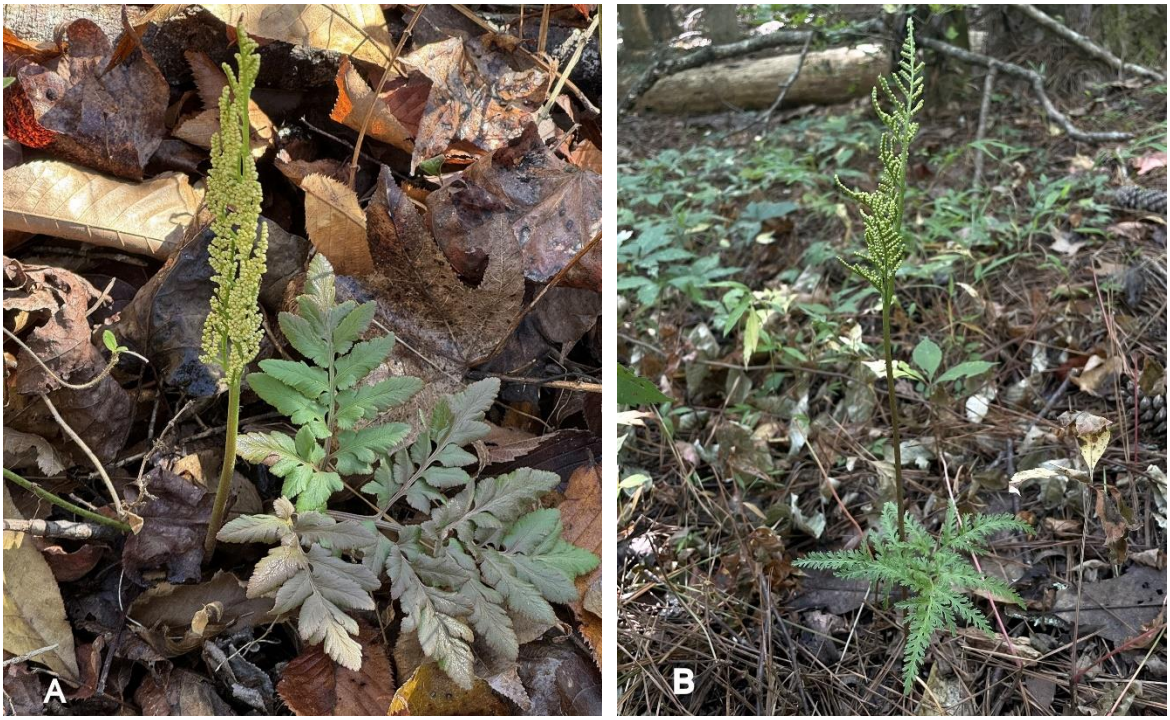


Figure 124. A. *Sceptridium dissectum* f. *obliquum*, Cleburne Co., Alabama, 16 Nov 2024. Photo: Dan Spaulding. **B.** *S. dissectum* f. *dissectum*, DeKalb Co., Georgia, 31 Aug 2024. Photo: John P. Van Valen.

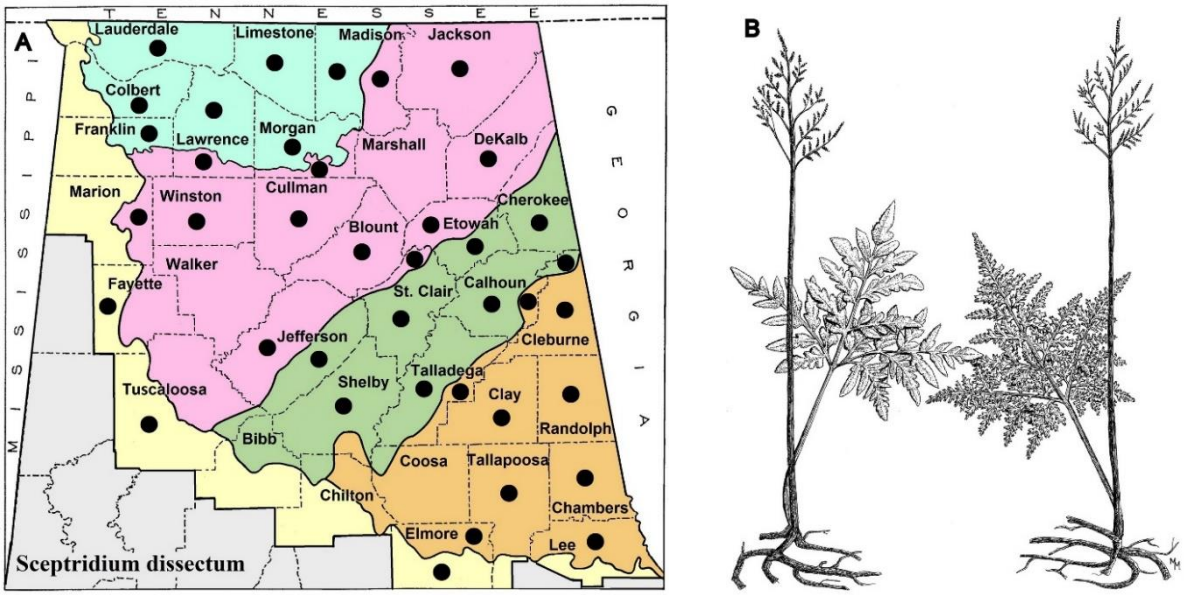


Figure 125. *Sceptridium dissectum*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Sceptridium dissectum is a highly variable species with two recognized forms, distinguished by the degree of leaf dissection. Forma *obliquum* has finely toothed but otherwise uncut segment margins, while forma dissectum exhibits deeply cut margins with numerous slender projections, giving the fronds a distinctly lacy appearance (Fig. 126). In Alabama, *S. dissectum* f. *obliquum* is the more widespread form and is often mistaken for *S. biternatum*. The more finely divided f. *dissectum* predominates in the northern parts of eastern North America. Where their ranges overlap, the two forms intergrade, producing plants with intermediate leaf segmentation.

Figure 126. A. *Sceptridium dissectum* f. *obliquum*, Cleburne Co., Alabama, 3 Aug 2013. Photo: Alan Cressler. **B.** *S. dissectum* f. *dissectum*, Autauga Co., Alabama, 6 Aug 2023. Photo: Charles Birding. **C.** *S. dissectum* f. *dissectum*, Allegheny Co., Pennsylvania, 25 Feb 2024. Photo: Noah Yawn.

The primary features that distinguish *Sceptridium dissectum* f. *obliquum* from *S. biternatum* are leaf texture and segment shape. In *S. dissectum*, the leaf blades are somewhat leathery, with trowel-shaped segments that taper to pointed tips. In contrast, *S. biternatum* has thinner leaves, with pinnae and elongated pinnules that have nearly parallel sides and relatively blunt tips. Wagner and Wagner (1993a) noted that fronds of *S. biternatum* typically remain green throughout winter, while those of *S. dissectum* often take on a bronze hue when exposed to sunlight—hence the common name "bronze fern." However, this color change is not a reliable diagnostic feature, as winter coloration is variable and may not occur consistently.

3. Sceptridium jenmanii (Underw.) Lyon {for George S. Jenman (1845–1902), British botanist} — ALABAMA GRAPE FERN; DIXIE GRAPE FERN, JENMAN'S GRAPE FERN (Fig. 127). [*Botrychium alabamense* Maxon; *Botrychium jenmanii* Underw.; *Sceptridium alabamense* (Maxon) Holub]

Figure 127. *Sceptridium jenmanii*. **A.** Rabun Co., Georgia, 16 Oct 2022. Photo: Alan Cressler. **B.** Laurens Co., South Carolina, 6 Feb 2022. Photo: Noah Yawn.

Plants terrestrial; evergreen. Hardwood or pine forests, lawns, cemeteries, and other open grassy areas. Sporulates August–October; very rare in the Piedmont; rare in the lower Coastal Plain (Fig. 128). Scattered in the southeastern USA, from western Virginia south to northern Florida and eastern Louisiana, and also in the Caribbean islands (Wagner & Wagner 1993a). The Alabama Natural Heritage Program (2023) lists this species as critically imperiled (S1) within the state.

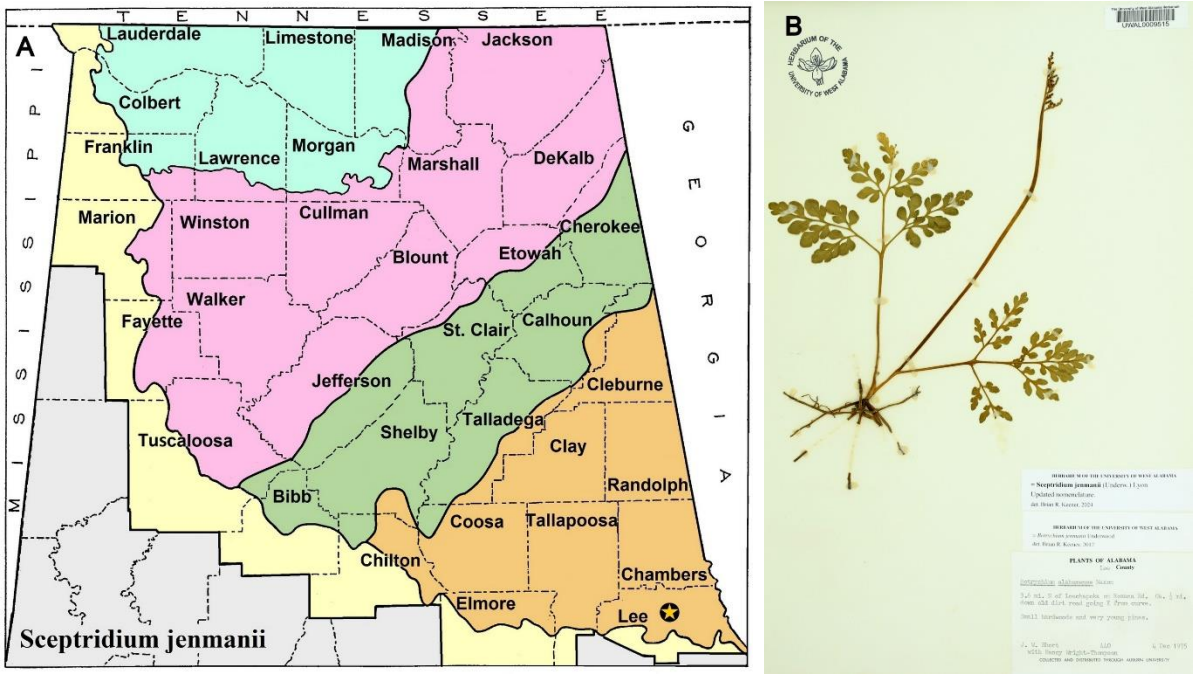


Figure 128. *Sceptridium jenmanii*. **A**. Distribution map. **B**. Herbarium specimen (UWAL), *Short 440*, Lee Co., Alabama, 4 Dec 1975.

Wagner and Wagner (1993a) proposed that *Sceptridium jenmanii* originated through hybridization between *S. biternatum* and *S. lunarioides*, followed by chromosome doubling (allopolyploidy). This process stabilized its genome, resulting in a fertile, self-sustaining taxon that functions as a distinct species. Notably, *S. jenmanii* is the only known tetraploid species within the New World *Sceptridium*, a genomic distinction that sets it apart from its diploid relatives. This polyploidy may have played a crucial role in its ecological and evolutionary success, potentially enhancing its adaptability and reproductive viability. Morphologically, *S. jenmanii* exhibits a mosaic of traits inherited from both parental species, further supporting its hybrid origin.

Lucien M. Underwood described *Sceptridium jenmanii* as *Botrychium jenmanii* in 1900, based on a specimen from Jamaica. However, Underwood (1896) had already examined similar plants from Alabama as a different species. In 1906, William R. Maxon documented this grape fern from the campus of Spring Hill College in Mobile, Alabama, naming it *Botrychium alabamense*. In his 1938 monograph of the Ophioglossaceae, Robert T. Clausen recognized both taxa as distinct, noting that *B. jenmanii* was endemic to the dry grasslands of the West Indies, while *B. alabamense* occurred in open woods and grassy areas in the southeastern United States. Subsequent studies determined that these two ferns were the same species, with *B. jenmanii* having nomenclatural priority (Lellinger 1985). Despite this reclassification, the common name "Alabama grape fern" remains widely used. Later research prompted the revision of *Botrychium* (sensu lato) into four genera. Consequently, researchers reassigned *B. jenmanii* and related species to *Sceptridium*, a genus established by Harold L. Lyon in 1905 (Hauk et al. 2003; Kato 1987).

4. Sceptridium lunarioides (Michx.) Holub {like *Botrychium lunaria*; Moonwort} — WINTER GRAPE FERN; PROSTRATE GRAPE FERN (Fig. 129). [*Botrychium lunarioides* (Michx.) Sw.; *Botrypus lunarioides* Michx.; *Holubiella lunarioides* (Michx.) Škoda]

Figure 129. *Sceptridium lunarioides*. **A.** Lee Co., Alabama, 28 Feb 2012. **B.** Lowndes Co., Alabama, 11 Mar 2010. Photos: Wayne Barger.

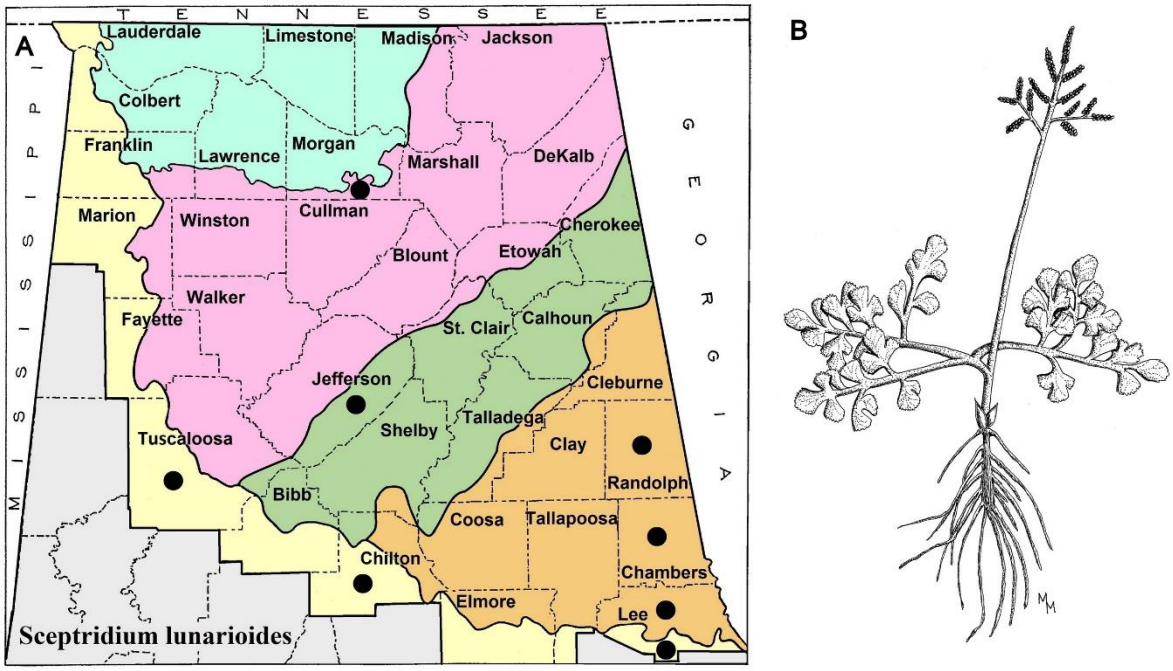


Figure 130. *Sceptridium lunarioides.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Plants terrestrial; deciduous, with fleshy leaves emerging in winter or early spring and withering by late summer. Lawns, pastures, cemeteries, churchyards, granitic flatrocks, and dry woodlands. Sporulates January–April; very rare in the Cumberland Plateau and Ridge & Valley; rare in the Piedmont; frequent in the Coastal Plain (Fig. 130). Primarily distributed in the southeastern Coastal Plain from North Carolina to northern Florida and west to eastern Texas (Wagner & Wagner 1993a). Also reported from southeast Oklahoma and extirpated in North Carolina (Kartesz 2025). The Alabama Natural Heritage Program (2003) initially ranked it as critically imperiled (S1), but by 2008, they ceased tracking the species after determining it was more widespread than previously thought.

For many years, fern manuals described *Sceptridium lunarioides* as exceptionally rare (Lellinger 1985). However, recent collections by southern botanists have demonstrated that this species is quite common in the Coastal Plain. It thrives in grassy, regularly mowed habitats, especially in rural cemeteries. Its historical oversight is understandable, given its small size and the tendency of its leaf blades to lie flat against the ground—a trait that inspired the common name, "Prostrate Grape Fern." Another vernacular name, "Winter Grape Fern," highlights its winter growth period. Notably, the sporophores of *S. lunarioides* remain curled through late fall and early winter, usually becoming erect in February (Wagner & Wagner 1993a).

Figure 131. *Sceptridium lunarioides*, Jefferson Co., Alabama, 13 Dec 2024. Photos: Dan Spaulding.

Sceptridium lunarioides closely resembles *S. jenmanii* (the Alabama Grape Fern), but several consistent traits distinguish the two. *Sceptridium lunarioides* has smooth roots, sessile or short-stalked fronds, and leaf segments that lack midribs (Fig. 131). In contrast, *S. jenmanii* features ribbed roots, distinctly stalked leaves held above the ground, and leaf segments with faint midribs (Fig. 127). The prostrate growth habit of *S. lunarioides* enables it to thrive in grassy, regularly mowed habitats, while the more upright leaves of *S. jenmanii* reflect its adaptation to slightly different ecological niches.

Wagner (1992) recognized the Winter Grape Fern as a distinct species within the monotypic section *Hiemobotrychium*. More recently, Zhang et al. (2020) proposed reclassifying it into a separate monotypic genus, *Holubiella*, based on molecular evidence suggesting it represents the earliest-diverging lineage within *Sceptridium*. However, Weakley et al. (2025) argue that its key role in the origin of the allopolyploid species *S. jenmanii* supports retaining it within *Sceptridium*.

8. **OSMUNDACEAE** (Royal Fern Family) – in Osmundales

The ferns of the Osmundaceae hold a distinguished place in both botany and horticulture, celebrated for their ancient lineage and distinctive appearance. Their robust growth and graceful fronds have captivated plant enthusiasts, making them favorites of gardeners and horticulturalists. As Clute (1901) observed, "Among ferns as among flowering plants, there are certain species that so persistently force themselves upon our attention as to make it almost impossible not to know them. The members of the Osmunda family belong to this class." Their historical significance as "living fossils" (Fig. 132a) adds to their intrigue, as these ferns have existed relatively unchanged for millions of years, offering a glimpse into prehistoric plant life (Metzgar et al. 2008, Yatabe et al. 1999).

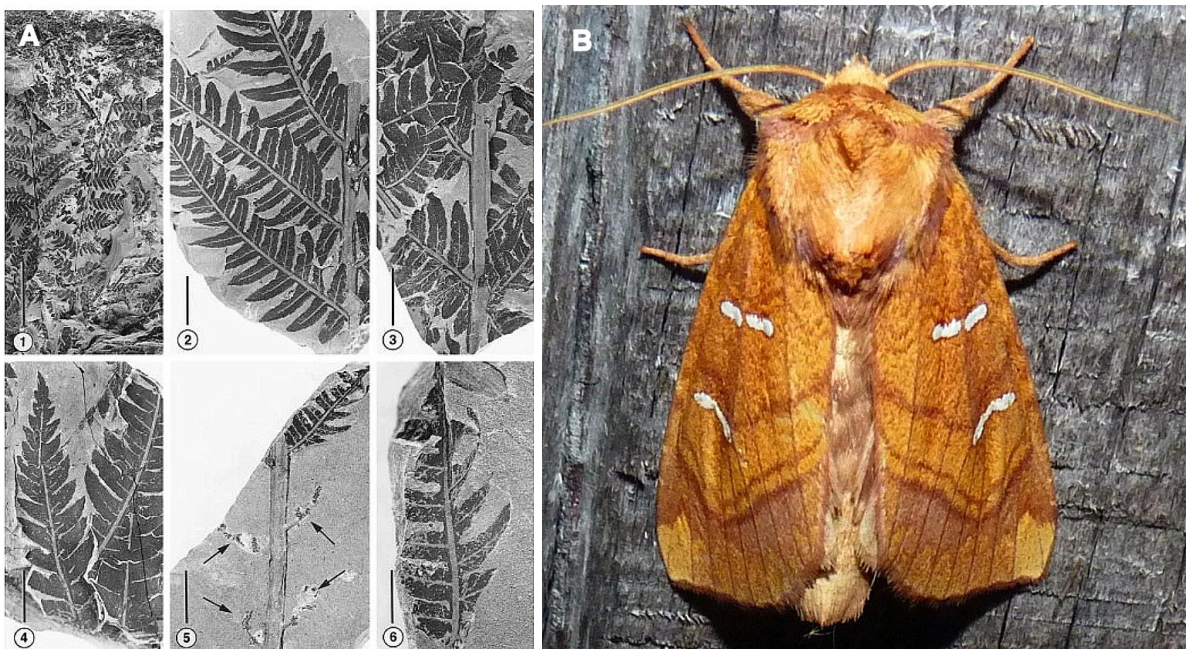


Figure 132. A. *Osmunda claytoniites*, an extinct relative of modern *Osmunda* that lived in Antarctica during the Late Triassic (<www.prehistoric-wiki.fandom.com/wiki/Osmunda_claytoniites>). **B.** Osmunda Borer Moth (*Papaipema speciosissima*), Randolph Co., Alabama, 26 Oct 2022 (@a24, iNaturalist observation).

Members of the Royal Fern Family serve as host plants for the Osmunda Borer Moth (*Papaipema speciosissima*; Fig. 132b). Bird (1938) describes how the larvae develop into pinkish caterpillars, which might seem to threaten the longevity of the host plants. However, this is not necessarily the case, as female moths preferentially lay their eggs on older plants. Adult moths live for about two weeks in the fall, laying eggs that overwinter. In late spring, the larvae hatch, bore through the stems of young fronds, and mine the rhizome until mid-summer. By then, they pupate and later emerge as adults, completing their life cycle.

1. Leaves 2-pinnate; veins Y-forked twice (each vein forming 4 veinlets); leaf segment margins finely toothed; spores borne on modified pinnae at the terminal portion of the blade.....***Osmunda***
1. Leaves pinnate-pinnatifid (cut once with deeply lobed pinnae); veins Y-forked once (each vein forming 2 veinlets); leaf segment margins entire to crenulate (with obscure, rounded teeth); spores borne either on fully fertile, specialized leaves or on fertile pinnae located in the middle of the blade, with sterile pinnae above and below.

2. Leaves dimorphic (of two distinct forms), blades either completely sterile and photosynthetic or entirely fertile and ephemeral (withering by summer); tufts of persistent rust-colored hairs present beneath the axils where pinnae join the rachis on sterile fronds ..... ***Osmundastrum***
2. Leaves hemidimorphic (partially diphorphic), with fertile pinnae located in the middle of the blade that wither later in the season, leaving a gap; tufts of hairs initially present in the axils of sterile pinnae on young fronds but absent at maturity..... ***Claytosmunda***

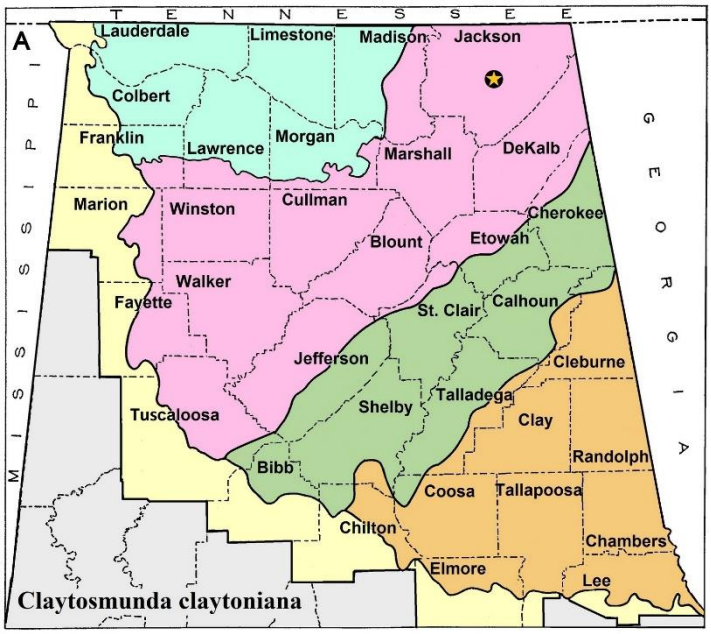
1. CLAYTOSMUNDA Metzgar & Rouhan 2016 {clay-toz-MUN-duh}
[Rev. John Clayton, an 18th-century American botanist; the fern genus *Osmunda*]

1. Claytosmunda claytoniana (L.) Metzgar & Rouhan {for John Clayton, 1695–1773, pioneer botanist of Virginia} — INTERRUPTED FERN; CLAYTON'S FERN (Fig. 133). [*Osmunda claytoniana* L.; *Osmundastrum claytonianum* (L.) Tagawa]

Figure 133. *Claytosmunda claytoniana*, Fannin Co., Georgia, 7 May 2011. Photos: Alan Cressler.

Plants terrestrial; deciduous. Mesic forests. Sporulates March–June; very rare in the Jackson County Mountains District of the Cumberland Plateau (Fig. 134). Native to the eastern USA and adjacent Canada, from Newfoundland west to Minnesota, south to Tennessee, and northern Georgia; disjunct in Asia (Whetstone & Atkinson 1993). The Alabama Natural Heritage Program (2023) lists this species as critically imperiled (S1) within the state.

Claytosmunda is a monotypic genus characterized by its distinctive arrangement of spore-bearing pinnae located in the middle of the blade, flanked above and below by sterile, green pinnae. This discontinuous pattern gave rise to its common name, "Interrupted Fern." The fertile pinnae emerge nearly black, transition to a golden-green color (Fig. 135a), and eventually turn brown as they release spores (Parsons 1899). As these pinnae wither, they leave a conspicuous gap in the center of the blade where the fertile segments were once located (Fig. 135b).



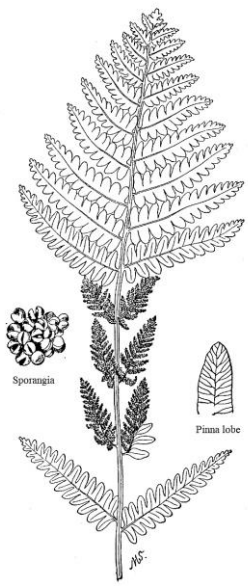


Figure 134. *Claytosmunda claytoniana*. **A.** Distribution map. **B.** Illustration: Marion Satterlee, 1899.

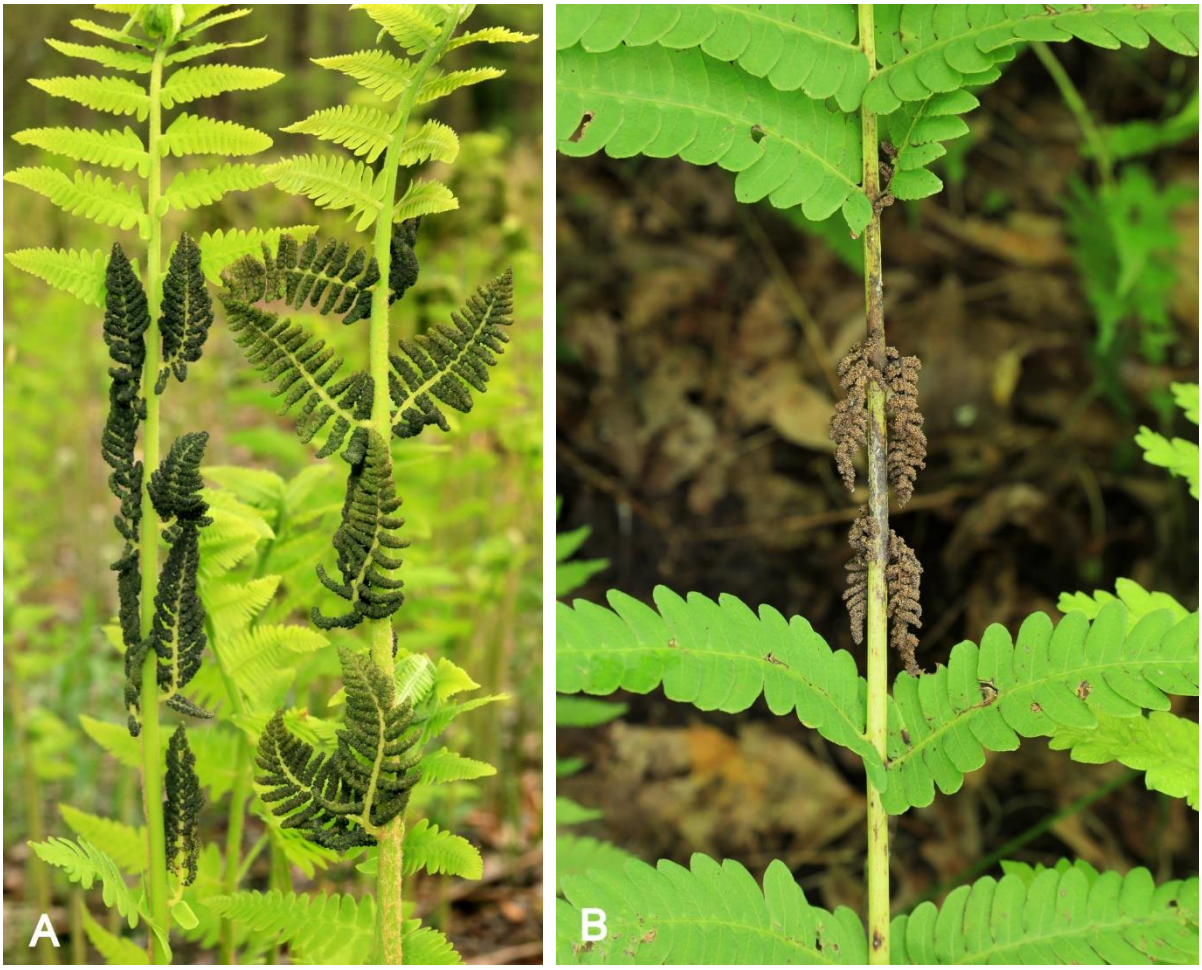


Figure 135. *Claytosmunda claytoniana*. **A.** Young fertile fronds, Westmoreland Co., Pennsylvania, 5 May 2024. **B.** Old fertile fronds, Rabun Co., Georgia, 3 Jul 2024. Photos: Noah Yawn.

The sterile fronds of *Claytosmunda claytoniana* (Interrupted Fern) are frequently confused with those of *Osmundastrum cinnamomeum* (Cinnamon Fern) because of their similar size and form (Fig. 136). Both species produce reddish woolly hairs on young fronds, but *C. claytoniana* sheds most of these hairs as the fronds mature. A key distinguishing feature of *C. claytoniana* is the absence of hair tufts on the undersides of sterile leaflets at the points where each pinna attaches to the rachis. Additionally, *C. claytoniana* typically inhabits upland forests, produces smaller fronds, and has pinna lobes with rounded tips. In contrast, *O. cinnamomeum* thrives in wetlands, grows more robustly, and has pinna lobes with pointed tips.

Figure 136. *Claytosmunda claytoniana*, Jackson Co., Alabama, 17 May 2011. Photo: Wayne Barger.

Radford et al. (1968) listed *Claytosmunda claytoniana* as occurring in Alabama, but botanists did not officially confirm its presence until the spring of 2011 (Fig. 136). At that time, Alan Cressler, Wayne Barger, and Brian Holt documented the species in Jackson County (Barger et al. 2012). Earlier reports were likely the result of misidentifications, with observers mistaking atypical fronds of Cinnamon Fern (*Osmundastrum cinnamomeum*) for those of the Interrupted Fern.

The discovery of *Claytosmunda claytoniana* in Alabama is noteworthy, as the species is primarily northern in distribution and reaches the southern limit of its range in the state's northeastern corner. Its presence underscores the unique ecological conditions of this region, which support several species at the edges of their geographic ranges. However, cultivating the Interrupted Fern presents challenges in our state due to its preference for cooler environments. While gardeners can often grow it successfully, maintaining healthy plants in Alabama's climate requires extra care, including careful attention to moisture, shade, and soil composition (Hoshizaki & Moran 2001).

2. OSMUNDA Linnaeus 1753 {oz-MUN-duh}
[*Osmunder*, Saxon, name for Thor, Norse god of war]

1. Osmunda spectabilis Willd. {showy; the fronds} — AMERICAN ROYAL FERN (Fig. 137). [*Osmunda regalis* L. var. *spectabilis* (Willd.) A. Gray]

Figure 137. *Osmunda spectabilis*, Randolph Co., Alabama, 2 May 2022. Photos: Lee Kelly.

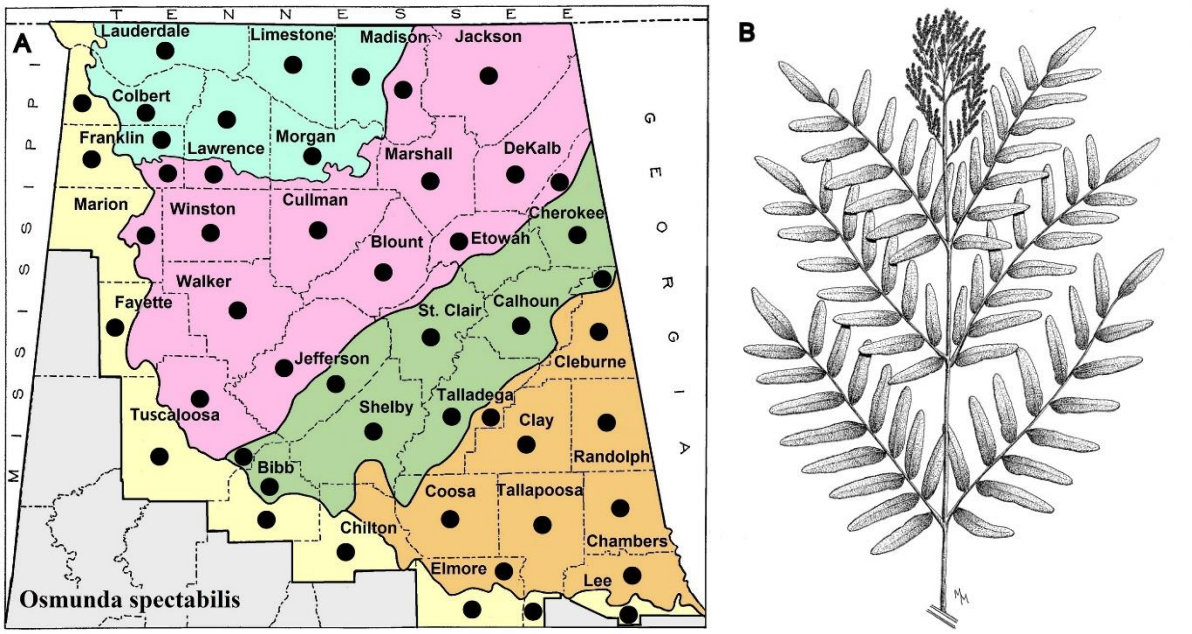


Figure 138. *Osmunda spectabilis.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Plants terrestrial; deciduous. Swamps, bogs, stream/lake banks, floodplains, marshes, seepage slopes, wet meadows, and ditches. Sporulates March–June; frequent throughout Alabama (Fig. 138). In eastern North America, from Newfoundland west to Manitoba, south to East Texas and Florida; also in the West Indies and Mexico, south through Central America to South America (Weakley et al. 2025).

Figure 139. *Osmunda spectabilis*, Jekyll Island, Glynn Co., Georgia, 26 Mar 2008. Photo: Alan Cressler.

The generic name *Osmunda* likely originates from the Saxon word "Osmunder," associated with Thor, the Norse god of war. Underwood (1899) speculated that this connection arose because the European Royal Fern, *Osmunda regalis*, commonly grows in bogs rich in bog iron—an essential material in early northern European weapon-making. Clute (1901), however, offered an alternative origin, citing an English folktale in which Osmond the Boatman hides his wife and child from Viking invaders in the 9th century by concealing them within a dense thicket of this fern on an island (Fig. 139). Occasionally, some refer to this species as the "flowering fern" because its attractive terminal fertile pinnae resemble a panicle of flowers (Frankel 1981).

Figure 140. *Osmunda spectabilis*. **A.** Calhoun Co., Alabama, 17 Apr 2025. Photo: Dan Spaulding. **B.** Jefferson Co., Alabama, 27 Apr 2024. Photo: Joel Reach.

The American Royal Fern can grow over seven feet tall in moist to wet soils, making it an intriguing addition to gardens. Orchid growers prize its dense, tangled rhizomes and roots as a superior growth substrate. Historically, people used its fibers to make twine, rope, netting, and mats (Dunbar 1989). The white, edible portion of the rhizome—known for its pungent taste—earned it the nickname "bog onion" (Abbe 1981). Notably, its spores contain chlorophyll, imparting a green hue that also colors the young sporangia (Fig. 140). As the spores mature and are released, the sporangia turn a distinctive rusty brown.

3. **Osmundastrum** C. Presl 1847 {oz-muhn-DAS-truhm}
[Genus *Osmunda*, and Latin suffix, *astrum*, incomplete resemblance]

1. Osmundastrum cinnamomeum (L.) C. Presl {cinnamon-colored; frond hairs} — CINNAMON FERN (Fig. 141). [*Osmunda cinnamomea* L. var. *cinnamomea*; *Osmunda cinnamomea* var. *frondosa* A. Gray; *Osmunda cinnamomea* var. *glandulosa* Waters; *Osmundastrum cinnamomeum* var. *glandulosum* (Waters) McAvoy]

Figure 141. *Osmundastrum cinnamomeum*, Cleburne Co., Alabama, 27 Apr 2025. Photo: Jimmy Triplett.

Plants terrestrial in wet soil or occasionally in thin soil on rocks; deciduous. Swamps, bogs, marshes, seepage slopes, stream/lake banks, ditches, floodplains, and wet sandstone bluffs. Sporulates March–May; frequent throughout Alabama (Fig. 142). This species occurs in eastern North America from Newfoundland west to Ontario and south to East Texas and Florida, and also extends to the West Indies, Mexico, Central and South America, and eastern Asia (Whetstone & Atkinson 1993).

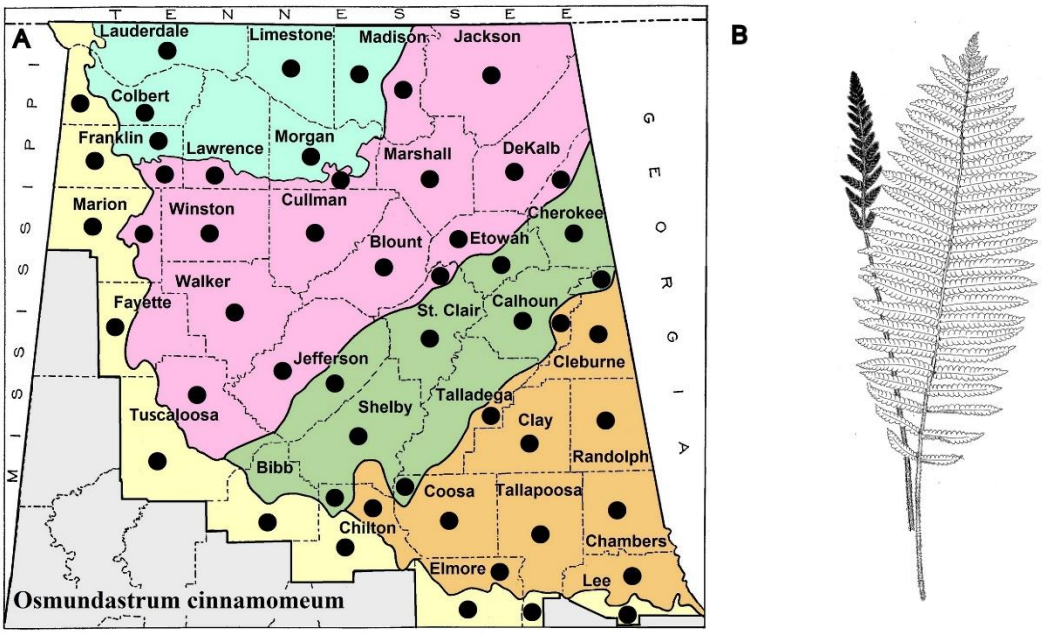


Figure 142. *Osmundastrum cinnamomeum*. **A.** Distribution map. **B.** Illustration: Forrest Bonner (Dean 1969).

In early spring, the tightly coiled croziers of the Cinnamon Fern emerge, their surfaces densely coated in silvery-white hairs (Clute 1901). As they unfurl with warming weather, the hairs take on a cinnamon-brown hue (Fig. 143a), giving the species its common name (Dean 1969). These fiddleheads mature into two distinct types of fronds: one is leafy, grass-green, and photosynthetic; the other is cinnamon-brown, lacks leafy tissue, and is specialized for spore production (Fig. 143b).

Figure 143. *Osmundastrum cinnamomeum*. **A.** Fiddleheads, Baldwin Co., Alabama, 11 Apr 2006. Photo: Wayne Barger. **B.** Fertile and sterile fronds, Gadsden Co., Florida, 29 Mar 2008. Photo: Alan Cressler.

The fertile fronds appear first, forming a ring around the outer edge of the rhizome's crown. Slender and erect, they bear reduced pinnae densely covered in globular sporangia. Initially green (Fig. 144a), they mature to a rich cinnamon color—hence the nickname "cinnamon sticks." Soon afterward, sterile fronds emerge from the center of the crown, arching outward to form a vase-like cluster around the fertile fronds (Clute 1901). Once spores are released, the fertile fronds wither and collapse to the base of the plant, while the leafy sterile fronds persist through summer.

Figure 144. *Osmundastrum cinnamomeum*. **A.** Young fertile fronds with sterile fronds, Calhoun Co., Alabama, 8 Apr 2025. **B.** Tufts of hair, Calhoun Co., Alabama, 27 Mar 2023. Photos: Dan Spaulding.

Figure 145. *Osmundastrum cinnamomeum*, growing with *Amauropelta noveboracensis* (New York fern), Talladega National Forest, Cleburne Co., Alabama, 12 Jun 2024. Photo: Dan Spaulding.

In spring, Cinnamon Fern produces sterile fronds densely covered with cinnamon-colored woolly hairs. Most hairs are shed as the season advances, but small tufts remain along the lower petiole and at the leaflet bases (Fig. 144b). This feature helps distinguish *Osmundastrum cinnamomeum* from the similar *Anchistea virginica* (Virginia chain fern), which has netted venation, purplish-black petioles, and long creeping rhizomes. By autumn, the sterile fronds of Cinnamon Fern turn brilliant gold, orange, or scarlet, adding vivid seasonal color to wetland habitats (Fig. 146).

Figure 146. *Osmundastrum cinnamomeum*, Green Swamp Ecological Preserve, Brunswick Co., North Carolina, 2 Nov 2013. Photo: Alan Cressler.

The central portion of Cinnamon Fern's large rhizome, known as the "heart of Osmund," is edible and has a tender, crisp texture with a taste reminiscent of cabbage (Clute 1901). The Cherokee used the plant medicinally as a 'chew root' for treating snake bites. They chewed portions of the rhizome, swallowing some and applying the rest directly to a wound. Native Americans also prepared a decoction from the rhizome to treat chills and relieve rheumatism (Dunbar 1989). Gardeners and landscapers prize Cinnamon Ferns for their hardiness, beauty, and dramatic displays, especially in mass plantings.

Osmundastrum cinnamomeum, the sole member of its genus, is common in boggy habitats across the eastern United States, often forming large, lush populations (Fig. 145). Given the fern's widespread abundance, it is not surprising that several variants occur. In some plants, fertile fronds are partly leafy, retaining traces of blade tissue—a form historically named *Osmunda cinnamomeum* L. var. *frondosa* A. Gray. Clute (1901) attributed this condition to stress or injury and regarded it only as a form. Another variant, *Osmundastrum cinnamomeum* var. *glandulosum* (Waters) McAvoy, bears dense glandular pubescence. Weakley et al. (2025) treat this as a form rather than a distinct variety, citing its scattered and inconsistent distribution.

9. HYMENOPHYLLACEAE (Filmy Fern Family) – in Hymenophyllales

1. Gametophytes ribbon-like; sporophytes (if present) less than 1 cm long, with stellate hairs; sori absent ..... ***Hymenophyllum***
1. Gametophytes entirely filamentous; sporophytes (if present) 0.5–20 cm long, glabrous or with simple hairs; sori present.

    2. Gametophyte generation dominant, sporophytes absent; reproduction by gemmae; plants forming felt-like mats that resemble colonies of moss or algae..... ***Crepidomanes***
    2. Sporophyte generation dominant; reproduction by spores; plants not forming felt-like mats.

        3. Leaf blades 0.5–2.5 cm long, undivided to slightly lobed, margins with dark hairs; plants resembling liverworts rather than ferns..... ***Didymoglossum***
        3. Leaf blades 4–20 cm long, deeply pinnately lobed, margins lacking dark hairs; plants distinctly fern-like ..... ***Vandenboschia***

1. CREPIDOMANES C. Presl 1851 {kreh-pih-doh-MAHN-neez}

[Greek *krepis*, slipper, and *manes*, cup-shaped, alluding to the shape of the involucre enclosing sori]

1. Crepidomanes intricatum (Farrar) Ebihara & Weakley {entangled; tangled filaments} — WEFT FERN; GROTTO-FELT; APPALACHIAN BRISTLE FERN (Fig. 147). [*Trichomanes intricatum* Farrar]

Figure 147. *Crepidomanes intricatum*, Cherokee Co., Alabama, 8 May 2022. Photo: Alan Cressler.

Plants epipetric, with evergreen, independent gametophytes. Deeply sheltered rock overhangs and grotto walls (often on ceilings or back walls), especially in humid gorges and in the spray zones near or behind waterfalls. Reproduction by gemmae; rare in the Highland Rim, Cumberland Plateau, and Ridge & Valley; very rare in the Coastal Plain (Fig. 148). The species occurs in scattered localities across the eastern United States, from Vermont and New Hampshire south through the Appalachians to northern Alabama, and west to southern Illinois and Indiana (Farrar 1993a).

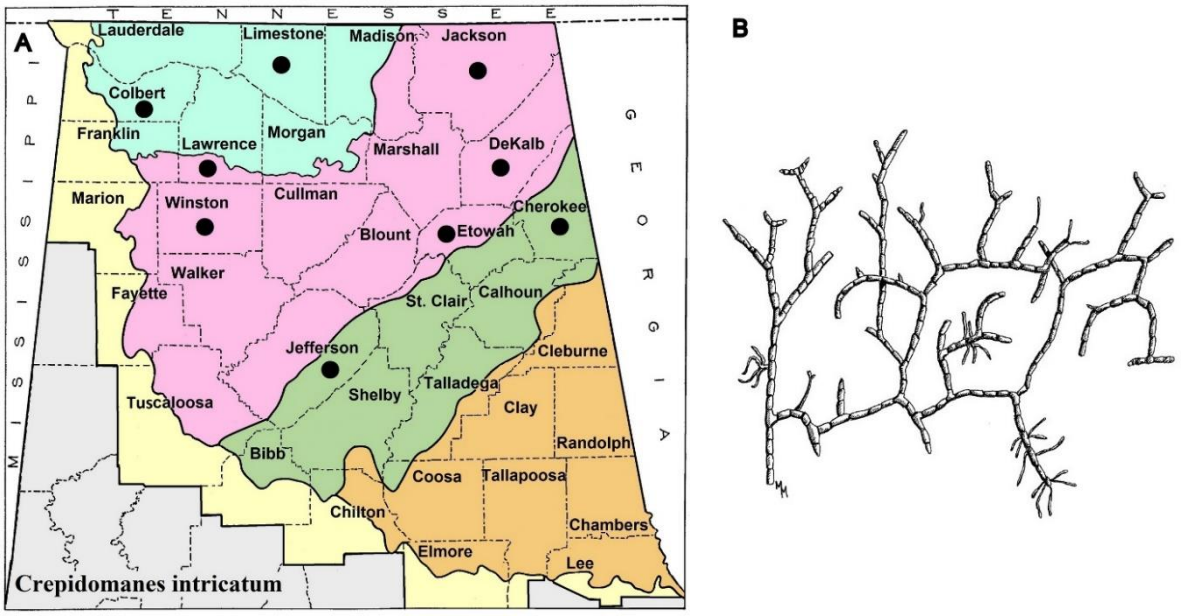


Figure 148. *Crepidomanes intricatum.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 2000.

The gametophytes of *Crepidomanes intricatum* thrive in sheltered, temperate rock crevices and grottoes, where they form dense, felt-like mats that can cover up to a square meter or more of rock surface. These populations do not produce sporophytes; instead, they reproduce by forming vegetative buds (gemmae) and through the persistent growth and branching of the gametophytes (Farrar 1993a). The name "grotto felt" derives from the fern's preferred habitat and distinctive growth form. The term "weft fern" highlights the fern's unique, interconnected growth pattern, drawing a parallel to the *weft* in textiles—the crosswise threads woven through the lengthwise threads to create fabric.

Figure 149. *Crepidomanes intricatum*. **A.** Colbert Co., Alabama, 3 Mar 2023. Photo: Wayne Barger. **B.** Guess Creek Cave, Jackson Co., Alabama, 6 May 2012. Photo: Alan Cressler.

These tiny, gametophyte-only ferns are often overlooked in the field, blending in with surrounding mosses and liverworts and making detection and identification challenging. As a result, they may be more widespread than current records suggest. Their filamentous alga-like form (Fig. 149a) sets them apart from liverworts and from the three other ferns in northern Alabama that also exhibit dominant gametophyte generations—those having flat, ribbon-like or leaf-like gametophytes rather than thread-like ones. Dr. Warren H. Wagner once described *Crepidomanes intricatum* to Dan Spaulding (pers. comm. 1997) as resembling "green steel wool" (Fig. 149b).

2. DIDYMOGLOSSUM Desvaux 1827 {dih-dee-moh-GLOSS-um}
[Greek *didymos*, twin, and *glossum*, tongue, alluding to bilabiate cup-like indusium and frond shape]

1. Didymoglossum petersii (A. Gray) Copel. {for Thomas M. Peters, 1810–1888} — DWARF FILMY FERN; DWARF BRISTLE FERN; PETERS' FILMY FERN (Fig. 150). [*Trichomanes petersii* A. Gray]

Figure 150. *Didymoglossum petersii*, Cleburne Co., Alabama, 14 Nov 2021. Photo: Noah Yawn.

Plants epipetric or epiphytic; evergreen. Shaded, moist rock faces, ledges, narrow gorges, and occasionally on tree trunks. Sporulates June–August; rare in the Cumberland Plateau; very rare in the Piedmont, restricted to high ridges of the Talladega Mountain range (Fig. 151). Chiefly in the Appalachians from western North Carolina and northwestern South Carolina south to northern Alabama, with disjuncts in Florida, Mississippi, Louisiana, Arkansas, Mexico, and Central America (Farrar 1993a). The Alabama Natural Heritage Program (2023) ranks this species as imperiled (S2).

The Dwarf Filmy Fern has long been one of Alabama's most celebrated ferns. It was first discovered in 1853 in Winston County by Judge Thomas M. Peters, a distinguished amateur lichen collector and a graduate of the University of Alabama (Thieret 1980). While exploring sandstone cliffs, Peters encountered two previously unknown ferns. He collected specimens and sent them to Asa Gray at Harvard University for identification.

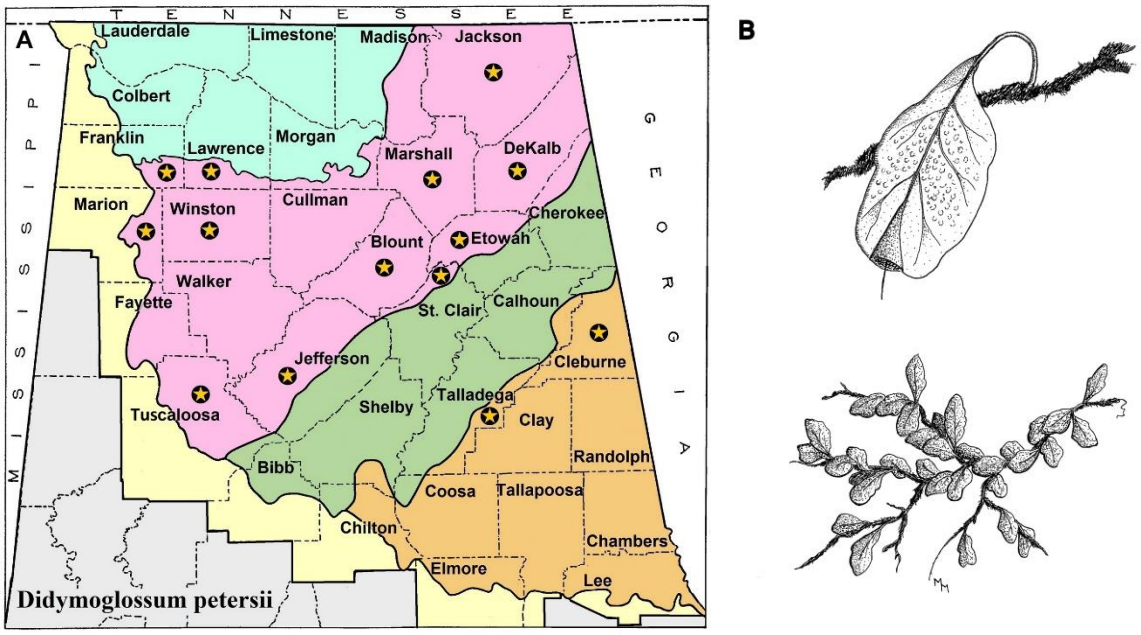


Figure 151. *Didymoglossum petersii.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Gray (1853) was astonished by Peters' discovery, remarking, *"*With one exception, no Hymenophyllaceous fern has been supposed to grow within the limits of the United States; nor, when the nature of our climate is considered, would any such fern be expected to occur, except, perhaps, in Florida.*"* He identified one of the ferns as a new species, naming it *Trichomanes petersii* in Peters' honor. Initially, he believed the second specimen to be *T. radicans* Sw. from tropical America. However, in 1861, Johann Sturm recognized it as a distinct species and named it *Trichomanes boschianum* (Shaver 1954).

Figure 152. *Didymoglossum petersii*, Cleburne Co., Alabama, 14 Nov 2021. Photo: Noah Yawn.

In 1880, Charles Mohr discovered *Didymoglossum petersii* on sandstone walls at Noccalula Falls, extending its known range beyond the original site in Winston County. Expansion of the parking lot in the mid-20th century destroyed the type locality at what is now the Sipsey River Picnic Area in the Bankhead National Forest (Dean 1969). By the early 1900s, botanists had documented the species at only three North American sites, all in Alabama. Since then, they have recorded it more broadly across the southeastern United States. Though inconspicuous, it often forms extensive mats resembling liverwort colonies (Fig. 152). It grows chiefly on rocks in highland regions, especially the Cumberland Plateau, but recent discoveries reveal it also thrives on trees in the Coastal Plain.

Subsequent research prompted a reevaluation of filmy fern taxonomy (Ebihara et al. 2006). Weakley et al. (2011) highlighted that recent phylogenetic and other studies of *Hymenophyllaceae* have underscored the diversity of evolutionary lineages, particularly within the traditionally broad concept of *Trichomanes*. As a result, botanists reassigned the ferns discovered by Peters to separate genera. Today, we recognize these species as *Didymoglossum petersii* and *Vandenboschia boschiana*.

3. HYMENOPHYLLUM J.E. Smith 1793 {hye-men-oh-FIL-um}
[Greek *hymen*, membrane, and *phyllon*, leaf; alluding to very thin fronds]

1. Hymenophyllum tayloriae Farrar & Raine (A. Gray) Copel. {for Mary S. Taylor, 1885–1976} — GORGE FILMY FERN; TAYLOR'S FILMY FERN (Fig. 153).

Figure 153. *Hymenophyllum tayloriae*, Lawrence Co., Alabama, 20 Mar 2021. Photo: Alan Cressler.

Plants epipetric; evergreen (gametophytes dominant, sterile sporophytes occasionally present). Deeply shaded, moist crevices in acidic rock, often narrow gorges, and spray cliffs near waterfalls. Reproducing by gemmae; very rare in the Warrior Basin District of the Cumberland Plateau (Fig. 154). Endemic to the southern Appalachians, it occurs in eastern Kentucky, western North Carolina, northwestern South Carolina, northeastern Georgia, eastern Tennessee, and northern Alabama (Kartesz 2025). The Alabama Natural Heritage Program (2023) ranks it as critically imperiled (S1).

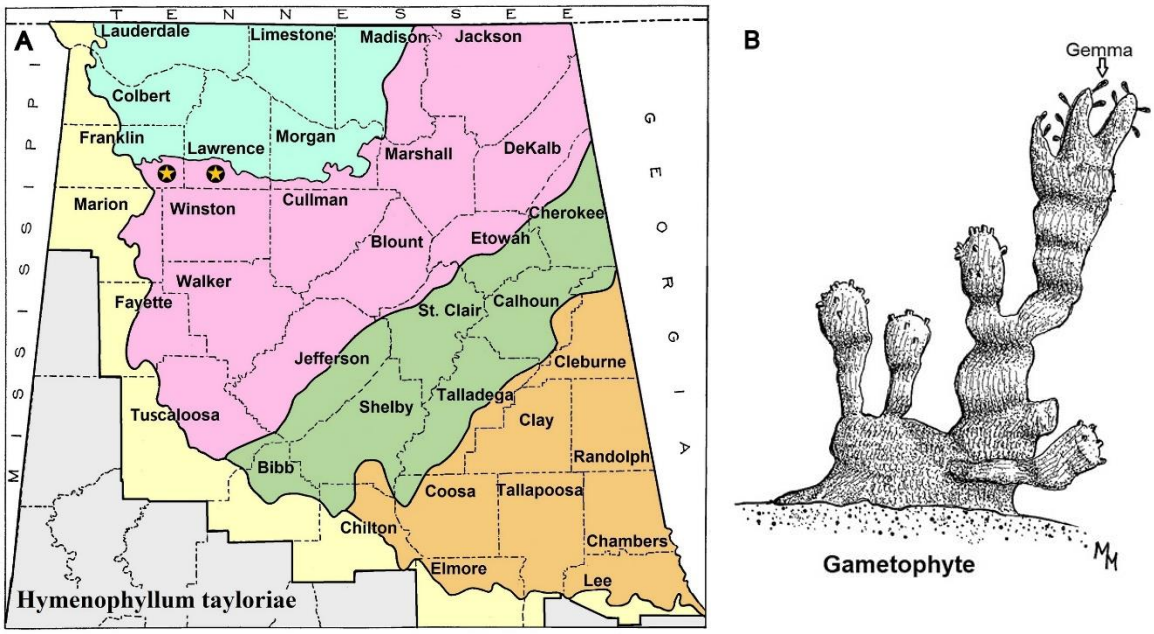


Figure 154. *Hymenophyllum tayloriae*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 155. *Hymenophyllum tayloriae* gametophytes, Sipsey Wilderness, Bankhead National Forest, Lawrence Co., Alabama, 22 Dec 2023. Photo: Noah Yawn.

The Gorge Filmy Fern (*Hymenophyllum tayloriae*) is notable for existing primarily in its gametophyte stage (Fig. 155), a rare condition among ferns. It thrives in deeply shaded, moist crevices of acidic rock, forming inconspicuous colonies that cling tightly to the substrate. Sporophytes are uncommon, but when present (Fig. 156), they are diminutive, with a short stem and typically only four leaves, the largest under 1 cm long. These delicate leaves consist of a single cell layer between the veins, lack sori, and bear stalked, star-shaped hairs. The ribbon-like gametophytes resemble liverworts but differ in having a single cell layer, lacking a midrib; in contrast, liverworts are usually thicker and often have a midrib. Another member of the filmy fern family, *Crepidomanes intricatum*, produces independent gametophytes, but its thread-like, filamentous structure contrasts with the strap-shaped gametophytes of *Hymenophyllum*.

Figure 156. *Hymenophyllum tayloriae* sporophytes, Sipsey Wilderness, Bankhead National Forest, Lawrence Co., Alabama, 22 Dec 2023. Photo: Noah Yawn.

In 1994, bryologist Paul G. Davison of the University of North Alabama discovered sporophytes of *Hymenophyllum tayloriae* growing alongside gametophytes in the Sipsey Wilderness of Lawrence County, Alabama. The species had first been collected much earlier, in 1936, by botanist Mary S. Taylor in South Carolina. Although her specimen included sporophytes, it remained undescribed for decades. In 1967, Farrar and Raine formally described the species as *H. tayloriae*, naming it in Taylor's honor. Based on their studies of independent gametophytes, they concluded that Taylor's specimen represented a distinct species. The later discovery in Alabama of gametophytes with attached sporophytes confirmed their conclusion (Farrar & Davison 1994).

3. VANDENBOSCHIA Copeland 1938 {van-den-BOSH-ee-uh}

[In honor of Roelof Benjamin van den Bosch, 1810–1862, Dutch pteridologist]

1. Vandenboschia boschiana (J.W. Sturm ex Bosch) Ebihara & K. Iwats. {for Roelof van den Bosch} — APPALACHIAN FILMY FERN; APPALACHIAN BRISTLE FERN (Fig. 157). [*Trichomanes boschianum* J.W. Sturm ex Bosch]

Plants epipetric; evergreen. On vertical or overhanging rock outcrops, usually in deeply shaded, moist grottoes. Sporulates June–September; rare in the Highland Rim, uncommon in the Cumberland Plateau, very rare in the Ridge & Valley, Piedmont, and upper Coastal Plain (Fig. 158). Native to the Appalachian region and the southern Ohio Valley, this species ranges from southern Illinois, Indiana, and Ohio south to West Virginia and northern Alabama, with a disjunct population in the Arkansas Ozarks (Farrar 1993a). Kartesz (2025) also reports it from northeastern Mississippi. The Alabama Natural Heritage Program ranked it as vulnerable (S3) in 1994, but later found it to be more widespread in the state than previously recognized. In other states, it remains ranked from vulnerable to critically imperiled (Hill 2003a).

Figure 157. *Vandenboschia boschiana*, Winston Co., Alabama, 6 Jul 2022. Photo: Noah Yawn.

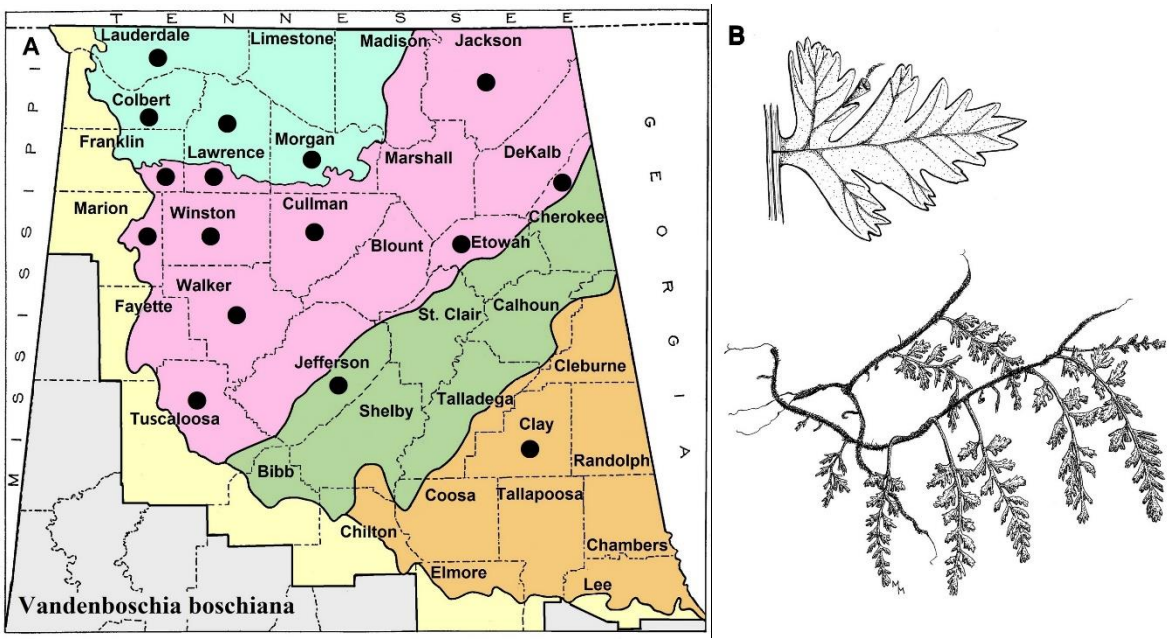


Figure 158. *Vandenboschia boschiana*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

In 1853, Judge Thomas M. Peters discovered the Appalachian Filmy Fern in what is now Winston County, Alabama, along with another member of the same family. These delicate plants, known as filmy or bristle ferns, have nearly transparent leaves and bristle-like sporangial receptacles that extend from an involucral cone (Fig. 159)—features that give rise to their common names. *Vandenboschia boschiana* is the largest filmy fern in North America and one of the few members of the primarily tropical family Hymenophyllaceae to occur in the United States. Initially identified by Asa Gray in 1853 as the tropical *V. radicans* (Sw.) Copel., the Appalachian plants were later recognized by Sturm as a distinct species and formally described as *V. boschiana* in 1861 (Shaver 1954).

Figure 159. *Vandenboschia boschiana*, Winston Co., Alabama. **A.** 19 Mar 2022. Photo: Brian Keener. **B.** 13 Jun 2024. Photo: Dan Spaulding. **C.** 6 Apr 2024. Photo: Courtney Hallmark.

The Appalachian Filmy Fern thrives in highly specialized habitats, anchoring itself with roots on long-creeping rhizomes that cling to vertical or horizontal rock faces. It typically occurs on moist, well-weathered sandstone cliffs, often beneath overhangs or in shallow caves that provide deep shade. Its fronds are frequently pendulous from these outcroppings, forming dense mats in formations known as rock shelters or rock houses. Although the fern can tolerate occasional drying and freezing, its delicate structure depends on consistently high moisture and humidity, similar to that of its tropical relatives. Several threats—including quarrying, mining, hydrological changes, recreational rock climbing, and over-collecting—could cause localized extirpation if the species is not adequately protected (Hill 2003a).

10. LYGODIACEAE (Climbing Fern Family) – in Schizaeales

1. LYGODIUM Swartz 1800 {lie-GOH-dee-um}
[Greek *lygodes*, flexible; in referring to its twining habit]

1. Sterile pinnae pinnately divided into numerous pinnules with serrated margins; fertile pinnae pinnately divided into segments fringed with linear lobes.....***Lygodium japonicum***
1. Sterile pinnae forked into two palmately lobed pinnules with entire (toothless) margins; fertile pinnae 3- to 5-forked into deeply palmate or irregularly lobed segments ..... ***Lygodium palmatum***

1. Lygodium japonicum (Thunb.) Sw. {of Japan; its origin} — JAPANESE CLIMBING FERN (Fig. 160).

Plants terrestrial; deciduous. Moist woods, stream banks, swamp margins, roadbanks, roadside ditches, low fields, and other disturbed areas. Sporulates June–November; uncommon in the Highland Rim and Cumberland Plateau; frequent in the Ridge & Valley and Piedmont; common in the Coastal Plain (Fig. 161). Native to eastern Asia; invasive in the southeastern USA from North Carolina to East Texas (Nauman 1993a).

Figure 160. *Lygodium japonicum*, Calhoun Co., Alabama, 16 Aug 2022. Photos: Dan Spaulding.

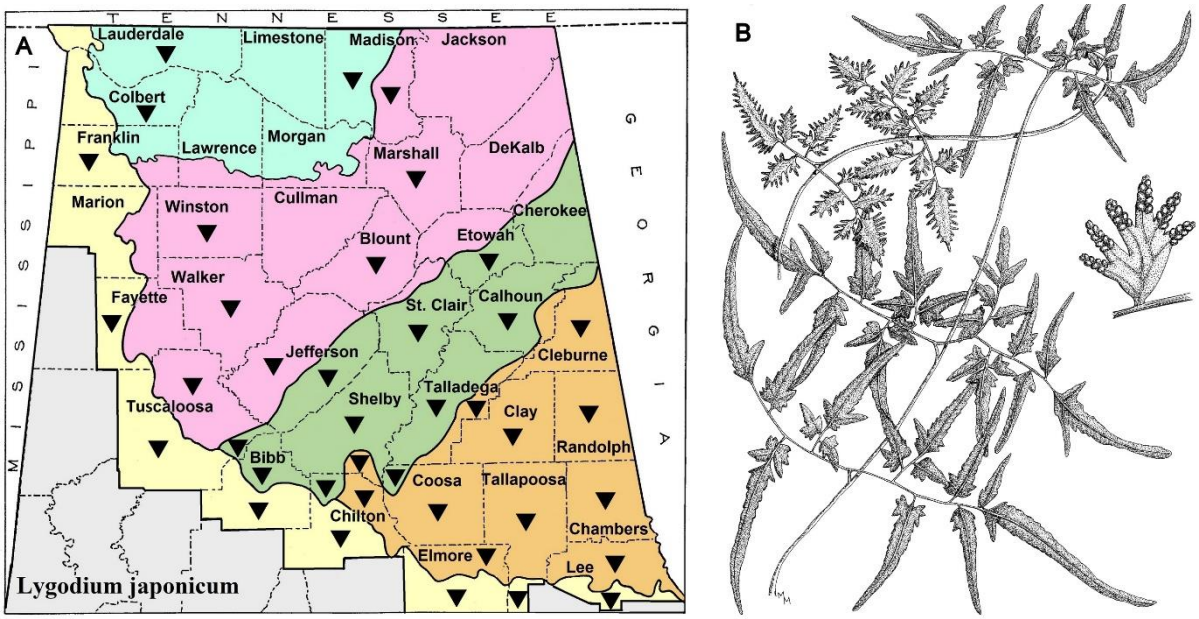


Figure 161. *Lygodium japonicum.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

The Japanese Climbing Fern, long cultivated in southern gardens, was first recorded escaping cultivation in Thomasville, Georgia, in the early 1900s (Nelson 2000). Since then, it has naturalized across the southeastern United States. Like many non-native plants, this fern exhibits highly weedy behavior. It grows so densely that it can completely cover shrubs and small trees (Fig. 162). The vine-like fronds, which can reach lengths of up to 30 meters, climb into the canopy of trees in swamp forests and other natural habitats (Weakley et al. 2025). This dense growth often shades out and kills the underlying vegetation, earning it the nickname "kudzu fern." The U.S. Department of Agriculture (2009) classifies this fern as a pest species.

Figure 162. *Lygodium japonicum*, roadbank, Calhoun Co., Alabama, 16 Aug 2022. Photo: Dan Spaulding.

Lygodium japonicum is particularly noxious in the Coastal Plain of the southeastern United States. Its unchecked spread disrupts natural communities and outcompetes native species, posing significant challenges to the tourism industry by damaging the biological resources of parks and other natural ecosystems. In pine plantations, it interferes with harvest periods and increases the risk of severe wildfires. The fern's growth habit acts as a "fuel ladder," potentially spreading fire into forest canopies and creating more devastating impacts (Nietes & Buot 2022).

Figure 163. *Lygodium japonicum*, Bibb Co., Alabama, 6 Jul 2024. **A.** Sterile pinna. **B.** Fertile pinna Photos: Dan Spaulding.

The pinnae of *Lygodium japonicum* are distinctly dimorphic, with sterile and fertile forms differing markedly in structure (Fig. 163). The sterile pinnae have pinnately divided pinnules with serrate margins, while the fertile pinnae, though also pinnately divided, develop narrow, entire linear lobes fringed with sporangia. Like *L. japonicum*, the American Climbing Fern (*L. palmatum*) spreads through its environment using a vine-like rachis, but its leaf morphology sets it apart. Instead of pinnately divided pinnae, *L. palmatum* produces broad, hand-shaped (palmately lobed) leaflets, giving it a distinctive appearance among North American climbing ferns.

2. Lygodium palmatum (Bernh.) Sw. {hand-like; the pinnae} — AMERICAN CLIMBING FERN; HARTFORD FERN (Fig. 164).

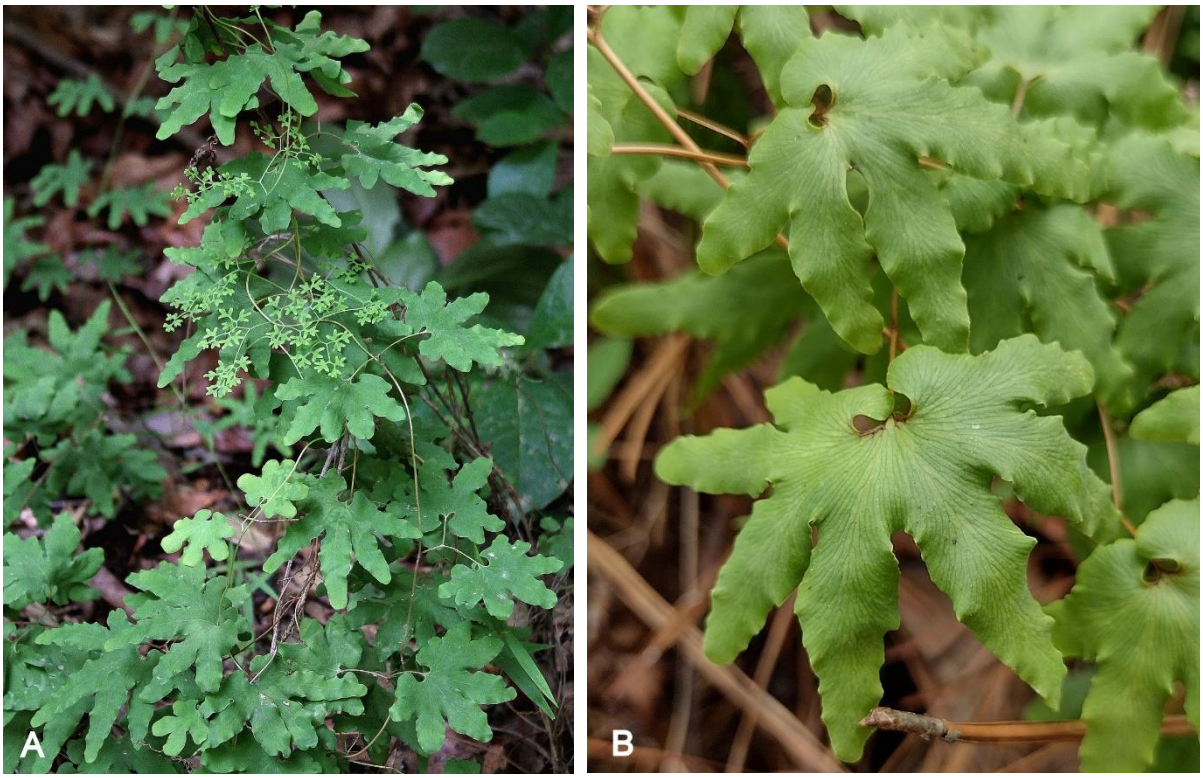


Figure 164. *Lygodium palmatum*. **A.** Cherokee Co., Alabama, 15 Jun 2011. Photo: Wayne Barger. **B.** Randolph Co., Alabama, 4 Mar 2024. Photo: Lee Kelly.

Plants terrestrial; evergreen. Streambanks, roadbanks, and moist woodlands (further north, it inhabits bogs, wet thickets, swamp forests, and sandstone outcrops). Sporulates July–September; very rare in the Lookout Mountain District of the Cumberland Plateau and Ashland Plateau District of the Piedmont (Fig. 165). Widely scattered in the eastern USA, from southern New Hampshire to southern Michigan, south to South Carolina, northern Alabama, and Georgia (Kartesz 2025). The Alabama Natural Heritage Program (2023) lists this species as critically imperiled (S1) within the state.

Lygodium palmatum, the only member of its genus native to North America, thrives in temperate regions with remarkable resilience. At first glance it scarcely resembles a fern, instead appearing as a slender, twining vine with alternately arranged, palmately lobed, hand-shaped leaflets. This impression, however, is deceptive: what seems to be a twining stem is in fact the elongated petiole and rachis of a single frond. Unlike most leaves, which reach a fixed size, this frond grows indeterminately, lengthening continuously in the manner of a climbing vine.

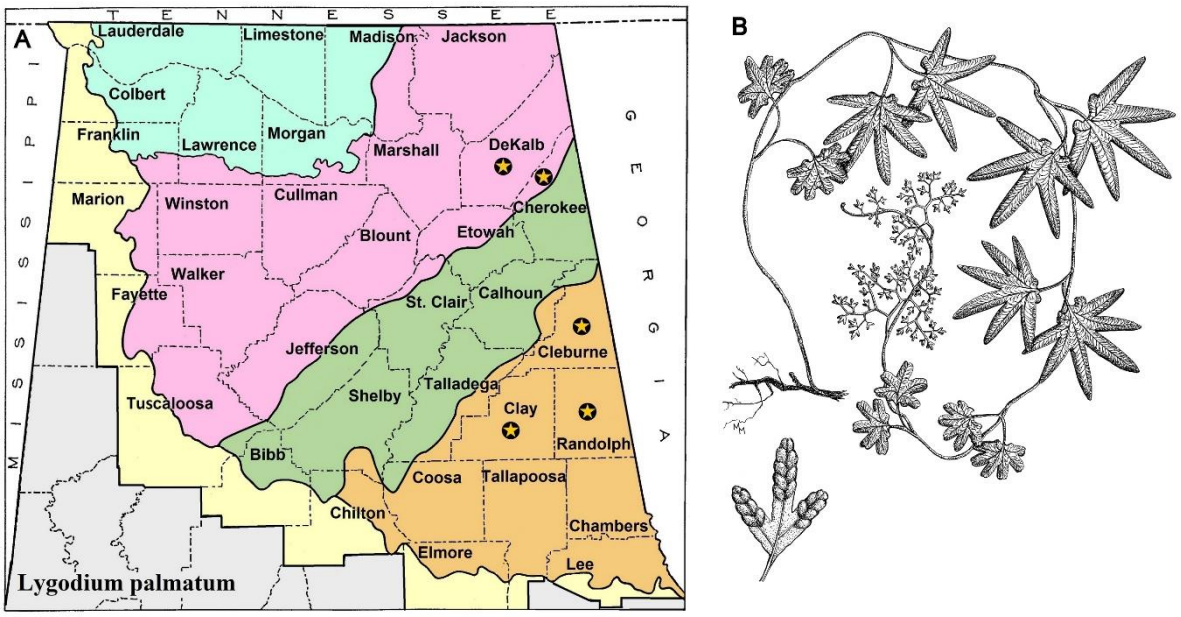


Figure 165. *Lygodium palmatum.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Henry David Thoreau discovered *Lygodium palmatum* on November 24, 1851, while walking through Ministerial Swamp in Concord, Massachusetts (Angelo 1985). In his journal, he described it as "a most beautiful slender and delicate fern, twining like a vine about the stem… our most beautiful fern, and most suitable for wreaths or garlands." By the early 20th century, Clute (1901) noted that city vendors sold fronds for decorative use, and this demand nearly drove the species to extinction in some areas. In response, the Connecticut legislature enacted a law in Hartford penalizing anyone who uprooted or removed specimens from another's land, earning the plant the nickname "Hartford Fern." It was among the first plants in the United States to receive legal protection (Mehrhoff 1980).

Figure 166. *Lygodium palmatum*, Union Co., Georgia, 22 Sep 2012. Photo: Alan Cressler.

The leaves of *Lygodium palmatum* are dimorphic, with distinct sterile and fertile forms. The sterile pinnae fork into two palmately lobed pinnules, while the fertile pinnae divide into three to five smaller segments that range from deeply palmate to irregularly lobed (Fig. 166). Hasan et al. (2016) investigated the potential medicinal properties of *L. palmatum* leaves. They found that a methanol extract of the leaves exhibits significant sedative and anxiolytic (anti-anxiety) effects, suggesting that *L. palmatum* may hold promise for treating anxiety and related neuropsychiatric disorders.

11. SALVINIACEAE (Floating Fern Family) – in Salviniales

1. Leaves tiny (< 1 mm), green to reddish-brown, numerous, alternately arranged on branches; upper surface hairless ..... ***Azolla***
1. Leaves larger (5–50 mm), bright green, arranged in threes with two round floating leaves and one root-like submerged leaf; upper surface hairy ..... ***Salvinia***

1. AZOLLA Lamarck 1783 {ah-ZOH-lah}

[Greek *azo*, to dry, and *ollyo*, to kill; alluding to drought killing this aquatic fern]

1. Azolla caroliniana Willd. {of Carolina; where first discovered} — EASTERN MOSQUITO FERN; WATER FERN; CAROLINA MOSQUITO FERN (Fig. 167). [*Azolla cristata* Kaulf.]

Figure 167. *Azolla caroliniana*, Talladega Co., Alabama, 1 May 2024. Photos: Dan Spaulding.

Plants free-floating aquatics; evergreen. Stagnant or slow-moving water of lakes, ponds, marshes, streams, ditches, and sloughs may be stranded on wet muck when the water level drops. Sporocarps produced June–September; uncommon in the Tennessee Valley District of the Highland Rim and Sequatchie Valley District of the Cumberland Plateau; rare in the Ridge & Valley and Piedmont; frequent in the Coastal Plain (Fig. 168). Widespread across the eastern USA, from southern New England west to Minnesota and south to Florida and Texas (Lumpkin 1993). It is particularly common in the southeastern Coastal Plain and extends into tropical regions (Weakley et al. 2025).

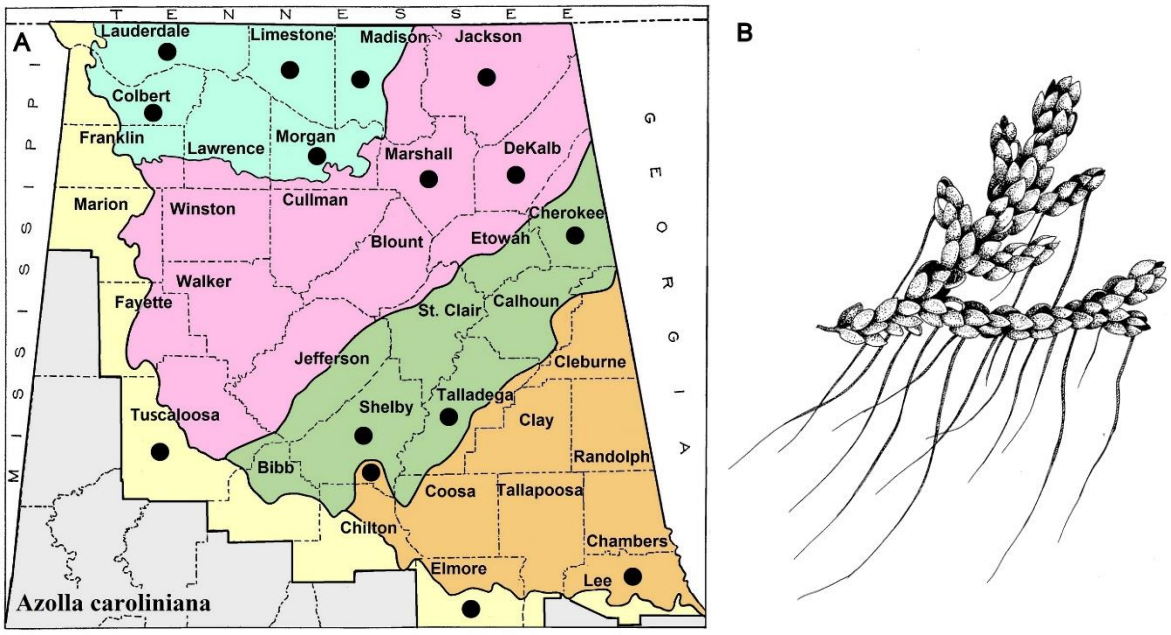


Figure 168. *Azolla caroliniana.* **A.** Distribution map. **B.** Illustration: Miriam Wysong Meyer 1967.

Populations of this tiny aquatic fern often form dense mats on the surface of stagnant water, resembling pond scum or duckweed more than a typical fern (Fig. 169). When the water takes on a distinctive red or bronze hue (Fig. 170), *Azolla* is usually the cause—a color change often triggered by heat stress or nutrient deficiency (Tran et al. 2020). By blanketing the surface, *Azolla* suppresses mosquito larvae, earning it the common name "mosquito fern" (Snyder & Bruce 1986). *Azolla caroliniana* rarely produces sporocarps—hard, pea-like structures that house spores (Lumpkin 1993). Rather, waterfowl serve as the primary agents of both short- and long-distance dispersal, as the fern clings to their breast feathers while they wade through or feed on these nutrient-rich mats (Brunton & Bickerton 2018).

Figure 169. *Azolla caroliniana*, Houston Co., Alabama, 14 Mar 2024. Photos: Alvin Diamond.

Mosquito ferns hold significant economic and ecological value through their symbiotic relationship with the nitrogen-fixing cyanobacterium *Anabaena azollae* (Lumpkin 1993). This mutualism enables *Azolla* to naturally enrich its environment with nitrogen-containing nutrients, making it an effective organic fertilizer. In Southeast Asia, *Azolla pinnata* R. Br., commonly known as Feathered Mosquito Fern, is widely cultivated in rice paddies, where it fertilizes the soil as it decomposes. However, this species has become invasive in Florida and has spread to other southeastern states (Madeira et al. 2013). In addition to fertilizing crops, mosquito ferns provide a nutrient-rich supplement for livestock feed, enhancing animal health (Dunbar 1989). Additionally, scientists have utilized *Azolla caroliniana* in phosphate mine pit lakes due to its ability to hyperaccumulate radium-226, thereby reducing radioactive contamination (Wilson & Hanlon 2012).

Figure 170. A. *Azolla caroliniana* Murray Co., Georgia, 3 Jul 2011. **B.** *Azolla pinnata*, Martin Co., Florida, 7 Mar 202. Photos: Alan Cressler.

Ahad et al. (2012) argue that previous classifications of *Azolla caroliniana* were based on misapplied names, necessitating a revision of its taxonomic designation, with *A. cristata* being the oldest valid name. Sessa (2024) states that *A. cristata* technically has precedence. However, Weakley et al. (2025) note that the taxonomy and nomenclature of *Azolla* remain highly contentious, with ongoing debates about the recognition of distinct taxa and significant uncertainty regarding the correct application of names based on taxonomic priority. While many authors initially classified *Azolla* in its own monotypic family, Azollaceae, recent studies have placed it alongside *Salvinia* in the Salviniaceae (Metzgar et al. 2007).

2. SALVINIA Séguier 1754 {sal-VIN-ee-uh}

[In honor of Antonio Maria Salvini, 1633–1729, an Italian naturalist and Greek scholar]

1. Floating leaves 1.5–3 cm long, often folded along the midrib; hairs on upper leaf surface with branches fused together at their tips, forming an egg-beater-like structure .....***Salvinia molesta***
1. Floating leaves 0.5–1.5 cm long, flat or concave; hairs of upper leaf surface with free, spreading branches not apically fused .....***Salvinia minima***

1. Salvinia minima Baker {smallest} — WATER SPANGLES; COMMON SALVINIA; FLOATING FERN (Fig. 171). [*Salvinia auriculata* Aubl., misapplied; *Salvinia rotundifolia* Willd., misapplied]

Plants free-floating aquatics; evergreen. Stagnant waters of ponds, canals, and slow streams, but may be stranded on wet muck when the water level drops. Sporocarps produced nearly year-round; rare in the Highland Rim, Cumberland Plateau, and Piedmont; uncommon in the Coastal Plain (Fig. 172). Native to tropical America, from Mexico to South America (Nauman 1993c); invasive in the southern USA, especially in the southeast (Kartesz 2025).

Figure 171. *Salvinia minima*, Colbert Co., Alabama, 20 Sep 2024. Photo: Jeff Garner.

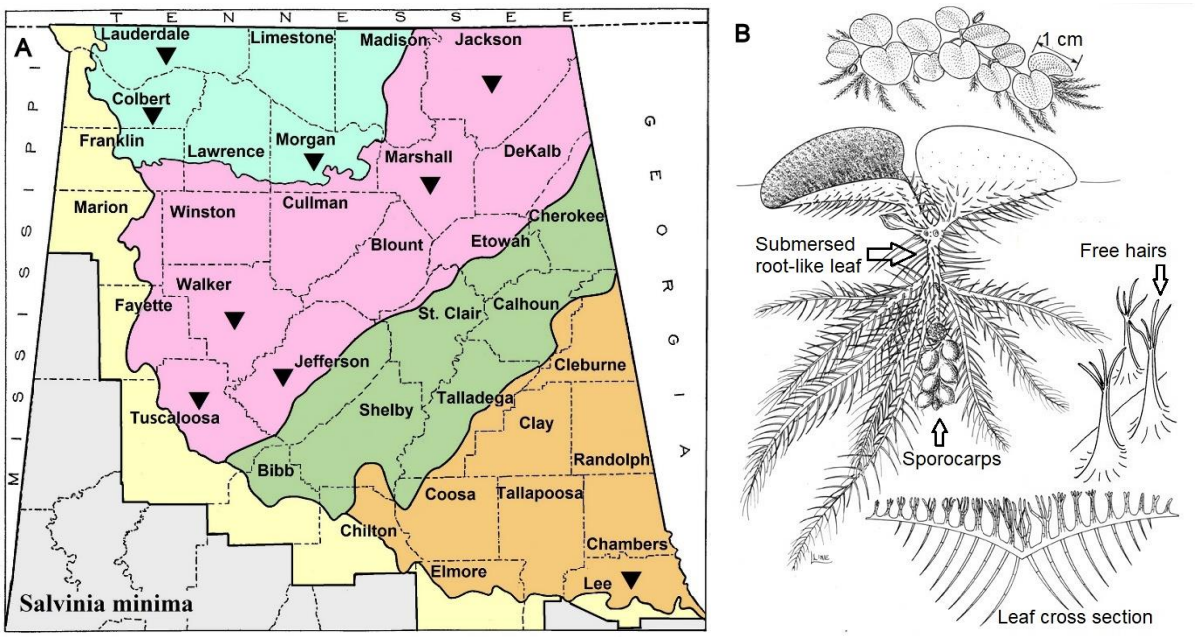


Figure 172. *Salvinia minima.* **A.** Distribution map. **B.** Illustration: Center for Aquatic and Invasive Plants. <www.plants.ifas.ufl.edu/>

Since the late 1880s, people have cultivated this aquatic fern in North American greenhouses and gardens. Initially introduced through the aquarium trade, *Salvinia minima* has become invasive in some southeastern states, where it is now considered a pest. Botanists first recorded its presence in Florida's St. Johns River in 1928, likely due to the flooding of cultivated pools or intentional release. It now thrives in many natural and artificial freshwater habitats, including sloughs, cypress swamps, lakes, and canals throughout the southeastern United States (Jacono et al. 2001; Tipping et al. 2012).

Figure 173. *Salvinia minima*, Hillsborough Co., Florida, 16 Mar 2016. Photo: Alan Cressler.

Water spangles rapidly produce daughter plants throughout the growing season by continuously branching and fragmenting their rhizomes. These fragments cling to boats, trailers, and a variety of animals—including alligators, turtles, birds, and other wildlife— facilitating the fern's spread between water bodies. The dense, hairy covering on the floating leaves helps prevent rapid desiccation when the fern is out of water. Although it may seem to vanish during cold weather or drought, its lateral buds remain dormant, deeply embedded within the rhizome and sheltered by surrounding vegetation. When conditions improve, these buds regenerate new growth. The branched hairs on the upper leaf surface also create a water-repellent shield (Fig. 173), distinguishing water spangles from similar-looking duckweeds (*Lemna*, *Spirodela*), which lack such hairs.

2. Salvinia molesta D.S. Mitch. {annoying or troublesome} — KARIBA WEED; GIANT SALVINIA (Fig. 174). [*Salvinia* ×*molesta* D.S. Mitch.]

Figure 174. *Salvinia molesta*, Jefferson Co., Alabama, 10 Sep 2023. Photo: Martha D. Anderton.

Plants free-floating aquatics; evergreen. Still waters of ditches, canals, ponds, rivers, and lakes. Primarily reproduces vegetatively, does not produce functional sporocarps; rare throughout Alabama (Fig. 175). Native to Brazil, this species has spread from its native range to tropical and subtropical regions worldwide (McFarland et al. 2004).

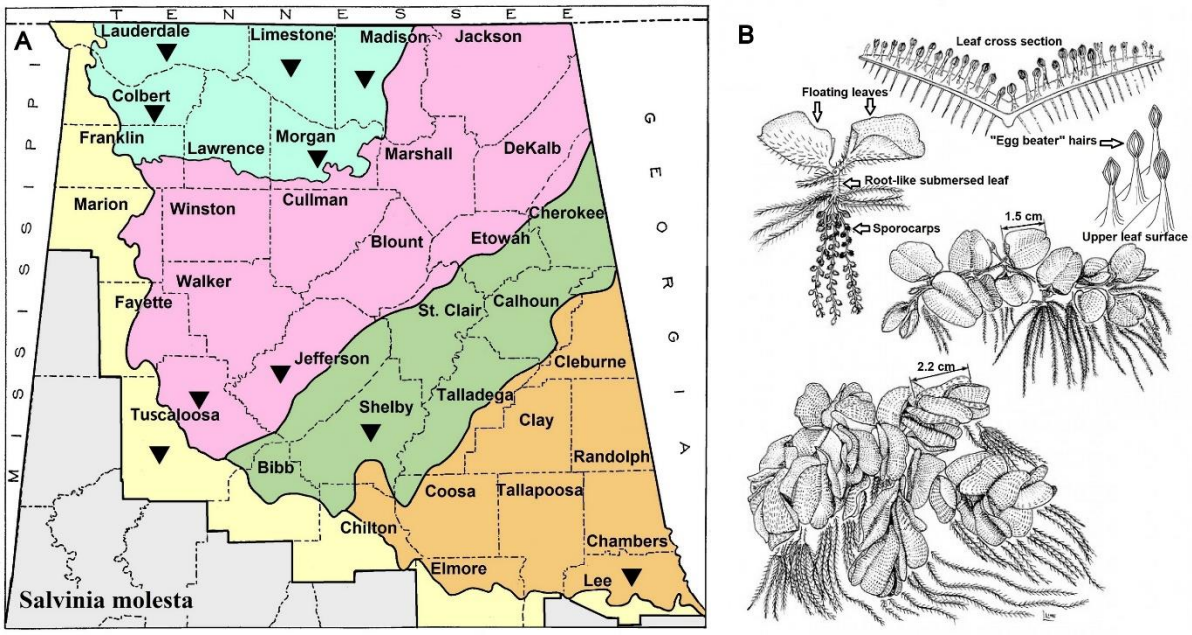


Figure 175. *Salvinia molesta*. **A.** Distribution map. **B.** Illustration: Center for Aquatic and Invasive Plants. <www.plants.ifas.ufl.edu/>

Figure 176. *Salvinia molesta*, Mobile Bay, Baldwin Co., Alabama, 31 Jul 2023. Photo: Howard Horne.

South African botanist David S. Mitchell first observed *Salvinia molesta* in 1959 at Lake Kariba, Zimbabwe, well outside its native range. Mitchell (1973) formally described the species based on material collected from this site, giving rise to its common name, "Kariba Weed." Although Nauman (1993c) did not record *S. molesta* as present in North America, he noted its cultivation in Florida and warned of its potential escape into the wild. Originally from Brazil, *S. molesta* has spread extensively across tropical and subtropical regions worldwide since the mid-20th century, becoming a highly invasive and destructive species (Coetzee & Hill, 2020).

The rapid spread of *Salvinia molesta* is remarkable. Mitchell & Tur (1975) found that its biomass can double in just five days, demonstrating an exponential growth rate in new environments (Fig. 176). Due to its aggressive expansion and severe ecological impacts, scientists rank *S. molesta* among the world's 100 worst invasive species (Luque et al. 2014). Traditional control methods, such as herbicides and mechanical removal, are labor-intensive and costly. However, biological control offers a more effective and sustainable solution. In 1980, Australia introduced the host-specific weevil *Cyrtobagous salviniae* as a biological control agent, a strategy that multiple countries have since adopted to combat infestations of this noxious aquatic fern (Coetzee & Hill 2020).

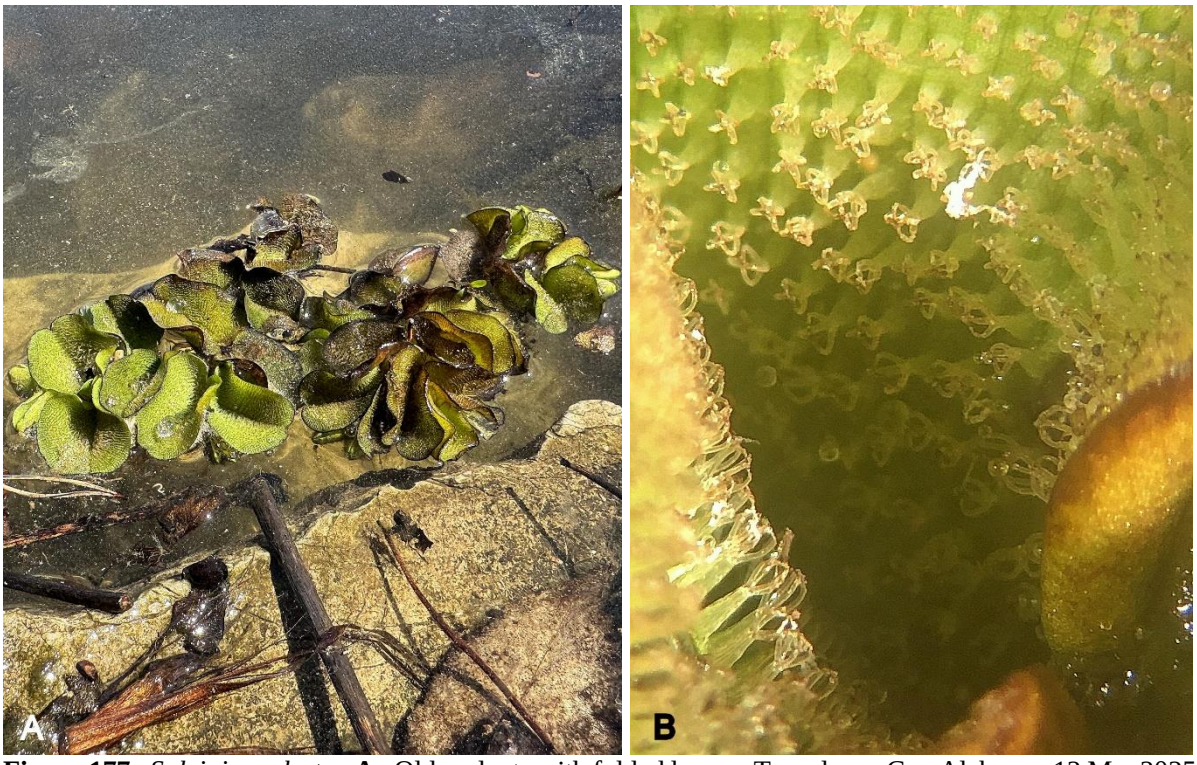


Figure 177. *Salvinia molesta*. **A.** Older plants with folded leaves, Tuscaloosa Co., Alabama, 12 Mar 2025. Photo: Dan Spaulding. **B.** "Egg-beater" hairs, Baldwin Co., Alabama, 11 Sep 2019. Photo: Howard Horne.

Salvinia molesta closely resembles *S. minima* but differs in key morphological traits. *Salvinia molesta* has larger floating leaves (1.5–3 cm long) that fold along the midrib as they mature (Fig. 177a), whereas the leaves of *S. minima* are smaller (0.5–1.5 cm long) and remain flat or concave. The most distinctive difference lies in their leaf hairs: in *S. molesta*, the hair branches fuse at their tips, forming an egg-beater-like structure (Fig. 177b), while in *S. minima*, the branches remain free. Holt et al. (2023) suggest that *S. molesta* is a polyploid hybrid of uncertain and debated parentage, though it bears morphological similarities to other South American species. They also emphasize that it primarily, and possibly exclusively, reproduces vegetatively, which indicates that the global invasion may consist of just one or a few clonal genotypes.

12. **MARSILEACEAE** (Water-Clover Family) – in Salviniales

1. Plants resembling 4-leaf clovers; leaf blades divided into 4 wedge-shaped leaflets borne at the summit of the petiole; sporocarps ovoid ..... ***Marsilea***
1. Plants grass-like; leaf blades absent, petioles narrowly winged; sporocarps spherical..... ***Pilularia***

1. **MARSILEA** Linnaeus 1753 {mar-sil-EE-uh}

[For Count Luigi Ferdinando Marsigli, 1656–1730, an Italian botanist at Bologna]

1. Marsilea mutica Mett. {without a point; sporocarps toothless} — AUSTRALIAN WATER-CLOVER; BANDED NARDOO; BANDED WATER-CLOVER (Fig. 178).

Figure 178. *Marsilea mutica*, Jefferson Co., Alabama, 8 Nov 2023. Photo: Wayne Barger.

Plants aquatic or amphibious; semi-evergreen. Shorelines of ponds and lakes. Sporocarps produced nearly year-round; very rare throughout Alabama (Fig. 179). Native to Australia and New Caledonia (Jacono & Johnson 2006); introduced and widely scattered in the southeastern and northwestern USA (Kartesz 2025).

Marsilea mutica resembles a four-leaf clover, with four palmately arranged leaflets positioned at the summit of each petiole. The leaflets display a striking two-tone pattern, with a light green base transitioning to a darker green upper region, separated by a reddish-brown band. This distinctive coloration, combined with the plant's Australian origin, inspired its common names. In deeper water, the leaves of this aquatic fern float on the surface (Fig. 178), while in shallower areas, they emerge above the water (Fig. 180a). Along muddy shorelines, terrestrial individuals are fully exposed, with their elongated petioles sprawling across the substrate (Fig. 180b).

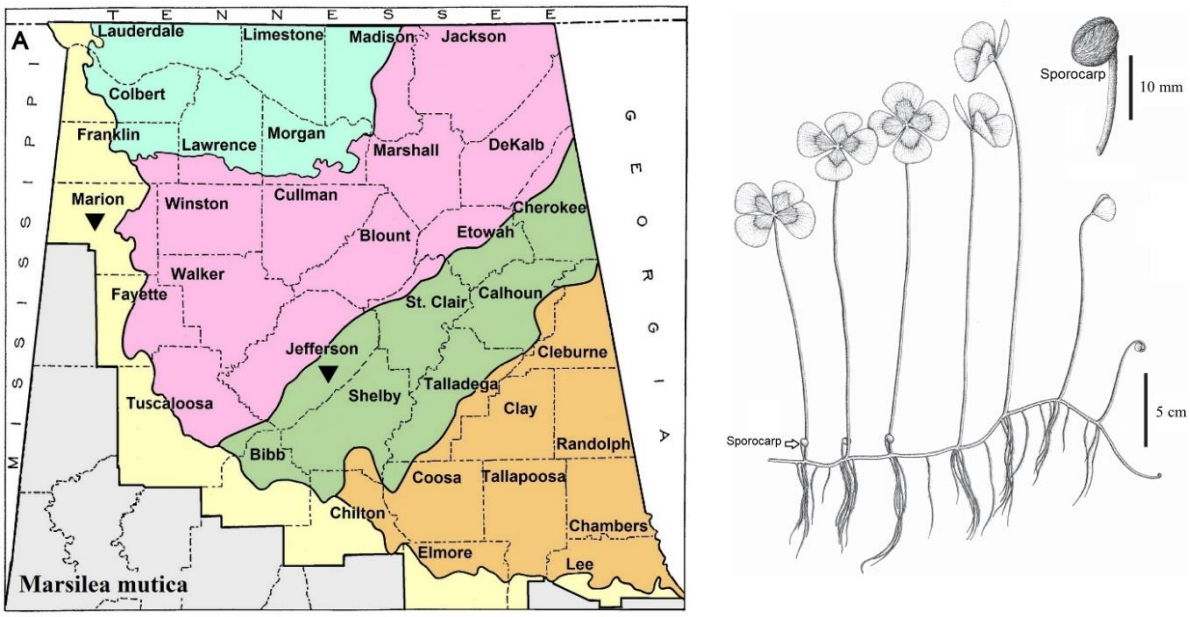


Figure 179. *Marsilea mutica.* **A.** Distribution map. **B.** Illustration from Petchsri et al. 2021.

Knepper et al. (2002) reported *Marsilea mutica* in North America, based on a collection made in Virginia in 1997. However, Jacono and Johnson (2006) documented an earlier specimen from South Carolina, collected in 1995. After these first records, botanists documented its spread to other states. In 2001, Chris J. Green discovered it in Marion County, Alabama. The recent introduction to the continent is more likely attributed to escape from horticultural cultivation rather than dispersal by waterfowl. Nurseries and garden centers commonly sell the Australian Water-Clover for use in aquatic gardens and aquariums. As people dispose of excess plant material by dumping it into streams, ponds, and lakes, *M. mutica* will likely become more widespread in Alabama. In Alabama, *M. mutica* will likely become more widespread, as it colonizes efficiently, grows prolifically, and survives drought and cold by producing dormant vegetative propagules instead of sporocarps (Jacono & Johnson 2006).

Figure 180. *Marsilea mutica* along margins of Lake Gulshan in Birmingham, Jefferson Co., Alabama, 23 Aug 2023. **A.** Plants in shallow water. **B.** Plants in muddy soil along the shore. Photos: Dan Spaulding.

Figure 181. A. *Marsilea minuta*, DeKalb Co., Georgia, 1 Nov 2020. Photo: Alan Cressler. **B.** *Marsilea macropoda*, Mobile Co., Alabama, 30 Jun 2011. Photo: Wayne Barger.

Two other species of *Marsilea* occur in Alabama's Coastal Plain: Dwarf Water-Clover (*M. minuta* L.; Fig. 181a) and Bigfoot Water-Clover (*M. macropoda* Engelm. ex A. Braun; Fig. 181b). The Australian Water-Clover (*M. mutica*) differs from both by having two-toned leaflets (Fig. 182a) and by lacking teeth on the back of its sporocarp—a hard, pea-shaped structure that bears sporangia (Fig. 182b). Like *M. minuta*, the Australian Water-Clover has nearly hairless leaves, unbranched sporocarp stalks, and rhizomes with roots both at the nodes and internodes (Fig. 182c). However, its sporocarps are solitary at the base of the petioles, whereas those of *M. minuta* cluster in groups of two to five (Petchsri et al. 2021). *Marsilea macropoda* differs from the other species by its hairy leaves, branched sporocarp stalks, and roots confined to the nodes. The leaflets of *M. minuta* resemble those of *M. macropoda* but are hairless and often display wavy, scalloped teeth or lobes along the terminal margins.

Figure 182. *Marsilea mutica.* **A.** Two-toned leaf, Jefferson Co., Alabama, 23 Aug 2023. Photo: Dan Spaulding. **B.** Toothless sporocarp, Marion Co., Alabama, 19 Nov 2002. Photo: Collette C. Jacono. **C.** Rhizome with roots at nodes and internodes, Jefferson Co., Alabama, 23 Aug 2023. Photo: Dan Spaulding.

Marsilea macropoda, native to Texas and Mexico, became part of Alabama's flora in 1972 when Robert Kral discovered it in downtown Mobile. This site was the state's only known occurrence until 1988, when Florida botanist James Burkhalter located another population near an old cemetery north of the city (SERNEC 2025). Burkhalter also documented *Marsilea minuta* in North America for the first time in 1992, collecting it in Escambia County, Florida (Burkhalter 1995). Native to tropical and subtropical regions of Southeast Asia and Africa, *M. minuta* ranks among the most troublesome weeds in rice paddies (Jacono & Johnson 2006). Its recent spread into Tennessee's Cumberland Plateau and Georgia's Piedmont suggests it may soon be found in northern Alabama (Kartesz 2025).

2. PILULARIA Linnaeus 1753 {pil-yoo-LAIR-ee-uh}
[Latin *pilula*, little ball; referring to the small, globose sporocarps]

1. Pilularia americana A. Braun {American} — AMERICAN PILLWORT (Fig. 183).

Figure 183. *Pilularia americana*, Walton Co., Georgia, 7 Apr 2012. Photo: Wayne Barger.

Plants aquatic or amphibious; evergreen. Rooted in the mud of temporary pools and shores along ponds, lakes, rivers, and stream margins. Sporocarps produced April–October; very rare in the Tennessee Valley District of the Highland Rim and Warrior Basin District of the Cumberland Plateau (Fig. 184). It occurs in disjunct regions with scattered populations throughout the USA (Dennis & Webb 1981). This species ranges along the Pacific Coast from Washington to Baja California, Mexico; across the Interior Plains and Highlands from Nebraska and Missouri south to Arkansas and Texas; and in the Southeast from Tennessee and northern Alabama east to Georgia and South Carolina (Johnson 1993b; Kartesz 2025). The Alabama Natural Heritage Program (2023) ranks it as critically imperiled (S1) within the state.

American Pillwort often goes unnoticed due to its grass-like appearance and small stature. This mat-forming fern spreads by creeping rhizomes, frequently forming dense underwater colonies (Fig. 185), but can also grow in bare mud (Johnson 1993b). Its thread-like leaves lack expanded blades and resemble those of quillworts (*Isoetes*) or rushes (*Juncus*). One way to distinguish *Pilularia americana* from these look-alikes is by its distinctive fiddleheads—coiled young fronds that unfurl as they mature (Fig. 184b). The common name "pillwort" refers to its underground, pill-shaped sporocarps (Fig. 186), which aid the plant in surviving drought (Dean 1969).

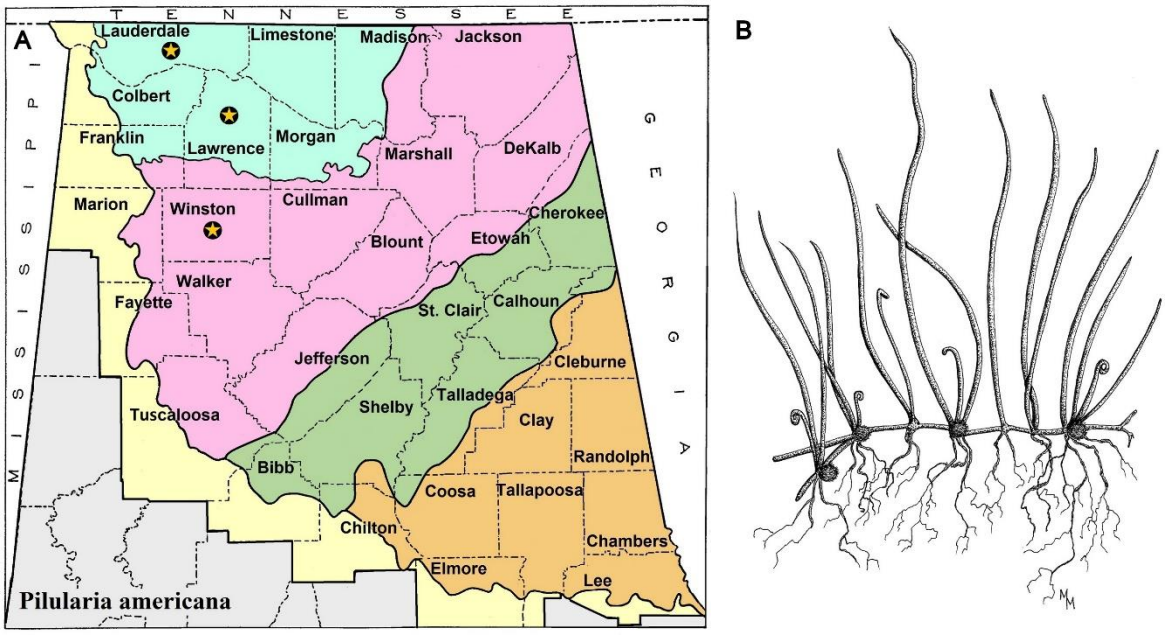


Figure 184. *Pilularia americana*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

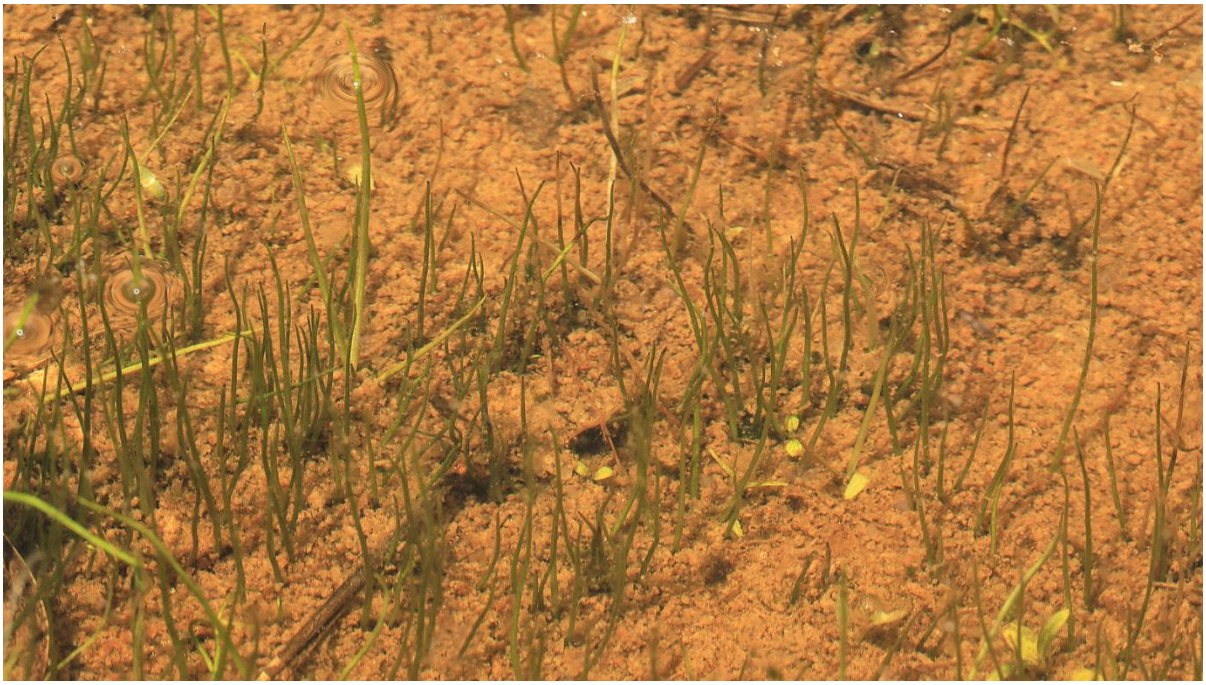


Figure 185. *Pilularia americana* submersed, Walton Co., Georgia, 30 Apr 2017. Photo: Alan Cressler.

Pilularia americana, the only pillwort native to the New World, was first discovered by Thomas Nuttall during his expedition along the Arkansas River between 1818 and 1820. In the late 19th century, explorers collected additional specimens in California and Oregon, and by the 20th century, botanists had documented scattered populations across the southeastern United States (Dennis & Webb 1981). In 1996, David Webb and Paul Davison recorded the species in Lauderdale County, Alabama, along the Tennessee River. The American pillwort is so inconspicuous that it often escapes notice and is seldom collected. The best time to find it is during autumn reservoir drawdowns, when water levels recede and reveal its preferred muddy habitat (Diggs et al. 2006).

Figure 186. *Pilularia americana* sporocarps, Oglethorpe Co., Georgia, 12 May 2023. Photo: Alan Cressler.

13. **PTERIDACEAE** (Maidenhair Fern Family) – in Polypodiales

1. Gametophyte generation dominant, liverwort-like; leaves of sporophyte (if present) undivided, linear, and less than 20 mm wide ..... ***Vittaria***
1. Sporophyte generation dominant, not liverwort-like; leaves of sporophyte dissected, not linear, and more than 20 mm wide.

    2. Blade segments mostly diamond- or fan-shaped, lacking midveins; sori oblong, distinct, and separate on recurved marginal lobes along pinnule margins; leaves bright green, glabrous, herbaceous, delicate, and flexible ..... ***Adiantum***
    2. Blade segments round, oblong, or linear, with well-developed midveins; sori confluent, appearing as continuous bands along recurved or flat margins, sori either covered or completely exposed; leaves mostly dark green, often pubescent, coriaceous, tough, and stiff.

        3. Leaf blade covered with stellate (star-shaped) and ciliate-fringed (hair-edged) scales; margins of leaf segments flat, not recurved over sori; leaves 1-pinnate to pinnate-pinnatifid, pinnae entire or lobed; petiole with 2 vascular bundles ..... ***Astrolepis***
        3. Leaf blade pubescent, scaly, or glabrous (smooth), but lacking stellate or ciliate-fringed scales; margins of leaf segments recurved over sori, forming false indusia; leaves 1–4-pinnate; petiole with 1 vascular bundle.

            4. Leaves 2–4-pinnate; pinnules distinctly lobed or divided; ultimate leaf segments less than 5 mm long; leaf blade densely pubescent to glabrous (smooth) ..... ***Myriopteris***
            4. Leaves 1–2-pinnate or palmately 3-divided; pinnules (or pinnae) entire or toothed; ultimate leaf segments more than 5 mm long; leaf blade sparsely pubescent to glabrous.

                5. Petiole dark brown to black, not grooved; terminal leaflets usually less than 5 cm long; fronds deciduous, dying back in winter ..... ***Pellaea***
                5. Petiole green to yellowish, grooved; terminal leaflets usually more than 5 cm long; fronds evergreen to semi-evergreen, often persisting through winter ..... ***Pteris***

1. ADIANTUM Linnaeus 1753 {ad-ee-AN-tum}
[Greek *adiantos*, unwetted; alluding to the water-repellent leaves]

1. Fronds broader than long (fan-shaped); petiole forked near the apex, producing twin rachises (branches) curving away from each other; leaflets borne on one side of each rachis; plants typically growing in soil ..... ***Adiantum pedatum***
1. Fronds longer than broad; petiole continuing as a single central rachis; leaflets borne on both sides of the rachis; plants often growing on rock..... ***Adiantum capillus-veneris***

1. Adiantum capillus-veneris L. {hair of Venus} — SOUTHERN MAIDENHAIR FERN; VENUS-HAIR FERN; BLACK MAIDENHAIR FERN; VENUS' MAIDENHAIR FERN (Fig. 187).

Figure 187. *Adiantum capillus-veneris*, Bibb Co., Alabama, 6 Jul 2024. Photos: Dan Spaulding.

Plants epipetric or terrestrial in thin soil; deciduous. Damp calcareous rock ledges, cliffs, stream banks, ravines, and old mortar of buildings. Sporulates June–October; rare in the Highland Rim, Cumberland Plateau, and Ridge & Valley; very rare in the Piedmont; uncommon in the Coastal Plain (Fig. 188). This species occurs mainly in the southern United States from Virginia to California, with scattered populations extending north to Ohio and south into Mexico, the West Indies, Central and South America, and tropical to warm-temperate regions of Eurasia and Africa (Paris 1993).

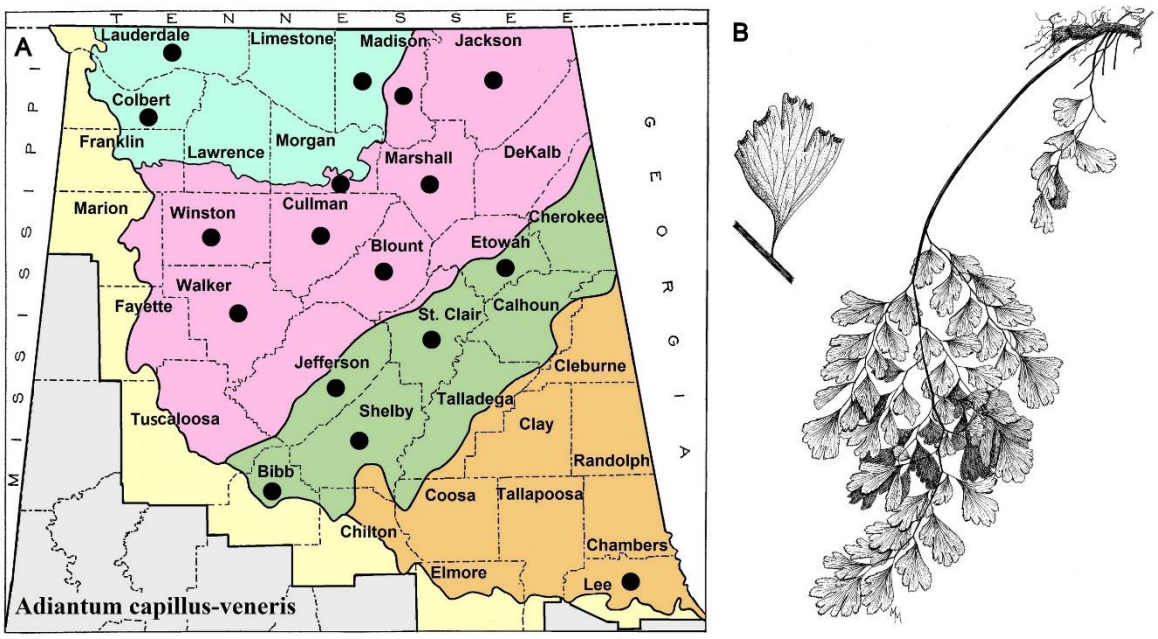


Figure 188. *Adiantum capillus-veneris.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 189. *Adiantum capillus-veneris*, in cracks of old masonry walls at Sloss Furnaces National Historic Landmark in Birmingham, Jefferson Co., Alabama, 1 Aug 2024. Photo: Dan Spaulding.

The Southern Maidenhair Fern flourishes on steep, wet limestone banks along rivers and creeks. It also takes root in the crevices of old wells and damp, shaded stone walls (Fig. 189). Delicate fronds arch gracefully from rock faces, their tips hanging gently downward. Gardeners often cultivate this fern in shaded landscapes or as a houseplant. Although more common in the southern United States, this species ranges north to southern Canada. The name "maidenhair" refers to its slender black leaflet stalks, which resemble the fine strands of Venus's hair, the Roman goddess of love (Abbe 1981).

Historically, people valued *Adiantum capillus-veneris* for its medicinal uses, though it is seldom employed today. Early European herbalists burned the fern to produce lye, combining it with fat and oil to create medicinal shampoos and skin treatments. They also used the plant to treat asthma, spleen disorders, snakebites, and as a general tonic. In France, traditional healers prepared "syrup of capillaire" by steeping the fern's leaves in boiling orange blossom water—the fragrant distillate of bitter orange flowers—then sweetening it with honey (Dunbar 1989).

2. Adiantum pedatum L. {palmately forking; the fronds} — NORTHERN MAIDENHAIR FERN; AMERICAN MAIDENHAIR FERN (Fig. 190).

Figure 190. *Adiantum pedatum*. **A.** Tallapoosa Co., Alabama, 15 Jun 2007. Photo: Wayne Barger. **B.** Jackson Co., Alabama, 30 Sep 2023. Photo: Helen A. Czech.

Plants terrestrial; deciduous. Moist deciduous forests, slopes, and shaded cliffs. Sporulates June–October; frequent throughout northern Alabama; uncommon in the Coastal Plain (Fig. 191). This species occurs primarily in eastern North America, from Nova Scotia to Michigan, south to Louisiana, and Georgia (Paris 1993).

Botanists and horticulturists treasure *Adiantum pedatum* for its distinctive beauty and unmistakable leaf structure, making it one of the most recognizable species of fern. Its graceful fronds sweep outward in a broad, horizontal arc, evoking the delicate appearance of a green bridal veil (Dunbar 1989). The glossy black stems contrast sharply with the elegantly forked blades, each adorned with fan-shaped leaflets. Gardeners value this fern's striking form and often incorporate it into shaded gardens and naturalistic landscapes. It thrives readily in cultivation, propagating with ease when divisions of the rhizome are separated and replanted (Mikel 1994). The plant's slender, freely branching rhizome frequently forms small colonies, further enhancing its natural charm (Fig. 192).

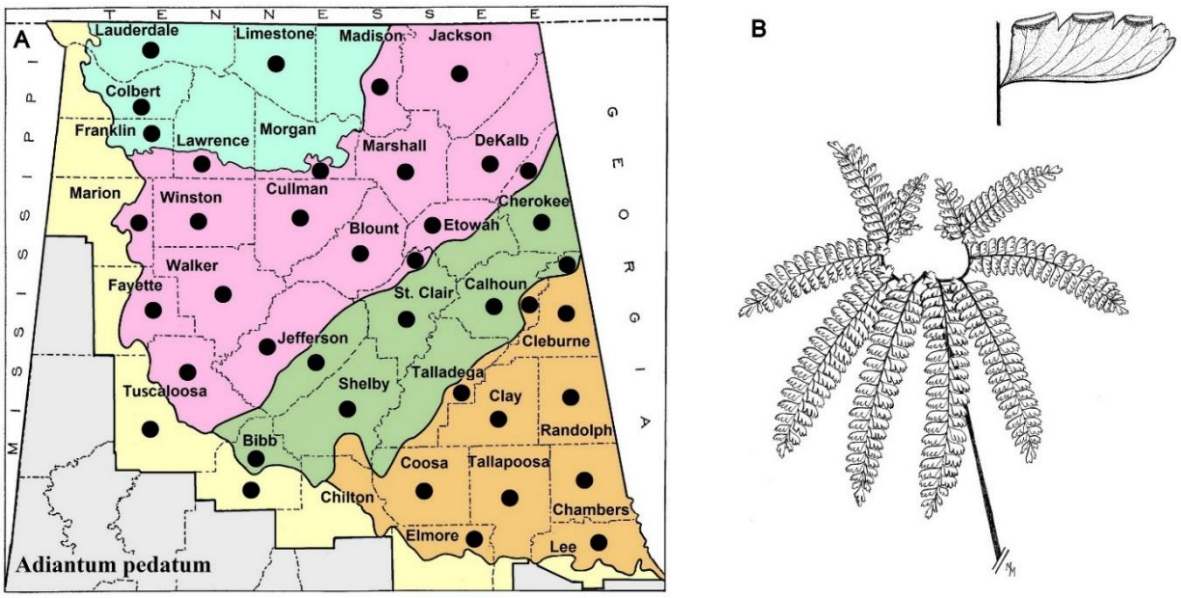


Figure 191. *Adiantum pedatum.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 192. *Adiantum pedatum*, Talladega Co., Alabama, 4 Jul 2024. Photo: Dan Spaulding.

The Cherokee used *Adiantum pedatum* in a variety of medicinal and practical ways. They brewed tea from the leaves to ease rheumatism and smoked powdered leaves to help relieve heart ailments and asthma. To treat sore muscles afflicted by rheumatism, they prepared a decoction by mixing rhizomes with water and applying it externally. Beyond its medicinal uses, the plant's glossy, blackish-brown stems held cultural significance in basketry. After softening the dried stalks, Cherokee artisans wove them into intricate designs, using the dark material to create striking black patterns that contrasted sharply with lighter plant fibers (Moerman 1998).

2. ASTROLEPIS D.M. Benham & Windham 1992 {as-stroh-LEP-iss}

[Greek *astro*, star, and *lepis*, scale, referring to the star-like scales on leaf blades]

1. Astrolepis integerrima (Hook.) D.M. Benham & Windham {absolutely entire; uncut leaflets} — SOUTHWESTERN CLOAK FERN; STAR-SCALED CLOAK FERN; HYBRID CLOAK FERN; FALSE CLOAK FERN; WHOLE-LEAF CLOAK FERN (Fig. 193). [*Astrolepis sinuata* (Lag. ex Sw.) Benham & Windham var. *integerrima* Hook.; *Cheilanthes integerrima* (Hook.) Mickel; *Hemionitis integerrima* (Hook.) Christenh.; *Notholaena integerrima* (Hook.) Hevly; *Notholaena sinuata* var. *integerrima* Hook.]

Figure 193. *Astrolepis integerrima*, Bibb Co., Alabama, 10 May 2011. Photo: Wayne Barger.

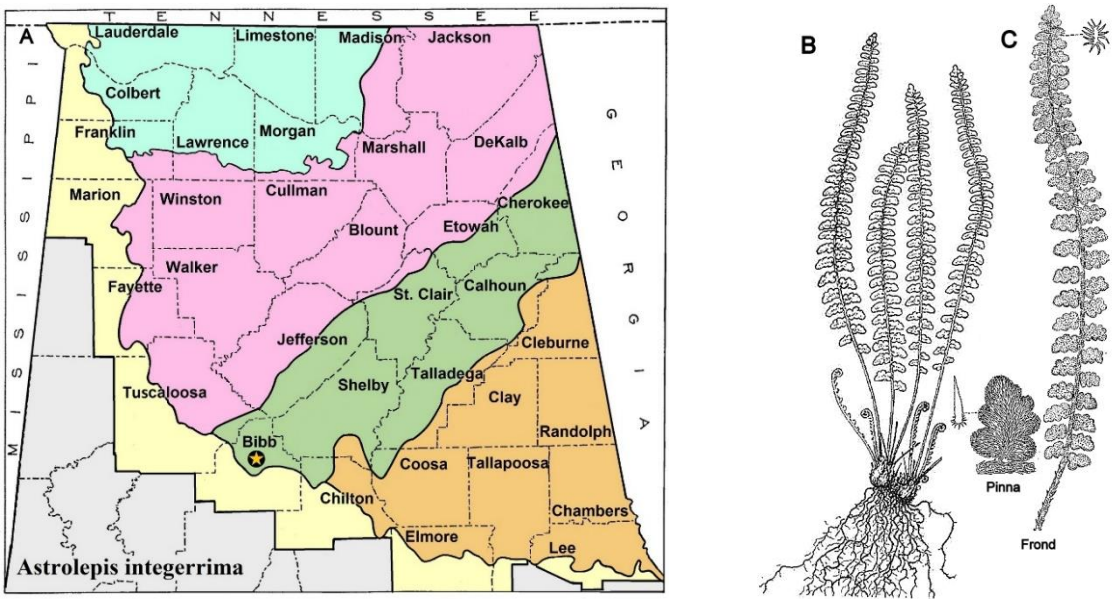


Figure 194. *Astrolepis integerrima*. **A.** Distribution map. **B.** Illustration of the whole plant by Lucretia Breazeale Hamilton, 1959. **C.** Illustration of frond and pinna by Jane W. Roller, 1967.

Plants epipetric; evergreen or semi-evergreen. Calcareous rock outcrops (Ketona dolomite in Alabama). Sporulates June–October; very rare in the Cahaba Ridges District of the Ridge & Valley (Fig. 194). This species occurs primarily in the southwestern United States and extends southward into Mexico (Paris 1993). It is disjunct in Bibb County, Alabama (Allison & Stevens 2001).

Astrolepis integerrima, one of several xerophytic rock ferns native to the arid regions of the southwestern United States and Mexico, is uniquely adapted to withstand harsh desert climates (Fig. 195). The rocky slopes and exposed cliff faces it inhabits offer little soil and receive intense solar exposure, demanding exceptional drought tolerance. The species meets this challenge with a suite of morphological and physiological traits that minimize water loss. Small, compact fronds reduce the surface area exposed to intense sunlight. A waxy cuticle and dense layer of hairs—features that inspired its common name—form a strong barrier against evapotranspiration. Stomata, responsible for gas exchange, are fewer than in most ferns and are recessed into specialized cavities called stomatal crypts, which trap moisture and protect them from dry air. During prolonged drought, the fronds curl tightly, an adaptive response that conserves water until favorable conditions return (Hevly 1963).

Figure 195. *Astrolepis integerrima*, Eddy Co., New Mexico, 10 May 2011. Photo: Alan Cressler.

The Southwestern Cloak Fern went undocumented east of the Mississippi River until June 1, 1992, when botanist Jim Allison discovered it growing on the Ketona dolomite glades of Bibb County, Alabama (Fig. 196). There, it thrived in thin soil pockets atop exposed rock ledges—an environment reminiscent of its arid southwestern habitat (Allison & Stevens 2001). This species is one of several southwestern ferns that have established disjunct, isolated populations in the eastern United States. The minuscule size and dust-like nature of fern spores make them ideally suited for long-distance wind dispersal, a likely explanation for the fern's unexpected presence in Alabama.

Figure 196. *Astrolepis integerrima*, dolomite glade, Bibb Co., Alabama, 11 Apr 2020. Photo: Alan Cressler.

Astrolepis integerrima is an apogamous allotriploid that arose through hybridization between two closely related species (Benham & Windham 1993). It carries three sets of chromosomes inherited from both parents, a combination that prevents sexual reproduction. Instead, it reproduces by apogamy, producing a new sporophyte directly from the gametophyte without fertilization. This strategy allows the species to bypass the sexual cycle while maintaining stable, self-sustaining populations.

3. **MYRIOPTERIS** Fée 1852 {mih-ree-OP-ter-iss}

[Greek *myrios*, countless, and *pteris*, fern; alluding to the numerous leaf segments of this fern]

Ferns in the genus *Myriopteris*, commonly known as lip ferns, owe their name to the distinctive morphology of their leaf margins, which often curl or roll under, resembling lips. These revolute margins create false indusia that shields the sori on the underside of the fronds, protecting the developing spores. The "lips" aid in spore maturation and dispersal by covering the sori, a crucial adaptation for *Myriopteris*, which often thrives in harsh, arid environments. These habitats, typically characterized by rocky outcrops and minimal soil, necessitate specialized strategies for moisture retention and successful reproduction.

1. Leaves essentially glabrous beneath, occasionally bearing a few obscure hairs; pinnules entire or lobed only at the base..... ***Myriopteris alabamensis***
1. Leaves distinctly pubescent beneath, villous-hirsute or tomentose; pinnules pinnatifid or pinnate.

    2. Rachis densely tomentose with woolly hairs interspersed with broader linear scales, surface nearly obscured; rachis hairs unsegmented, lacking dark bands; pinnules mostly cut to the midrib.....***Myriopteris tomentosa***
    2. Rachis villous-hirsute with shaggy and bristle-like hairs, lacking scales, surface visible through pubescence; rachis hairs segmented with several dark bands; pinnules deeply lobed, but not cut to the midrib.....***Myriopteris lanosa***

1. Myriopteris alabamensis (Buckley) Grusz & Windham {of Alabama} — ALABAMA LIP FERN, SMOOTH LIP FERN (Fig. 197). [*Cheilanthes alabamensis* (Buckley) Kunze; *Hemionitis alabamensis* (Buckley) Christenh.]

Figure 197. *Myriopteris alabamensis*, Marshall Co., Alabama, 11 May 2021. Photo: Alan Cressler.

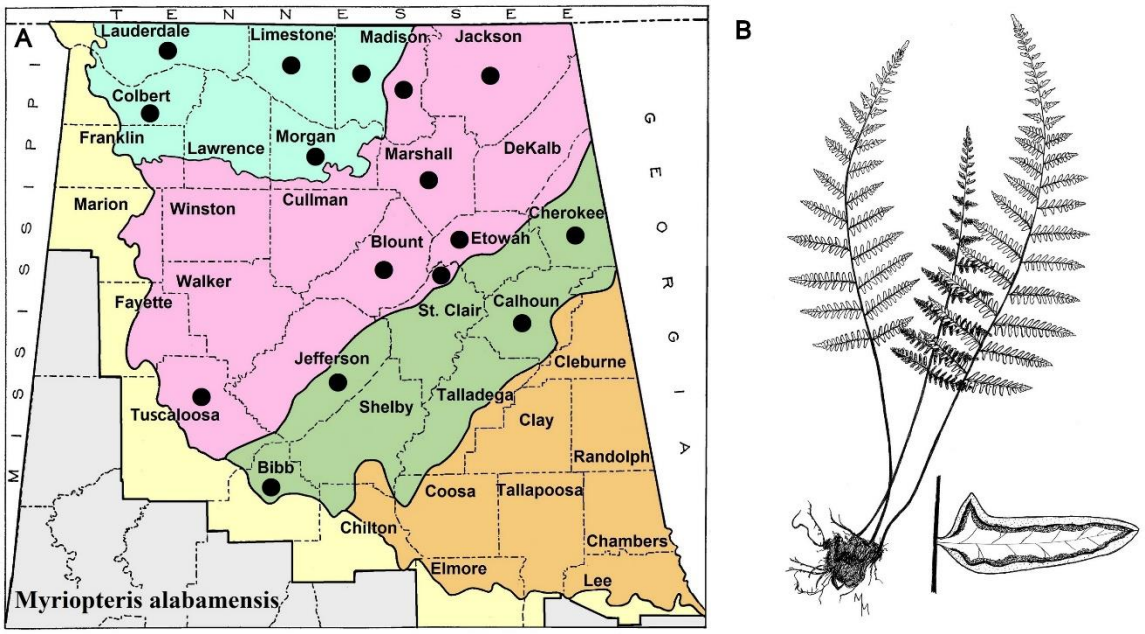


Figure 198. *Myriopteris alabamensis.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Plants epipetric; evergreen. Shaded crevices of calcareous cliffs and cracks in dolomitic rocks and boulders. Sporulates March–November; rare in the Highland Rim, Cumberland Plateau, and Ridge & Valley; very rare in the Lime Hills District of the Coastal Plain (Fig. 198). This widespread species ranges across the southeastern USA from Alabama north to western Virginia, extending westward to southeastern Kansas, Texas, and southern Arizona, and continuing south into Mexico (Windham & Rabe 1993). The Alabama Heritage Program (1994) previously classified this fern as vulnerable (S3) but now recognizes it as more frequent in Alabama.

In 1843, Samuel Buckley discovered *Myriopteris alabamensis* growing on limestone rocks along the Tennessee River at Muscle Shoals in Colbert County, Alabama (Small 1938). Although dam construction later submerged the original site beneath Wilson Lake, the fern persists in nearby habitats. Among Alabama's *Myriopteris* species, the Alabama Lip Fern is distinguished by its nearly hairless leaves (Fig. 199a), in contrast to the densely hairy foliage of *M. lanosa* and *M. tomentosa*. Despite this difference, all three species favor rocky, well-drained sites, often occurring on outcrops where they endure dry conditions and limited soil (Fig. 199b).

Figure 199. *Myriopteris alabamensis*, Bibb Co., Alabama, 15 May 2009. Photos: Alan Cressler.

Dean Whittier (1965) demonstrated that *Myriopteris alabamensis* reproduces asexually through apogamy, where the sporophyte develops directly from the gametophyte without fertilization. The species is predominantly apogamous and triploid across most of its range; however, in northern Mexico, it occurs as a sexual diploid. Windham and Rabe (1993) proposed that the triploid originated from the Mexican diploid through autopolyploidy, when an unreduced gamete (containing the full diploid chromosome set) fused with a normal haploid gamete, producing offspring with three chromosome sets. These findings highlight the complex interplay of reproductive modes and evolutionary processes that have enabled *M. alabamensis* to persist across a wide range of habitats.

2. Myriopteris lanosa (Michx.) Grusz & Windham {woolly} — (Fig. 200). HAIRY LIP FERN [*Cheilanthes lanosa* (Michx.) D.C. Eaton; *Hemionitis lanosa* (Michx.) Christenh.]

Figure 200. *Myriopteris lanosa*, Lee Co., Alabama, 16 Apr 2023. Photo: Noah Yawn.

Plants epipetric; evergreen. Dry, thin soil mostly on acidic rocks of slopes, bluffs, and granite flatrocks. Sporulates March–November; uncommon in northern Alabama; rare in the Coastal Plain (Fig. 201). This species occurs chiefly in the eastern USA from Connecticut to southeastern Kansas, south to East Texas and northern Florida (Kartesz 2025).

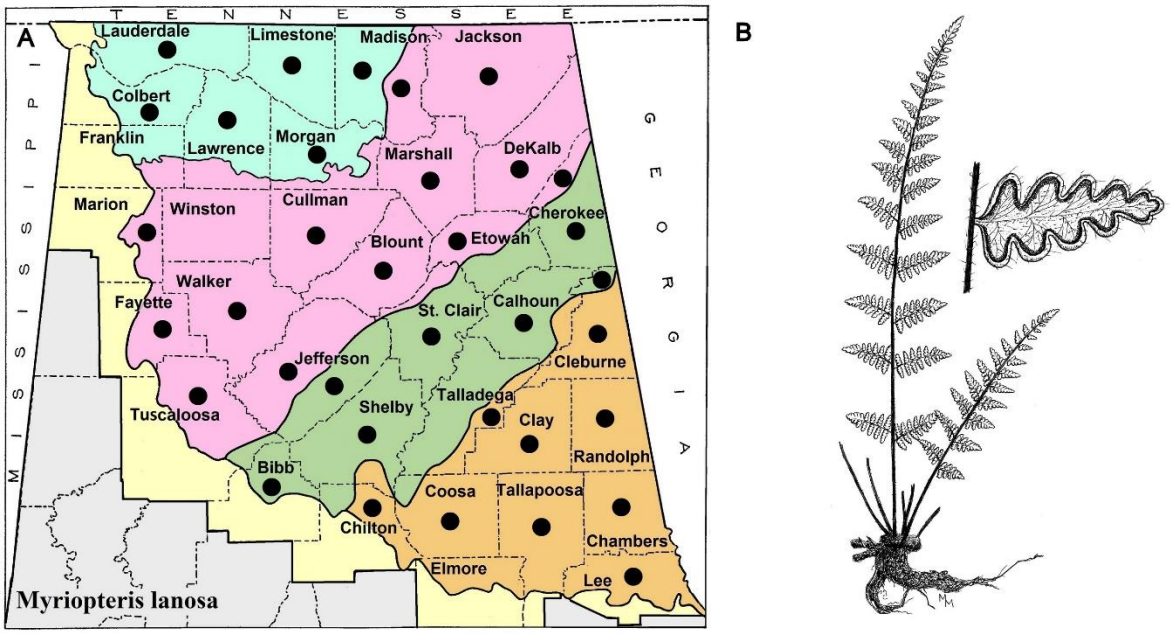


Figure 201. *Myriopteris lanosa.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

The Hairy Lip Fern is a xerophytic species uniquely adapted to the harsh, arid conditions of rock outcrops and cliff crevices. It thrives in environments where moisture is scarce, relying on several key morphological adaptations. A dense covering of hairs on the fronds helps reduce water loss by trapping moisture and protecting against desiccating winds. In addition, a waxy cuticle on the fronds further minimizes evapotranspiration. During periods of extreme drought, the fronds curl tightly, resembling withered, lifeless leaves—an effective strategy for conserving water.

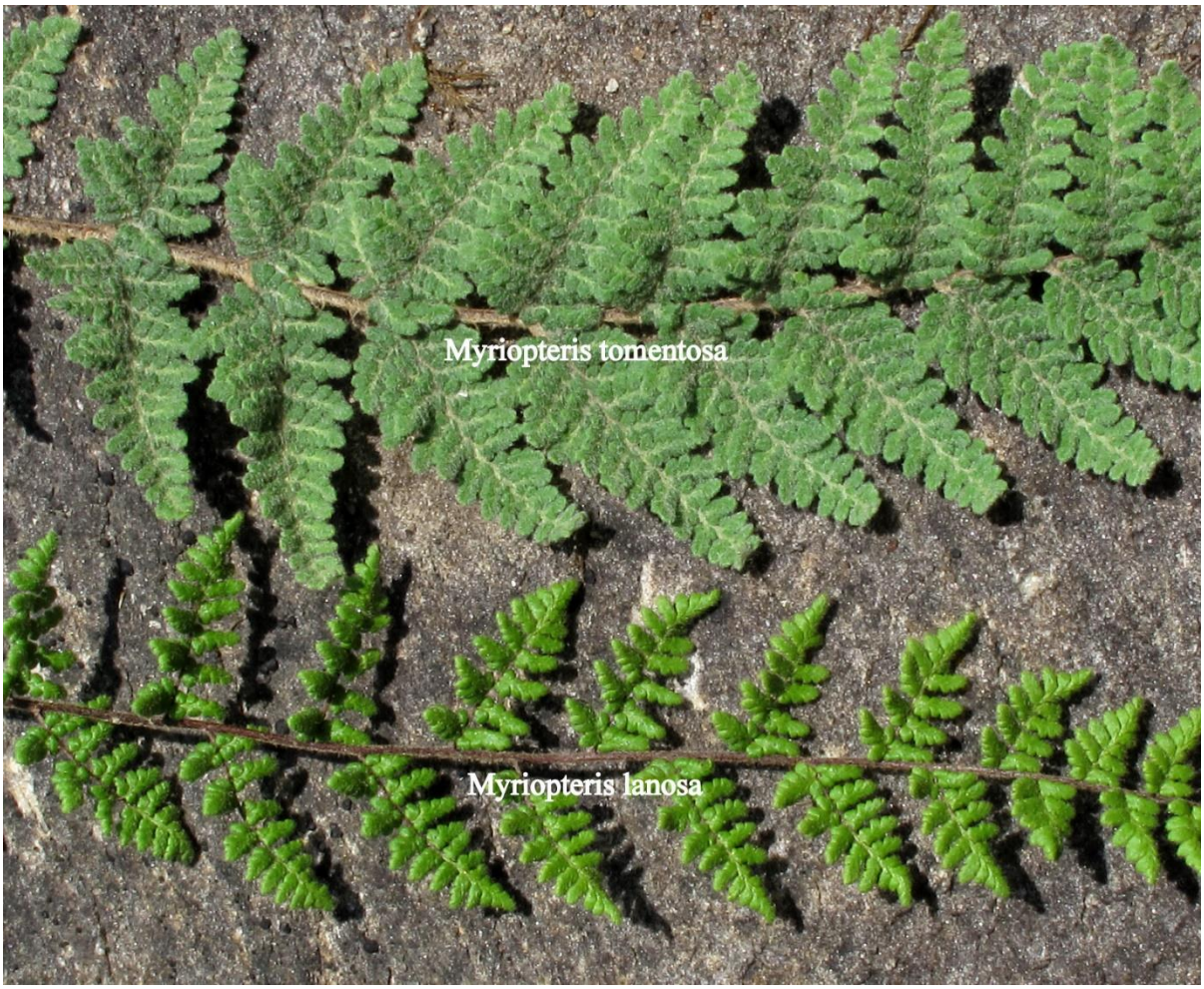


Figure 202. Frond comparisons between *Myriopteris lanosa* and *Myriopteris tomentosa*, Stephens Co., Georgia, 7 Jun 2009. Photo: Alan Cressler.

Myriopteris lanosa is often confused with *M. tomentosa* (Woolly Lip Fern) due to their similarly hairy appearance and shared affinity for rocky habitats (Fig. 202). However, the two species differ markedly in rachis pubescence and pinnule dissection. *Myriopteris lanosa* has a villous-hirsute rachis covered with shaggy, bristle-like hairs and lacks scales, allowing the surface to remain visible through the pubescence (Fig. 203a). In contrast, *M. tomentosa* bears a densely tomentose rachis with interspersed broader, linear scales that often obscure the surface. Pinnule morphology further separates them: in *M. tomentosa*, the pinnules are regularly cut to the midrib, whereas those of *M. lanosa* are deeply lobed but not fully divided (Fig. 203b). A key diagnostic trait of *M. lanosa* is its multicellular hairs, which exhibit distinct dark bands along their length—a feature absent in *M. tomentosa*. The bands appear faint to the naked eye but become readily visible under magnification, providing a reliable means of identification.

Figure 203. *Myriopteris lanosa*, Cleburne Co., Alabama, 30 Apr 2023. Photos: Dan Spaulding.

3. Myriopteris tomentosa (Link) Fée {densely woolly} — WOOLLY LIP FERN; WEBBY LIP FERN (Fig. 204). [*Cheilanthes tomentosa* Link; *Hemionitis bradburii* (Hook.) Christenh.]

Figure 204. *Myriopteris tomentosa*, Calhoun Co., Alabama, 14 Feb 2025. Photos: Dan Spaulding.

Plants epipetric; evergreen. Rocky slopes, ledges, and cliffs. Sporulates March–November; uncommon in northern Alabama; rare in the Coastal Plain (Fig. 205). This species occurs through the Appalachians from Virginia south to Georgia, Alabama, and Tennessee, west to Arkansas and Arizona, and south to Texas and Mexico (Windham & Rabe 1993).

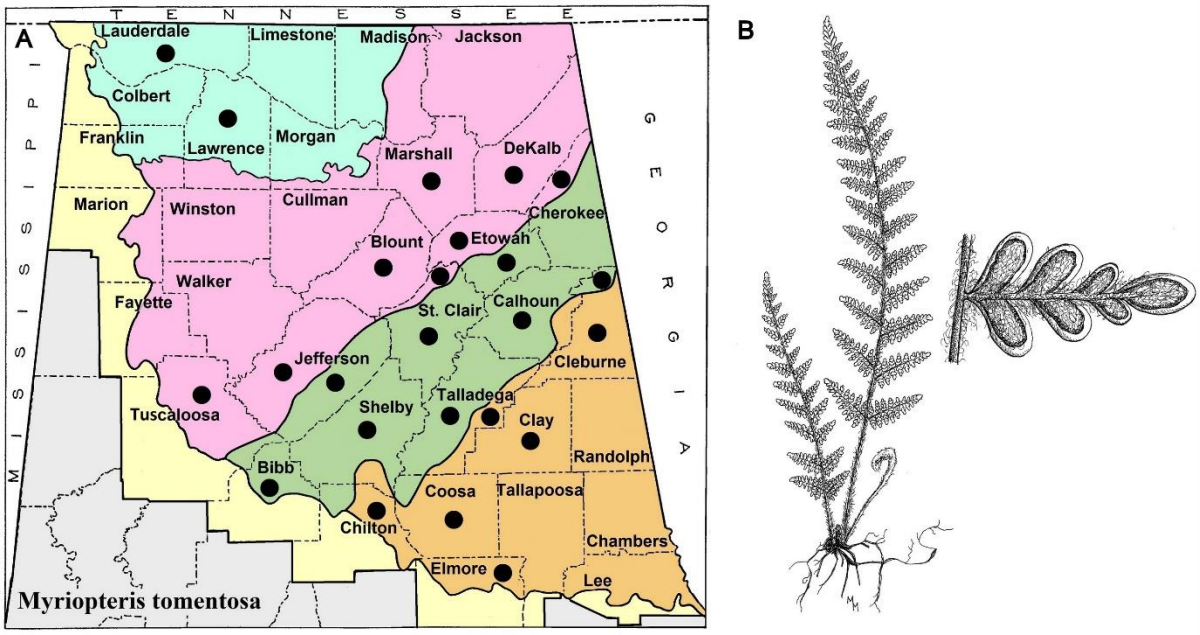


Figure 205. *Myriopteris tomentosa.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Myriopteris tomentosa thrives in arid, rocky environments, utilizing specialized adaptations to conserve water. Its woolly hairs densely cover the fronds, reducing moisture loss by limiting transpiration (Fig. 206). During extended droughts, the fronds shrivel and turn brown to minimize evaporation, then rehydrate and regain function once moisture returns. Its reproductive strategy further enhances survival: as an apogamous triploid, it carries three sets of chromosomes and reproduces asexually through apogamy, in which the gametophyte produces the sporophyte directly, bypassing fertilization and the need for free water (Whittier 1965; Windham & Rabe 1993).

Figure 206. *Myriopteris tomentosa*, Shelby Co., Alabama, 6 Jul 2019. Photos: Vitaly Charny.

The Woolly Lip Fern also has considerable horticultural appeal. Well adapted to sunny, dry, and rocky habitats, it thrives in rock gardens, xeriscapes, and the crevices of stone walls. Young fronds are thickly clothed in white hairs that give them a striking silvery sheen. As they mature, this pubescence gradually diminishes, revealing green foliage that adds distinctive texture and color to the landscape (Hoshizaki & Moran 2001).

A similar species, the Hairy Lip Fern (*Myriopteris lanosa*), resembles *M. tomentosa* but differs in several key traits. *Myriopteris lanosa* is generally smaller and has sparser pubescence, exposing more leaf surface. Its pinnae are twice-cut, with more widely spaced pinnules, creating a more open appearance. A distinctive feature of *M. lanosa* is its hairs, which have conspicuous dark bands along their length. In contrast, *M. tomentosa* typically has thrice-cut pinnae with densely packed pinnules, giving it a more finely divided and compact look (Fig. 202). Additionally, *M. tomentosa* lacks the dark-banded hairs that characterize *M. lanosa*, making this feature a reliable way to distinguish the two species.

4. PELLAEA Link 1841 {pell-EE-uh}

[Greek *pellos*, dusky, possibly referring to its bluish-gray leaves]

1. Petiole and rachis sparsely to moderately pubescent; stem surfaces dull; lower pinnae with long stalks 5–15 mm long; leaves somewhat dimorphic, with fertile fronds larger and bearing longer, narrower leaf segments than sterile fronds..... ***Pellaea atropurpurea***
1. Petiole and rachis glabrous or nearly so, with at most a few scattered hairs; stem surfaces shiny; lower pinnae sessile or on short stalks up to 6 mm long; leaves monomorphic, with fertile and sterile fronds similar in size and segment shape..... ***Pellaea glabella***

1. Pellaea atropurpurea (L.) Link {blackish-purple} — PURPLE CLIFFBRAKE; HAIRY CLIFFBRAKE; PURPLE-STEM CLIFFBRAKE; WINTER BRAKE (Fig. 207). [*Hemionitis atropurpurea* (L.) Christenh.]

Figure 207. *Pellaea atropurpurea*, Marshall Co., Alabama, 3 May 2023. Photo: Wayne Barger.

Plants epipetric; evergreen. Limestone rocks, ledges, cliffs, mortar of bricks, and stone walls. Sporulates March–November; frequent in the Highland Rim; uncommon in the Cumberland Plateau and Ridge & Valley; very rare in the Piedmont; rare in the Black Prairie District of the Coastal Plain (Fig. 208). Widespread in North America from Quebec and Ontario westward to the Rocky Mountains and south to northern Florida, Texas, and southeastern Nevada, continuing south through Mexico and Guatemala (Windham 1993a).

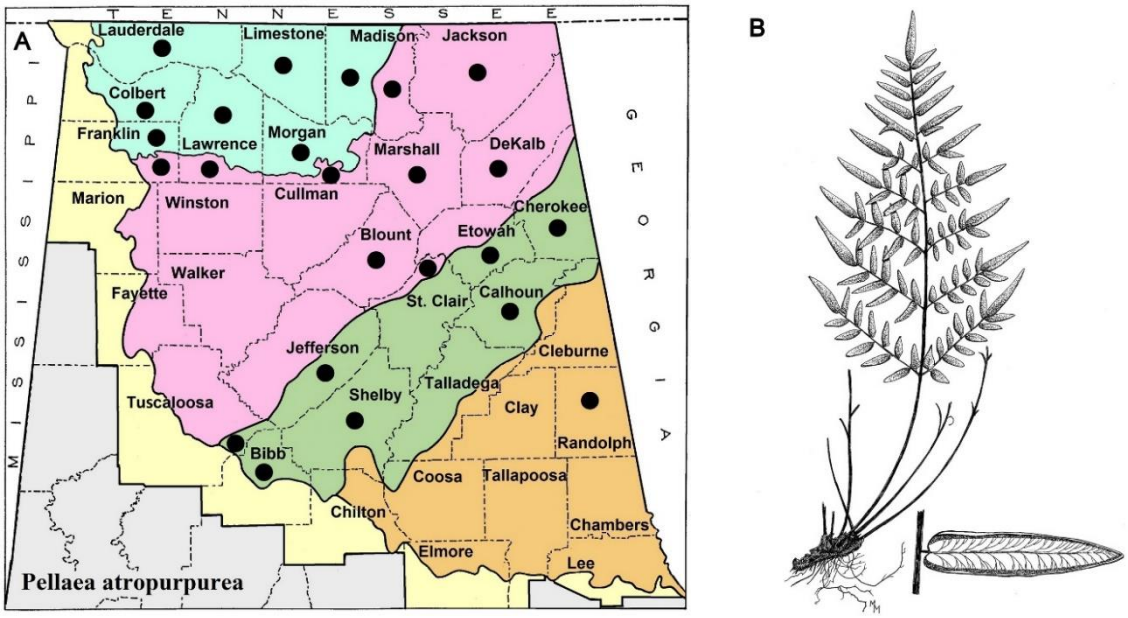


Figure 208. *Pellaea atropurpurea*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

In the early 1700s, colonial plant collector John Clayton (1694–1773) first documented *Pellaea atropurpurea* along the Rappahannock River in Virginia (Snyder & Bruce 1986). This fern is a triploid species that reproduces asexually via apogamy. Windham (1993a) proposed that it originated as an autopolyploid from a single diploid ancestor, likely arising when an unreduced gamete fused with a normal haploid gamete, producing offspring with three complete chromosome sets. Although triploids are generally sterile because their chromosomes cannot pair properly during meiosis, the Purple Cliffbrake bypasses this barrier by reproducing apogamously, with the sporophyte developing directly from the gametophyte without fertilization.

Figure 209. *Pellaea atropurpurea*, Jefferson Co., Alabama, 1 Aug 2024. Photos: Dan Spaulding.

The Purple Cliffbrake is a distinctive fern recognized for its striking dark, purplish-black stems and blue-green fronds. Its leathery blades are remarkably resilient, enabling it to withstand cold temperatures and remain evergreen through winter. It thrives in rocky habitats, especially on limestone outcrops, and frequently colonizes old stone walls and brick mortar laden with lime, anchoring its rhizomes in narrow crevices (Fig. 209). It is also well suited to cultivation, performing particularly well in rock gardens with limestone (Mickel 1994). However, as older fronds die back, their segments detach from the rachis, leaving behind a tangle of blackened stems that creates an unsightly contrast with the fresh growth.

Figure 210. *Pellaea atropurpurea*, Jefferson Co., Alabama, 1 Aug 2024. Photos: Dan Spaulding.

Although *Pellaea atropurpurea* closely resembles *P. glabella* (Smooth Cliffbrake) and often occurs in similar habitats, the two species are readily distinguished in the field by differences in pubescence and leaf dimorphism. *Pellaea atropurpurea* has moderately to sparsely pubescent stems and somewhat dimorphic leaves, with fertile fronds larger and bearing longer, narrower segments than the sterile ones (Fig. 210). In comparison, *P. glabella* has essentially glabrous stems and monomorphic leaves, with fertile and sterile fronds similar in size and segment shape. These traits provide reliable field characters for separating the two species in their natural habitats.

2. Pellaea glabella Mett. ex Kuhn subsp. **glabella** {hairless} — SMOOTH CLIFFBRAKE; SLENDER CLIFFBRAKE (Fig. 211). [*Hemionitis glabella* (Mett. ex Kuhn) Christenh.; *Pellaea atropurpurea* (L.) Link var. *bushii* Mackenzie]

Plants epipetric; evergreen. Calcareous cliffs and ledges. Sporulates May–September; very rare in the Tennessee Valley District of the Highland Rim and the Sequatchie Valley of the Cumberland Plateau (Fig. 212). Distributed across the eastern United States and adjacent Canada, from Quebec and Vermont west to Ontario and Michigan, and southward through the Appalachians to northern Alabama and west to north Texas (Windham 1993a). The Alabama Natural Heritage Program does not currently track this species; we recommend recognizing it as critically imperiled (S1) within the state.

Figure 211. *Pellaea glabella*, Marshall Co., Alabama, 16 Jun 2017. Photo: Alan Cressler.

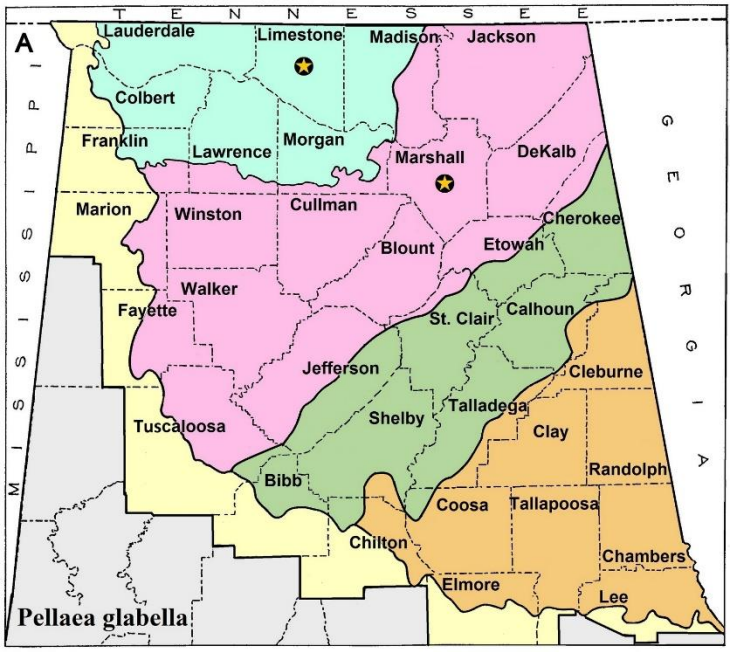


Figure 212. *Pellaea glabella.* **A.** Distribution map. **B.** Illustration: Ruth Sinclair George, 1938.

The first documented occurrence of *Pellaea glabella* in Alabama dates to January 15, 1958, when James P. Gillespie, then a biology instructor at Athens College, collected it from a quarry north of Elkmont in Limestone County. He deposited a specimen at Florida State University (SERNEC 2025), but his record went unnoticed, remaining absent from state floras for decades (Dean 1969; Kral et al. 2011; Short & Spaulding 2012; Spaulding et al. 2001c). More than half a century later, on May 3, 2015, Alan Cressler discovered a second occurrence of the species in Marshall County (Barger et al. 2019). While photographing prehistoric rock art at Painted Bluff, he encountered this fern growing on limestone cliffs along the Tennessee River (pers. comm., Dan Spaulding, 17 Feb 2025).

Figure 213. *Pellaea glabella* growing on Warren Point Sandstone, Marion Co., Tennessee. **A.** Denny Cove, 26 Sep 2020. **B.** Foster Falls Small Wild Area, 9 Dec 2012. Photos: Alan Cressler.

Pellaea glabella is very similar to *P. atropurpurea* (Purple Cliffbrake) but differs in its nearly smooth stems, similar fertile and sterile fronds, and sessile or short-stalked lower pinnae (Fig. 213a). In contrast, *P. atropurpurea* bears hairy stems, long-stalked lower pinnae, and fertile fronds that are larger than the sterile ones. Butters (1917a) observed that *P. glabella* often inhabits more exposed sites, such as exposed calcareous cliffs and ledges, where its rhizomes penetrate deep into rock crevices, enabling survival on dry, sunbaked outcrops. He also noted that the species occasionally grows on calcareous sandstone (Fig. 213b), a rock type cemented with calcium carbonate ($CaCO_3$), often derived from dissolved limestone or marine sediments. By comparison, *P. atropurpurea* is most often associated with limestone or dolomite and frequently colonizes lime-rich mortar in old masonry walls.

In North America, *Pellaea glabella* consists of four geographically isolated subspecies, most of which are sexual diploids. The exception is *P. glabella* subsp. *glabella*, an apogamous tetraploid believed to have arisen from subsp. *missouriensis* (Gastony) Windham. Unlike its sexually reproducing relatives, this subspecies reproduces through apogamy, a form of asexual reproduction in which the sporophyte develops directly from the gametophyte without fertilization (Gastony 1988; Wagner et al. 1965; Windham 1993a). This strategy enables the fern to persist in harsh, dry habitats, where fertilization often fails because sperm cannot swim to the eggs without a film of free-standing water.

5. PTERIS Linnaeus 1753 {TAIR-iss}
[Greek *pteris*, a fern; derived from *pteron*, wing or feather, referring to the frond's shape]

1. Petioles and rachis with scales; pinnae all simple, lacking lobes or pinnules..... ***Pteris vittata***
1. Petioles and rachis smooth, without scales; pinnae, at least the lower ones, lobed or pinnate.

   2. Rachis winged most of its length, at least the upper half; petiole much shorter than the blade; plants typically epipetric, often on rocks or old walls..... ***Pteris multifida***
   2. Rachis winged only below the terminal pinnae or entirely unwinged; petiole much longer than blade; plants typically terrestrial, often in disturbed sites in Alabama..... ***Pteris cretica***

1. Pteris cretica L. subsp. **cretica** {from Crete} — CRETAN BRAKE; RIBBON FERN; TABLE FERN (Fig. 214). [*Pycnodoria cretica* (L.) Small]

Figure 214. *Pteris cretica* subsp. *cretica*, Citrus Co., Florida, 29 Dec 2022. Photo: Alan Cressler.

Plants terrestrial, occasionally epipetric; evergreen or semi-evergreen. Growing in sheltered, disturbed sites (rocky or limy soils in Florida). Sporulates April–December; very rare in the southern Piedmont and Coastal Plain (Fig. 215). This species originated in the Paleotropics and has become naturalized in California and along the southeastern Coastal Plain, especially in Florida (Kartesz 2025).

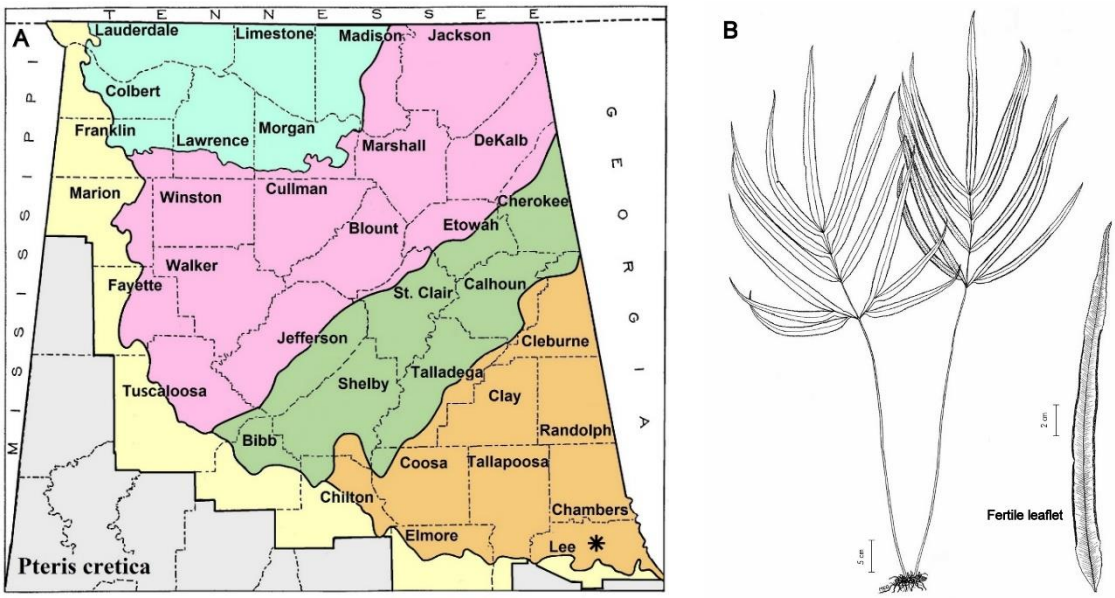


Figure 215. *Pteris cretica*. **A.** Distribution map. **B.** Illustration by María del Carmen Otero Cabada, 2011.

Katie Lawson, Assistant Professor at Auburn University, was the first person to collect *Pteris cretica* in the study area of this paper. She discovered the exotic fern growing beneath an old shed porch in Lee County on May 12, 2022. Due to its widespread cultivation and frequent escapes in warmer climates, its native range remains uncertain, making its natural distribution difficult to determine (Nauman 1993b). Small (1938) believed that *P. cretica* was native to Florida, citing its ability to thrive in undisturbed habitats (Fig. 216a). However, he noted that its specific epithet suggested Linnaeus believed it originated from the Greek island of Crete.

Figure 216. A. *Pteris cretica* subsp. *cretica*, Alachua Co., Florida, 7 Jan 2021. Photo: Jeannie Mounger. **B.** *Pteris parkeri*, Marion Co., Florida, 12 Jul 2024. Photo: Eric C. Maxwell.

Pteris cretica is a widely distributed tropical fern of the Old World and one of the most commonly cultivated species worldwide (Morton 1957). Its adaptability and ornamental appeal make it a popular houseplant, particularly the crested varieties with fan-like or forked leaf tips. Preferring indirect light, minimal watering, and good drainage, it thrives indoors (Olsen 2007).

A variegated variant, commonly classified as *Pteris cretica* var. *albolineata* Hook. has become established in Florida and southern Alabama (Fig. 216b). This striking fern, with green fronds marked by silvery-white central stripes, is commonly called the White-lined Cretan Brake or Silver Ribbon Fern. While taxonomists traditionally classified it as a variety of *P. cretica*, Jaruwattanaphan et al. (2013) argue that it warrants recognition as a distinct species, *P. parkeri* hort. ex J.J. Parker.

Taxonomists recognize two subspecies of *Pteris cretica*. Only subsp. *cretica* is naturalized in the southeastern United States (Weakley et al. 2025). The other, *P. cretica* subsp. *laeta* (Wall. ex Ettingsh.) Fraser-Jenk., native to tropical Asia, is now naturalized in South America. It differs from subsp. *cretica* by its brown, scabrous petioles and wavy pinna margins, whereas subsp. *cretica* has smooth, straw-colored petioles and pinnae with flat margins (Arana et al. 2020).

2. Pteris multifida Poir. {much divided; leaves} — SPIDER BRAKE; HUGUENOT FERN; SAW-LEAVED BRACKEN; WALL BRAKE; SPIDER FERN (Fig. 217). [*Pteris serrulata* auct. non L. f.; *Pycnodoria multifida* (Poir.) Small]

Figure 217. *Pteris multifida*, Talladega Co., Alabama, 9 Feb 2024. Photos: Dan Spaulding.

Plants epipetric; evergreen to semi-evergreen. On old walls with lime mortar, steep streambanks, rocky ledges behind waterfalls, and limestone gravel riprap along bridge abutments. Sporulates April–December; rare in northern Alabama; uncommon in the Coastal Plain (Fig. 218). Native to East Asia and naturalized primarily in the southeastern USA (Wyatt 2020).

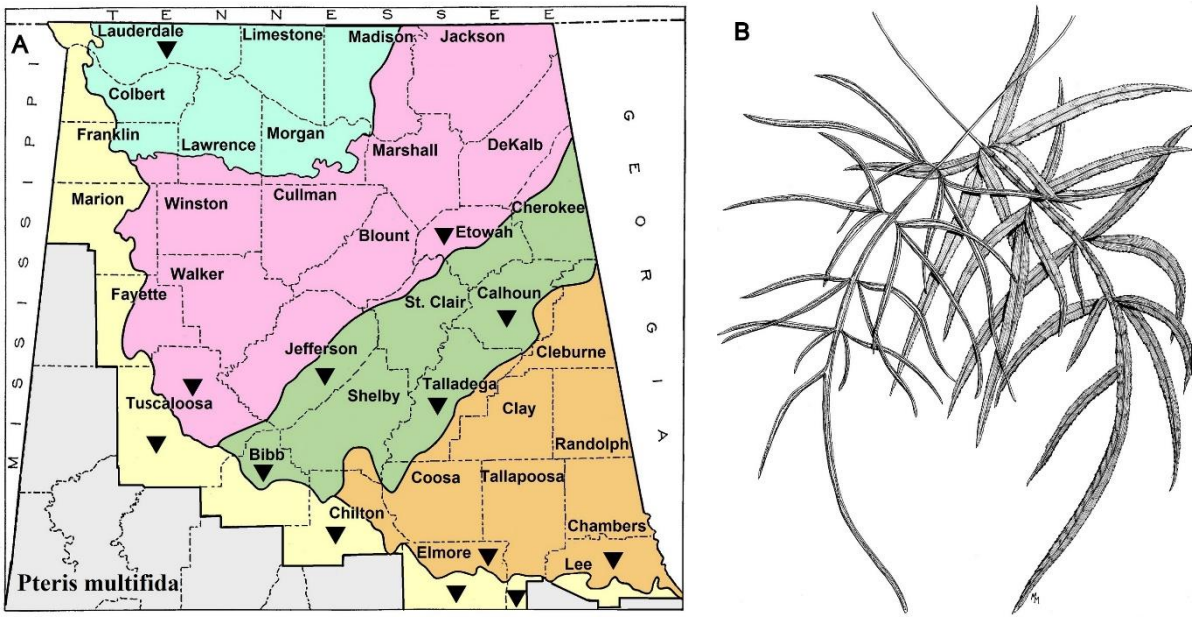


Figure 218. *Pteris multifida*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Horticulturists originally introduced *Pteris multifida* to the Southeast as a cultivated fern, but it quickly naturalized and integrated into the local flora. This non-native species adapts remarkably well, thriving in a wide range of artificial habitats. It commonly grows on brick walls, in crevices of old structures, along riprap at bridge bases, in narrow alleys, around stone wells, and on sheltered rocky ledges in natural settings. Its ability to prosper beyond cultivated gardens demonstrates its resilience and capacity for widespread colonization (Jones 1955).

Figure 219. *Pteris multifida*, Calhoun Co., Alabama, 2 Mar 2024. **A.** Sterile frond. **B.** Fertile frond. Photos: Dan Spaulding.

The common name "spider brake" likely refers to its spider-like appearance, while "brake" is an archaic term once widely applied to ferns or fern-like plants. Small (1938) noted that "Huguenot fern" originated from its 1868 discovery at a Huguenot cemetery in Charleston, South Carolina. The name "saw-leaved bracken" highlights the serrated margins of the sterile fronds (Fig. 219a), which contrast with the mostly untoothed fertile fronds (Fig. 219b). "Wall brake" reflects the fern's habit of growing on vertical surfaces, often in crevices and sheltered spots. Although *Pteris multifida* primarily thrives in human-influenced habitats, it occasionally inhabits natural sites, such as shaded rock shelters beneath waterfalls, illustrating its ecological adaptability (Fig. 220).

Figure 220. *Pteris multifida*, Noccalula Falls, Etowah, Co., Alabama, 25 Sep 2016. Photo: Alan Cressler.

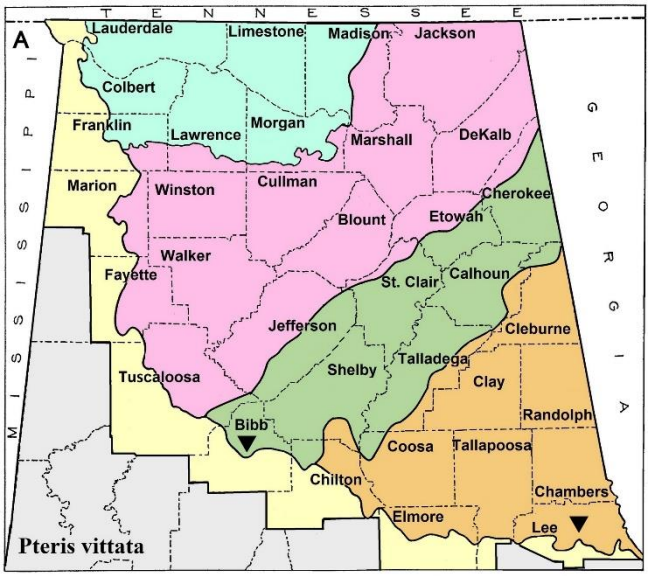
Botanists sometimes mistake juvenile *Pteris multifida* for *P. cretica* (Cretan brake). In its early stages, *P. multifida* produces only decurrent terminal pinnae, creating a wing along the rachis—a feature that mimics mature *P. cretica*. Juvenile *P. multifida*, however, can be recognized by its thinner leaves and uppermost pinnae with long, tapering tips, whereas *P. cretica* typically bears thicker leaves and terminal pinnae that generally are blunt or rounded (Nauman 1993b). Both species reproduce asexually through apogamy, in which the sporophyte arises directly from the gametophyte without fertilization (Huang et al. 2011; Kawakami et al. 1995).

3. Pteris vittata L. {ribbon} — LADDER BRAKE; CHINESE BRAKE; RUSTY BRAKE (Fig. 221). [*Pycnodoria vittata* (L.) Small]

Plants epipetric, rarely terrestrial; evergreen. Lime mortar of brick and stone walls, under bridges, old masonry walls, building crevices, and with rock along small drainages. Sporulates year-round; very rare in the Cahaba Valley District of the Ridge & Valley and the southern Piedmont; rare in the Coastal Plain (Fig. 222). Native to Asia and naturalized primarily in the Coastal Plain of the southeastern USA, as well as in California, the West Indies, and South America (Nauman 1993b).

Figure 221. *Pteris vittata,* Auburn, Lee Co., Alabama, 17 Jul 2024. Photos: Roger Birkhead.

Ladder Brake is most often associated with older coastal cities in the United States, where it thrives in the mossy crevices of historic masonry, including weathered walls and cemetery monuments. In southeastern Louisiana—particularly within the historic districts of New Orleans—it frequently carpets the edges of open crawl spaces beneath houses and sprawls across aged brickwork. In Alabama, the species persists on masonry at several sites in Mobile's historic quarters. It also grows in Auburn, where it emerges between the bricks of century-old school buildings on the Auburn University campus.



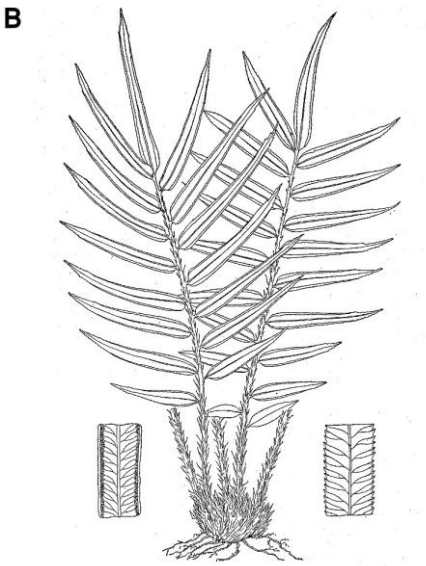


Figure 222. *Pteris vittata.* **A.** Distribution map. **B.** Illustration: Ruth Sinclair George, 1938.

In 2024, the senior author documented a small population of *Pteris vittata* growing in dolomitic rock within a roadside drainage ditch in Bibb County (Fig. 223), demonstrating the fern's ability to persist beyond strictly urban settings. John Short had earlier reported it from old masonry at the Sloss Furnaces National Historic Landmark in Birmingham (Short & Spaulding 2012). However, recent surveys at that site have failed to locate any plants, suggesting the population may no longer be extant.

Figure 223. *Pteris vittata*, on Ketona Dolomite, Bibb Co., Alabama, 6 Jul 2024. Photos: Dan Spaulding.

Pteris vittata is remarkable for its exceptional tolerance to arsenic, a trait rare among plants. While most vegetation struggles or dies in arsenic-contaminated environments, this fern thrives, enduring arsenic concentrations up to 1,000 times greater than those tolerated by other species. Its extraordinary ability to absorb arsenic makes it an ideal candidate for long-term phytoremediation, offering promising potential for the cleanup of contaminated soils (Yan et al. 2019).

6. VITTARIA Smith 1793 {vih-TAIR-ee-uh}

[Latin *vitta*, ribbon or band; referring to narrow strap-like leaves of the sporophyte]

1. Gemmae (asexual buds) uniform in length, each with 4 body cells; sporophytes occasionally present; plants found in the Piedmont of Alabama..... ***Vittaria graminifolia***
1. Gemmae variable in length, with 2–12 body cells; sporophytes absent; plants found in the Highland Rim and Cumberland Plateau in Alabama.....***Vittaria appalachiana***

1. Vittaria appalachiana Farrar & Mickel {Appalachian} — APPALACHIAN SHOESTRING FERN; APPALACHIAN VITTARIA; APPALACHIAN GAMETOPHYTE (Fig. 224).

Plants epipetric gametophytes; evergreen. Shaded, moist cavities and crevices of sandstone bluffs and grottoes. Reproduces by gemmae; very rare in the Highland Rim; rare in the Cumberland Plateau (Fig. 225). The species primarily occurs in the Appalachians, extending from southwestern New York and Pennsylvania south to northern Georgia and Alabama (Farrar 1993b).

Botanists often overlook the Appalachian Shoestring Fern because of its small size and unassuming appearance. The gametophytes commonly form dense colonies on deeply shaded rock surfaces (Fig. 226), with their upturned thallus lobes orienting perpendicular to the strongest light. Unlike most ferns, this species has lost the ability to produce sporophytes and reproduces exclusively through tiny, club-shaped gemmae. Researchers have successfully induced sporophytes in laboratory settings, but none have survived beyond infancy (Farrar 1978).

Figure 224. *Vittaria appalachiana*, Etowah Co., Alabama, 2 Sep 2022. Photo: Noah Yawn.

The gametophytes of *Vittaria appalachiana* superficially resemble liverworts at first glance, yet they differ in several diagnostic traits. Whereas liverwort thalli are typically several cells thick, *Vittaria* gametophytes consist mostly of a single layer of cells, giving them a more delicate, translucent appearance. Their slender, root-like rhizoids also form distinctive clusters along one margin of the plant, in contrast to liverwort rhizoids, which spread more evenly across the entire underside. In addition, these gametophytes share close similarities with those of *V. graminifolia*, but differ in gemma structure: in *V. appalachiana*, gemmae vary in length, containing 2–12 body cells (Fig. 227), whereas in *V. graminifolia*, they are uniform, each consistently composed of four body cells.

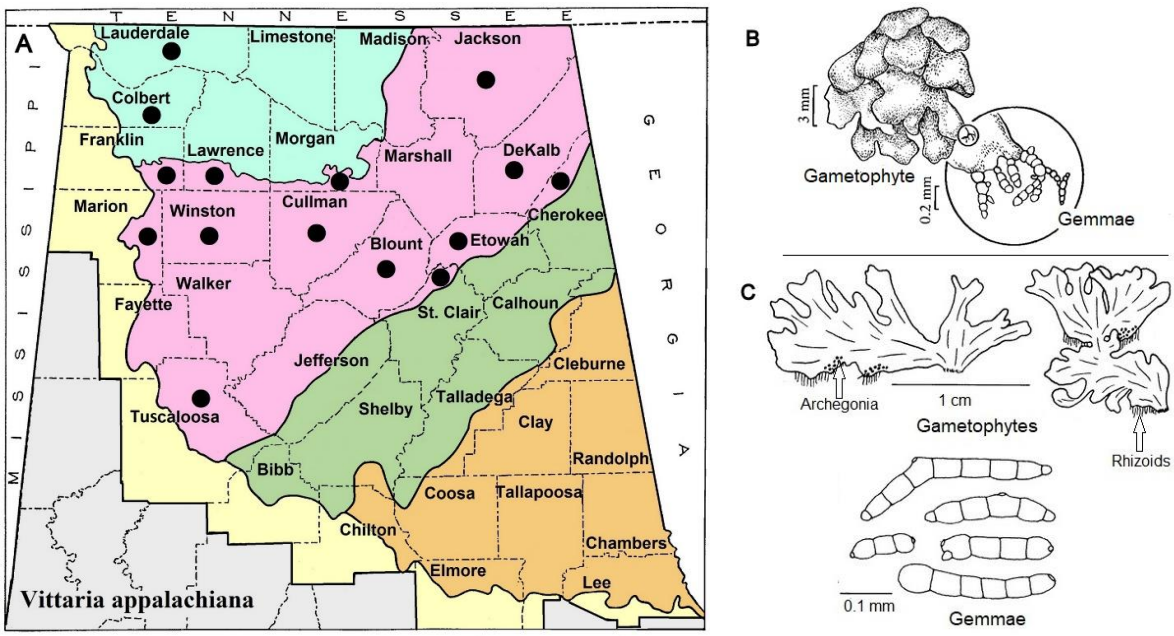


Figure 225. *Vittaria appalachiana.* **A.** Distribution map. **B.** Illustration by John Myers (in Flora of North America 1993). **C.** Illustration by Donald R. Farrar (in Farrar & Mickel 1991).

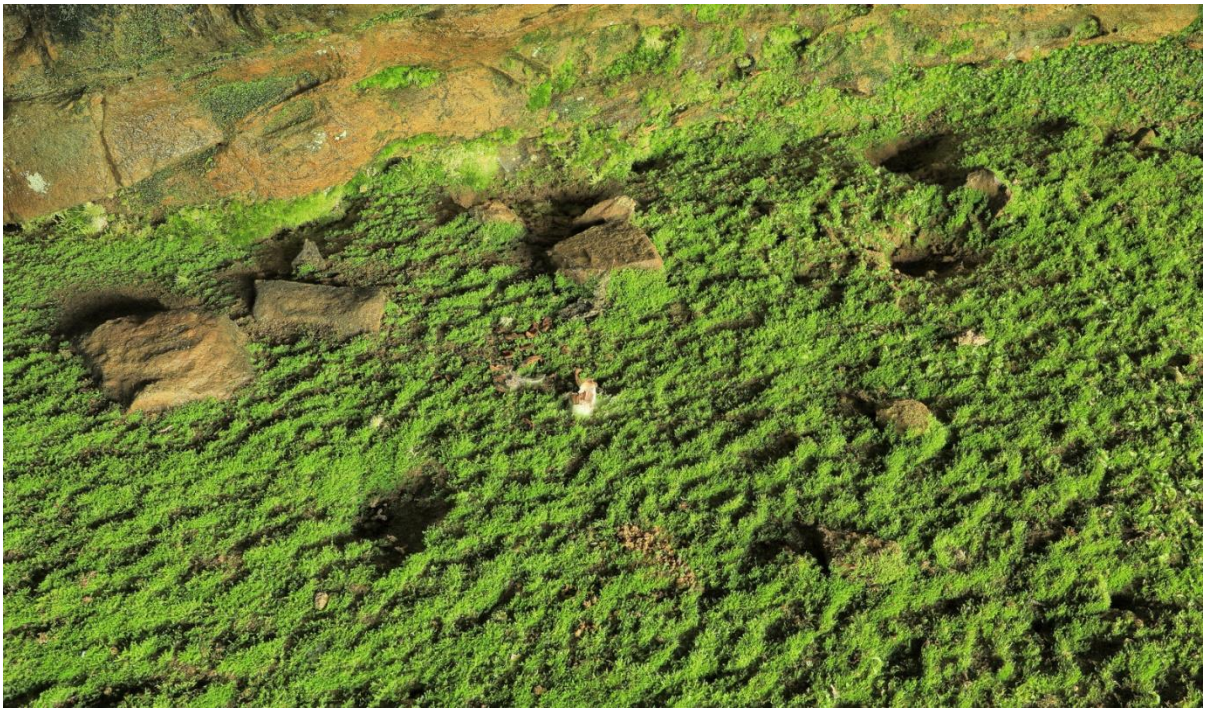


Figure 226. *Vittaria appalachiana* colony, St. Clair Co., Alabama, 12 Aug 2023. Photo: Alan Cressler.

This fern species remained unclassified formally as a distinct species for many years. In 1824, German-American botanist Lewis David von Schweinitz was the first to document it, although he mistakenly identified it as a leafy liverwort in the genus *Jungermannia*. More than a century later, in 1930, American bryologist Aaron John Sharp correctly identified the plant as the gametophyte of a fern, similar to the sporophyte-producing species of *Vittaria*. In 1963, Warren H. Wagner and Sharp hypothesized that the Appalachian fern's gametophytes likely belonged to *Vittaria lineata* (L.) Sm., the Shoestring Fern. Nearly 30 years later, Don Farrar and John Mickel (1991) formally described the "Appalachian gametophyte" as *Vittaria appalachiana*.

Figure 227. *Vittaria appalachiana* gemmae, Cherokee Co., Alabama, 25 Feb 2022. Photo: Noah Yawn.

2. Vittaria graminifolia Kaulf. {grass-leaved} — GRASS FERN; SLENDER SHOESTRING FERN; GRASS-LEAF SHOESTRING FERN (Fig. 228). [*Vittaria filifolia* Fée]

Figure 228. *Vittaria graminifolia* gametophytes, Elmore Co., Alabama, 29 Nov 2021. Photo: Noah Yawn.

Plants epipetric or epiphytic in other regions; evergreen. In Alabama, it grows in deep, moist recesses and cracks of quartzite rock. Outside the tropics, it reproduces asexually by gemmae; very rare in the Piedmont (Fig. 229). Native mainly to the Neotropics, ranging from Mexico to South America (Pinson et al. 2017a), but occurs sporadically in the southeastern USA, where it persists almost exclusively as clonal gametophyte colonies. Although the Alabama Natural Heritage Program does not currently track this fern, we consider it critically imperiled (S1) in the state.

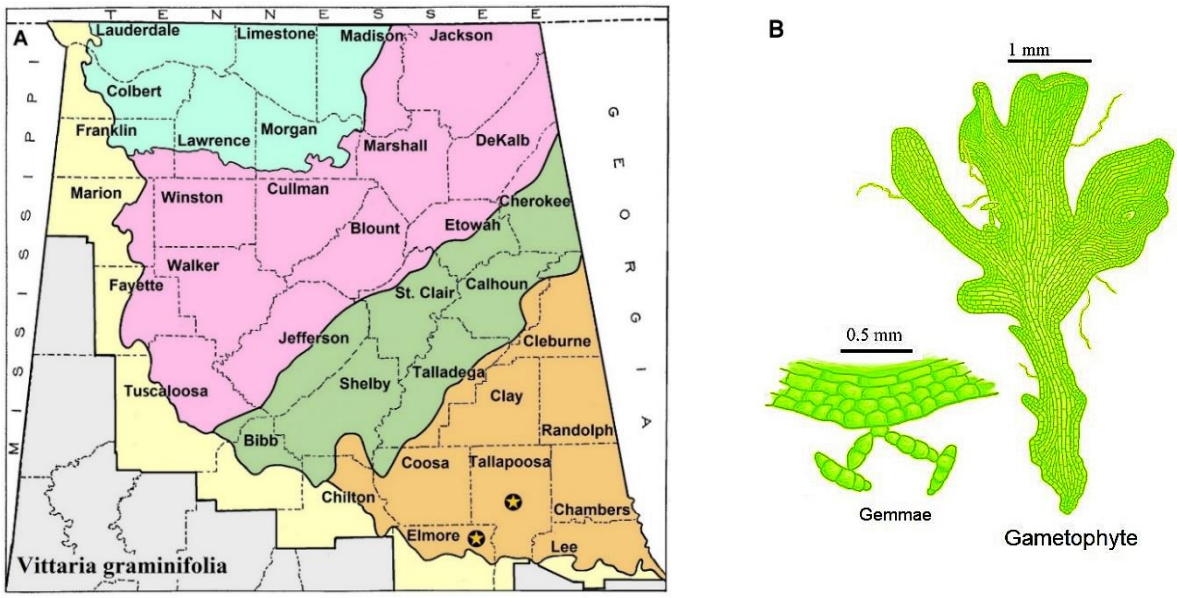


Figure 229. *Vittaria graminifolia*. **A**. Distribution map. **B**. Illustration: Simon Parsons (Pinson et al. 2017a).

Figure 230. *Vittaria graminifolia*, Broxton Rocks, Coffee Co., Georgia, 29 Jul 2017. Photo: Alan Cressler.

Vittaria graminifolia primarily inhabits mid- to high-elevation montane rainforests of tropical America, where it typically grows as an epiphyte and readily produces sporophytes (Mickel & Smith 2004). In 1982, Don Farrar and Gary Landry made the first North American discovery of *V. graminifolia* gametophytes, which they found growing on the buttresses of beech trees in St. Helena Parish, Louisiana (Farrar & Landry 1987). In 2015, researchers documented clonal gametophytes, immature sporophytes, and occasional mature, reproductive sporophytes (Fig. 230) in shaded rock shelters and crevices at Broxton Rocks Preserve in Coffee County, Georgia (Pinson et al. 2017b). More recently, in 2021, Noah Yawn discovered gametophytes along with a few immature sporophytes (Fig. 231) growing on rocks in the lower Piedmont of Alabama (Yawn et al. in prep.).

Figure 231. *Vittaria graminifolia*, Elmore Co., Alabama, 29 Nov 2021. Photo: Noah Yawn.

Figure 232. *Vittaria lineata*. **A.** Clonal gametophytes and immature sporophytes, Hillsborough Co., Florida, 1 Nov 2019. Photo: Alan Cressler. **B–C.** Mature sporophytes growing on *Sabal palmetto*, Baldwin Co., Alabama, 15 Feb 2012. Photos: Wayne Barger.

A closely related species, the Shoestring Fern, *Vittaria lineata* (L.) Sm., is native to southeast Georgia, Florida, and tropical regions of the Americas (Fig. 232). It is adventive in southern Alabama, often growing on planted Cabbage Palmetto (*Sabal palmetto*) trunks. Due to their similar appearance, Edgar T. Wherry (1964) mistakenly reported *V. graminifolia* in Collier County, Florida, based on a specimen collected by John Beckner in 1960 (Gastony 1980). Both species produce sporophytes with linear, grass-like leaves, and their gametophytes can persist in long-lasting populations even in the absence of sporophytes.

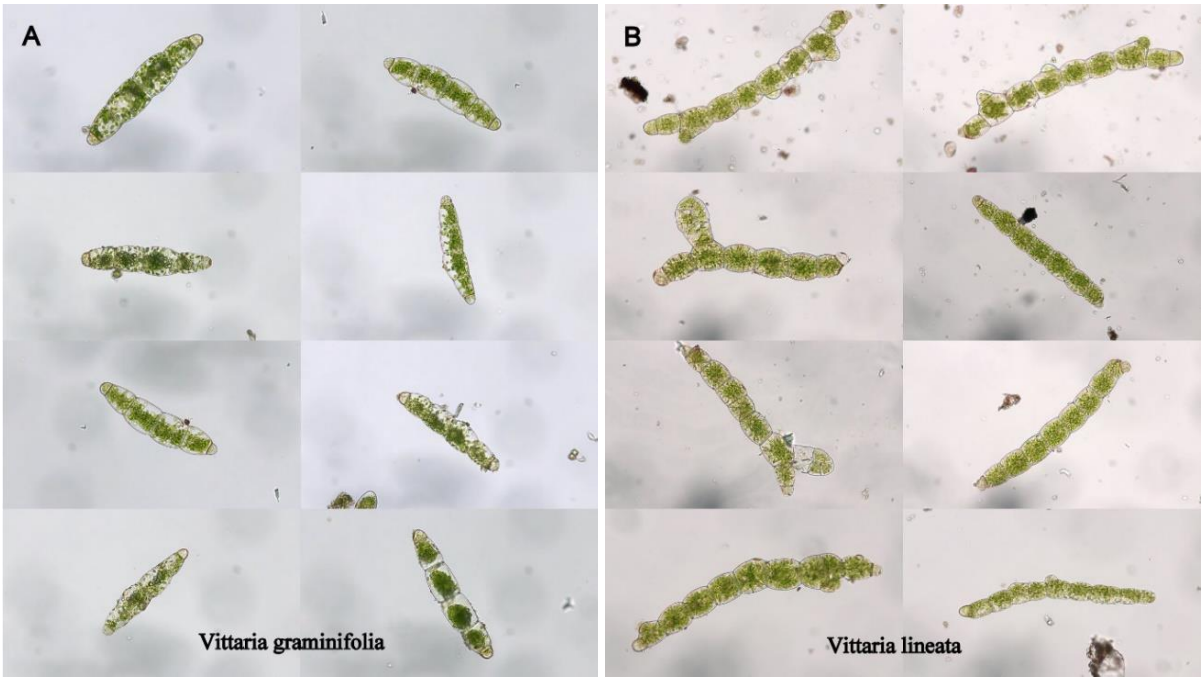


Figure 233. A. Gemmae of *Vittaria graminifolia*, Elmore Co., Alabama, 29 Nov 2021. **B.** Gemmae of *Vittaria lineata*, Collier Co., Florida, 28 Dec 2022. Photos: Noah Yawn.

The differences between *Vittaria graminifolia* and *V. lineata* are subtle but diagnostic. Gametophytes of *V. graminifolia* produce uniform gemmae, each with six cells, including four body cells (Fig. 233a), while those of *V. lineata* vary from 4 to 16 cells (Fig. 233b). Sporophytes also differ: *V. graminifolia* has narrow fronds 1.5–2 mm wide, trilete (tetrahedral) spores, and rhizome scales 4–6 mm long that lack a hair-like tip; *V. lineata* has slightly broader fronds 2–3 mm wide, monolete (bilateral) spores, and rhizome scales 6–7 mm long with prominent hair-like tips (Weakley et al. 2025).

14. DENNSTAEDTIACEAE (Bracken Fern Family) – in Polypodiales

1. Leaves subcoriaceous (somewhat leathery), lacking glands; sori confluent, forming continuous linear bands along revolute (in-rolled) margins of leaf segments ..... ***Pteridium***
1. Leaves membranaceous (thin and flexible), with long-stalked glands; sori distinct, forming separate globular clusters in the sinuses along leaf segment margins.

   2. Leaves 2-pinnate-pinnatifid; sori at the edge of leaf margins, enclosed in a tubular or cuplike indusium ..... ***Sitobolium***
   2. Leaves 3–4-pinnate-pinnatifid; sori near the leaf margins on the lower surface, often partially covered by a marginal, flap-like indusium ..... ***Hypolepis***

1. HYPOLEPIS Bernhardi 1806 {hi-poh-LEE-pis}

[Greek *hypo*, below, and *lepis*, scale, in referring to the flap-like indusia covering sori]

1. Hypolepis tenuifolia (G. Forst.) Bernh. {slender leaved} — SPINELESS BRAMBLE FERN; SOFT GROUND FERN (Fig. 234).

Figure 234. *Hypolepis tenuifolia*, cultivated, Jefferson Co, Alabama, 8 May 2024. Photos: Dan Spaulding.

Plants terrestrial; deciduous. Shaded disturbed areas. Sporulates May–November; very rare waif in northern Alabama (Fig. 235). Native to East Asia and the South Pacific islands (Brownsey 1987). It has escaped cultivation in Alabama and Arkansas in the southeastern USA (Peck 2011).

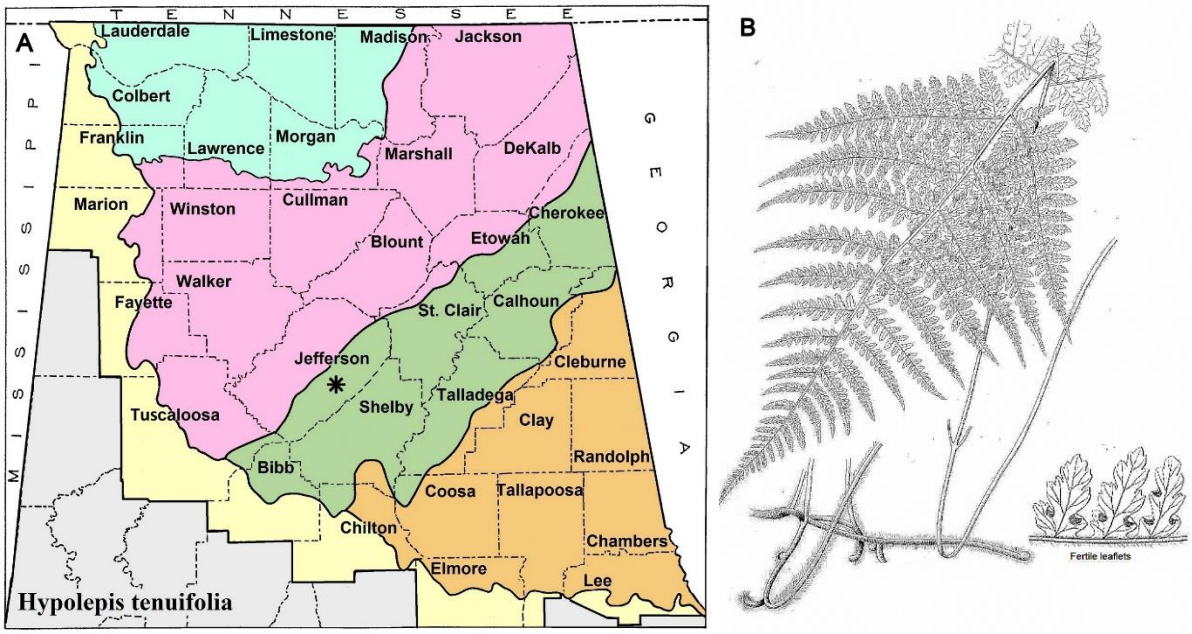


Figure 235. *Hypolepis tenuifolia*. **A**. Distribution map. **B**. Illustration: Georg Heinrich Mettenius, 1856.

Figure 236. *Hypolepis tenuifolia*, cultivated, Jefferson Co, Alabama, 8 May 2024. Photos: Dan Spaulding.

Hypolepis tenuifolia is the most widely cultivated species of the genus in the United States (Hoshizaki & Moran 2001). This robust fern spreads aggressively through long-creeping rhizomes, sometimes invading nearby woodlands and vacant lots. Its common name, "soft ground fern," refers to the numerous downy hairs interspersed with glands covering its fronds (Fig. 236). The species rarely produces sori, suggesting that spores contribute little to its dispersal. Instead, it propagates primarily through vegetative growth via rhizomes. Although native to tropical regions, its deeply buried rhizomes enable it to withstand winter temperatures, making it surprisingly resilient in colder climates.

Figure 237. A. *Hypolepis repens*, Orocovis, Puerto Rico, 5 May 2023. Photo: Octavio Rivera Hernández. **B.** *Hypolepis barringtonii*, Clay Co., Florida, 16 Aug 2011. Photo: Alan Cressler.

For decades, gardeners in and around Birmingham, Alabama, have cultivated the Asian *Hypolepis tenuifolia*, often misidentifying it as *H. repens* (L.) K. Presl (Fig. 237a), a species native to the tropical Americas. Schwartsburd (2018) recognized Florida populations as a distinct species, *H. barringtonii* (Fig. 237b), which he distinguished by its fewer stem bristles and shorter, membranous fronds—reaching up to 1.5 meters in length—compared to the larger, parchment-like fronds of *H. repens*. While the fronds of *H. repens* and *H. barringtonii* are sparsely hairy, those of *H. tenuifolia* are densely pubescent. The common name "bramble fern" refers to the dense, scrambling growth and prickly stems characteristic of many *Hypolepis* species, though *H. tenuifolia* lacks prickles, further setting it apart from both *H. repens* and *H. barringtonii*.

Superficial similarities between *Hypolepis tenuifolia* and other large, triangular-bladed ferns often result in misidentification. Bracken ferns (*Pteridium* spp.) resemble *H. tenuifolia* at first glance, but they differ in their glabrous petioles and linear, confluent sori that run continuously along the in-rolled pinna margins. Another species commonly mistaken for *H. tenuifolia* is the Mariana Maiden Fern (*Macrothelypteris torresiana*), which bears erect to arching blades on relatively lax stalks with only fine, inconspicuous hairs. By contrast, *H. tenuifolia* carries its broad blades nearly horizontally on stiff, upright stalks, clothed in long, soft hairs, which give the entire plant a distinctly downy texture. The hairy petioles and horizontal fronds make *H. tenuifolia* readily distinguishable.

2. PTERIDIUM Gleditsch ex Scopoli 1760 {tuh-RID-ee-um}
[Greek, *pteridion*, diminutive of *Pteris*, a wing or feather; an ancient name for a fern]

1. Terminal segments of well-developed pinnules noticeably elongated, generally 6–15 times as long as wide; leaves essentially glabrous ..... ***Pteridium pseudocaudatum***
1. Terminal segments of well-developed pinnules slightly elongated, generally 2–4 times as long as wide; leaves distinctly pubescent underneath .....***Pteridium latiusculum***

1. Pteridium latiusculum (Desv.) Hieron. {broad} — EASTERN BRACKEN FERN; EAGLE FERN; PASTURE BRAKE (Fig. 238). [*Pteridium aquilinum* (L.) Kuhn subsp. *latiusculum* (Desv.) Hultén; *Pteridium aquilinum* (L.) Kuhn var. *latiusculum* (Desv.) Underw. ex A. Heller; *Pteris latiuscula* Desv.]

Figure 238. *Pteridium latiusculum*, Kenora Dist., Ontario, Canada, 11 Jul 2024. Photo: Cory Chioppone.

Plants terrestrial; deciduous. Woodlands, barrens, pastures, roadsides, and other open areas. Sporulates July –September; rare in northern Alabama; very rare in the Coastal Plain (Fig. 239). This species occurs mainly in eastern North America, from Newfoundland west to Manitoba and south to Florida and Louisiana, with outliers in Alberta and British Columbia. Its range also extends into Mexico, Europe, and Asia (Jacobs & Peck 1993).

The Eastern Bracken Fern (*Pteridium latiusculum*) thrives in open woodlands with partial shade but spreads aggressively in abandoned fields and pastures. Resistant to browsing, it often increases under grazing pressure as livestock avoid it in favor of more palatable vegetation. However, cattle may consume bracken fern in overgrazed pastures where forage is scarce, exposing them to toxic compounds. Notably, the fronds of this fern contain shikimic acid, a carcinogenic compound that can contaminate milk, posing potential health risks to humans (Fenwick 1989).

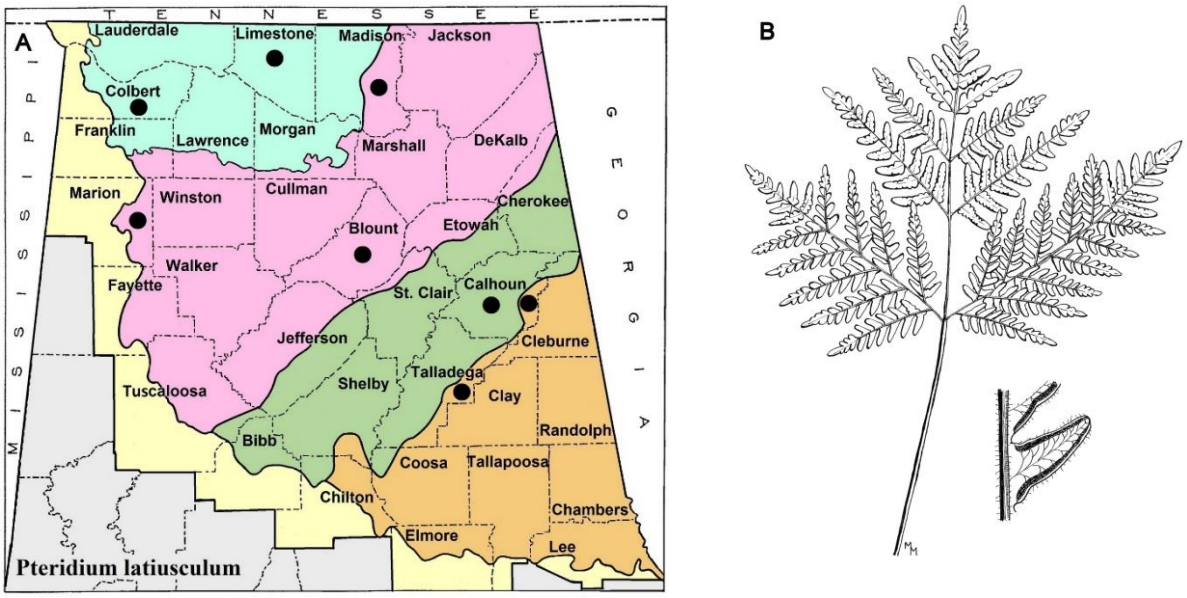


Figure 239. *Pteridium latiusculum*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 240. *Pteridium latiusculum*, Talladega Co., Alabama, 4 Jul 2024. Photos: Dan Spaulding.

During grain shortages in 18th-century Europe, peasants ground the rhizomes of bracken ferns (*Pteridium aquilinum*) to extend scarce flour supplies. Farmers also put the plant to practical use, employing its dried fronds as bedding for various livestock (Abbe 1981). In addition, its alkaline ashes provided potash vital for glassmaking and soap, while the sturdy stalks served as durable thatching for rural roofs (Lankester 1881). Herbalists brewed rhizome tea to treat spleen swelling, blended it with oil for wound ointments, and applied powdered rhizomes to hasten the healing of ulcers (Dunbar 1989). Before the advent of modern pharmaceuticals, practitioners relied on bracken as a vermifuge to expel intestinal worms (Frankel 1981). Taxonomists at that time regarded all bracken populations as a single, broadly defined *Pteridium aquilinum*, whereas today they recognize multiple distinct species.

Pteridium latiusculum resembles *P. pseudocaudatum* (Southern Bracken Fern) but differs in its pubescence and pinnule morphology. The leaves of *P. pseudocaudatum* are essentially glabrous, whereas those of *P. latiusculum* are distinctly pubescent, at least along segment margins. In terms of pinnule shape, the terminal segments of well-developed pinnules in *P. pseudocaudatum* are noticeably elongated, typically 6–15 times as long as wide, while in *P. latiusculum*, they are only slightly elongated, generally 2–4 times as long as broad (Fig. 240).

2. Pteridium pseudocaudatum (Clute) Christenh. {false-tail} — SOUTHERN BRACKEN FERN; SOUTHERN BRAKE (Fig. 241). [*Pteridium aquilinum* (L.) Kuhn subsp. *pseudocaudatum* (Clute) Hultén; *Pteridium aquilinum* (L.) Kuhn var. *pseudocaudatum* (Clute) A. Heller; *Pteridium latiusculum* (Desv.) Hieron. var. *pseudocaudatum* (Clute) Maxon]

Figure 241. *Pteridium pseudocaudatum*, Coosa Co., Alabama, 24 Apr 2022. Photo: Noah Yawn.

Plants terrestrial; deciduous. Sandy woodlands, savannas, woodlands, barrens, fields, pastures, and roadsides. Sporulates July–September; common throughout Alabama (Fig. 242). Native to the eastern USA, from Massachusetts to Missouri, south to East Texas, and Florida (Jacobs & Peck 1993).

The Southern Bracken Fern (*Pteridium pseudocaudatum*) is widespread across Alabama and other southeastern states. Unlike most native ferns, it can become a noxious weed due to its aggressive spread via deep underground rhizomes. These rhizomes make the fern notoriously difficult to eradicate and provide exceptional resistance to fire, as the surrounding soil insulates them from most wildfires. Because of this, the fern's fiddleheads are often among the first green shoots to emerge after a fire, quickly reestablishing a dense colony that covers the burned site.

Pteridium pseudocaudatum closely resembles *P. latiusculum* (Eastern Bracken Fern) but can be recognized by its distinctly elongated, "tailed" terminal pinnule segments—typically 6–15 times longer than wide—and its smooth, nearly hairless leaves (Fig. 243). By contrast, *P. latiusculum* bears terminal segments only 2–4 times as long as wide and has fine hairs on the lower leaf surface. Another similar species, *P. caudatum* (L.) Maxon (Lacy Bracken Fern), native to Florida and tropical America, is reminiscent of a skeletonized form of *P. pseudocaudatum* (Fig. 244).

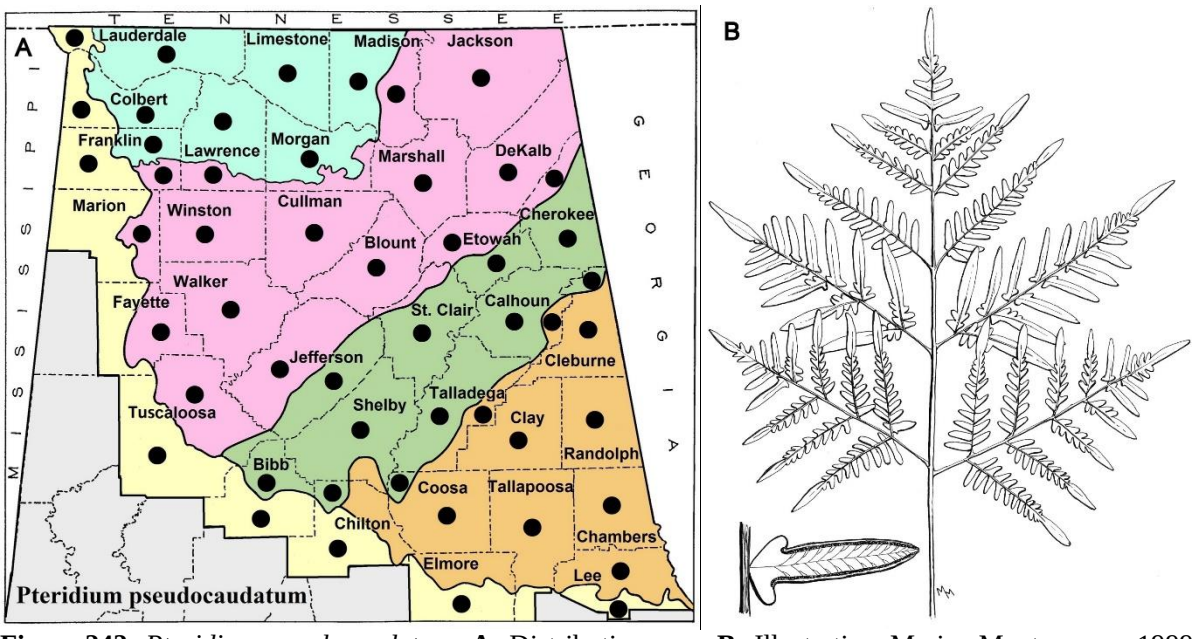


Figure 242. *Pteridium pseudocaudatum.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 243. *Pteridium pseudocaudatum*, Winston Co., Alabama, 3 Jul 2021. Photos: Dan Spaulding.

Bracken ferns produce the enzyme thiaminase, which can be toxic to livestock when consumed in large quantities, leading to thiamine deficiency and related health issues (Kingsbury 1964). Although some sources promote bracken fiddleheads as a wild edible—praised for their delicate flavor and mucilaginous texture reminiscent of okra—recent research has raised significant health concerns. Scientists have identified carcinogenic compounds in the plant and linked the traditional consumption of bracken fiddleheads in Japan to increased rates of stomach cancer (Thieret 1980).

Figure 244. *Pteridium caudatum*, Big Pine Key, Monroe Co., Florida, 27 Dec 2024. Photo: Alan Cressler.

The Cherokee used bracken fern in various medicinal preparations. They brewed a tonic believed to restore vitality and promote overall well-being, applied poultices to wounds for its antiseptic qualities, and relied on its antiemetic effects to ease nausea. Other Native American tribes also recognized the plant's versatility. Its long, sturdy rhizomes were woven into baskets, rugs, and mats, providing durable household materials. The young fiddleheads were boiled or steamed as a seasonal vegetable, and the rhizomes were roasted and ground into a starchy flour that could supplement other food sources during times of scarcity (Moerman 1998).

3. SITOBOLIUM Desvaux 1827 {sih-toh-BOH-lee-um}

[Greek *sitos*, grain, and *bolos*, lump; globular sori resemble grains of wheat or barley]

1. Sitobolium punctilobulum (Michx.) Desv. {dotted lobes; sori on leaf margins} — HAY-SCENTED FERN; BOULDER FERN; PASTURE FERN (Fig. 245). [*Dennstaedtia punctilobula* (Michx.) T. Moore]

Plants terrestrial; deciduous. Shaded sandstone bluffs, cliffs, and rocky slopes; further north, other habitats include woodland borders, clearings, pastures, thickets, and roadbanks. Sporulates June–September; rare in the Cumberland Plateau, Ridge & Valley, and Piedmont (Fig. 246). Occurs in eastern North America from eastern Canada south to northern Alabama and Georgia, extending westward to the Great Lakes, the upper Mississippi Valley, and north Arkansas (Nauman & Evans 1993). The Alabama Heritage Program (1994) initially classified this fern as vulnerable (S3) but now recognizes it as more common in the state than previously believed.

In the northern regions of its range, the Hay-Scented Fern is highly prolific, spreading aggressively through its rhizomes to the extent that some people regard it as a weed. The fern releases allelopathic chemicals—substances that inhibit the growth and germination of neighboring plants. Research has demonstrated that these ferns play a crucial role in maintaining open patches in their habitat by hindering the germination and growth of competing species, particularly tree seedlings, in their vicinity (Hill 2003b).

Figure 245. *Sitobolium punctilobulum*, Randolph Co., Alabama, 24 Apr 2024. Photos: Lee Kelly.

The fronds of this fern are finely glandular-hairy and release a strong, sweetish fragrance when bruised. The scent becomes especially noticeable as the plants dry, reminiscent of freshly mown hay; hence its common name, "hay-scented fern." Other vernacular names like "boulder fern" and "pasture fern" reflect some of its habitats (Clute 1901). The Cherokee brewed tea from the fern to help control chills, while other tribes used the small, swollen nodules at the base of the plant's crown—likely modified leaf bases or rhizome swellings—to treat lung hemorrhages (Dunbar 1989).

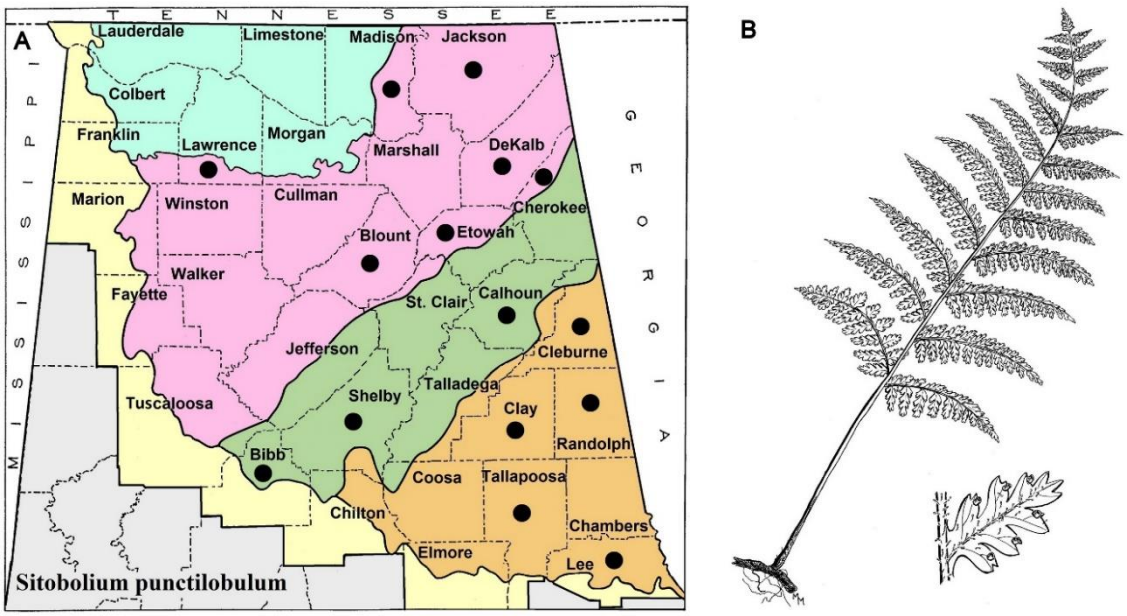


Figure 246. *Sitobolium punctilobulum*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 247. *Sitobolium punctilobulum*, DeKalb Co., Georgia, 10 Jun 2024. Photo: Alan Cressler.

The Hay-scented Fern is readily distinguished from other woodland ferns of similar size and appearance—such as the Southern Lady Fern (*Athyrium asplenioides*), Intermediate Wood Fern (*Dryopteris intermedia*), and New York Fern (*Amauropelta noveboracensis*)—by several consistent traits. *Sitobolium punctilobulum* fronds are yellow-green to pale green and usually bear fine, whitish-gray glandular hairs. The silvery-pilose petioles lack scales, and the species spreads by long-creeping rhizomes that form scattered clonal patches. Another key diagnostic feature is its tiny sori, less than 0.5 mm in diameter, positioned near the margins of the leaf segments and enclosed by distinctive whitish, cup-shaped indusia (Fig. 247).

15. CYSTOPTERIDACEAE (Brittle Fern Family) – in Polypodiales

1. Cystopteris Bernhardi 1806 {sis-TOP-ter-iss}
[Greek *kystos*, bladder, and *pteris*, fern; young indusia inflated]

1. Rhizome elongated, the apex projecting more than 1 cm beyond the leaf bases; blades usually widest near the middle; pinnules at mid-blade pinnate (dissected to midrib); fronds lacking glandular hairs; bulblets absent; plants terrestrial.....***Cystopteris protrusa***
1. Rhizome short, the apex scarcely extending beyond the leaf bases; blades usually widest near base; pinnules at mid-blade pinnatifid (deeply lobed but not dissected to midrib); fronds with or without glandular hairs; bulblets absent or present; plants epipetric (growing on rock).

   2. Leaf apex gradually long-tapered (attenuate), often elongated; leaf blades narrowly triangular, at least 3 times as long as broad and 2–3 times longer than the petioles; gland-tipped hairs usually scattered along rachis and leaflets; bulblets usually present, spherical, smooth except for a few glandular hairs, 2–3 mm in diameter, and found on the rachis and leaflets.....***C. bulbifera***
   2. Leaf apex acute to acuminate, not long-tapered; leaf blades spearhead-shaped, about 2 times longer than broad and about the same length as the petioles; gland-tipped hairs absent or scarce; bulblets often absent, if present, deformed, densely scaly, 1.5 mm in diameter or smaller, and found only on rachis.....***C. tennesseensis***

1. Cystopteris bulbifera (L.) Bernh. {bearing bulbs} — BULBLET BLADDER FERN; BULBLET FERN (Fig. 248). [*Filix bulbifera* (L.) Underw.]

Figure 248. *Cystopteris bulbifera*, Etowah Co., Alabama, 25 Sep 2016. Photo: Alan Cressler.

Plants usually epipetric, rarely terrestrial; deciduous. Shaded cliffs, ledges, bluffs, and talus slopes, often on calcareous rock. Sporulates May–September; uncommon in the Highland Rim and Cumberland Plateau; rare in the Ridge & Valley; very rare in the Piedmont (Fig. 249). Distributed primarily in eastern North America from Nova Scotia to Ontario, south to northern Arkansas, and through the Appalachians to north Alabama, with outlier populations in the Southwest (Haufler et al. 1993a).

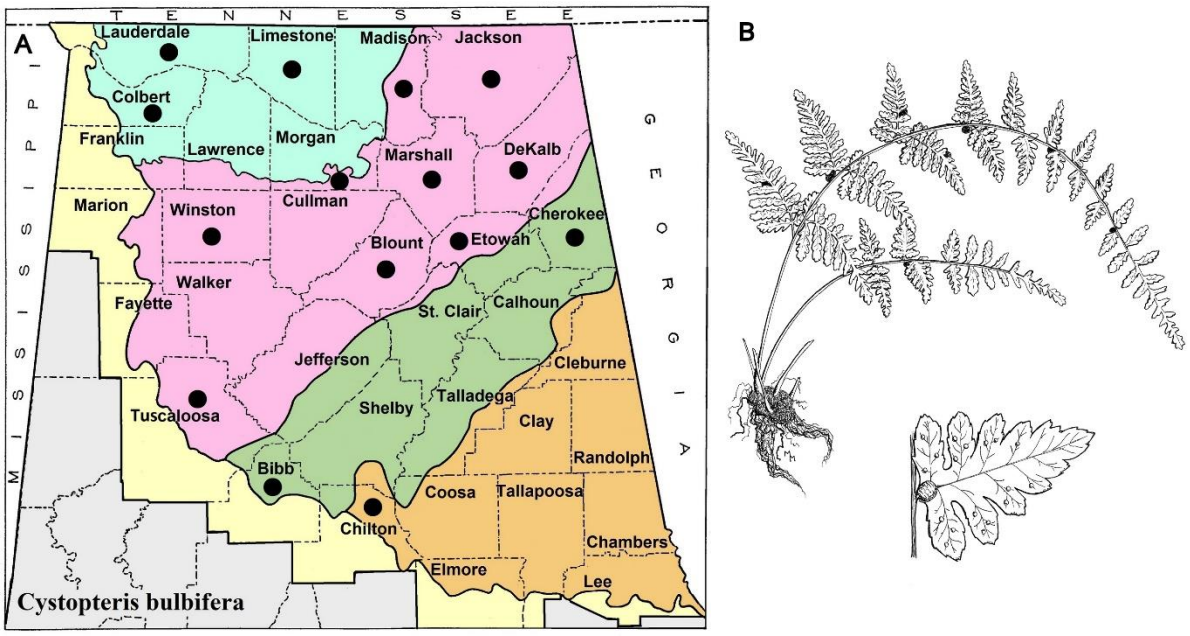


Figure 249. *Cystopteris bulbifera*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 250. *Cystopteris bulbifera*, Warren Co., Tennessee, 4 Sep 2011. Photo: Alan Cressler.

The common name "bulblet bladder fern" refers to the bladder-like appearance of its indusia and the small vegetative buds (bulblets) that form on the underside of mature leaves (Fig. 250). These bulblets, about half the size of a pea, can develop roots and grow into new plants once detached from the parent. Occasionally, they begin to sprout while still attached, accelerating the reproductive process. However, the bulblets are highly deciduous and often fall off soon after collection, making them rare in herbarium specimens.

Figure 251. *Cystopteris bulbifera*, Jackson Co., Alabama, 18 May 2011. Photo: Wayne Barger.

Cystopteris bulbifera is easily recognized by its long, narrowly triangular fronds (Fig. 251), smooth, well-formed bulblets, and preference for moist, rocky habitats. Young fronds of the Bulblet Bladder Fern may resemble those of *C. tennesseensis*, but *C. bulbifera* often displays a reddish rachis during early development. Gland-tipped hairs provide a more reliable distinction: *C. bulbifera* typically produces numerous such hairs, while *C. tennesseensis* bears few, if any. The bulblets offer further diagnostic value; those of *C. tennesseensis*, when present, are usually misshapen and covered in scales.

2. Cystopteris protrusa (Weath.) Blasdell {protruding} — LOWLAND BRITTLE FERN; SPREADING BLADDER FERN; LOWLAND BLADDER FERN (Fig. 252). [*Cystopteris fragilis* (L.) Bernh. var. *protrusa* Weath.; *Filix fragilis* (L.) Underw.]

Figure 252. *Cystopteris protrusa*, Lauderdale Co., Alabama, 16 Mar 2020. Photo: Chesley Rogers.

Plants terrestrial; deciduous. Rich, moist woods. Sporulates April–July; uncommon in the Highland Rim, Cumberland Plateau, and Ridge & Valley; rare in the Piedmont and Coastal Plain (Fig. 253). Native to the eastern USA and adjacent Canada, from Massachusetts to Ontario and Wisconsin, south to Georgia, the Florida Panhandle, and East Texas (Kartesz 2025).

The common name "lowland brittle fern" reflects two defining characteristics of the species. First, its fronds are delicate and easily damaged. Second, while many related ferns thrive on rocky substrates, this species prefers rich, moist forest soils (Fig. 254). *Cystopteris protrusa* is also known as the "spreading bladder fern" due to its distinctive creeping rhizomes extending beyond the fronds and producing buds for the following year's growth. This feature distinguishes it from other ferns in the genus, where fronds typically emerge near the rhizome apex. The term *bladder* refers to the bladder-like indusium that covers the sori.

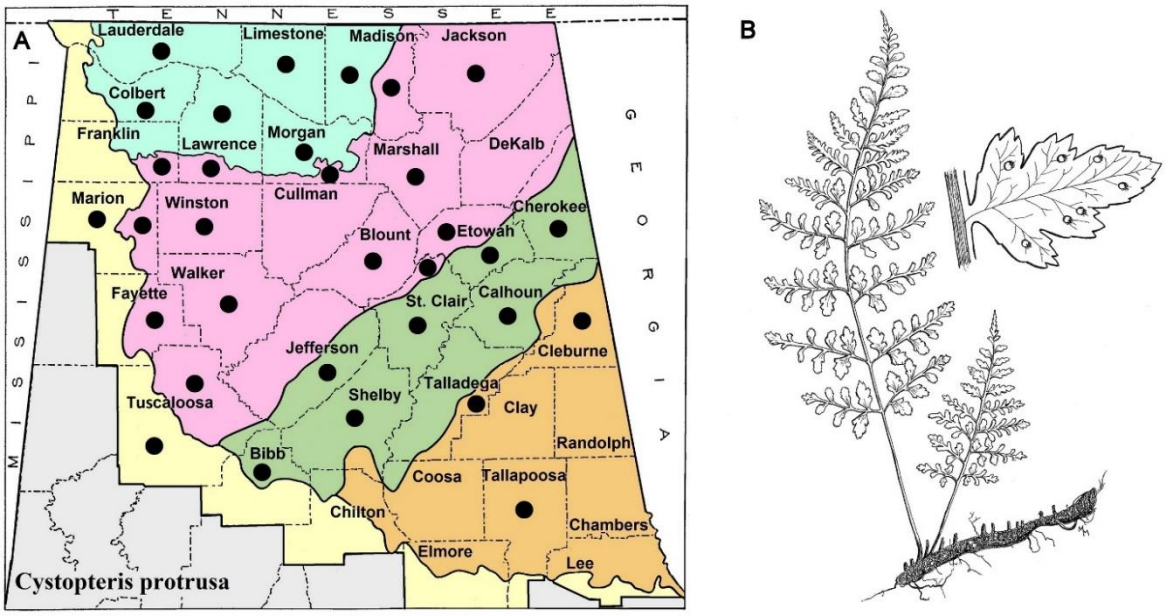


Figure 253. *Cystopteris protrusa.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 254. *Cystopteris protrusa.* **A.** Protruding rhizome apex, Etowah Co., Alabama, 17 Sep 2024. Photo: Dan Spaulding. **B.** Rhizome with mature leaves, Fannin Co., Georgia, 5 Jun 2011. Photo: Alan Cressler.

3. Cystopteris tennesseensis Shaver {of Tennessee} — TENNESSEE BLADDER FERN; TENNESSEE BULBLET FERN (Fig. 255). [*Cystopteris* ×*tennesseensis* Shaver]

Figure 255. *Cystopteris tennesseensis*, Madison Co., Alabama, 8 May 2021. Photo: Alan Cressler.

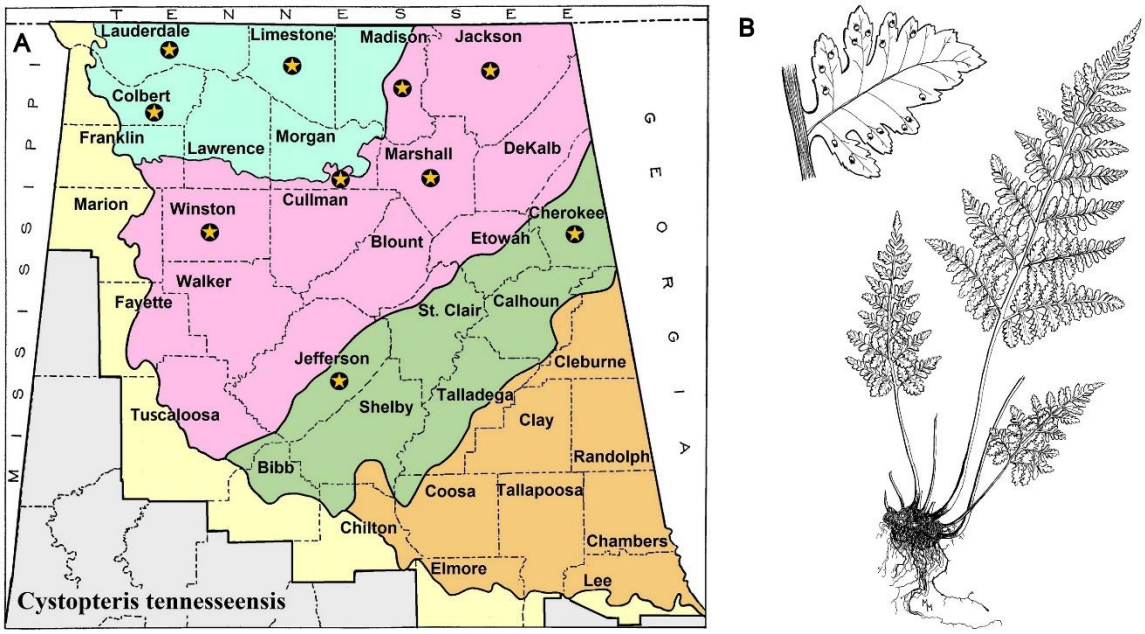


Figure 256. *Cystopteris tennesseensis.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Plants epipetric; deciduous. Shaded limestone rocks on slopes, cliffs, and ledges. Sporulates April–October; rare in the Highland Rim and Cumberland Plateau; very rare in the Ridge & Valley (Fig. 256). Native to the eastern USA from Southern Pennsylvania to southern Michigan, south to Oklahoma, north Georgia, and northern Alabama (Haufler et al. 1993a). The Alabama Natural Heritage Program (2023) lists this species as imperiled (S2) within the state.

In *Ferns of Tennessee*, Jesse Shaver (1954) described *Cystopteris tennesseensis* as a fertile allotetraploid, identifying its parent species as *C. bulbifera* and *C. protrusa* (then classified as *C. fragilis var. protrusa*) based on its intermediate traits (Fig. 257). He collected the type specimen from a north-facing limestone bluff along a creek in Smith County, Tennessee. Before Shaver's work, botanists frequently misidentified *C. tennesseensis* as *C. fragilis*. Consequently, historical records of *C. fragilis* from Alabama likely refer to *C. tennesseensis* or *C. protrusa* instead.

Figure 257. *Cystopteris tennesseensis*, Walker Co., Georgia, 2 May 2009. Photo: Alan Cressler.

Haufler et al. (1990) characterized *Cystopteris tennesseensis* as a robust, recently evolved species that has successfully adapted to ecological niches unoccupied by its parent species. Their study documented instances of sympatry, where two or all three species coexisted. In these situations, *C. protrusa* typically occupied the forest floor, *C. bulbifera* thrived on moist cliffs and nearby talus slopes, while *C. tennesseensis* inhabited drier cliffs. The more terrestrial *C. protrusa* is easily recognized by its long internodes, with a rhizome apex extending beyond the current season's leaves. In contrast, the two rock-dwelling species, *C. bulbifera* and *C. tennesseensis*, have short rhizomes.

In *Flora of North America*, Haufler et al. (1993) noted that *Cystopteris tennesseensis* occasionally inhabits human-made structures such as rock walls and bridge abutments. Reichgelt (2024) emphasizes that many lithophytic (rock-dwelling) ferns readily colonize artificial vertical surfaces in urban environments. He suggests that these stone structures can function as novel niches for native species, although their success often hinges on their resilience to urban heat-island effects. Recently, the senior author of this paper documented a population of *C. tennesseensis* thriving at Birmingham's historic Sloss Furnaces, growing alongside other lithophytic ferns (Fig. 258). Similarly, Cusick (1989) reported *C. tennesseensis* colonizing the mortar of a furnace stack in Maryland. Reichgelt (2024) proposes that *C. tennesseensis* exemplifies a species adapting to "urban cliffs" in the eastern United States, a noteworthy development given its uncommon or rare status within its range.

Figure 258. *Cystopteris tennesseensis*, in cracks of old masonry walls at Sloss Furnaces National Historic Landmark in Birmingham, Jefferson Co., Alabama, 26 Oct 2024. Photos: Dan Spaulding.

Morphologically, *Cystopteris tennesseensis* resembles other *Cystopteris* species found in Alabama but exhibits traits indicative of its hybrid origin. As an allotetraploid, it carries the combined genomes of two diploid progenitors and displays intermediate characteristics (Haufler et al. 1990). *Cystopteris bulbifera* has elongated leaf blades, typically four to five times longer than wide and broadest at the base. Its fronds bear numerous glandular hairs and round, fleshy bulblets. In contrast, the leaf blades of *C. tennesseensis* are only slightly more than twice as long as wide and are widest just above the base. Its fronds produce fewer glandular hairs, and its bulblets are spindle-shaped and scaly. *Cystopteris protrusa*, by comparison, has leaf blades that are broadest near the middle and tapering toward the base. Unlike the other two species, its fronds lack both glandular hairs and bulblets.

16. DIPLAZIOPSIDACEAE (Glade Fern Family) – in Polypodiales

1. HOMALOSORUS Small ex Pichi Sermolli 1977 {hoh-MAL-oh-sor-us}

[Greek *homalos*, even or level, *sorus*, a heap or collection; alluding to the regular lines of sori]

1. Homalosorus pycnocarpos (Spreng.) Pichi Sermolli {densely fruited; numerous sori} — NARROW-LEAF GLADE FERN; NARROW-LEAF-SPLEENWORT (Fig. 259). [*Asplenium pycnocarpon* Spreng.; *Asplenium angustifolium* Michx.; *Athyrium angustifolium* Milde; *Athyrium pycnocarpon* (Spreng.) Tidestrom; *Diplaziopsis pycnocarpos* (Spreng.) M.G. Price; *Diplazium pycnocarpon* (Spreng.) Broun]

Figure 259. *Homalosorus pycnocarpos*, Jackson Co., Alabama, 12 May 2007. Photo: Alan Cressler.

Plants terrestrial; deciduous. Rich hardwood forests, shaded cliff bases, limestone sinks, cave entrances, and moist woods in basic or neutral soils. Sporulates July–September; uncommon in the Highland Rim and Cumberland Plateau; very rare in the Ridge & Valley, Piedmont, and Coastal Plain (Fig. 260). Native to the eastern USA and adjacent Canada from Quebec to Ontario, south to western Louisiana, and northern Florida (Kato 1993c). Freeman et al. (1979) initially designated *Homalosorus pycnocarpos* as a Species of Special Concern in the state, but later determined it to be more widespread than previously believed.

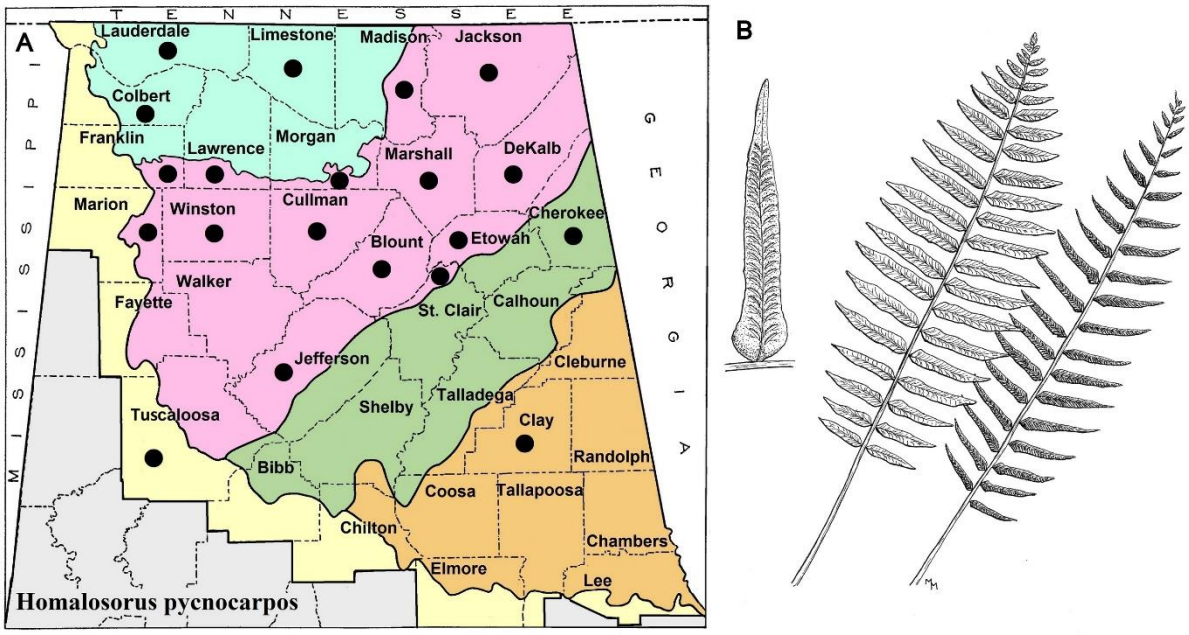


Figure 260. *Homalosorus pycnocarpos.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 261. *Homalosorus pycnocarpos*, Crawford Co., Pennsylvania, 12 Aug 2023. Photo: Noah Yawn.

Figure 262. *Homalosorus pycnocarpos*, Etowah Co., Alabama, 17 Sep 2024. Photos: Dan Spaulding.

Homalosorus pycnocarpos is a distinctive fern recognized by a unique combination of traits that separate it from other southeastern species. Its large, once-pinnate fronds bear entire or shallowly toothed pinnae with linear sori (Fig. 261). The elongated sori, reminiscent of those in *Asplenium* (spleenworts), prompted André Michaux in 1803 to describe the species as *Asplenium angustifolium*. This species exhibits weak dimorphism, producing fertile fronds with narrower pinnae than sterile ones (Fig. 262a). Commonly known as the "glade fern" for its preference for moist, rocky openings (Fig. 262b), it also forms extensive populations in rich calcareous forests (Fig. 263).

Figure 263. *Homalosorus pycnocarpos* population, Stephens Co., Georgia, 4 Jul 2022. Photo: Noah Yawn.

Pichi Sermolli (1977) established *Homalosorus* as a monotypic genus, recognizing only *H. pycnocarpos*, a fern native to temperate eastern North America. Kato and Darnaedi (1988) proposed a close relationship between *Homalosorus* and the Asian genus *Diplaziopsis*, leading Price (1990) to transfer *Homalosorus* into *Diplaziopsis*, a reclassification supported by Weakley et al. (2025). However, Christenhusz et al. (2011) maintained *Homalosorus* as a distinct genus, citing differences in blade apex shape, venation patterns, and chromosome numbers, despite shared traits such as pinna shape, rachis grooving, indusium structure, and spore morphology. DNA sequencing by Chunxiang et al. (2011) further supports the recognition of *Homalosorus* as a separate monotypic genus.

17. **ASPLENIACEAE** (Spleenwort Family) – in Polypodiales

1. **Asplenium** Linnaeus. 1753 {as-PLEE-nee-um}

[Greek *splen*, for spleen; Dioscorides thought it helped treat diseases of the spleen]

The common name "spleenwort" applies to many species within this genus and reflects their long-standing use in traditional medicine, particularly for treating ailments related to the spleen (Frankel 1981). This association dates back to at least the sixteenth century, when the English herbalist John Gerard recommended decoctions of these ferns for conditions such as an enlarged or obstructed spleen (Dunbar 1989). The name combines 'spleen' with the Old Germanic word *wurt* (or *wyrt* in Old English), meaning plant or herb, highlighting the fern's historical identity as a medicinal remedy.

Hybridization is well documented in *Asplenium*. In 1925, Edgar T. Wherry proposed that rock-dwelling spleenworts of the southern Appalachian Mountains originated from a northern ancestor that later hybridized with a southern lineage. Expanding on this idea, Wagner (1954) investigated the reticulate evolution of the Appalachian *Asplenium* complex (Fig. 264). He demonstrated that three diploid progenitors—*A. montanum, A. platyneuron*, and *A. rhizophyllum*—gave rise to a series of sterile and fertile hybrids across the eastern United States (Fig. 265). Recent research has identified 10 taxa within this hybrid complex, including three fertile allotetraploid species—*A. bradleyi, A. pinnatifidum*, and *A. tutwilerae*—and seven sterile hybrids: *A. ×boydstoniae, A. ×ebenoides, A. ×gravesii, A. ×kentuckiense, A. ×reverterum, A. ×trudellii*, and *A. ×wherryi*. All occur in Alabama except for *A. ×wherryi*.

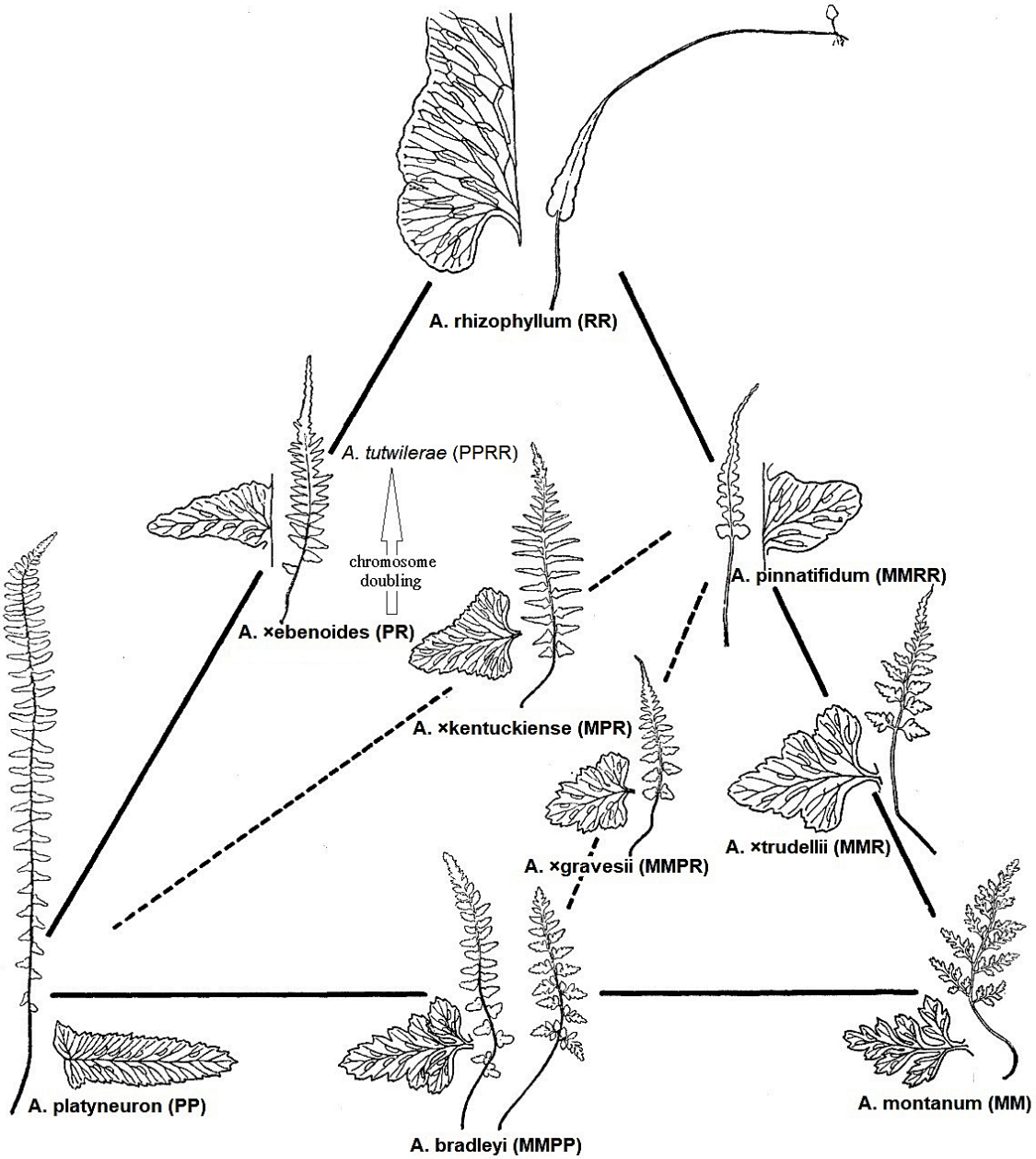


Figure 264. Reticulate evolution in Appalachian *Asplenium*, with genomic formulas in parentheses (adapted from Wagner 1954).

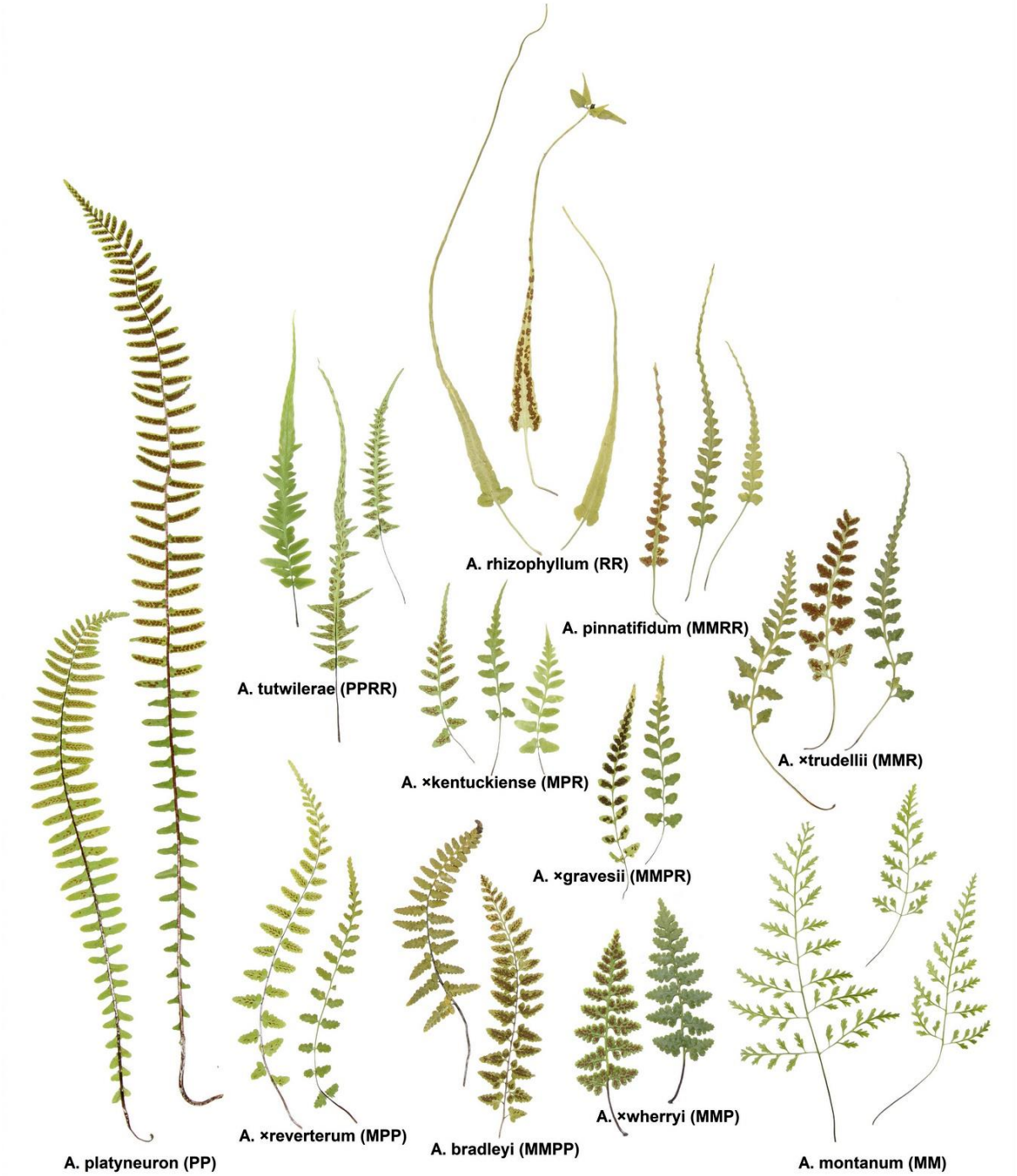


Figure 265. The Appalachian *Asplenium* complex with all taxa except *A.* ×*boydstoniae* (PPPR) and *A.* ×*ebenoides* (PR). Genomic formulas are in parentheses. Poster created by Noah Yawn, 2024.

1. Leaves simple and unlobed, except for small basal ears.

    2. Leaf apex long-attenuate (long-tapering) or caudate (tail-like), often rooting at the tip; veins forming areoles; sori solitary along veins .....***Asplenium rhizophyllum***
    2. Leaf apex acute to acuminate, not rooting at the tip; veins free, not forming areoles; sori paired along veins .....***Asplenium scolopendrium***

1. Leaves deeply lobed (pinnatifid) or divided to the rachis (pinnate to tripinnate); leaf apex often long-tapering.

    3. Leaves pinnatifid or pinnate in the lower portion, pinnatifid above, at least in the upper third of the blade, the apex unlobed.

        4. Leaf blades pinnatifid throughout, or with only the lowest pair of pinnae divided to the rachis; spores well-developed and viable..... ***Asplenium pinnatifidum***
        4. Leaf blades pinnatifid above and pinnate below for at least two pairs of pinnae; spores shrunken and sterile.

            5. Leaf blades irregular or asymmetric, with lobes or pinnae differing in size and shape; rachis brown along three-fourths of its length, green near the apex; leaves sometimes rooting at the tip; plants typically growing on calcareous rocks such as limestone, often associated with *A. platyneuron* and *A. rhizophyllum*.....***Asplenium ×ebenoides***.
            5. Leaf blades generally regular and symmetric, with lobes or pinnae mostly uniform in size and shape; rachis brown less than half its length or green throughout; leaves not rooting at the tip; plants typically growing on acidic rocks such as sandstone.

                6. Leaf blade narrowly triangular, broadest at the basal or next-to-basal pair of pinnae; petiole usually brown below and green above, with dark pigmentation extending about halfway up the petiole; rachis green throughout; often associated with *A. montanum* and *A. pinnatifidum* .....***Asplenium ×trudellii***.
                6. Leaf blade oblong or linear-attenuate, usually broadest one-fourth to one-half the distance from the base of blade; petiole usually brown throughout, dark pigmentation occasionally extending into the blade; rachis green throughout or brown below to the first or second pair of pinnae and green above; lowermost pinnae margins shallowly lobed, crenate (with rounded teeth), or nearly entire.

                    7. Blades not tapering at the base except for an occasional reduced pinna, lower three or four pinnae pairs approximately equal in size; frond texture somewhat leathery; often associated with *A. bradleyi* and *A. pinnatifidum* .....***Asplenium ×gravesii***
                    7. Blades tapering at the base, with the second or third lower pinna pairs shorter than the upper fourth or fifth; frond texture membranous (more papery); often associated with *A. pinnatifidum* and *A. platyneuron*..... ***Asplenium ×kentuckiense***

    3. Leaves pinnate, pinnate-pinnatifid, bipinnate, or tripinnate (sometimes pinnatifid above); leaf apex not long-tapering, except in *Asplenium abscissum*.

        8. Rachis shiny black or dark brown throughout its length, not grooved on upper surface; leaves 1-pinnate; leaf blade linear, lanceolate, or oblanceolate, with more-or-less parallel sides for much of its length.

            9. Pinnae asymmetrical, with the main vein running along the basal margin of a pinna; sori usually 1 (rarely 2 or 3) per leaflet, positioned along the basal edge of the vein; indusium translucent, whitish.....***Asplenium monanthes***
            9. Pinnae symmetrical, with the main vein running more or less along the middle of a pinna; sori numerous (more than 4) per leaflet, positioned on both sides of the vein; indusium opaque, greenish.

10. Pinnae mostly alternate, with prominent auricles (basal lobes); pinna bases usually overlapping the rachis; leaves dimorphic, with larger, upright fertile fronds and smaller, spreading sterile fronds; leaflet margins usually finely serrate, occasionally incised; plants terrestrial or growing on rock.....***Asplenium platyneuron***
10. Pinnae mostly opposite, with auricles absent or small; pinna bases usually not overlapping the rachis; leaves monomorphic, with fertile and sterile fronds similar; leaflet margins crenulate (with rounded teeth) or nearly entire; plants mainly growing on rock.

    11. Pinnae oblong, longer than wide, usually over 7 mm long; pinna auricles present at the bases of leaflets, sometimes obscure.....***Asplenium resiliens***
    11. Pinnae mostly oval, nearly as wide as long, usually under 7 mm long; pinna auricles absent at the bases of leaflets .....***Asplenium trichomanes***

8. Rachis shiny black or dark brown throughout its length, not grooved on upper surface; leaves 1-pinnate; leaf blade linear, lanceolate, or oblanceolate, with more-or-less parallel sides for much of its length.

8. Rachis brown for up to half its length or green throughout, usually grooved on the upper surface (at least in the green portion); leaves pinnate, pinnate-pinnatifid, bipinnate, or tripinnate; leaf blade often narrowly to broadly triangular, widest at or just above the base, or lance-oblong or lanceolate with sides of the blade not parallel.

    12. Leaves 1-pinnate; blade over 5 cm wide at its widest point; lower pinnae more than 2.5 cm long with acuminate tips; leaf apex long-tapering .....***Asplenium abscissum***
    12. Leaves pinnate-pinnatifid (at least basally), bipinnate, or tripinnate; blade under 5 cm wide at the widest point; lower pinnae less than 2.5 cm long; leaf apex rounded, acute, or acuminate.

        13. Leaves usually with 2–5 pairs of pinnae; petioles entirely green; pinnae on distinct stalks; ultimate segments lacerate toward apex; plants usually on calcareous rock (e.g., limestone) .....***Asplenium ruta-muraria***
        13. Leaves with more than 5 pairs of pinnae; petioles dark brown, at least at base; pinnae short-stalked (upper pinnae often sessile); plants usually on acidic rock (e.g., sandstone, quartzite).

            14. Petiole dark brown at the base, green above; rachis green throughout; leaf blades bipinnate-pinnatifid for most of their length or pinnate-pinnatifid above and bipinnate below; segment margins with only a few teeth; blade usually triangular or ovate-lanceolate.....***Asplenium montanum***
            14. Petioles dark brown throughout; rachis brown up to at least the first few pinnae; leaf blades mostly 1-pinnate, shallowly to deeply lobed, occasionally the lowest 1 or 2 pairs of leaflets compound; segment margins serrated; blade usually lanceolate**.**

                15. Rachis brown only up to about half its length; sori mostly opposite; spores well-developed and viable.....***Asplenium bradleyi***
                15. Rachis brown up to about three-quarters of its length; sori mostly alternate, forming a herringbone pattern; spores shrunken and sterile; (associated with *A. bradleyi* and *A. platyneuron*) .....***Asplenium ×reverterum***

1. Asplenium abscissum Willd. var. **abscissum** {cut off; the leaves} — CUTLEAF SPLEENWORT; ABSCISED SPLEENWORT; CUT SPLEENWORT (Fig. 266).

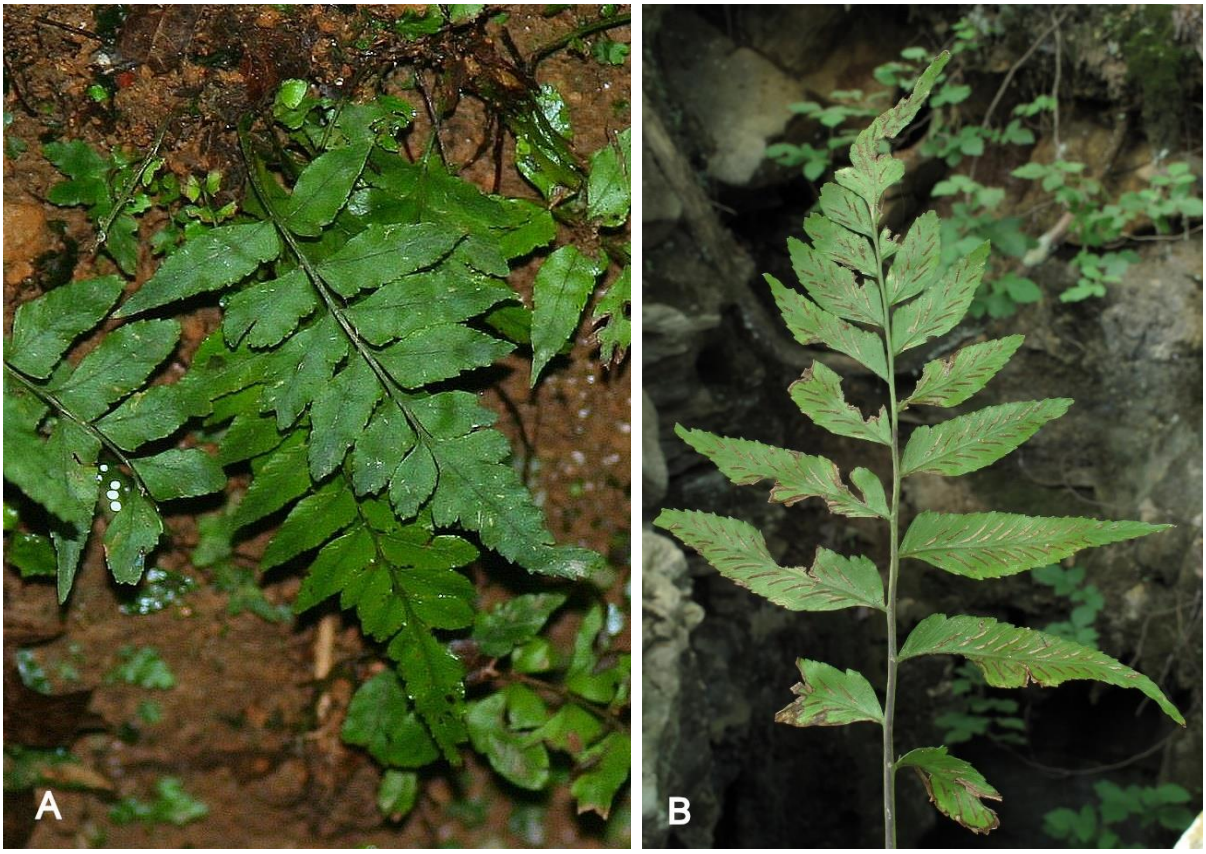


Figure 266. *Asplenium abscissum.* **A.** Jackson Co., Alabama, 10 Jul 2009. Photo: Wayne Barger. **B.** Jackson Co., Alabama, 20 Jun 2009. Photo: Alan Cressler.

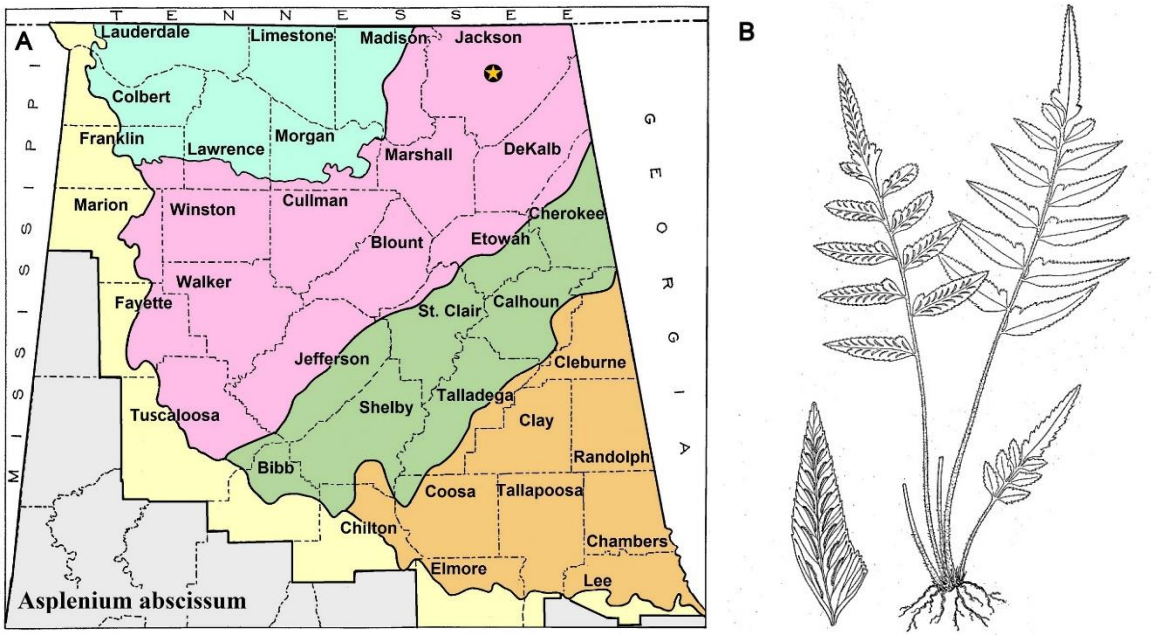


Figure 267. *Asplenium abscissum.* **A**. Distribution map. **B**. Illustration: Ruth Sinclair George, 1938.

Plants epipetric; evergreen. Walls of limestone sinkholes or pits and vertical limestone ledges of caves. Sporulates year-round; very rare in the Jackson County Mountains District of Cumberland Plateau (Fig. 267). This species occurs chiefly in central and south Florida, south through the West Indies, Mexico, Central America, and South America (Wagner et al. 1993). Disjunct in northeast Alabama (Barger et al. 2010). The Alabama Natural Heritage Program (2023) lists this species as critically imperiled (S1) within the state.

On May 20, 1989, Alan Cressler (pers. comm. 2025) made a significant discovery in northern Jackson County, Alabama, of a population of *Asplenium abscissum* var. *abscissum* far beyond its typical range. This fern usually grows in the limestone regions of peninsular Florida, particularly along the southeastern coast. The nearest population lies roughly 800 kilometers (500 miles) away, in Alachua County, Florida, near Gainesville. The other variety of this species, *A. abscissum* var. *subaequilaterale* Rosenst., native to Bolivia and Peru, is distinguished by its long-acuminate pinnae, which feature more than 18 pairs of veins (Kessler & Smith 2018).

Figure 268. *Asplenium abscissum* in a sinkhole, Jackson Co., Alabama, 20 Jun 2009. Photo: Alan Cressler.

The Alabama colony of *Asplenium abscissum* grows about 7.6 m (25 ft) down a vertical pit that drops more than 46 m (150 ft). The plants anchor themselves to moist, weathered limestone inside the sinkhole (Fig. 268). This tropical fern survives in this otherwise temperate region because the cave generates a "chimney effect." The narrow entrance regulates the microclimate, keeping the ambient temperature around the plants from dropping below 14 °C (56 °F) throughout the year. In winter, when surface air cools below this threshold, warmer cave air rises through the sinkhole, and colder, denser air flows in through other openings. This circulation in the pit maintains a steady flow of air at about 14 °C (56 °F), shielding the plants from freezing. A perennial stream, approximately 18 m (60 ft) below the ferns, sustains high relative humidity and provides a favorable microhabitat (Barger et al. 2010).

2. Asplenium bradleyi D.C. Eaton {for Frank H. Bradley, 1838–1879, American geologist} — BRADLEY'S SPLEENWORT; CLIFF SPLEENWORT (Fig. 269). [*Asplenium stotleri* Wherry]

Figure 269. *Asplenium bradleyi*, Cherokee Co., Alabama, 9 Jun 2011. Photo: Alan Cressler.

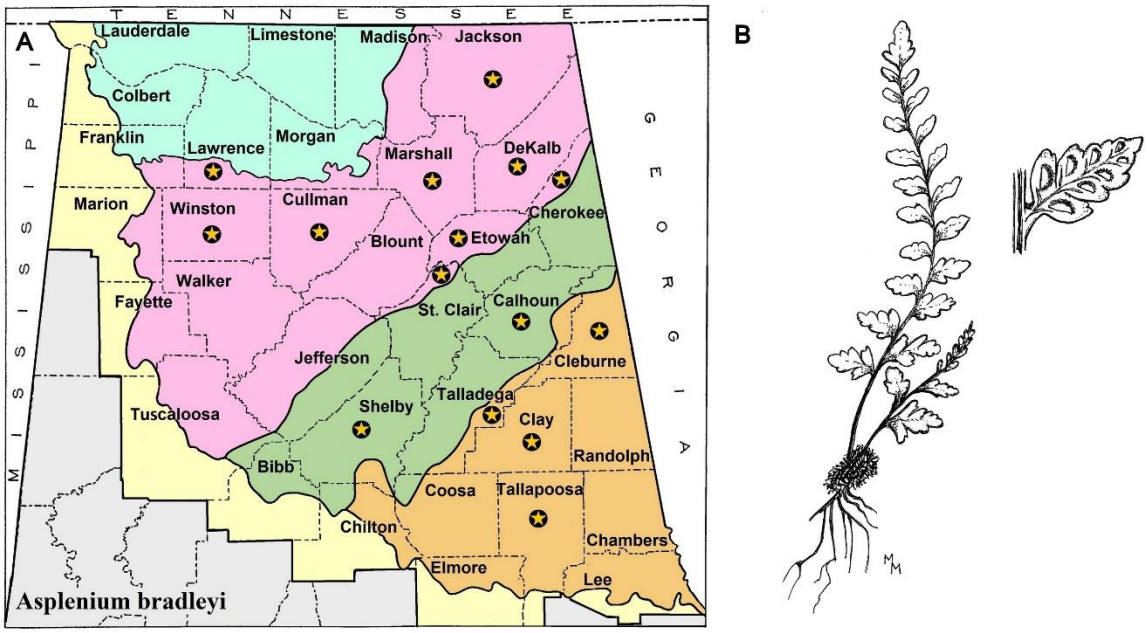


Figure 270. *Asplenium bradleyi.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Plants epipetric; evergreen. Acidic rock cliffs and ledges, usually composed of sandstone, in shady, dry-mesic habitats. Sporulates April–October; rare in the Cumberland Plateau, Ridge & Valley, and Piedmont (Fig. 270). Endemic to the eastern USA, scattered from central Georgia and northern Alabama north to New York and Ohio, and west to Arkansas and southeastern Oklahoma (Wagner et al. 1993). The Alabama Natural Heritage Program (2023) ranks this species as imperiled (S2) within the state.

Frank Howe Bradley discovered *Asplenium bradleyi* in Tennessee in 1870, and Harvard botanist Daniel Cady Eaton formally described the species three years later, in 1873, naming it in Bradley's honor (Dean 1969). This allotetraploid fern arose as a hybrid between *A. montanum* and *A. platyneuron*, achieving fertility through chromosome doubling. Morphologically, Bradley's spleenwort exhibits traits intermediate between those of its parents. Its fertility also enables it to cross with *A. pinnatifidum*, producing the hybrid *A.* × *gravesii*.

Figure 271. *Asplenium bradleyi*, Stephens Co., Georgia, 7 Jun 2009. Photo: Alan Cressler.

Wagner (1954) provided detailed comparisons of the rachises of *Asplenium bradleyi* and its parent species. In *A. platyneuron*, the rachis is uniformly dark brown, nearly circular in cross-section, with two fine ridges along the upper surface spaced about half the diameter of the rachis. By contrast, *A. montanum* has a green rachis with a flattened-triangular shape, bearing two rounded flanges separated by a broad, shallow groove and a central bulge. The rachis of *A. bradleyi* is intermediate: brown only on the lower half, slightly flattened, with ridges spaced about the same distance as the diameter of the rachis, and the upper groove shows only a slight central bulge (Fig. 272).

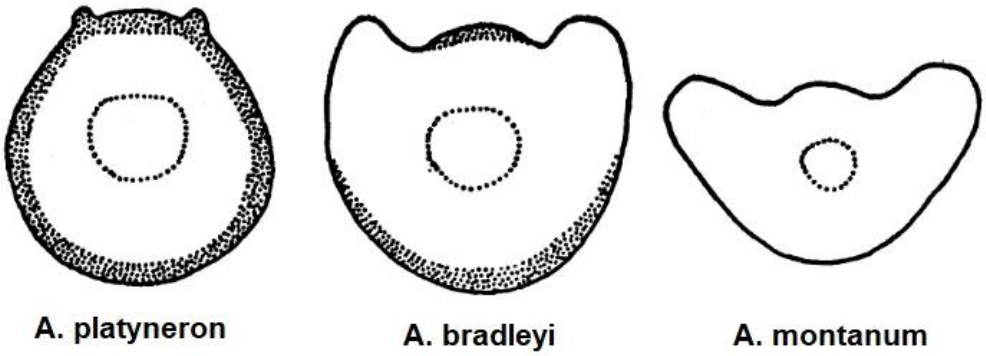


Figure 272. Rachis cross-sections of *Asplenium bradleyi* and its progenitors (Wagner 1954).

Without close examination of the rachis, one might mistake *Asplenium bradleyi* for a smaller form of *A. platyneuron*. Careful inspection of the basal leaflets, however, reveals clear distinctions: in *A. bradleyi*, the leaflets attach by tiny stalks, while in *A. platyneuron*, they join the rachis directly without stalks. *Asplenium bradleyi* also differs from *A. montanum* in petiole coloration—its petiole is dark brown throughout, whereas in *A. montanum* it is darkened only at the base or for up to half its length (Fig. 271).

3. Asplenium ×ebenoides R.R. Scott {resembling ebony spleenwort; one of its parents} — SCOTT'S SPLEENWORT; DRAGON-TAIL FERN (Fig. 273). [×*Asplenosorus ebenoides* (R.R. Scott) Wherry]

Figure 273. *Asplenium ×ebenoides*, Rock Bridge Co., Virginia, 11 Sep 2024. Photo: Joey Thompson.

Plants epipetric; evergreen. Moist outcrops of calcareous sedimentary rocks, such as limestone and dolomite. Sterile hybrid [*Asplenium platyneuron* × *rhizophyllum*], spores abortive; rare in the Highland Rim and Cumberland Plateau (Fig. 274). The hybrid occurs sporadically in the eastern United States, ranging from New Hampshire and Vermont west to southern Ohio, Missouri, and Arkansas, and south through the Appalachians to northwestern Georgia and northern Alabama (Kartesz 2025). The Alabama Natural Heritage Program (2023) ranks it as critically imperiled (S1) in the state.

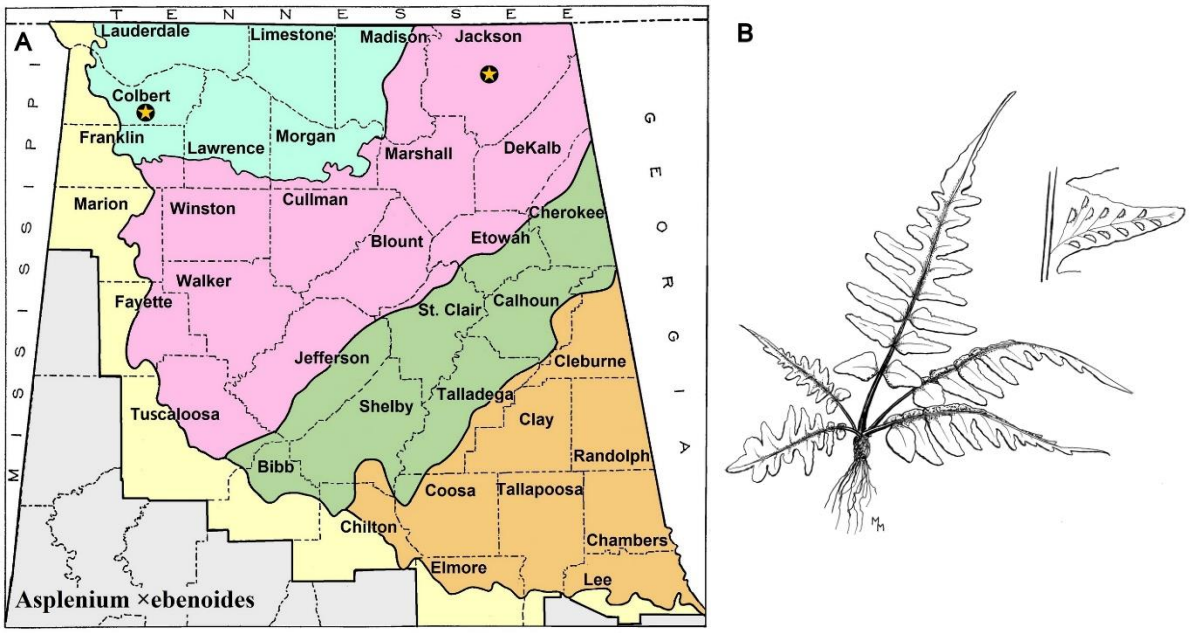


Figure 274. *Asplenium ×ebenoides.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 275. Leaves of *Asplenium ×ebenoides* showing extreme irregularity (Wagner 1954).

In 1862, Robert R. Scott discovered *Asplenium* ×*ebenoides* along the banks of the Schuylkill River near Philadelphia, Pennsylvania. He published his findings in 1865, initially describing the fern as a distinct species, though some botanists suspected it was a hybrid (Maxon 1900a). Margaret Slosson (1902) later confirmed its hybrid origin, demonstrating that *A.* ×*ebenoides* resulted from a cross between *A. platyneuron* and *A. rhizophyllum* (Fig. 264). She successfully synthesized the hybrid by deliberately crossing its parent species in a laboratory. Recognizing the significance of her work, Wagner (1954) called *A.* ×*ebenoides* the most famous hybrid fern. He also noted that wherever the parent species occur together, the hybrid often appears, though typically as a solitary plant.

Figure 276. *Asplenium* ×*ebenoides*, Rock Bridge Co., Virginia, 11 Sep 2024. Photos: Joey Thompson.

Asplenium ×*ebenoides* is a highly variable hybrid, displaying considerable diversity in leaf shape and form (Fig. 275). Its fronds are typically deeply lobed (pinnatifid) with a long, tapering tip, though many individuals exhibit pinnate divisions near the base. The uneven length of the leaf lobes gives the fern an irregular, somewhat asymmetrical outline. Another distinguishing characteristic is the dark coloration of the leaf stalk, which often extends into the lower part of the rachis (Fig. 276).

In Hale County, Alabama, a population of *Asplenium* ×*ebenoides* underwent chromosome doubling, resulting in a fertile allotetraploid (Fig. 264). Julia L. Tutwiler discovered this distinctive spleenwort in 1874 at Havana Glen. Although many botanists visited the site over the years, the plant remained unnamed until Brian Keener and Larry Davenport formally described it as *A. tutwilerae* in 2007 (Fig. 277). Wagner (1954) had earlier referred to the population informally as "fertile *ebenoides*."

Figure 277. *Asplenium tutwilerae*, Hale Co., Alabama, 15 Jul 2009. Photo: Wayne Barger.

Tutwiler's Spleenwort has also backcrossed with *Asplenium platyneuron* at the same site, producing the sterile hybrid *A.* × *boydstoniae* (K.S. Walter) J.W. Short (1983). Katherine Boydston first synthesized this hybrid in 1954 during crossbreeding experiments at the University of Michigan. In 1971, Kerry Walter discovered *A.* × *boydstoniae* in the wild and later named it in her honor (Walter et al. 1982). Remarkably, Havana Glen remains the only known locality worldwide for both ferns.

4. Asplenium ×gravesii Maxon {for Edward Willis Graves, 1882–1936, American Pteridologist} — GRAVES' SPLEENWORT; SAND MOUNTAIN SPLEENWORT (Fig. 278). [×*Asplenosorus gravesii* (Maxon) Mickel]

Figure 278. *Asplenium* ×*gravesii*, Jackson Co., Alabama, 19 Dec 2020. Photo: Alan Cressler.

Plants epipetric; evergreen. Crevices of cliffs and boulders of sandstone rock. Sterile hybrid [*Asplenium bradleyi* × *pinnatifidum*], spores abortive; very rare in the Cumberland Plateau (Fig. 279). The hybrid occurs sporadically from Pennsylvania west to Missouri and south to Arkansas and northeastern Alabama (Kartesz 2025). Although the Alabama Natural Heritage Program does not currently track this taxon, it should be ranked as critically imperiled (S1) in the state.

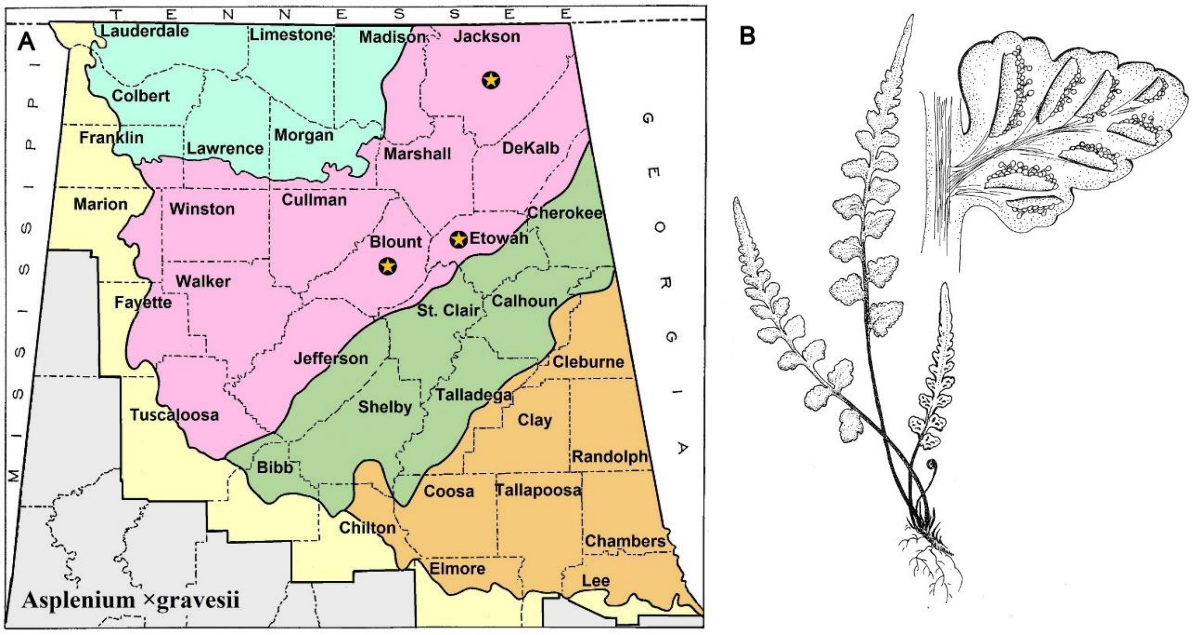


Figure 279. *Asplenium ×gravesii.* **A.** Distribution map. **B.** Illustration: Miriam Wysong Meyer, 1967.

Figure 280. *Asplenium ×gravesii* with *Asplenium pinnatifidum* (one of its parents), Black Creek Canyon, Lookout Mountain, Etowah Co., Alabama, 16 Jun 2017. Photo: Alan Cressler.

Graves's Spleenwort is a sterile tetraploid hybrid produced by a backcross between *Asplenium bradleyi* and *A. pinnatifidum* (Wagner 1954). William R. Maxon (1918) named the hybrid in honor of Edward Graves, who discovered it in 1917 on sandstone cliffs near Trenton, Georgia. Historically, Edgar T. Wherry and Graves reported this fern from Jackson and Etowah counties, Alabama (Wagner & Darling 1957). More recently, Noah Yawn, Wayne Barger, and Alan Cressler rediscovered *A.* ×*gravesii* in these two counties and documented a new occurrence in Blount County (Yawn et al. 2024).

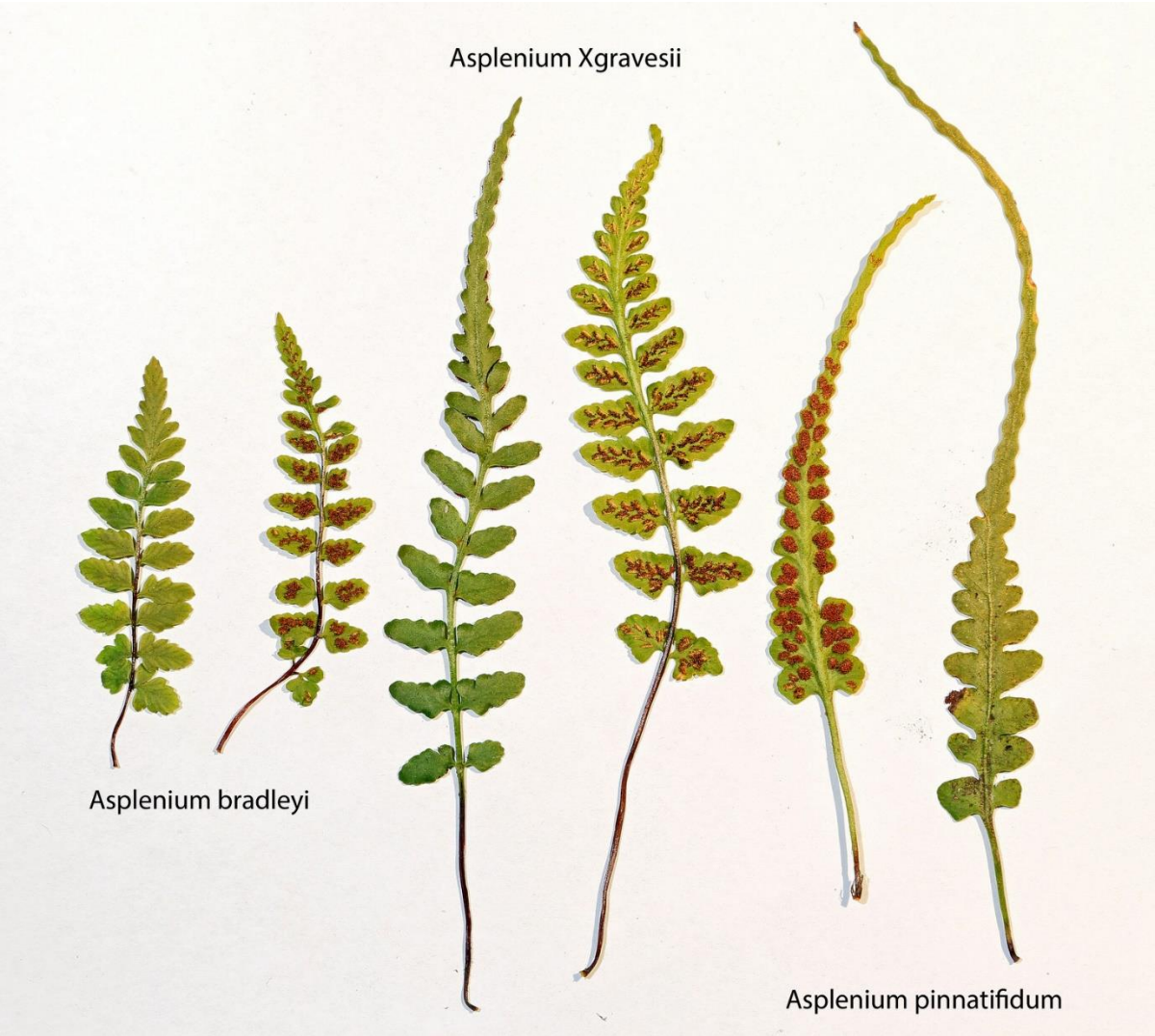


Figure 281. *Asplenium* ×*gravesii* and its parents, Etowah Co., Alabama, 24 Jan 2016. Photo: Alan Cressler.

In the southeastern United States, *Asplenium* ×*gravesii* occurs primarily on Pottsville sandstone bluffs of the Cumberland Plateau (Yawn et al. 2024). This rare hybrid usually grows as scattered individuals near its parental species (Fig. 280). Thomas Darling (1957) attributed its scarcity to the restricted distribution of *A. bradleyi*. Morphologically, *A.* ×*gravesii* exhibits pinnatifid (deeply lobed) blades in the upper portion and pinnate in the lower portion, intermediate between its parents: *A. pinnatifidum* has predominantly pinnatifid blades, while *A. bradleyi* is almost entirely pinnate. Additional traits that separate *A.* ×*gravesii* from *A. pinnatifidum* include brown petioles and darker brown sori, which often coalesce as they mature (Fig. 281). Compared to *A. bradleyi*, the hybrid has less deeply lobed pinnae and a rachis that is at least slightly winged (Maxon 1918; Wherry 1920).

5. Asplenium ×kentuckiense T.N. McCoy {of Kentucky} — KENTUCKY SPLEENWORT (Fig. 282). [*Asplenium pinnatifidum* Nutt. var. *kentuckiense* (T.N. McCoy) Clute; ×*Asplenosorus kentuckiensis* (T.N. McCoy) Mickel]

Figure 282. *Asplenium ×kentuckiense*, Blount Co., Alabama, 27 Jun 2022. Photo: Noah Yawn.

Plants epipetric; evergreen. Crevices and ledges of sandstone cliffs. Sterile hybrid [*Asplenium pinnatifidum* × *platyneuron*], spores abortive; very rare, known only from Blount County, in the Sand Mountain District of the Cumberland Plateau (Fig. 283). This hybrid occurs sporadically in the eastern United States, from Virginia west to Illinois and south to Arkansas, Mississippi, and Georgia (Kartesz 2025). Although the Alabama Natural Heritage Program does not currently track it, the hybrid should be ranked as critically imperiled (S1) in the state.

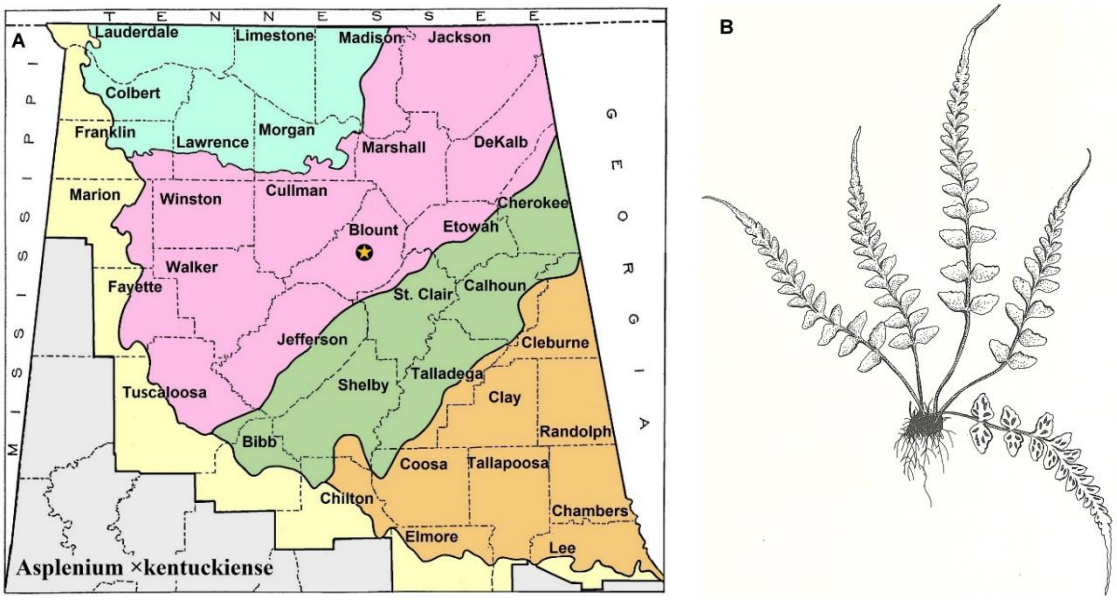


Figure 283. *Asplenium ×kentuckiense*. **A.** Distribution map. **B.** Illustration: Miriam Wysong Meyer, 1967.

Figure 284. *Asplenium ×kentuckiense*, Blount Co., Alabama, 27 Jun 2022. Photo: Noah Yawn.

McCoy (1936) described *Asplenium ×kentuckiense* from a specimen he collected in 1934 in Boyd County, Kentucky. In 2022, Noah Yawn and Alan Cressler documented it in Alabama (Fig. 284), growing in crevices of a sandstone bluff on Sand Mountain in Blount County (Yawn et al. 2024). This sterile triploid hybrid arose from a cross between *A. pinnatifidum* and *A. platyneuron* (Fig. 285). Wagner (1958) recognized the Kentucky Spleenwort as among the rarest hybrids in the Appalachian *Asplenium* complex, noting that the contrasting habitat preferences of its parent species often prevent them from occurring together. The Alabama record represents a significant range extension for this exceedingly rare hybrid.

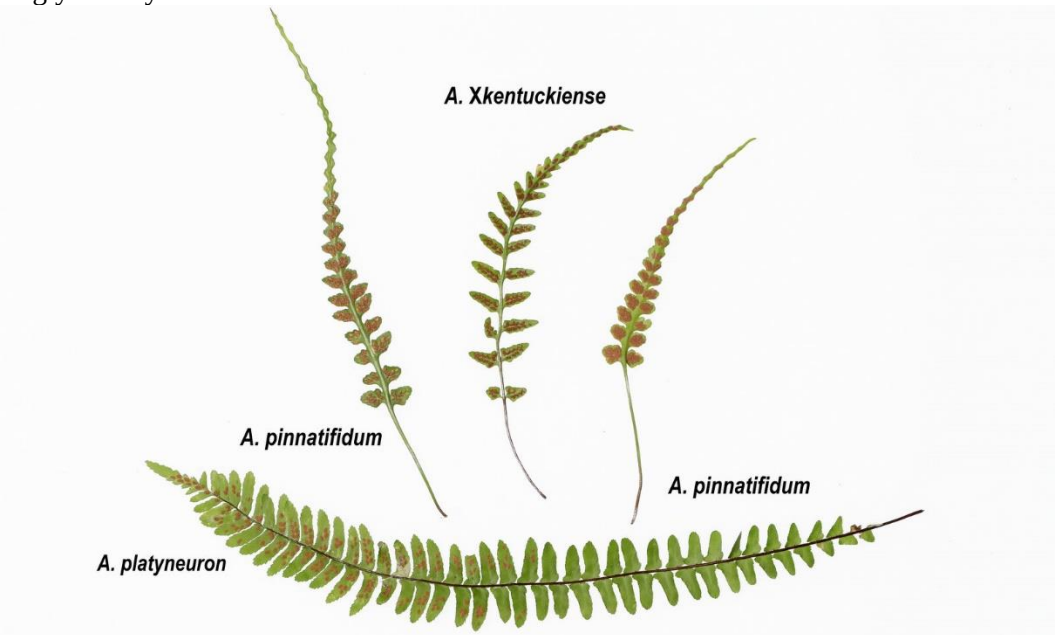


Figure 285. Fronds of *Asplenium ×kentuckiense* and its two parents, *Asplenium pinnatifidum* and *Asplenium platyneuron*, Macon-Bibb Co., Georgia, 29 Jan 2022. Photo: Noah Yawn.

Figure 286. *Asplenium ×kentuckiense* fronds, Bibb Co., Georgia, 24 Apr 2013. Photo: Alan Cressler.

Asplenium ×kentuckiense strongly resembles both *A. ×gravesii* and *A. ×trudellii*, making it difficult to distinguish between them due to only subtle morphological differences. *Asplenium ×trudellii* typically produces a narrowly triangular blade, broadest at the basal or next-to-basal pair of pinnae. Its petiole appears brown only at the base, turning green in the upper portion. In contrast, *A. ×gravesii* and *A. ×kentuckiense* usually bear blades that are widest between one-fourth and one-half of the distance from base to tip, and their petioles display brownish-black pigmentation that extends at least to the rachis. A key trait distinguishing *A. ×kentuckiense* from *A. ×gravesii* is its tapering leaf base, where the second and third lower pinnae pairs are shorter than the fourth and fifth (Fig. 286). In *A. ×gravesii*, the leaf base generally does not taper, and the three or four lowest pinnae pairs remain nearly equal in length (Wagner & Darling 1957).

6. Asplenium monanthes L. {one-flowered} — SINGLE-SORUS SPLEENWORT (Fig. 287).

Figure 287. *Asplenium monanthes*, Jackson Co., Alabama, 27 Jan 2010. Photos: Wayne Barger.

Plants epipetric; evergreen. Found on moist limestone ledges in deep ravines, sinkholes, and around cave mouths. Sporulates April–October; very rare in the Jackson County Mountains District of Cumberland Plateau (Fig. 288). Scattered in highly humid parts of the tropics, subtropics, and warm temperate areas (Weakley et al. 2025). In the continental United States, the species occurs in northeastern Alabama, northwestern South Carolina, western North Carolina, northern Florida, and southeastern Arizona (Kartesz 2025). Its broader range extends through Mexico, the West Indies, Central and South America, Africa, Madagascar, and the Hawaiian Islands (Wagner et al. 1993). The Alabama Natural Heritage Program (2023) ranks this species as critically imperiled (S1) within the state.

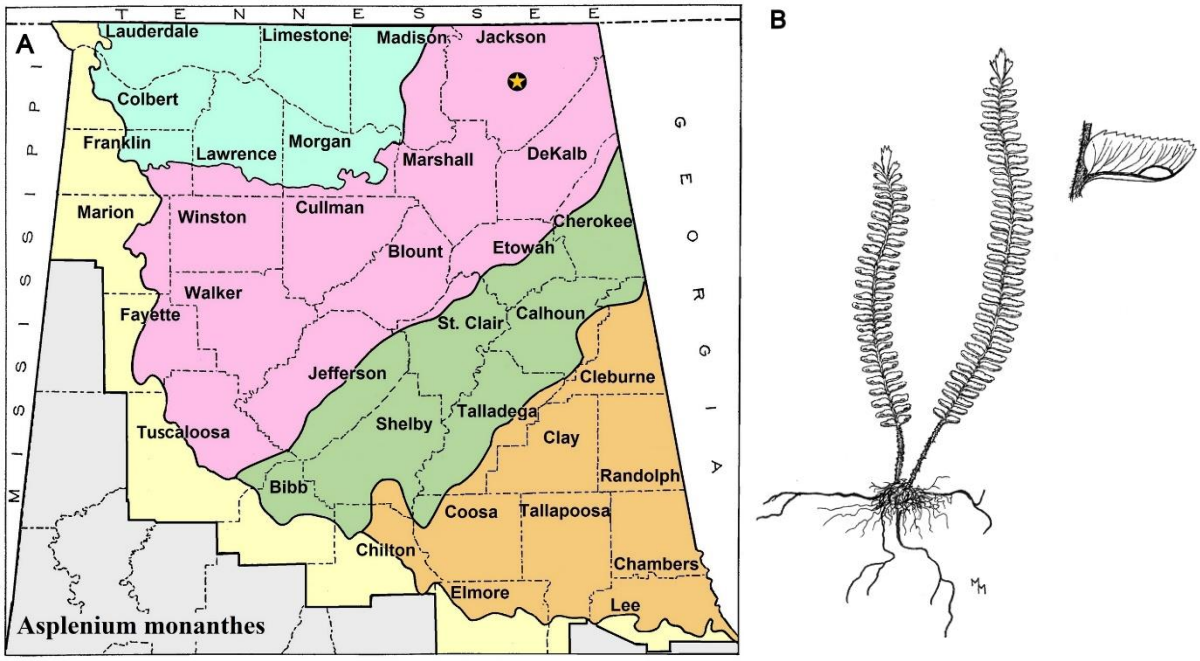


Figure 288. *Asplenium monanthes.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

In 1946, Rufus Morgan, an early advocate for the Appalachian Trail, made a significant botanical discovery: the first documented occurrence of *Asplenium monanthes* in the southeastern United States. He found the spleenwort growing on rocks beneath Whitewater River Falls in Oconee County, South Carolina (Blomquist 1948). Prior to this, the only known location in the continental United States was the Huachuca Mountains of southwestern Arizona. Subsequent fieldwork revealed additional populations in North Carolina and Florida. On June 18, 1983, biological explorer and photographer Alan Cressler (pers. comm. 2025) made another notable discovery, finding the Single-Sorus Spleenwort growing in a sinkhole associated with a cave in Jackson County, Alabama (Fig. 289). John Short visited the site on July 3, 1984, and made the first specimen collection for the state.

Asplenium monanthes has a broad distribution across tropical and subtropical regions, extending into temperate areas of the southeastern United States. Notably, these populations are significantly isolated from the nearest Neotropical occurrences (Shaw 2003). Edgar T. Wherry (1964) suggested that hurricanes may have transported spores from Mexico, leading to the scattered populations observed in the Southeast. However, Allison Shaw (2003) pointed out that the precise origin of these founding spores remains uncertain, although evidence indicates that the Caribbean is a more probable source than Mexico. Furthermore, she emphasized that the populations in the southeastern United States are relatively small and limited in number, raising conservation concerns despite the fern's extensive global distribution.

Figure 289. *Asplenium monanthes*, Jackson Co., Alabama, 22 May 2021. Photo: Alan Cressler.

The Single-Sorus Spleenwort acquired its common name from typically bearing a solitary sorus on each leaflet. It is an apogamous triploid fern that forms sporophytes without fertilization, with spores developing directly into new plants and bypassing sexual reproduction. It is an apogamous triploid that forms sporophytes without fertilization, with spores developing directly into new plants and bypassing sexual reproduction. In triploid apogamous ferns, this process compensates for chromosomal imbalances that would otherwise prevent fertility. This clonal mode of reproduction enables the species to persist across a variety of environments. Although apogamous ferns often originated through hybridization, researchers treat them as distinct species because they produce viable spores and reproduce independently (Dyer et al. 2012; Evans 1969; Shaw 2003).

7. Asplenium montanum Willd. {montane} — MOUNTAIN SPLEENWORT (Fig. 290).

Plants epipetric; evergreen. Crevices of ledges, cliffs, bluffs, sandstone boulders, and other acidic rock. Sporulates May–October; infrequent in the Cumberland Plateau; rare in the Ridge & Valley, and Piedmont (Fig. 291). This species occurs mainly in the Appalachians, from southern New England and New York south through Ohio and Virginia to northern Georgia and Alabama, and is disjunct in the Ozarks of Arkansas and Missouri (Wagner et al. 1993).

André Michaux, the esteemed French botanist and explorer, was the first to collect Mountain Spleenwort from the rugged mountains of North Carolina. In his 1803 *Flora Boreali-Americana*, Michaux initially misidentified the fern as the Black Spleenwort, *Asplenium adiantum-nigrum* L., a common European species. He later sent specimens to Carl Ludwig Willdenow, a prominent German botanist of the late 18th and early 19th centuries. In 1810, Willdenow identified the fern as a distinct species and formally described it as *Asplenium montanum* (Wherry 1942).

Figure 290. *Asplenium montanum*, DeKalb Co., Alabama, 14 May 2010. Photo: Wayne Barger.

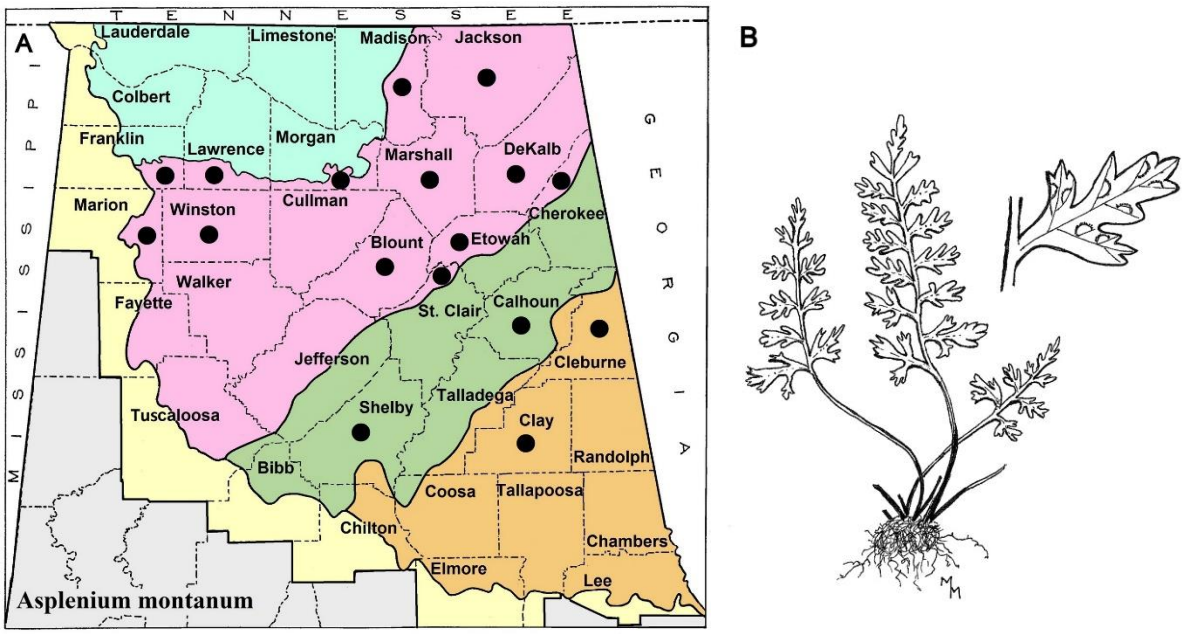


Figure 291. *Asplenium montanum*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 292. *Asplenium montanum*, DeKalb Co., Alabama, 12 Apr 2015. Photo: Vitaly Charny.

The Mountain Spleenwort, a diploid progenitor within the reticulately evolved Appalachian *Asplenium* complex, serves as a parent of *A. pinnatifidum*, *A. bradleyi*, and *A.* ×*trudellii* (Fig. 264). Wagner (1954) highlighted several distinct characteristics of *A. montanum*: (1) its triangular, long-petiolate fronds with blades dissected two to three times, (2) the dark-brown coloration of the leaf axis, confined to the base of a flattened petiole, (3) the glossy appearance of the upper leaf surface, attributed to the elongated, nearly straight-walled epidermal cells, and (4) its exclusive occurrence in acid-rock crevices (Fig. 292).

8. Asplenium pinnatifidum Nutt. {pinnately lobed} — LOBED SPLEENWORT (Fig. 293). [×*Asplenosorus pinnatifidus* (Nutt.) Mickel]

Figure 293. *Asplenium pinnatifidum*, Cullman Co., Alabama, 11 May 2011. Photo: Wayne Barger.

Plants epipetric; evergreen. Cliffs, ledges, and boulders of sandstone and other acidic rocks. Sporulates May–October; rare in the Highland Rim and Ridge & Valley; uncommon in the Cumberland Plateau (Fig. 294). The species occurs from northeastern Oklahoma east to southern New York, south through the Appalachians to northern Georgia and Alabama, with scattered outliers elsewhere in the eastern United States (Wagner et al. 1993).

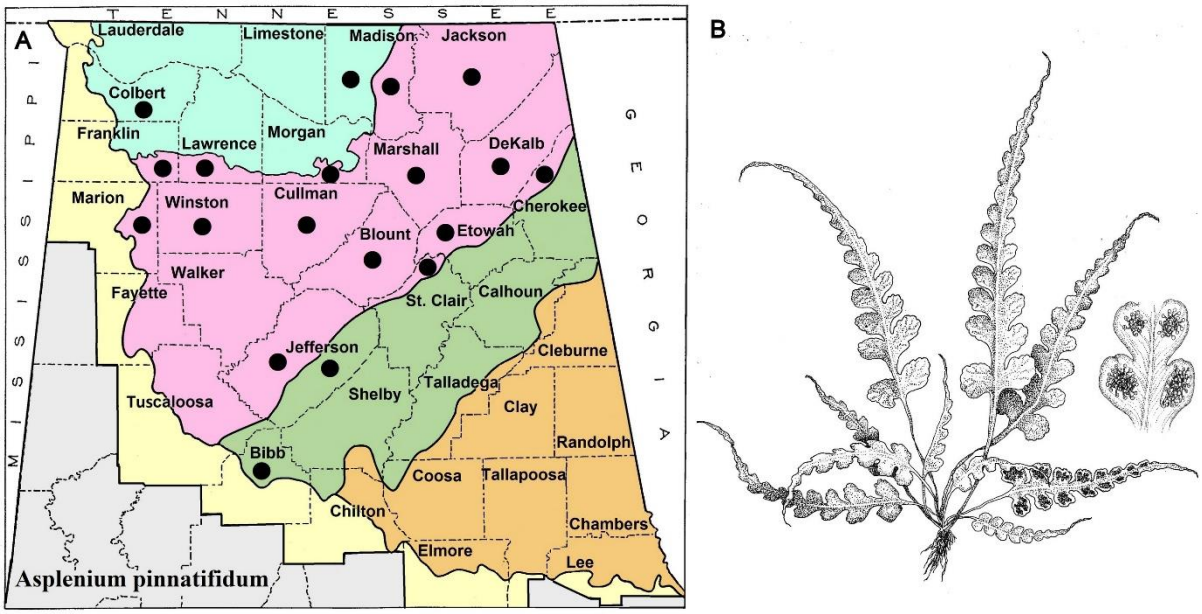


Figure 294. *Asplenium pinnatifidum*. **A.** Distribution map. **B.** Illustration: Miriam Wysong Meyer, 1967.

Figure 295. *Asplenium pinnatifidum*, Winston Co., Alabama, 5 Apr 2024. Photo: Helen A. Czech.

Asplenium pinnatifidum is an allotetraploid fern with four sets of chromosomes, derived from the hybridization of *A. montanum* and *A. rhizophyllum*. It is the most widespread hybrid-derived spleenwort in the Appalachian region. In Alabama, *A. pinnatifidum* forms additional hybrids within the *Asplenium* complex: crossing with *A. montanum* to yield *A.* ×*trudellii*, with *A. bradleyi* to give rise to *A.* ×*gravesii*, and with *A. platyneuron* to produce *A.* ×*kentuckiense*. Each of these hybrids exhibits a blend of traits inherited from both parents (Wagner et al. 1993).

A distinctive feature of *Asplenium pinnatifidum* that reflects its hybrid origin is its irregularly shaped leaf blades. Some forms resemble *A.* ×*ebenoides*, another spleenwort with variable fronds, which can lead to occasional misidentifications. Typically, however, *A. pinnatifidum* has pinnatifid (deeply lobed) blades, with the lowest pair of pinnae sometimes fully divided to the rachis (Fig. 295). Its petiole is dark brown only near the base, remaining green above and along the midrib. By contrast, *A.* ×*ebenoides* usually combines pinnatifid upper blades with pinnate lower blades, often with at least two pairs of pinnae fully divided to the rachis. Its petiole is uniformly blackish-brown, with the dark pigmentation extending into the midrib (Wagner 1954).

9. Asplenium platyneuron (L.) Britton, Sterns, & Poggenb. {broad nerved} — EBONY SPLEENWORT; BROWNSTEM SPLEENWORT (Fig. 296). [*Asplenium ebeneum* Aiton; *Asplenium platyneuron* var. *bacculum-rubrum* (Featherm.) Fernald]

Figure 296. *Asplenium platyneuron*. **A.** Typical form, Lauderdale Co., Alabama, 1 Jan 2022. Photo: Chesley Rogers. **B.** 'Bacculum-rubrum' form, Monroe Co., Alabama, 31 May 2011. Photo: Wayne Barger.

Plants terrestrial or epipetric; evergreen. Various habitats, ranging from moist to dry, include forests, woodlands, old fields, rock outcrops, masonry crevices, under shrubs in landscaped beds, and roadside banks. Sporulates April–November; common throughout Alabama (Fig. 297). Occurs in eastern North America from Quebec to Ontario, south to Texas and Florida, with outliers in the southwestern USA and disjunct populations in southern Africa (Jacobsen 1983; Wagner et al. 1993).

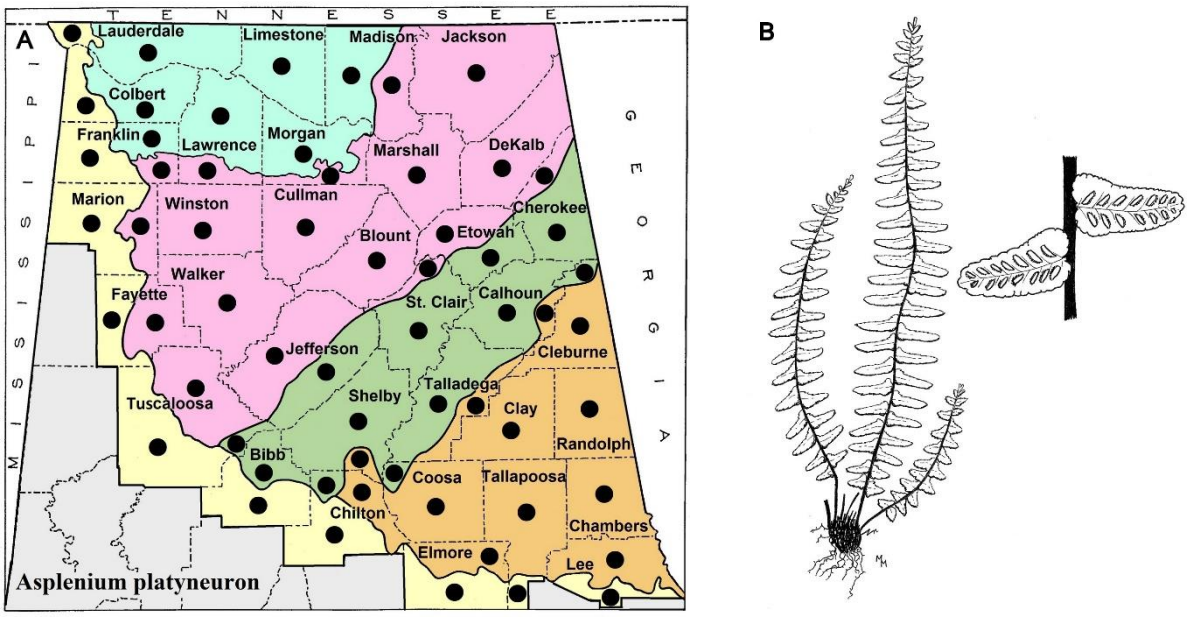


Figure 297. *Asplenium platyneuron.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

The Ebony Spleenwort is an ecological generalist, thriving in a wide variety of habitats, most often in disturbed woodland soils, but it also grows on rocky substrates (Fig. 298). Remarkably, it is the only North American *Asplenium* that typically grows away from rock (Wagner et al. 1993). It ranks among the most common and abundant ferns in eastern North America, with records from every county in Alabama (Keener et al. 2025). Its distribution is especially striking, spanning both eastern North America and southern Africa—regions separated by thousands of kilometers and the Atlantic Ocean. Although spores can disperse long distances on wind currents, especially during intense storms like hurricanes, prevailing westward wind patterns do not cross the equator. The resulting disjunct range remains one of the more intriguing biogeographic puzzles of the genus (Short & Spaulding 2012).

Figure 298. *Asplenium platyneuron*, Cleburne Co., Alabama, 28 Aug 2022. Photo: Noah Yawn.

The pronounced morphological variability of *Asplenium platyneuron* has led some botanists, including Fernald (1950) and Thieret (1980), to recognize multiple varieties and forms (Taylor et al. 1976). Fronds are typically unbranched, less than 35 cm in length, and 5 cm in width, with finely toothed pinnae. Yet naturalists have documented wide variation in frond size, branching, and the degree of serration (Fig. 299). Despite this variability, Wagner et al. (1993) treated *A. platyneuron* as a single, highly variable species, concluding that its forms and varieties do not merit taxonomic recognition. The Ebony Spleenwort also serves as a diploid progenitor in the reticulate evolution of the Appalachian *Asplenium* complex, where it is a parent of *A. bradleyi*, *A.* ×*ebenoides*, and *A.* ×*kentuckiense* (Fig. 264).

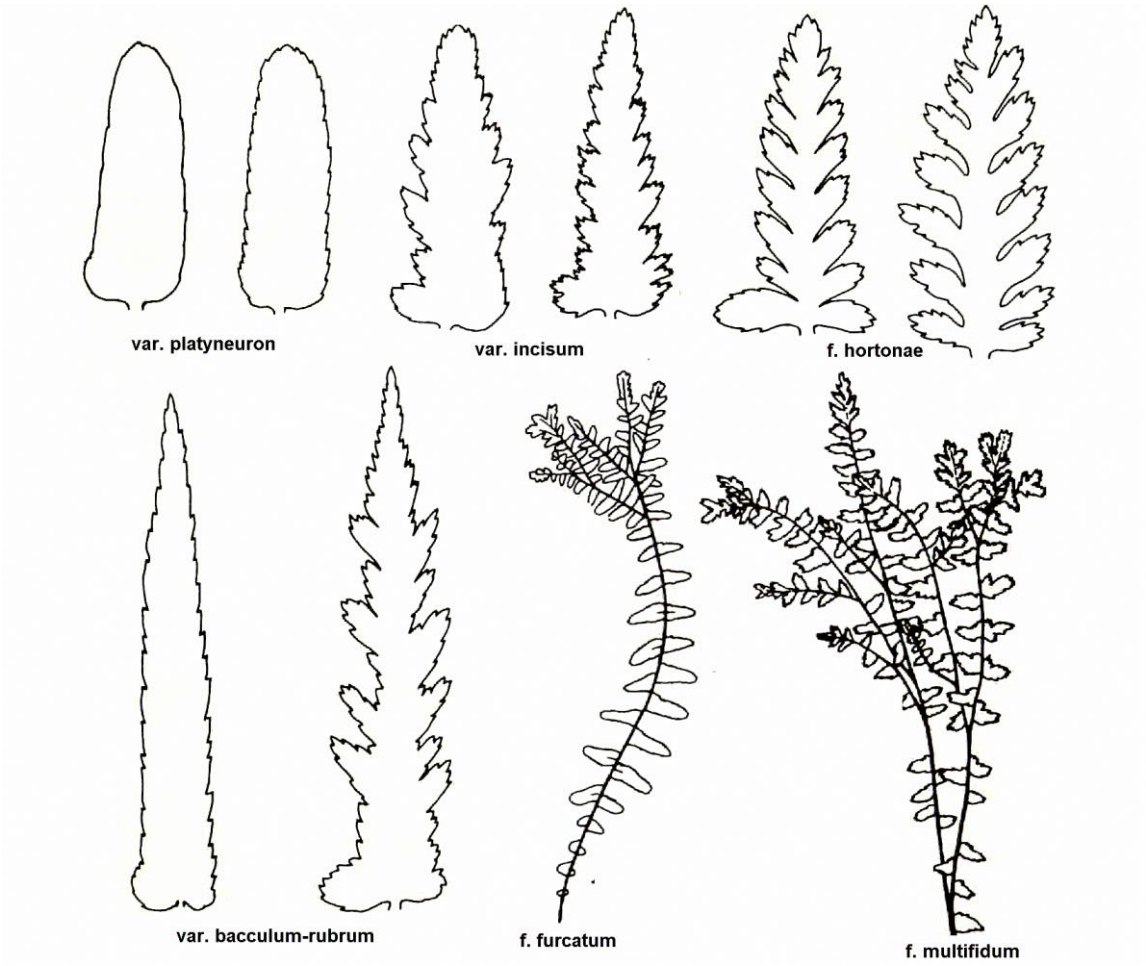


Figure 299. Variation in *Asplenium platyneuron* pinnae and fronds (Taylor et al. 1976).

At first glance, smaller individuals of the Christmas Fern (*Polystichum acrostichoides*) may resemble the Ebony Spleenwort (*Asplenium platyneuron*). However, the Christmas Fern has a light-colored, densely scaly petiole, unlike the smooth, dark brown petiole of *A. platyneuron* (Fig. 300a). In Alabama, the Blackstem Spleenwort (*A. resiliens*) is the most similar spleenwort to *A. platyneuron*. One key difference lies in their leaflet arrangement: *A. resiliens* bears opposite leaflets whose bases usually do not overlap the rachis, while *A. platyneuron* has alternate leaflets with bases that overlap the rachis (Fig. 300b). Additionally, *A. platyneuron* exhibits slight frond dimorphism, with sterile fronds smaller and less erect than fertile ones, while *A. resiliens* has monomorphic fronds. The specific epithet *platyneuron*, meaning "broad-nerved," is misleading and originates from an early illustration that exaggerated the width of the rachis (Nelson 2000).

Figure 300. *Asplenium platyneuron*. **A.** Calhoun Co., Alabama, 9 Nov 2024. Photo: Savannah Spaulding. **B.** Walker Co., Alabama, 13 Dec 2024. Photo: Dan Spaulding.

10. Asplenium resiliens Kunze {springing back; flexible petioles} — BLACKSTEM SPLEENWORT; LITTLE EBONY SPLEENWORT (Fig. 301). [*Asplenium parvulum* M. Martens & Galeotti]

Figure 301. *Asplenium resiliens*, Wilcox Co., Alabama, 4 May 2022. Photo: Wayne Barger.

Plants epipetric; evergreen. Moist to dry limestone rocks, boulders, and cliffs. Sporulates April–November; frequent in the Highland Rim, Cumberland Plateau, and Ridge & Valley; rare in the Piedmont and Coastal Plain (Fig. 302). In the USA, this species ranges from southern Pennsylvania south to Florida and west to New Mexico and southwestern Arizona. Its broader range extends through the West Indies, Mexico, Central America, and South America (Wagner et al. 1993).

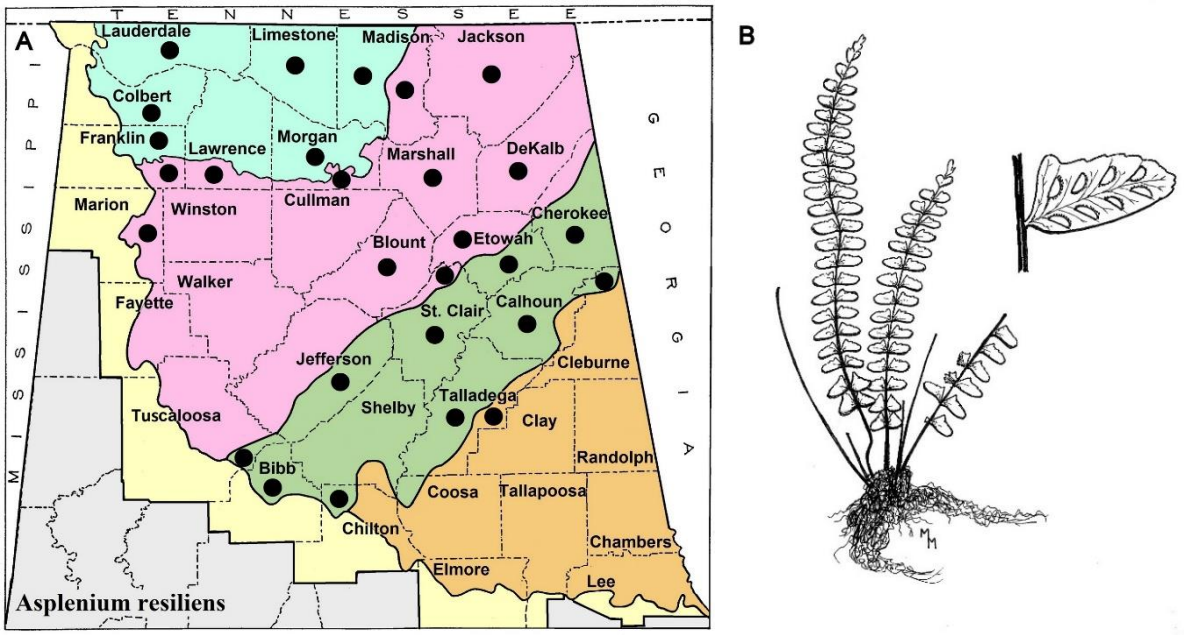


Figure 302. *Asplenium resiliens.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 303. *Asplenium resiliens*, Wilcox Co., Alabama, 4 May 2022. Photo: Wayne Barger.

The Blackstem Spleenwort (*Asplenium resiliens*) closely resembles the more common Ebony Spleenwort (*A. platyneuron*), but several clear traits separate them. In *A. resiliens*, the leaflets are arranged oppositely in pairs along the rachis, while in *A. platyneuron*, they alternate and attach singly. Furthermore, the bases of the pinnae of *A. resiliens* typically do not overlap the rachis, whereas the pinnae of *A. platyneuron* distinctly overlap it (Fig. 303). Habitat preference also sets these species apart—*A. resiliens* occurs almost exclusively on calcareous rock outcrops (Fig. 304), whereas *A. platyneuron* is an ecological generalist, thriving on both rock and soil.

Figure 304. *Asplenium resiliens*, Madison Co., Alabama, 26 May 2024. Photo: Courtney Alley.

Asplenium resiliens is a triploid fern, a condition that prevents it from producing viable gametes through normal sexual reproduction. Instead, it reproduces by apogamy, in which the gametophyte develops directly into a sporophyte without fertilization. Yet, despite relying on this asexual mode, *A. resiliens* can occasionally hybridize when irregular meiosis produces haploid spores that develop into functional gametophytes capable of crossing with compatible relatives. One such event involved the subtropical tetraploid *A. heterochroum* Kunze, producing *Asplenium heteroresiliens* W.H. Wagner—an allopentaploid with five chromosome sets inherited from both parents (Morzenti 1966). Because apogamy bypasses the sterility normally associated with odd chromosome numbers, *A. heteroresiliens* persists and reproduces clonally. Now treated as a distinct species, it remains rare and localized in the Coastal Plain of the Carolinas, Georgia, and northern Florida (Kartesz 2025). Recently, Noah Yawn and Alan Cressler discovered an Alabama population in Conecuh County (Yawn et al. 2024).

11. Asplenium ×reverterum Yawn, ined. {to turn back, returned} — REVERTED SPLEENWORT; YAWN'S SPLEENWORT (Fig. 305).

Figure 305. *Asplenium ×reverterum*, Walker Co., Georgia, 16 Jul 2024. Photo: Alan Cressler.

Plants epipetric; evergreen. Crevices and ledges of sandstone cliffs. Sterile hybrid [*Asplenium bradleyi* × *platyneuron*]; spores abortive; very rare in the Sand Mountain District of the Cumberland Plateau (Fig. 306). This hybrid is documented only from Alabama, Georgia, and Pennsylvania (Yawn & Spaulding in prep.). The Alabama Natural Heritage Program does not currently track this hybrid; however, we believe it warrants a status of critically imperiled (S1) within the state.

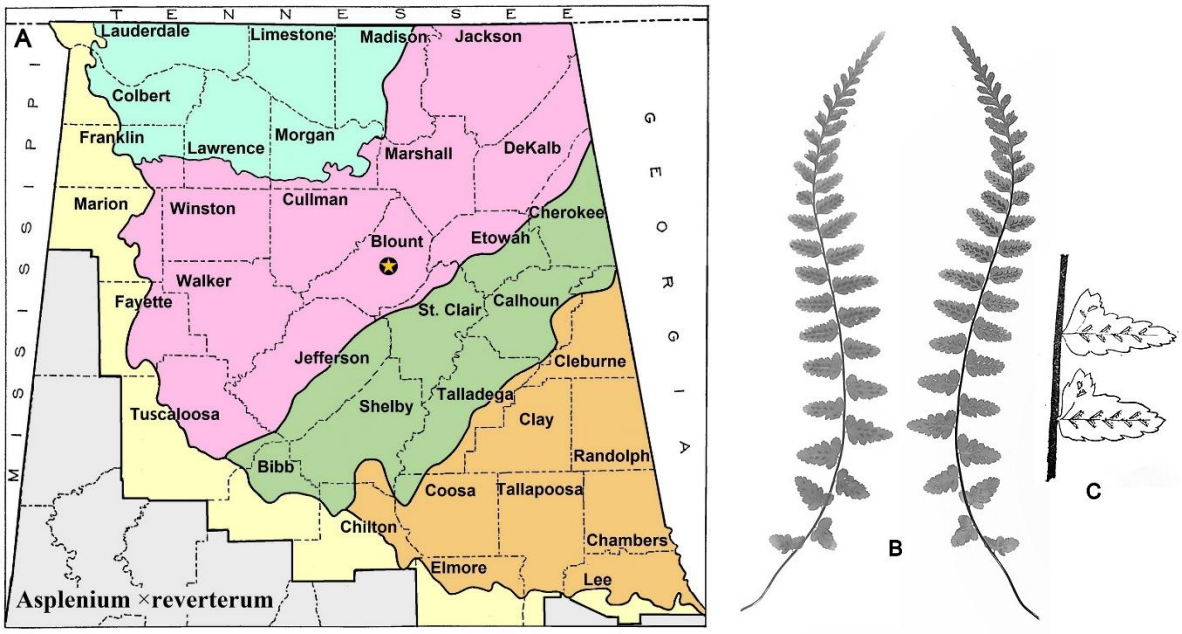


Figure 306. *Asplenium ×reverterum.* **A.** Distribution map. **B.** Photograph of fronds by Alan Cressler, Walker Co., Georgia, 16 July 2024. **C.** Illustration of two lower pinnae by Inez Rinninger (Wherry 1942).

In 2024, Noah Yawn documented the first collection of *Asplenium* ×*reverterum* in Alabama from Blount County. This sterile triploid hybrid is the result of a backcross between *A. bradleyi* and *A. platyneuron*. Wherry (1937a) first reported the hybrid in York and Lancaster counties, Pennsylvania, noting that it "shows close resemblance to both parents." The most distinctive character is rachis pigmentation: in *A. bradleyi*, the dark coloration extends only halfway up the rachis, while in *A. platyneuron*, it continues to the apex. In the hybrid, this pigmentation is intermediate, reaching nearly three-quarters the length of the rachis. Morphologically, *A.* ×*reverterum* resembles *A. bradleyi* more closely, though its sori exhibit a subtle herringbone arrangement reminiscent of *A. platyneuron*. Later in 2024, Alan Cressler reported the hybrid from Johns Mountain in Walker County, Georgia, with both parent species occurring at the site (Fig. 307).

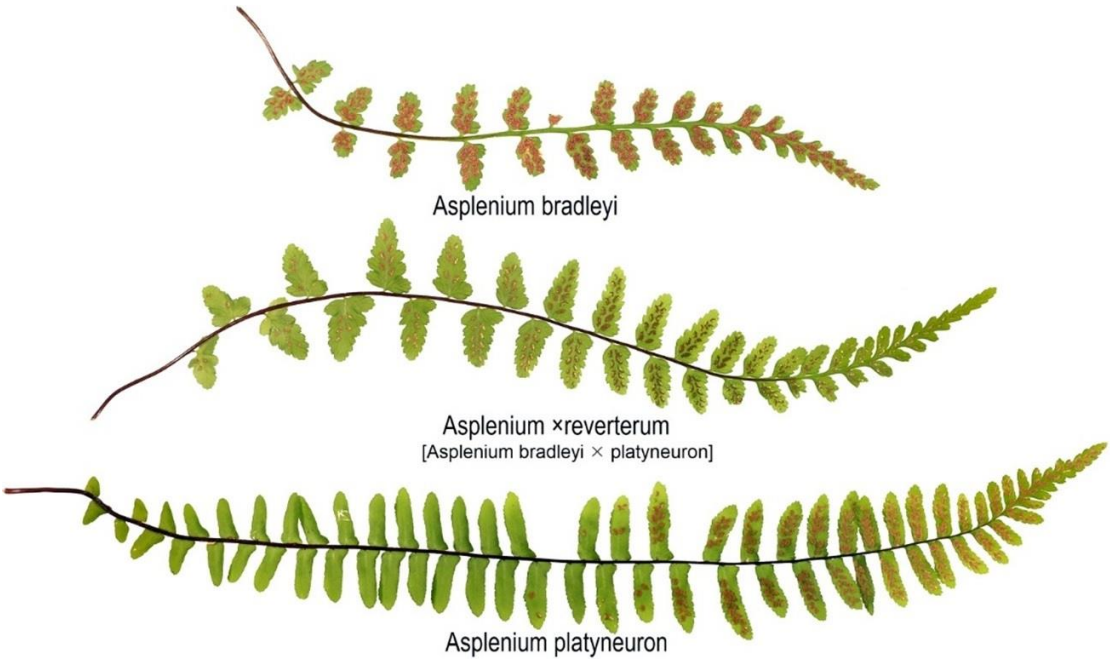


Figure 307. *Asplenium bradleyi, A.* ×*reverterum, A. platyneuron* from Walker Co., Georgia, 16 July 2024. Photo: Alan Cressler.

Another rare backcross hybrid within the Appalachian *Asplenium* complex, *A.* ×*wherryi* (Fig. 308a), arises from a cross between *A. bradleyi* and *A. montanum* (Fig. 264). First documented in Pennsylvania and New Jersey by Trudell (1935) and Wherry (1935), it was formally named by Smith et al. (1961) in honor of Edgar T. Wherry. Like other sterile hybrids in the complex, *A.* ×*wherryi* exhibits intermediate traits between its parent species, with frond shape and division reflecting a transitional form (Fig. 308b). A key distinguishing feature is the pigmentation of its petiole and rachis: in *A. bradleyi*, the dark color extends well onto the rachis, whereas in *A. montanum*, it is confined to the lower portion of the petiole. The hybrid displays an intermediate pattern, with the petiole darkened to the base of the leaf blade while the rachis remains mostly green (Smith et al. 1961).

Although rare, botanists have recorded additional populations of *A.* ×*wherryi* in Georgia, Kentucky, North Carolina, and Virginia since its original discovery. Wherry's Spleenwort typically occurs as scattered individuals where its parent species grow in proximity. Sterile and incapable of reproducing by spores, it nonetheless persists for years, suggesting a relatively long lifespan for individual plants. Continued field surveys may reveal further occurrences, including in Alabama.

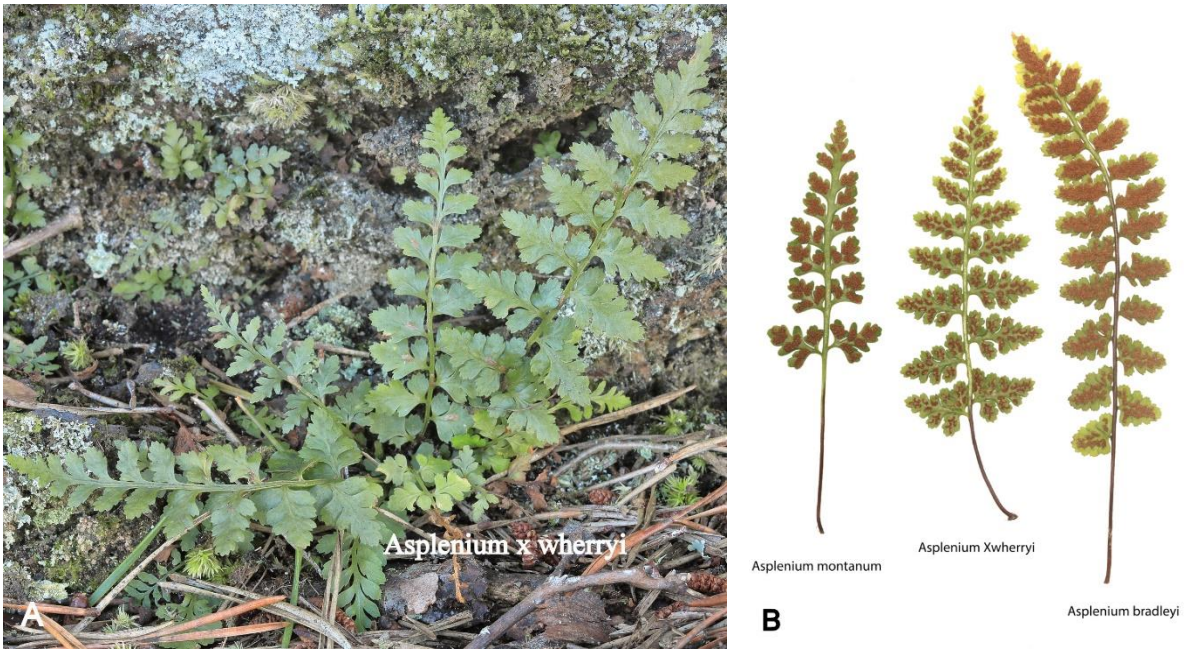


Figure 308. Spleenworts on Crowder's Mountain, Gaston Co., North Carolina, 5 Feb 2022. **A.** *Asplenium* ×*wherryi*. **B.** Comparison of *Asplenium montanum*, *A.* × *wherryi*, and *A. bradleyi*. Photos: Alan Cressler.

12. Asplenium rhizophyllum L. {rooting leaf} — WALKING FERN; WALKING SPLEENWORT (Fig. 309). [*Camptosorus rhizophyllus* (L.) Link]

Figure 309. *Asplenium rhizophyllum*, Jackson Co., Alabama, 28 Oct 2009. Photos: Wayne Barger.

Plants epipetric; evergreen. Shaded rock ledges and boulders, primarily on limestone. Sporulates May–October; uncommon in the Highland Rim, Cumberland Plateau, and Ridge & Valley; very rare in the Fall Line Hills District of the Coastal Plain (Fig. 310). This species ranges from southern Canada (Quebec and Ontario) south through the eastern United States to Georgia, Alabama, and southeastern Oklahoma (Kartesz 2025).

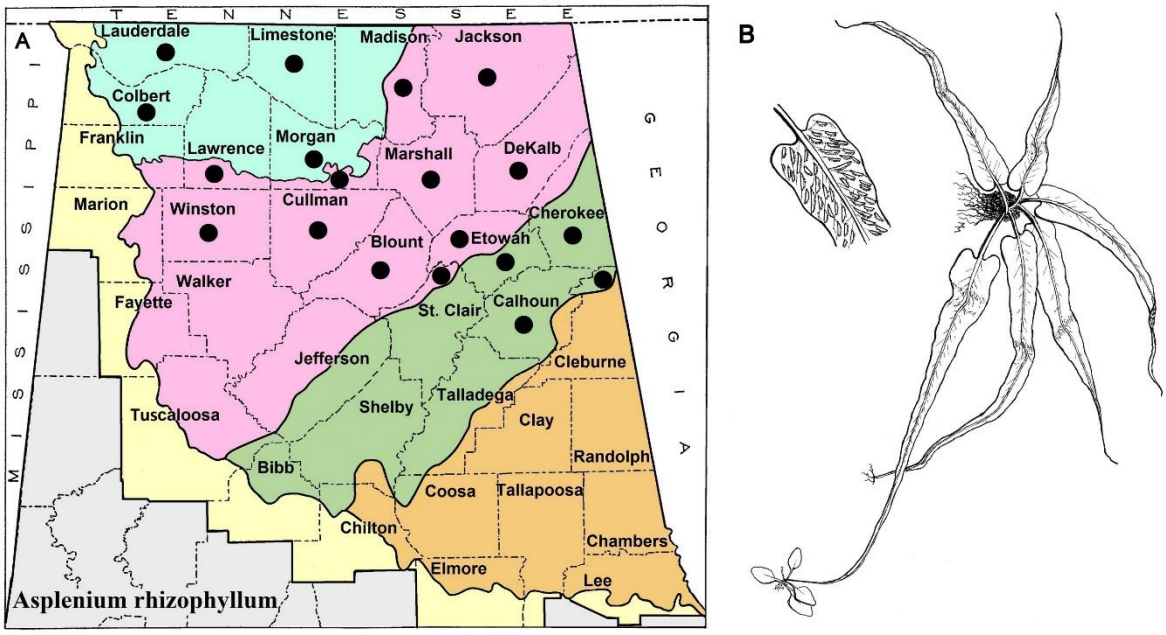


Figure 310. *Asplenium rhizophyllum*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 311. *Asplenium rhizophyllum*, Murray Co., Georgia, 5 Jun 2011. Photo: Alan Cressler.

Asplenium rhizophyllum is morphologically distinctive among the spleenworts, leading many early researchers to place it in a separate genus, *Camptosorus*. Wagner (1954) emphasized four key traits: (1) triangular-attenuate, simple blades with long, tapering tips capable of rooting; (2) a green axis except for the darker petiole base; (3) a distinctive anastomosing, web-like venation pattern; and (4) a preference for shaded, moss-covered calcareous rocks and boulders. Another diagnostic feature is the scattered distribution of sori across the entire underside of the leaf (Fig. 311).

Figure 312. *Asplenium rhizophyllum*, Stephens Co., Georgia, 25 Mar 2018. Photo: Alan Cressler.

The common name "walking fern" refers to the plant's ability to root at the tips of its leaves, producing new individuals (Fig. 312). This growth habit often creates dense, spreading clonal patches, in contrast to most other spleenworts, which frequently grow as solitary plants (Wagner et al. 1993). *Asplenium rhizophyllum* is also a diploid progenitor of the reticulately evolved Appalachian *Asplenium* complex (Fig. 264). In northern Alabama, it served as an ancestor of the hybrid-derived Lobed Spleenwort (*A. pinnatifidum*) and as a parent of Scott's Spleenwort (*A. ×ebenoides*), both of which inherited a reduced ability to form plantlets at their attenuate leaf tips (Wagner 1954).

12. Asplenium ruta-muraria L. {rue of walls} var. **cryptolepis** (Fernald) Wherry {with hidden scales; on lower petioles} — AMERICAN WALL-RUE; WALL-RUE SPLEENWORT (Fig. 313). [*Asplenium cryptolepis* Fernald; *Asplenium ruta-muraria* var. *ohionis* (Fernald) Wherry]

Plants epipetric; evergreen. Shaded crevices of limestone cliffs, ledges, and boulders. Sporulates May–October; very rare in the Tennessee Valley District of the Highland Rim, Jackson County Mountains District of the Cumberland Plateau, and Cahaba Ridge District of the Ridge & Valley (Fig. 314). This species occurs in eastern North America from Quebec and New England west to Ontario and the Great Lakes, and south along the Appalachians to northern Arkansas, north Georgia, and central Alabama (Kartesz 2025). The Alabama Natural Heritage Program (2023) ranks this species as critically imperiled (S1) in the state.

For many years, botanists considered *Asplenium ruta-muraria* a historical species in Alabama due to the absence of recent collections. Samuel B. Buckley first documented it in 1839 along the Tennessee River, though he did not specify a county. In the 1870s, Eugene A. Smith collected specimens in Bibb and Colbert counties (Keener et al. 2025; SERNEC 2025). Early 20th-century records include Elisha L. Lee from Jackson County in 1908 and Edward W. Graves from Lauderdale County in 1917 (Graves 1920). Charles Mohr (1901) reported it from Winston, DeKalb, and Etowah counties, but no voucher specimens support these occurrences. Short and Spaulding (2012) suggested the species might still exist in Alabama, noting its small size makes it easy to overlook. In 2015, Wayne Barger and Chris Taylor rediscovered the fern in Jackson and Lauderdale Counties (Barger et al. 2019).

Figure 313. *Asplenium ruta-muraria*, Jackson Co., Alabama, 9 Apr 2019. Photo: Wayne Barger.

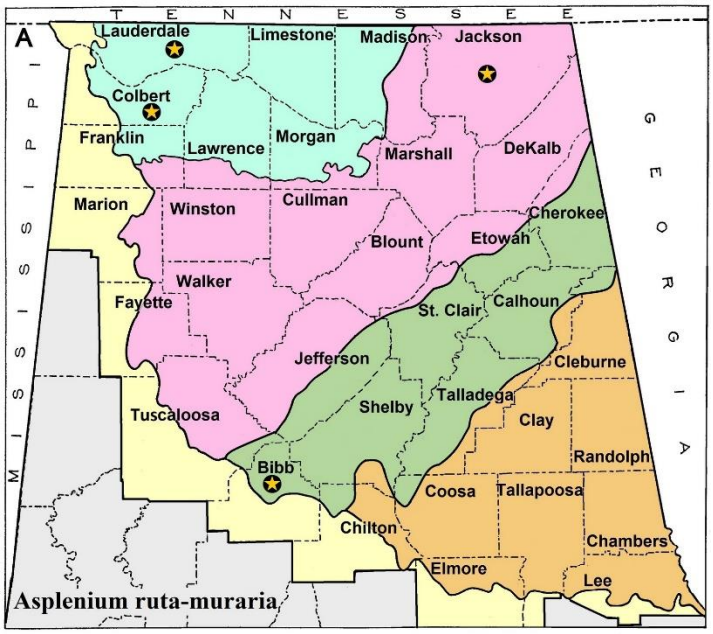


Figure 314. *Asplenium ruta-muraria.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

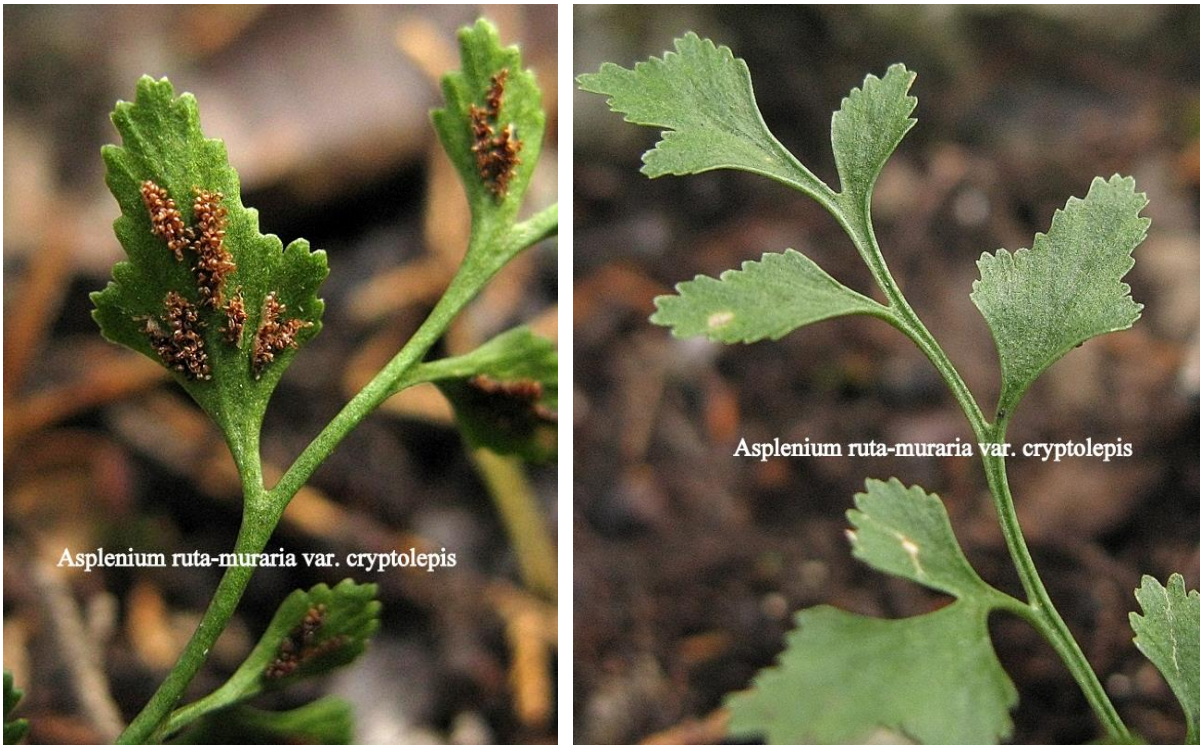


Figure 315. *Asplenium ruta-muraria*, Franklin Co., Tennessee, 29 Sep 2010. Photos: Todd Crabtree.

Asplenium ruta-muraria is a distinctive fern with unique morphological features and a strong preference for calcareous substrates. It thrives in pockets of well-weathered, relatively dry limestone outcrops, making it challenging to locate. This species is easily distinguished from other spleenworts by its fronds, which typically bear only 2–5 pairs of stalked pinnae with the lacerate ultimate segments (Fig. 315). Its petioles are entirely green, lacking the dark brown pigmentation seen in many related species.

Figure 316. *Asplenium ruta-muraria*, Bremen, Germany, 24 Oct 2023. Photo: Markus Klemke.

The specific epithet *ruta-muraria* translates to "rue of walls," referring both to the fern's frequent growth on European walls (Fig. 316) and its resemblance to Common Rue (*Ruta graveolens* L.). Fernald (1928) observed that, unlike their European counterparts, North American plants rarely occur on brick or stone walls. Noting this ecological difference, he questioned whether the species was truly uniform across continents. Based on additional morphological distinctions, he described the North American variant as a separate species, *Asplenium cryptolepis*.

Wherry (1940) attributed the differences in physical characteristics mainly to environmental factors: European specimens thrived in porous stone and humid conditions, while North American plants grew on solid limestone in drier conditions. After studying American populations on masonry, Wherry found them nearly indistinguishable from their European counterparts and reclassified them as *A. ruta-muraria* var. *cryptolepis*. However, Wagner et al. (1993) argued that the morphological differences were too subtle to justify separate taxonomic classifications. Still, Weakley et al. (2025) prefer not to assume that North American plants are identical to their European relatives.

14. Asplenium scolopendrium L. {centipede; alluding to the two rows of linear sori resembling feet} var. **americanum** (Fernald) Kartesz & Gandhi {American} — AMERICAN HART'S-TONGUE FERN; HOUND'S-TONGUE FERN; SEAWEED FERN; CATERPILLAR FERN; BUTTONHOLES (Fig. 317). [*Phyllitis fernaldiana* Á. Löve; *Phyllitis scolopendrium* (L.) Newman var. *americana* Fernald]

Figure 317. *Asplenium scolopendrium*, Morgan Co., Alabama, 30 Aug 2010. Photo: Alan Cressler.

Plants epipetric; evergreen. Deeply shaded limestone sinkholes with cool, humid air (in our region). Sporulates July–September; very rare in the northeastern Cumberland Plateau (Fig. 318). Chiefly distributed in the northeastern USA and southern Canada from upstate New York to the upper peninsula of Michigan, disjunct in northeast Alabama, eastern Tennessee, and New Mexico (Cibola County); also in the West Indies (Haiti) and Mexico (Weakley et al. 2025). The U.S. Fish and Wildlife Service lists *Asplenium scolopendrium* var. *americanum* as federally threatened (Currie 1993), and the Alabama Natural Heritage Program (2023) ranks it as critically imperiled (S1) within the state.

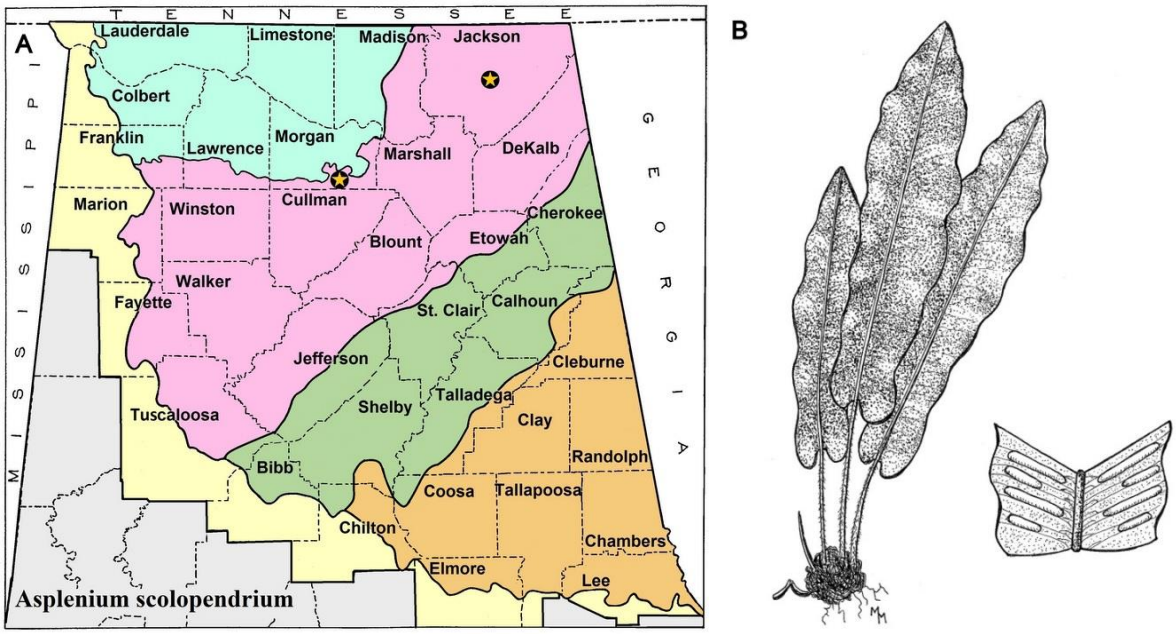


Figure 318. *Asplenium scolopendrium*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 319. *Asplenium scolopendrium*, Onondaga Co., New York, 17 Oct 2023. Photos: Noah Yawn.

Asplenium scolopendrium var. americanum is one of the rarest ferns in North America. In the northern part of its range, it thrives on cool, moist talus slopes under deep shade (Fig. 319a); in the southern Appalachians, it is restricted to humid limestone sinkholes (Fig. 320). Several of its common names, including "seaweed fern," "hound's-tongue," and "hart's-tongue," refer to its distinctive strap-shaped fronds. The term *hart* is an Old English word for a mature stag, referencing the resemblance of the fronds to a deer's elongated tongue. Other names, such as "caterpillar fern" and "buttonholes," allude to the linear sori (Fig. 319b) on the undersurface of the leaves (Clute 1901).

German-American botanist Frederick Pursh first documented the species near Syracuse, New York, in 1807 (Clute 1901). Decades later, in 1849, Dr. Augustin Gattinger discovered the first known population of the southeastern United States in Roane County, Tennessee. Unfortunately, this population disappeared by the early 1900s, likely due to over-collecting (Shaver 1954). In 1879, retired Confederate General Benjamin Cheatham located a second Tennessee population in a Marion County sinkhole near the Alabama border (Maxon 1900b). Initially estimated at around 200 plants, this population steadily declined, leaving only a few individuals by 1935 (McGilliard 1936). Remarkably, some ferns persist at the Marion County site to this day.

Figure 320. *Asplenium scolopendrium* habitat, Morgan Co., Alabama, 7 Mar 2016. Photo: Alan Cressler.

Nearly a century after the initial Tennessee discoveries, spelunkers uncovered two new populations of *Asplenium scolopendrium* var. *americanum* in northeastern Alabama. During a 1978 caving expedition, Eric Batchelder found the fern thriving in a Jackson County sinkhole (Short 1979). This discovery prompted further exploration, leading spelunkers to locate another population deep within a Morgan County sinkhole (Short 1980a). Scientists believe these southern populations are remnants from the Ice Ages, when the American Hart's-Tongue Fern's range extended farther southward. As the climate warmed, these ferns persisted in cool, sheltered sinkholes protected from summer heat (Short & Spaulding 2012). In 1980, Alan Cressler (pers. comm. 2025) observed seven plants at the Jackson County site, but none remain today—likely lost to ruthless plant collectors.

Carolus Linnaeus described *Asplenium scolopendrium* in 1753, based on European specimens. Nearly two centuries later, Fernald (1935) distinguished the American variety from its European counterpart, citing key morphological differences: North American specimens have smaller leaves, narrower scales with elongated, tapering tips, and sori concentrated primarily in the upper half of the blade rather than evenly distributed along its length. Britton (1953) highlighted cytology as the most definitive distinction, noting that American plants are tetraploid, whereas their European counterparts are diploid. This ploidy difference led Áskell Löve to reclassify the American variety as a separate species. However, Wagner (1955) argued that chromosome number alone was insufficient justification for taxonomic elevation.

15. Asplenium trichomanes L. {hair cup} — MAIDENHAIR SPLEENWORT (Fig. 321).

Figure 321. *Asplenium trichomanes*, Lauderdale Co., Alabama, 29 Jun 2010. Photo: Wayne Barger.

Plants epipetric; evergreen. Shaded acidic or calcareous rock crevices of cliffs, ledges, and boulders often covered with moss. Sporulates May–November; uncommon in northern Alabama; very rare in the Fall Line Hills District of the Coastal Plain (Fig. 322). This spleenwort is widespread in temperate North America but rare in the Great Plains and the southeastern Coastal Plain. It also occurs in Mexico and Europe (Weakley et al. 2025). Once considered imperiled to vulnerable (S2S3) in Alabama (ANHP 2022), it was delisted in 2023 after surveys revealed it to be more widespread than previously recognized.

Asplenium trichomanes closely resembles *A. resiliens* (Blackstem Spleenwort) but differs in having smaller, oval leaflets that lack basal lobes (Fig. 323). The specific epithet *trichomanes* derives from the Greek *thrix* ("hair") and *manes* ("cup"), though the fern is neither hairy nor cup-shaped. The name reflects a pre-Linnaean tradition, when botanists classified spleenworts under the genus *Trichomanes* (bristle ferns). In his landmark publication *Species Plantarum* (1753), Linnaeus reassigned these species to *Asplenium* and designated *A. trichomanes* as the type, retaining the old genus name as the species epithet in keeping with traditional taxonomic convention.

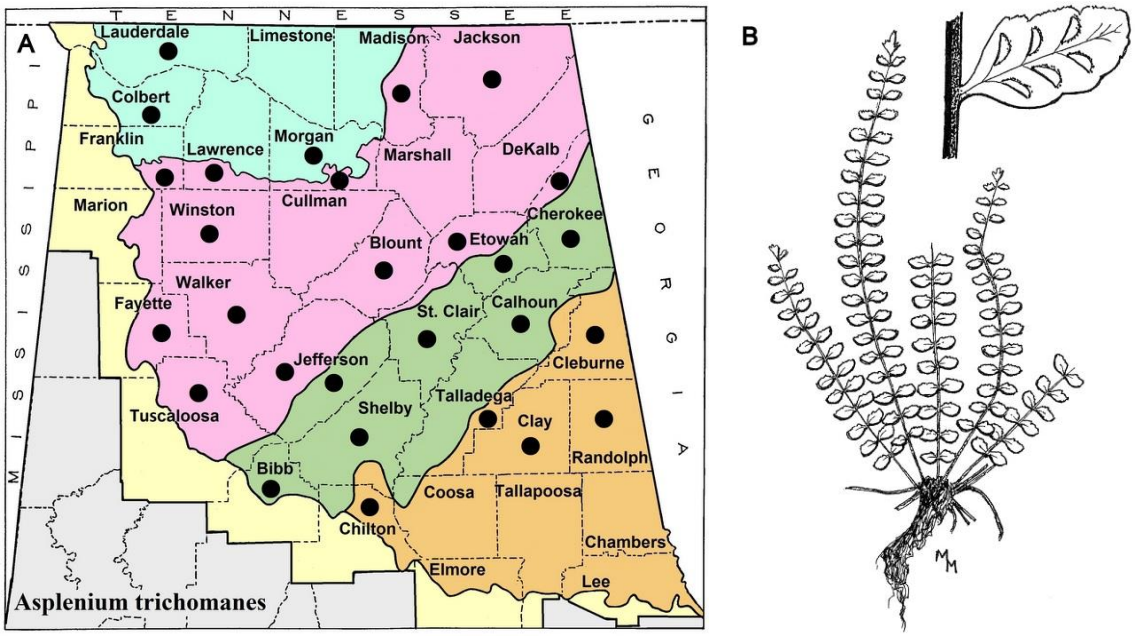


Figure 322. *Asplenium trichomanes.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 323. *Asplenium trichomanes*, Lauderdale Co., Alabama, 17 Mar 2010. Photo: Wayne Barger.

Asplenium trichomanes (sensu lato) represents a complex of diploid, tetraploid, and hexaploid cytotypes distributed across North America, Europe, Asia, Australia, and New Zealand (Moran 1982). Wagner et al. (1993) recognized two distinct North American elements at subspecific rank: the tetraploid *A. trichomanes* subsp. *quadrivalens* D.E. Mey. and the diploid *A. trichomanes* subsp. *trichomanes*. However, Weakley et al. (2025) treat these taxa at the species level. In North America, *A. trichomanes* is the more widespread of the two, typically occurring on non-calcareous rocks but occasionally found on limestone in Alabama. By contrast, *A. quadrivalens* (D.E. Mey.) Landolt is a calciphile restricted to calcareous substrates (Moran 1982). This tetraploid is rare in North America, occurring in isolated regions of Canada and the eastern and northwestern United States (Kartesz 2025).

16. Asplenium ×trudellii Wherry {for Harry William Trudell, 1879–1964, American botanist} — TRUDELL'S SPLEENWORT (Fig. 324). [*Asplenium pinnatifidum* Nutt. var. *trudellii* (Wherry) Clute; ×*Asplenosorus trudellii* (Wherry) Mickel]

Figure 324. *Asplenium ×trudellii*, Madison Co., Alabama, 23 May 2016. Photo: Wayne Barger.

Plants epipetric; evergreen. Crevices and ledges of sandstone cliffs. Sterile hybrid [*Asplenium montanum* × *pinnatifidum*], occasionally reproducing by unreduced spores; rare in the Cumberland Plateau (Fig. 325). Endemic to the eastern USA, mainly in the Appalachians from New Jersey west to Ohio and south to Alabama and Georgia, with disjunct populations in northern Illinois and Arkansas (Kartesz 2025). The Alabama Natural Heritage Program (2023) ranks it as critically imperiled (S1).

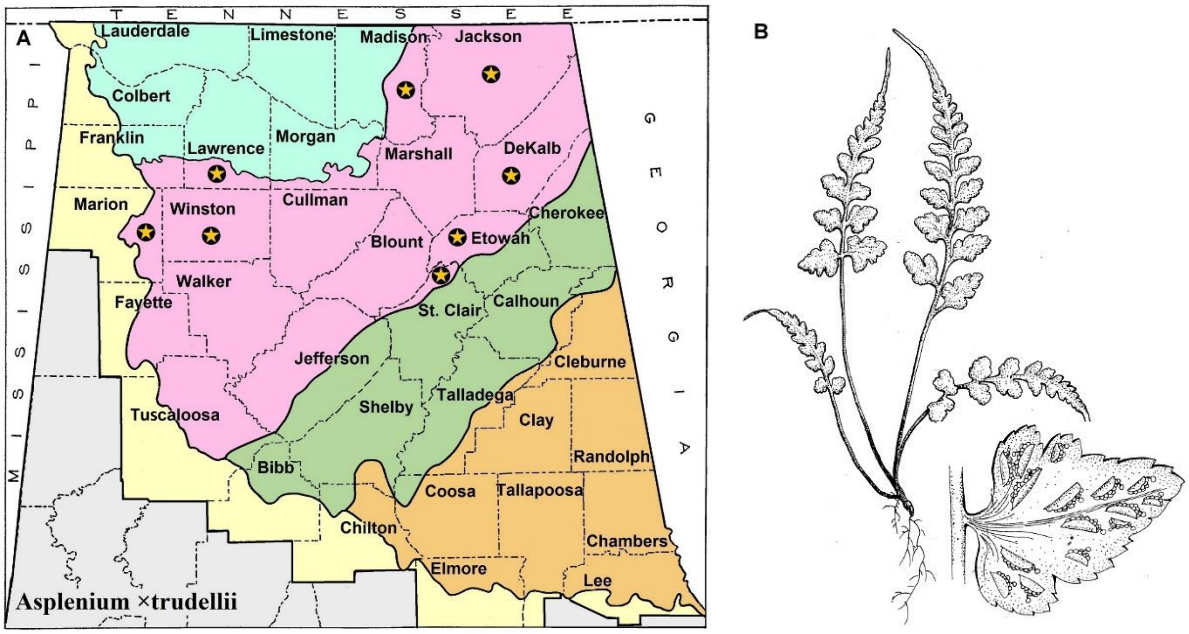


Figure 325. *Asplenium ×trudellii.* **A**. Distribution map. **B**. Illustration: Miriam Wysong Meyer, 1967.

Figure 326. *Asplenium ×trudellii* and parents, Marion Co., Tennessee, 9 Dec 2012. Photo: Alan Cressler.

In 1920, Harry Trudell, an amateur botanist from Philadelphia, discovered this fern growing along a ravine near the Susquehanna River in Pennsylvania. Later that same year, Edgar T. Wherry visited the site and documented a large, self-sustaining population. Impressed by its abundance and distinctiveness, Wherry (1925) classified the fern as a separate species and named it in Trudell's honor. He proposed that the plant likely originated through hybridization and remarked on its close resemblance to the Lobed Spleenwort (*Asplenium pinnatifidum*). However, he noted a key difference: in Trudell's Spleenwort (*A.* ×*trudellii*), the leaf blades are pinnate for about half their lower length, whereas in *A. pinnatifidum* they are chiefly pinnatifid. Decades earlier, on April 9, 1878, Eugene Smith had unknowingly collected this species in Marion County, Alabama, but identified it as *A. pinnatifidum* (Keener et al. 2025).

Figure 327. *Asplenium* ×*trudellii* with parents, Marion Co., Tennessee, 12 Feb 2012. Photo: Alan Cressler.

Wagner (1954) argued that cytological evidence strongly supported the classification of Trudell's spleenwort as an infertile hybrid between *Asplenium montanum* and *A. pinnatifidum* (Fig. 326). He noted that despite the sterility of its spores—distinguished microscopically by their irregular shape—the hybrid often thrives in surprising abundance in habitats where both parent species coexist (Fig. 327). At the time, Wagner emphasized that botanists had never recorded the fern in regions where both parent species were absent. He concluded that although *A.* ×*trudellii* can form large populations, its triploid chromosome complement likely prevents it from becoming a reproductively viable species. Nevertheless, Wagner (1983) later acknowledged evidence suggesting that *A.* ×*trudellii* might propagate through unreduced spores, which retain the full complement of chromosomes.

Weakley et al. (2025) treat *Asplenium* × *trudellii* as a species of hybrid origin rather than a sterile hybrid, omitting the hybrid "×" usually included in its name. They state that there is evidence of fertile spore production and emphasize that Trudell's Spleenwort is far more common than other sterile *Asplenium* hybrids. In some cases, it occurs where one or both parent species are absent, suggesting the capacity for independent dispersal. Cranfill (1980) likewise observed that the fern appeared more frequently in Kentucky than expected for a sterile hybrid, raising the possibility of apogamy. Yawn et al. (2024) further propose that apogamy or unreduced spore production may facilitate its slow, clonal spread, leading to localized or isolated colonies. They recommend further study to clarify the reproductive mechanisms of these self-sustaining populations and to determine whether this taxon warrants elevation from a nothospecies (formally named hybrid) to full species status.

18. **WOODSIACEAE** (Cliff Fern Family) – in Polypodiales

1. **WOODSIA** R. Brown 1810 {wood-ZEE-uh}
[For Joseph Woods, 1776–1864; English botanist]

1. Woodsia obtusa (Spreng.) Torr. subsp. **obtusa** {obtuse; tips of pinnules} — BLUNT-LOBED CLIFF FERN; COMMON WOODSIA; BLUNT-LOBED WOODSIA (Fig. 328).

Figure 328. *Woodsia obtusa*, Coosa Co., Alabama, 15 Aug 2024. Photos: Wayne Barger.

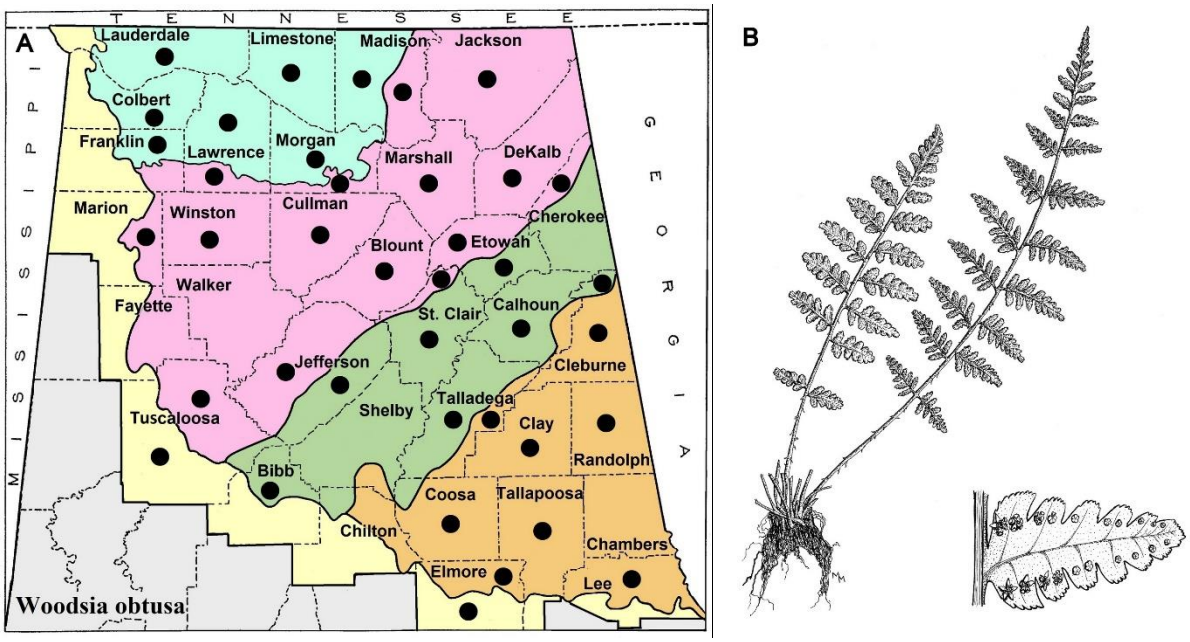


Figure 329. *Woodsia obtusa*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Plants epipetric or occasionally terrestrial; evergreen. Cliffs, ledges, rock outcrops, bluffs, rocky slopes, roadside embankments, well-drained wooded hillsides, rarely on urban walls. Sporulates May–October; uncommon in northern Alabama; rare in the Coastal Plain (Fig. 329). Native to the eastern USA and Canada from Quebec and Maine to southeastern Wisconsin, south to East Texas, and the Florida Panhandle (Windham 1993c).

The Blunt-Lobed Cliff Fern (*Woodsia obtusa*) is often mistaken for the bladder ferns (*Cystopteris* spp.), as both are small ferns with thin-textured fronds that grow on or near rock outcrops, sometimes in the same vicinity. Because of their overlapping habitats and similar appearance, they are frequently confused even by experienced naturalists. Several features, however, reliably separate them. *Woodsia* has distinctly scaly petioles (Fig. 330a), with old stalk bases that often persist through winter, and its indusia attach beneath the sori, splitting at maturity into a star-shaped cup (Fig. 330b). By contrast, *Cystopteris* has smooth or only lightly scaly petioles that wither away by the following season, and its indusia are pocket- or hood-shaped, attached along one side of the sorus. Venation also differs: in *Woodsia*, veins stop short of the leaflet margins, ending in enlarged *hydathodes*—specialized pores that exude water (Fig. 330c); in *Cystopteris*, veins extend fully to the margins.

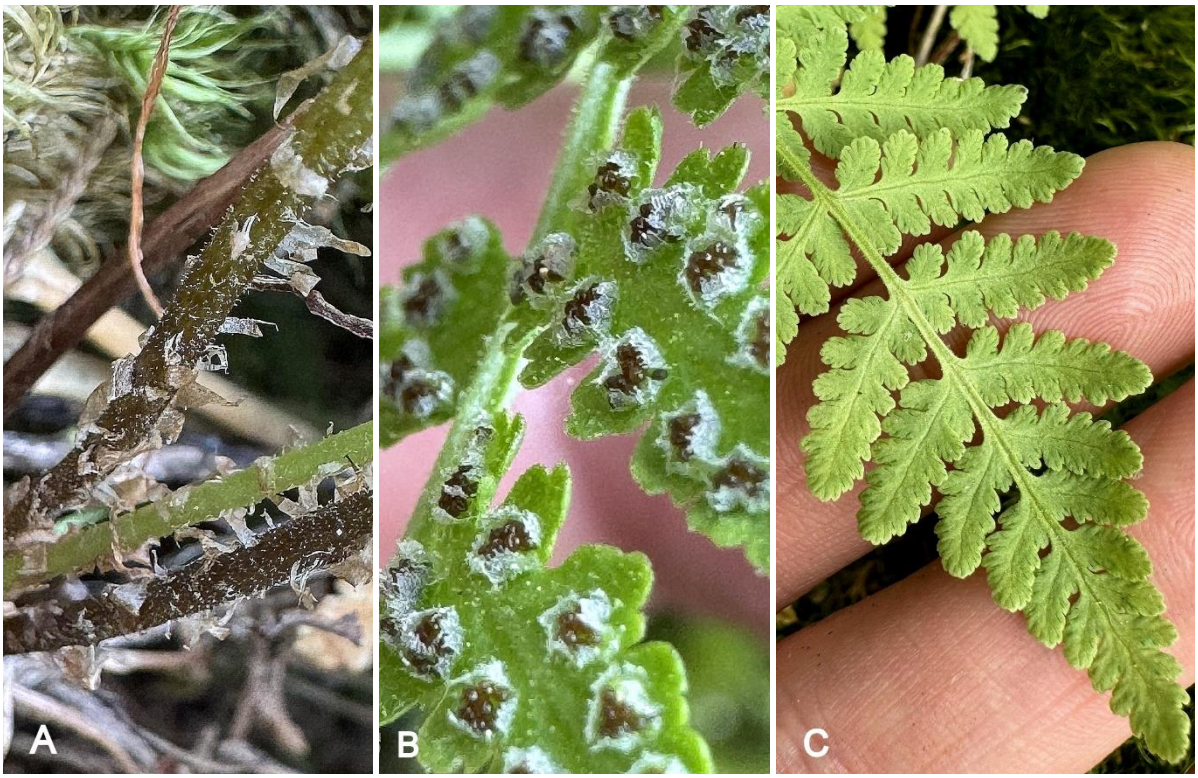


Figure 330. *Woodsia obtusa* Jefferson Co., Alabama, 8 May 2024. **A.** Scaly petioles. **B.** Indusia attached beneath sori. **C.** Veins not reaching the edge of leaf margins. Photos: Dan Spaulding.

Windham (1993b) recognized two cytotypes of *Woodsia obtusa* at the subspecific rank, distinguished by subtle morphological, ecological, and geographic differences. The tetraploid, *W. obtusa* subsp. *obtusa*, is widespread across the eastern United States, where it grows on a variety of rock types but shows a strong preference for limestone. In contrast, the diploid, *W. obtusa* subsp. *occidentalis* Windham, is restricted to the western portion of the range and typically occupies sandstone or granitic substrates. Morphologically, subsp. *occidentalis* bears more finely dissected, bipinnate-pinnatifid fronds, whereas subsp. *obtusa* tends to have coarser, primarily bipinnate blades.

19. ONOCLEACEAE (Sensitive Fern Family) – in Polypodiales

1. ONOCLEA Linnaeus 1753 {oh-noh-KLEE-uh}

[Greek *onos*, vessel, and *kleiein*, to close; pinnules roll up into bead-like segments, enclosing the sori]

1. Onoclea sensibilis L. {sensitive; to the first frost} — SENSITIVE FERN; BEAD FERN (Fig. 331).

Figure 331. *Onoclea sensibilis*, wet ditch, Cleburne Co., Alabama, 1 Aug 2021. Photos: Dan Spaulding.

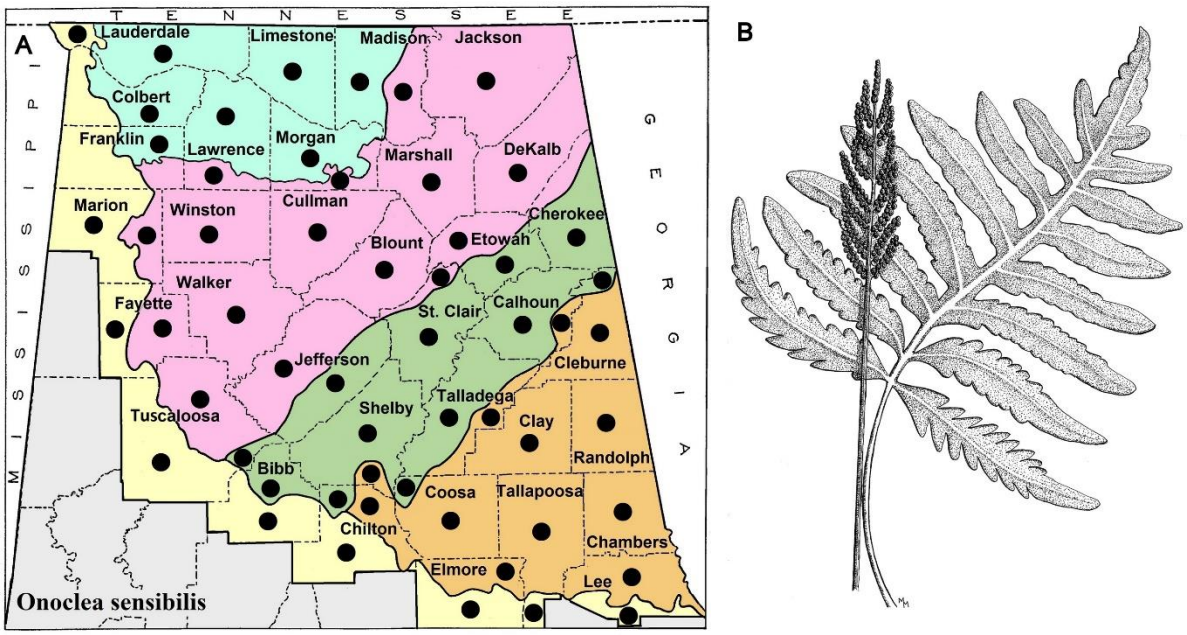


Figure 332. *Onoclea sensibilis.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Plants terrestrial; deciduous. Marshes, swamps, alluvial woods, bottomland forests, lake and pond margins, streambanks, ditches, and wet, disturbed habitats. Sporulates April–June; common throughout Alabama (Fig. 332). Native to the eastern USA and Canada from Newfoundland to southeastern Manitoba, south to East Texas and Florida (Johnson 1993a).

The common name "sensitive fern" refers to its vegetative leaves, which wither at the first frost, leaving only the upright fertile fronds (Fig. 333a). With their distinctive blackish-brown, bead-like spore clusters, these fronds have earned the plant the alternate name "bead fern" (Fig. 333b). Unlike the sterile leaves, they persist through winter, releasing green spores in early spring before new fronds appear (Lloyd & Klekowski 1970). Florists often use these long-lasting, fertile fronds in dried flower arrangements (Olsen 2007). Although gardeners sometimes cultivate the species, it spreads aggressively by rhizomes and can become weedy.

Figure 333. *Onoclea sensibilis*, Calhoun Co., Alabama, 9 Nov 2024. Photos: Emily Spaulding.

Onoclea sensibilis often thrives in low, moist fields, and its accidental inclusion in hay has resulted in livestock poisonings. Animals that ingest this fern may develop symptoms of incoordination, rendering them temporarily unable to walk or eat (Gibbons et al. 1990). In addition to its toxic properties, this fern is the larval host for the Sensitive Fern Borer Moth (*Papaipema inquaesita*, Fig. 334a). The caterpillars, commonly called cutworms, bore into the fern's stems and rhizomes, feeding internally and disrupting vascular tissues (Peterson et al. 1990).

The sterile leaves of the Sensitive Fern (*Onoclea sensibilis*, Fig. 334b) closely resemble those of the Netted Chain Fern (*Lorinseria areolata*, Fig. 334c), and the two often occur in similar habitats. Closer inspection, however, reveals consistent differences. *Onoclea* typically bears opposite leaf segments with rounded, blunt tips and smooth margins, whereas *Lorinseria* generally has alternate segments with sharper tips and finely serrated edges.

Figure 334. A. Sensitive Fern Borer Moth, Shelby Co. Alabama, 18 Sep 2024. Photo: John Morgan. **B.** Sterile frond of Sensitive Fern, Calhoun Co. Alabama, 9 Nov 2024. Photo: Emily Spaulding. **C.** Sterile frond of Netted Chain Fern, Calhoun Co. Alabama, 9 Nov 2024. Photo: Savannah Spaulding.

20. BLECHNACEAE (Chain Fern Family) – in Polypodiales

1. Leaves strongly dimorphic, sterile leaves mostly pinnatifid, fertile leaves pinnate; veins of sterile fronds conspicuously netted throughout or nearly so ..... ***Lorinseria***
1. Leaves monomorphic, sterile and fertile leaves pinnate-pinnatifid; veins mostly free except for limited netting along the midribs of leaf segments ..... ***Anchistea***

1. ANCHISTEA C. Presl 1851 {an-KISS-tee-uh}

[Greek *anchistos*, a relation; closely related to the genus *Woodwardia*]

1. Anchistea virginica (L.) C. Presl {Virginian; where first collected} — VIRGINIA CHAIN FERN; SOUTHERN CHAIN FERN (Fig. 335). [*Woodwardia virginica* (L.) Sm.]

Figure 335. *Anchistea virginica*. **A.** Baker's Pond, Bogan Mountain, Chattooga Co., Georgia, 15 Sep 2012. **B.** Fertile pinnae, Fall Line Sandhills Natural Area, Taylor Co., Georgia, 16 Oct 2011. Photos: Alan Cressler.

Plants terrestrial; deciduous. Bogs, swamps, woodland seeps, marshes, and roadside ditches in acidic, organic soils. Sporulates June–November; rare in the Cumberland Plateau, Ridge & Valley, and Piedmont; frequent in the Coastal Plain (Fig. 336). This species occurs in eastern North America, from the Great Lakes to Nova Scotia and New England, south through the Coastal Plain to Florida, and west to East Texas, with scattered populations farther north. It is also present in Bermuda (Cranfill 1993).

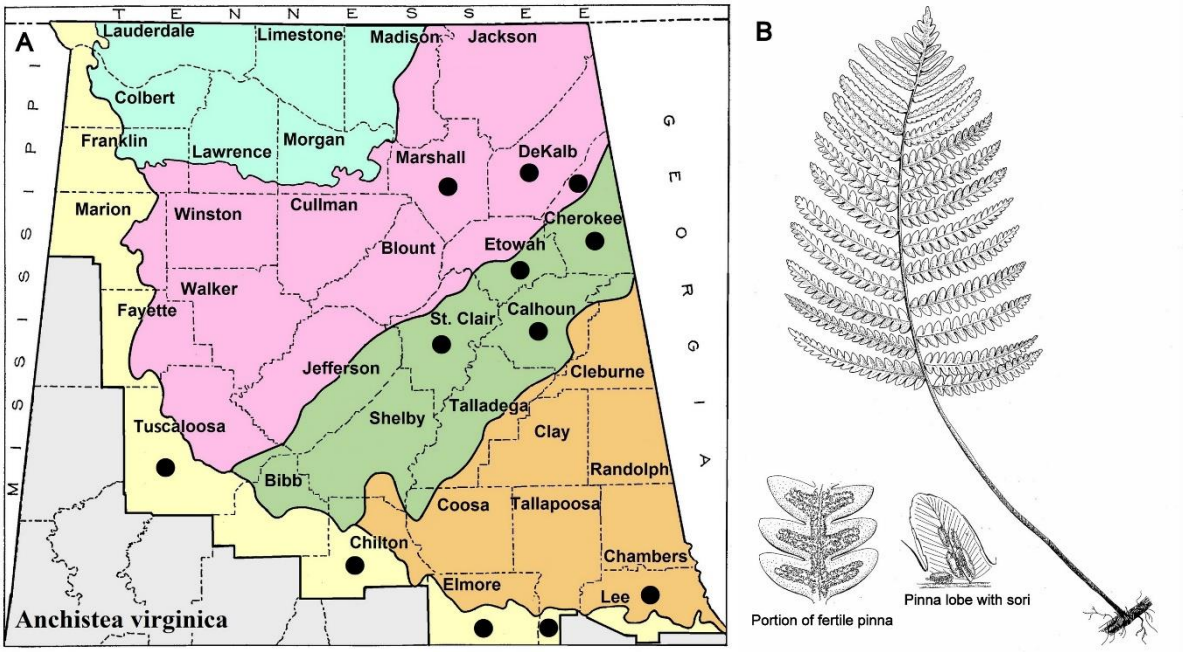


Figure 336. *Anchistea virginica*. **A.** Distribution map. **B.** Illustration: Miriam Wysong Meyer, 1967.

Figure 337. *Anchistea virginica*, Cherokee Co., Alabama, 18 May 2022. Photos: Zach Irick.

Figure 338. *Anchistea virginica*, Calhoun Co., Alabama, 11 Aug 2022. Photo: Noah Yawn.

In Alabama, *Anchistea virginica* primarily inhabits the Coastal Plain, with a few scattered populations occurring above the Fall Line. The sterile leaves of the Virginia Chain Fern closely resemble those of the Cinnamon Fern (*Osmundastrum cinnamomeum*), and both species thrive in similar wetland habitats. However, *A. virginica* stands out with its blackish leaf stalks, the interconnected veins of its pinnae forming a distinctive chain-like pattern near the midribs, and the absence of woolly brown hairs (Fig. 337). This species spreads through creeping, horizontal rhizomes, with fronds scattered along their length, often forming dense colonies (Fig. 338). In contrast, *O. cinnamomeum* has a brown to tan leaf stalk, unconnected veins, and young fronds covered in cinnamon-brown woolly hairs that persist in the axils of older leaflets. Unlike *A. virginica*, it typically grows in dense tufts, with fronds arranged in a circular pattern that emerges from short, ascending rhizomes.

2. LORINSERIA C. Presl 1849 {loh-RIN-seer-ee-uh}

[For Gustav Lorinser, 1811–1863, a Bohemian botanist and physician]

1. Lorinseria areolata (L.) C. Presl {with areoles; netted veins} — NETTED CHAIN FERN; NETVEIN CHAIN FERN; NETLEAF CHAIN FERN (Fig. 339). [*Woodwardia areolata* (L.) T. Moore]

Plants terrestrial; deciduous. Acidic bogs, seeps, swamps, wet woods, and seepage cliffs. Sporulates May–September; frequent throughout Alabama (Fig. 340). Native to the eastern USA from Maine to Arkansas, south to eastern Texas and Florida (Cranfill 1993).

The Netted Chain Fern (*Lorinseria areolata*) inhabits a range of wetlands and often forms dense, spreading colonies in saturated soils, sometimes blanketing large patches of ground (Fig. 341). It produces dimorphic fronds: broad, pinnatifid sterile leaves and taller, pinnate fertile fronds lined with rows of sori (Fig. 342a–b). Its common names emphasize two distinctive traits—the intricate network of veins on sterile fronds and the chain-like rows of sori on fertile fronds. The sterile leaves closely resemble those of the Sensitive Fern (*Onoclea sensibilis*), which often grows in the same habitats and can cause confusion. Examination of the leaf segments best separates the two: in *L. areolata*, they are alternate and finely toothed, whereas in *O. sensibilis*, they are typically opposite with smooth, toothless margins.

Figure 339. *Lorinseria areolata*, Calhoun Co., Alabama, 28 Aug 2024. Photos: Dan Spaulding.

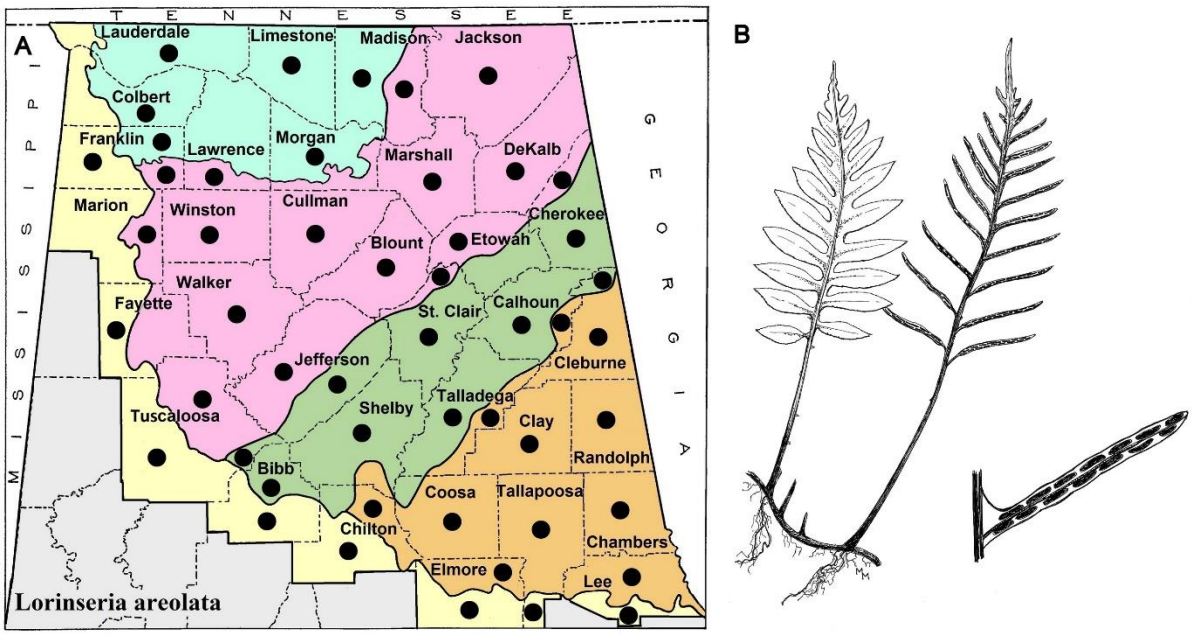


Figure 340. *Lorinseria areolata*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Native Americans crafted intricate basket designs using slender fibers from the stems of the Netted Chain Fern. They gathered the fronds and split the petioles to extract the leathery strands (Dunbar 1989). In addition to its cultural importance, this fern is a vital host plant for the Chain Fern Borer Moth (*Papaipema stenocelis*). Adult moths lay their eggs on the fronds, and once hatched, the larvae feed on the petioles and rhizomes of the fern (Peterson et al. 1990).

Figure 341. *Lorinseria areolata* population, Lee Co., Alabama, 17 Apr 2024. Photo: Dan Spaulding.

Figure 342. *Lorinseria areolata.* **A**–**B.** Calhoun Co., Alabama, 9 Nov 2024. Photos: Savannah Spaulding. **C.** Rows of sori on fertile frond, DeKalb Co., Alabama, 3 Aug 2023. Photo: Brittney M. Hughes.

21. ATHYRIACEAE (Lady Fern Family) – in Polypodiales

1. Leaves 1-pinnate; pinnae pinnatifid; sori mostly straight, not crossing the veins ..... ***Deparia***

1. Leaves 2–3-pinnate; pinnae at least 1-pinnate; sori mostly curved, extending across the veins.

    2. Leaves bright green, not variegated; veins all free (not netted); rhizomes erect; petiole bases swollen; native, widespread throughout Alabama .....***Athyrium***
    2. Leaves variegated, silvery gray to gray-green; veins both free and anastomosing (netted); rhizomes short-creeping to ascending; petiole bases not swollen; exotic, rarely naturalizing in Alabama .....***Anisocampium***

1. ANISOCAMPIUM C. Presl 1851 {ah-nee-soh-KAM-pee-um}
[Greek *anisos*, unequal, and *campe*, bend; vein areoles are few and irregular]

1. Anisocampium niponicum (Mett.) Y.C. Liu, W.L. Chiou, & M. Kato {of Japan} — JAPANESE PAINTED FERN (Fig. 343). [*Athyrium niponicum* (Mett.) Hance]

Figure 343. *Anisocampium niponicum*, Cleburne Co., Alabama, 10 Jun 2021. Photo: Wayne Barger

Plants terrestrial; deciduous. Moist woods along drainages. Sporulates May–September; very rare in northern Alabama (Fig. 344). This species is indigenous to southeastern Asia, including China, India, Japan, Korea, Myanmar, Nepal, and Vietnam. In its native range, it grows in forests, along streams, on shaded wet mountain slopes, and occasionally on shrubby or grassy slopes. Widely cultivated as an ornamental fern, it sometimes escapes from gardens and has become sparingly naturalized in parts of the eastern USA and Europe (Wang & Kato 2013; Wyatt & Harris 2022).

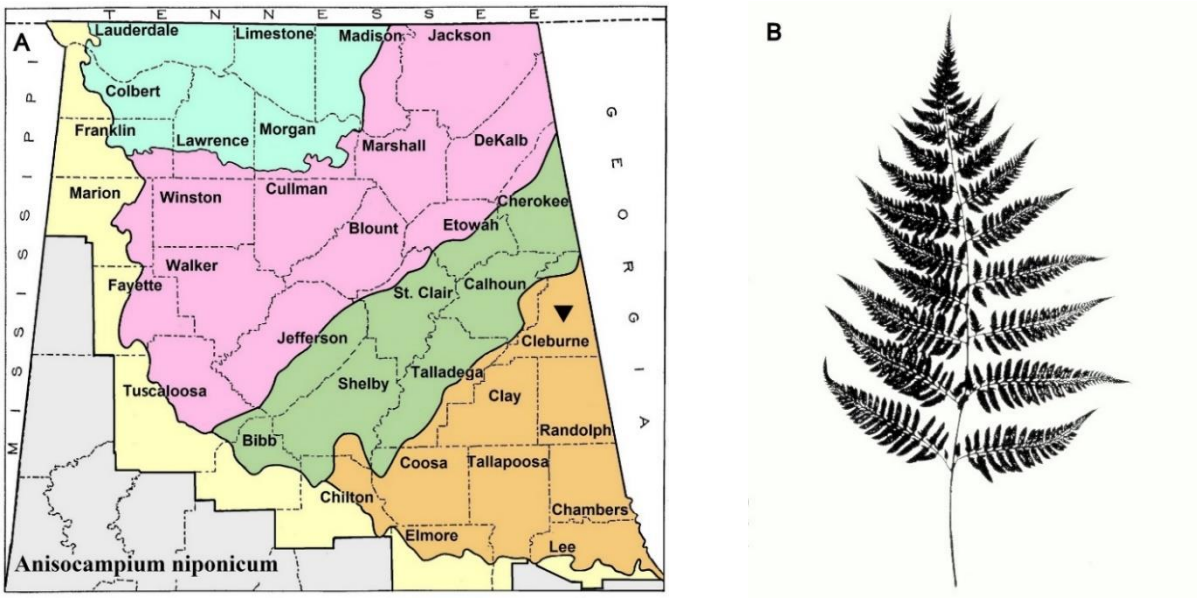


Figure 344. *Anisocampium niponicum.* **A.** Distribution map. **B.** Illustration: Barbara Joe Hoshizaki, 2001.

Figure 345. *Anisocampium niponicum*. **A.** Habitat in wild, Cleburne Co., Alabama, 10 Jun 2021. Photo: Wayne Barger. **B.** Cultivated, Cleburne Co., Alabama, 24 Mar 2024. **C.** Sori on a cultivated plant, Cleburne Co., Alabama, 27 Oct 2024. Photos: Dan Spaulding.

In 2021, Wayne Barger discovered *Anisocampium niponicum* on Cheaha Mountain in Cleburne County, Alabama (Fig. 345a), where three individuals were growing in an undisturbed area with no sign of nearby plantings (Yawn et al. 2024). Previously, James Peck (2011) documented the species in Arkansas, and Wyatt and Harris (2022) reported it from additional states across the eastern United States. Weakley et al. (2025) noted that this popular ornamental often spreads locally from cultivation and is expected to naturalize more broadly. However, it shows no signs of invasiveness and remains an attractive addition to shaded gardens.

The Japanese Painted Fern (*Anisocampium niponicum*), often sold under its former name *Athyrium niponicum* 'Pictum,' is highly valued for its striking tricolored fronds, which display a silvery sheen infused with deep burgundy along the main veins (Fig. 345b). Like its close relative, the Southern Lady Fern (*Athyrium asplenioides*), it bears linear sori (Fig. 345c). In cultivation, this fern thrives in moist, shaded gardens, where its vibrant foliage provides bold contrast against surrounding greenery. Its popularity is due to the distinctive coloration of its fronds, which often retain their ornamental appeal throughout the growing season. Under favorable conditions, it continuously produces fresh fronds from spring through fall, ensuring a dynamic and ever-changing display (Mickel 1994; Olsen 2007).

2. ATHYRIUM Roth 1799 {uh-THEER-ee-um}
[Greek *athyros*, doorless; sporangia tardily pushing open the outer edge of the indusium]

1. Athyrium asplenioides (Michx.) A.A. Eaton {like *Asplenium*; linear sori as in the spleenworts} — SOUTHERN LADY FERN; LOWLAND LADY FERN (Fig. 346). [*Athyrium filix-femina* (L.) Roth ex Mert. var. *asplenioides* (Michx.) Farw.]

Figure 346. *Athyrium asplenioides*. **A.** Madison Co., Alabama, 18 Apr 2011. Photo: Wayne Barger. **B.** Calhoun Co., Alabama, 9 Nov 2024. Photo: Emily Spaulding.

Plants terrestrial, occasionally in thin soil on rock; deciduous. Bottomland forests, wooded streambanks, alluvial woods, moist cliff bases, roadside ditches, and shaded pond or lake margins. Sporulates May–September; common throughout Alabama (Fig. 347). Native to the eastern USA from southern New Hampshire to southeastern Kansas, south to East Texas, and Florida (Kato 1993a).

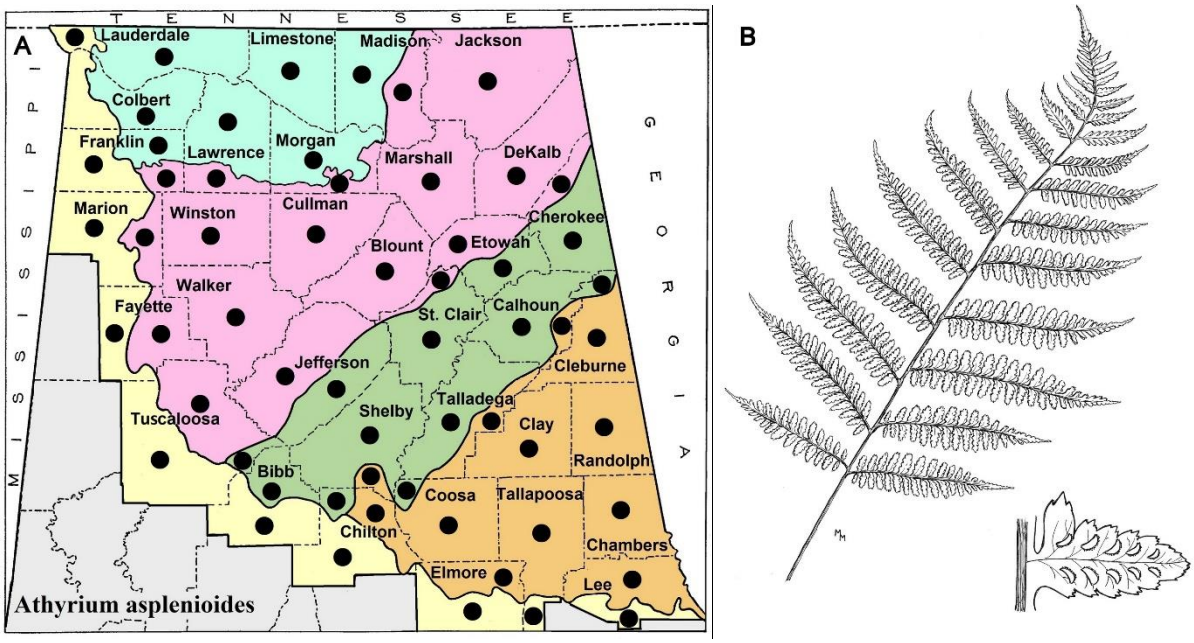


Figure 347. *Athyrium asplenioides.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

The "true" Lady Fern, *Athyrium filix-femina* (sensu stricto), is native to Eurasia and represents one member of a wide-ranging complex that botanists have classified at different ranks (Kelloff et al. 2002). Butters (1917b) and Wherry (1961) treated the North American entities as distinct species, whereas Lellinger (1985) reduced them to subspecies. In *Flora of North America*, Kato (1993a) placed *A. asplenioides* as one of four varieties of *A. filix-femina* in Canada and the United States. More recently, Weakley et al. (2025) recognized these taxa at the species level. In the eastern United States, the complex includes the Southern Lady Fern (*A. asplenioides*) and the Northern Lady Fern (*A. angustum* (Willd.) K. Presl), with additional species in western North America. Modern treatments now consistently restrict *A. filix-femina* s.s. to Eurasia, separating it from its North American relatives.

Figure 348. *Athyrium asplenioides*, Calhoun Co., Alabama, 13 May 2007. Photo: Vitaly Charny.

In 16th- and 17th-century Europe, the Lady Fern (*Athyrium filix-femina*) became closely associated with folklore surrounding the "mystic fern seed." During this era, many believed ferns bore seeds capable of granting invisibility to anyone who discovered them. This myth was prevalent at the time, and seekers would venture out on Midsummer's Eve to search for the elusive seeds, unaware that ferns reproduce not by seeds but by microscopic spores. With its graceful, lace-like fronds and preference for shaded woodlands, the Lady Fern embodied mystery and intrigue within this tradition. Known then as the "female fern," it was regarded as the counterpart to the coarser, robust Male Fern, *Dryopteris filix-mas* (L.) Schott (Clute 1901; Frankel 1981).

The Southern Lady Fern (*Athyrium asplenioides*) is a graceful addition to shaded gardens, thriving in rich, moist soils with little maintenance. Its common name reflects long-held associations with feminine qualities. The delicate, lacy fronds suggest a Victorian shawl or veil, evoking the charm of a bygone era. Reddish petioles recall the elegance of crimson stockings on a refined lady (Fig. 348), while the arching, linear sori resemble the gentle curve of a fair maiden's eyebrows (Fig. 349). Together, these traits reinforce the fern's subtle, feminine allure (Mickel 1994). Though admired for its beauty, it can spread vigorously and crowd out neighboring plantings.

Figure 349. *Athyrium asplenioides*, young sori, Colbert Co., Alabama, 13 Jul 2023. Photo: Vitaly Charny.

Some Native American tribes prepared a medicinal infusion known as "root tea" by steeping the rhizomes of lady fern in hot water. This herbal remedy served primarily as a gynecological aid, offering several benefits. Women traditionally drank the tea to stimulate lactation, relieve breast pain after childbirth, and ease labor pains. A more potent decoction of the rhizome also functioned as a diuretic, promoting urine flow (Foster & Duke 1990; Moerman 1998).

3. Deparia Hooker & Greville 1830 {dih-PAIR-ee-uh}
[Greek *depas*, saucer; from the saucer-like indusium of the type species, *Deparia prolifera*]

1. Leaves tapering toward the base; blade oblong-lanceolate, petiole bases swollen, with two rows of teeth; plants deciduous, native, growing in moist forests ..... ***Deparia acrostichoides***
1. Leaves broadest at the base, blade ovate-lanceolate; petiole bases not markedly swollen, lacking teeth; plants evergreen, exotic, growing in disturbed or natural habitats..... ***Deparia petersenii***

1. Deparia acrostichoides (Sw.) M. Kato {like *Acrostichum*; leather fern} — SILVERY GLADE FERN; SILVERY-SPLEENWORT; SILVER FALSE SPLEENWORT (Fig. 350). [*Asplenium acrostichoides* Sw.; *Athyrium thelypterioides* (Michx.) Desv.; *Diplazium acrostichoides* (Sw.) Butters]

Figure 350. *Deparia acrostichoides*, Winston Co., Alabama, 13 Jun 2024. Photos: Dan Spaulding.

Plants terrestrial or occasionally in thin soil on rock; deciduous. Moist forests, rich woods, cove forests, and wooded limestone sinks. Sporulates June–September; rare in northern Alabama; very rare in the Coastal Plain (Fig. 351). Native to eastern USA and Canada from Nova Scotia to Ontario, south to Arkansas and Georgia (Kato 1993b).

Deparia acrostichoides reaches the southern limit of its range in Alabama, where it is rare, though it becomes more common farther north. In the South, it typically grows in moist, rocky woodlands (Fig. 352). This species is the only representative of *Deparia* native to the New World (Kato 1993b). Although not a true spleenwort, Olof Swartz placed it in *Asplenium* in 1801 because of its linear sori. Its thick indusia retain a silvery-white sheen through much of the summer, giving rise to its common name (Clute 1901). Later in the season, the sori darken to brown (Fig. 353).

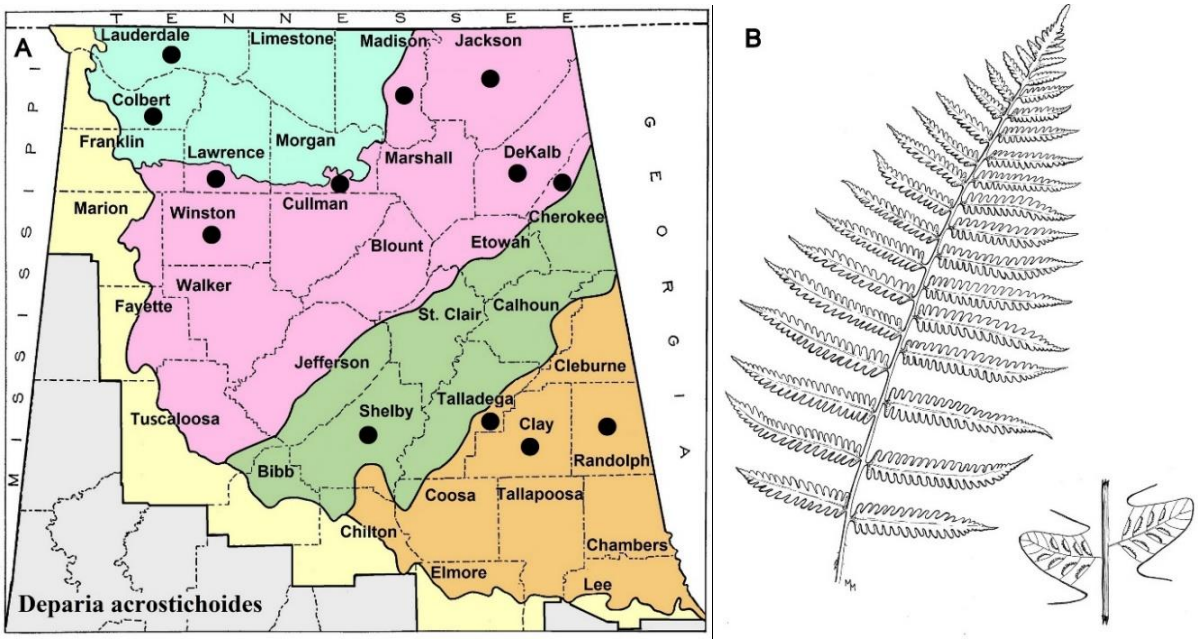


Figure 351. *Deparia acrostichoides.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 352. *Deparia acrostichoides*. **A.** Jackson Co., Alabama, 27 Apr 2008. Photo: Alan Cressler. **B.** Winston Co., Alabama, 13 Jun 2024. Photo: Dan Spaulding.

The Silvery Glade Fern (*Deparia acrostichoides*) superficially resembles the New York Fern (*Amauropelta noveboracensis*) because both have pinnate-pinnatifid fronds with narrowing leaf bases. Closer examination, however, reveals key differences. In *A. noveboracensis*, the blade tapers more abruptly at the base, with the lowermost three or four pairs of leaflets markedly reduced, producing a distinct narrowing. Its sori are also round, while those of *D. acrostichoides* are straight and elongated.

Figure 353. *Deparia acrostichoides*, Macon Co., North Carolina, 13 Sep 2009. Photo: Alan Cressler.

2. Deparia petersenii (Kunze) M. Kato {for Christian Wilhelm Petersen (1792–1859), a Danish botanist who collected the type specimen in China} — JAPANESE LADY FERN; PETERSEN'S LADY FERN; JAPANESE FALSE SPLEENWORT (Fig. 354). [*Asplenium petersenii* Kunze; *Diplazium japonicum* (Thunb.) Bedd., misapplied]

Figure 354. *Deparia petersenii*, Dale Co., Alabama, 25 Nov 2021. Photos: James Eddie Watkins.

Plants terrestrial; evergreen. Swamp forests, wet hammocks, moist banks, and disturbed areas. Sporulates June–October; rare in northern Alabama; uncommon in the Coastal Plain (Fig. 355). Native to southeast Asia, introduced and naturalized in the southeastern USA, chiefly in the Coastal Plain from Georgia and Florida, west to Louisiana (Kartesz 2025).

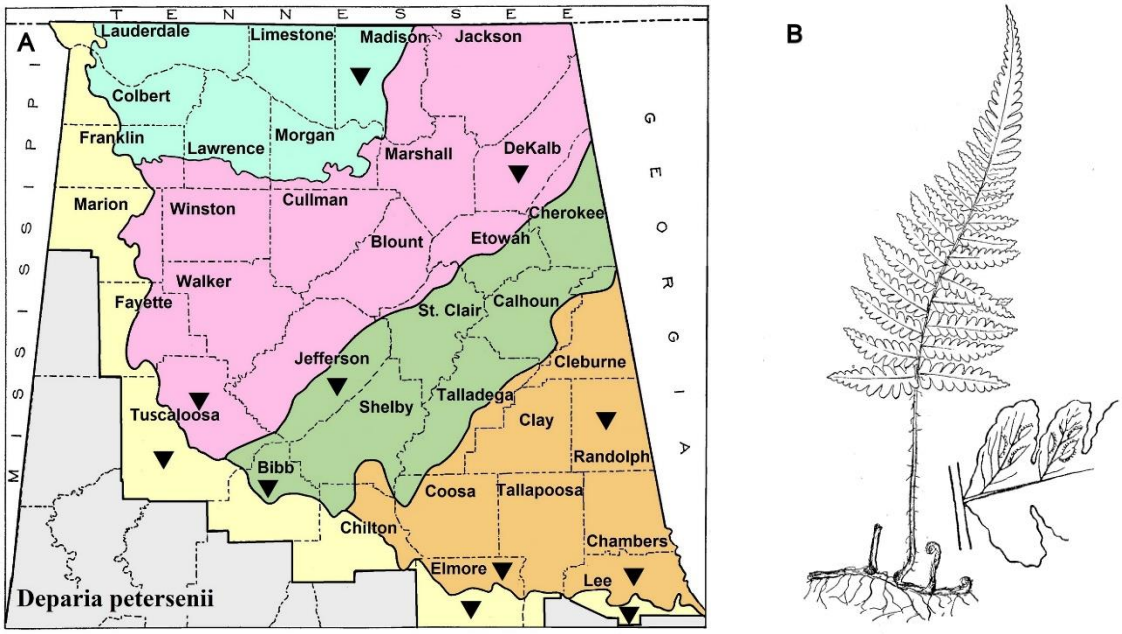


Figure 355. *Deparia petersenii.* **A.** Distribution map. **B.** Illustration: James C.W. Chen, 1964.

Figure 356. *Deparia petersenii*, bottomlands, Escambia Co., Alabama, 28 Dec 2020. Photo: Steven Kistler.

Edgar T. Wherry (1964) reported an Asian fern in North America from a plant that escaped cultivation in Gadsden County, Florida, in 1957. He identified it as the Japanese Twin-Sorus Fern, *Diplazium japonicum* (Thunb.) Bedd., and most subsequent floras adopted this name (Lellinger 1985). Kato (1993b) later corrected the error, noting that botanists had misapplied the name *Diplazium japonicum* (=*Deparia japonica* (Thunb.) M. Kato) to North American specimens. He determined that the fern naturalized in the southeastern United States is *Deparia petersenii*.

Figure 357. *Deparia petersenii*, under a bridge, Lee Co., Alabama, 13 Jun 2024. Photo: Dan Spaulding.

In 1977, John Short reported another North American occurrence of *Deparia petersenii* in Lee County, Alabama. It was Auburn University student Jason I. Glick who collected the specimen from a wooded campus ditch, initially mistaking it for *Deparia acrostichoides*. He brought it to Short, who identified it as *Diplazium japonicum*, now recognized as *D. petersenii* (Short 1980b). Soon afterward, botanists recorded the species in Georgia, Mississippi, and Louisiana (Faircloth 1981). Since these early discoveries, *D. petersenii* has spread further and is becoming an invasive species, thriving in both natural (Fig. 356) and disturbed habitats (Fig. 357). Its linear sori and stiff, silvery hairs, which often contrast with the dark brown petiole and lower rachis, provide reliable characters for identification.

22. **THELYPTERIDACEAE** (Marsh Fern Family) – in Polypodiales

Many species in the Thelypteridaceae are known as "maiden ferns," a common name that inspired the genus name *Thelypteris*, derived from the Greek *thelys* ("female" or "womanly") and *pteris* ("fern"), likely alluding to their delicate, graceful form. The family is one of the largest among ferns, occurring worldwide and especially diverse in tropical and subtropical regions. Because of this diversity, pteridologists have long debated its classification, advancing very different taxonomic interpretations over the past century. Some grouped more than 1,000 species into a single, broadly defined genus, *Thelypteris*, while others separated them into more than 30 smaller genera. Morton (1963) chose the broad approach and classified all species under *Thelypteris*, a treatment that Lellinger (1985) later adopted in his manual of North American ferns. In *Flora of North America*, Smith (1993b–d) recognized three genera, reflecting a more moderate viewpoint. Most recently, Fawcett and Smith (2021) greatly expanded the family to 37 genera worldwide, applying a modern system that integrates morphological traits, biogeographic patterns, and phylogenomic (DNA-based) evidence.

1. Leaves 1–2-pinnatifid, sometimes pinnate near the blade base; rachis with conspicuous wings connecting the bases of leaf segments ..... ***Phegopteris***
1. Leaves 1–3 pinnate; rachis not winged, pinnae free.

    2. Leaves bipinnate or tripinnate; blade broadly triangular; pinna midribs not grooved on the lower surface .....***Macrothelypteris***
    2. Leaves usually 1-pinnate to 1-pinnate-pinnatifid, rarely 2-pinnate; blade narrowly to broadly lanceolate; pinna midribs grooved on the lower surface.

        3. Sori elongate; indusia absent; sporangia minutely pubescent with hairs 0.1–0.2 mm long; fronds evergreen; plants growing in rock crevices of sandstone bluffs .....***Leptogramma***
        3. Sori round or slightly oblong; indusia present, occasionally inconspicuous; sporangia glabrous, but indusia occasionally pubescent; fronds evergreen or deciduous; plants typically terrestrial, occasionally growing on rock in thin soil.

            4. Leaf blade strongly tapering at base; lowermost pinnae significantly reduced, with the basal 3 or 4 pairs less than one-tenth the length of the longest pinnae..... ***Amauropelta***
            4. Leaf blade tapering slightly to moderately at base, or not at all; lowermost pinnae often as long as those above, or if reduced, then at least one-fourth the length of the longest pinnae.

                5. Veinlets (lateral veins) mostly Y-forked, with some simple, unbranched veinlets often present; pinnae cut to or nearly to the midvein; margins of fertile leaf segments strongly recurved; indusia sparsely hairy ..... ***Thelypteris***
                5. Veinlets simple, not forked; pinnae deeply lobed but not cut to the midveins; margins of pinnae slightly recurved to flat; indusia conspicuously hairy.

                    6. Basal veins from adjacent lobes of a pinna united below the sinus, forming a single excurrent vein to the sinus between lobes; costae (midribs) on the lower pinna surfaces pubescent with short hairs, 0.1–0.2 mm long; rachis and pinnae without stalked glands ..... ***Christella***
                    6. Basal veins from adjacent lobes of a pinna not united, each pair extending to the margins just above the sinus or converging at the sinus without fusing; costae on lower pinna surfaces pubescent with short and long hairs, 0.3–1.0 mm long; rachis and pinnae usually bearing stalked yellowish glands .....***Pelazoneuron***

1. AMAUROPELTA Kunze 1843 {ah-maw-ro-PEL-tuh}
[Greek *amauros*, dark or obscure, and *pelte*, shield; alluding to the small indusium]

1. Amauropelta noveboracensis (L.) S.E. Fawc. & A.R. Sm. {of New York} — NEW YORK FERN; TAPERING FERN (Fig. 358). [*Dryopteris noveboracensis* (L.) A. Gray; *Parathelypteris noveboracensis* (L.) Ching; *Thelypteris noveboracensis* (L.) Nieuwl.]

Figure 358. *Amauropelta noveboracensis.* **A.** Cleburne Co., Alabama, 7 May 2022. Photo: Dan Spaulding. **B.** Clay Co., Alabama, 3 Aug 2023. Photo: Joe Stockert.

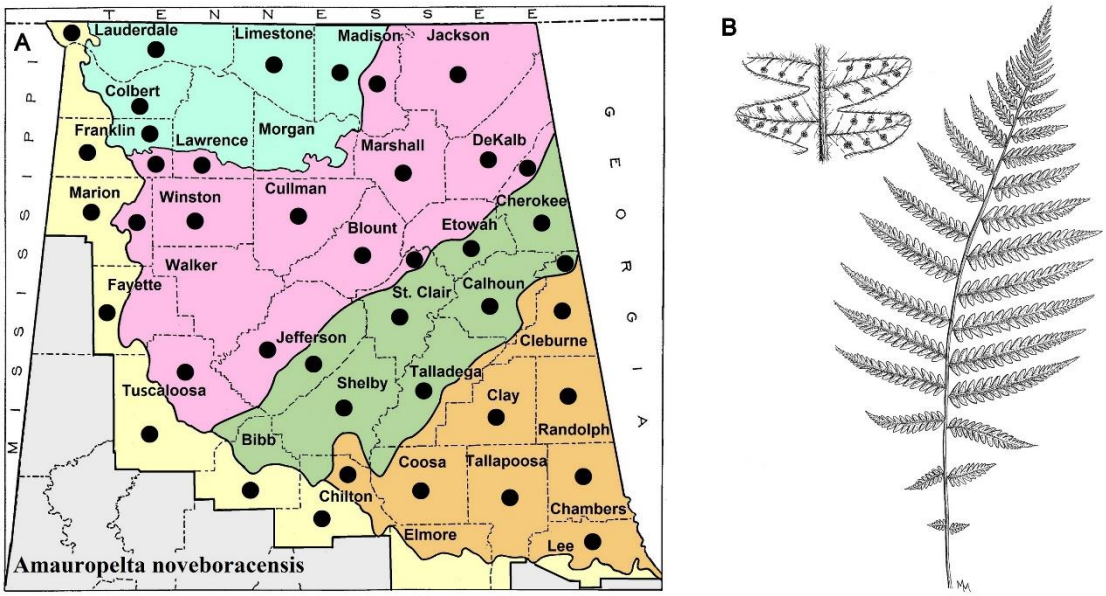


Figure 359. *Amauropelta noveboracensis.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 2000.

Plants terrestrial; deciduous. Mesic forests, bottomland forests, floodplains, wooded stream banks, and swamp margins. Sporulates May–August; frequent in northern Alabama; rare in the Coastal Plain (Fig. 359). It occurs in eastern North America, from Newfoundland to southern Ontario, south to Louisiana and Georgia (Smith 1993d).

Figure 360. *Amauropelta noveboracensis*, Gilmer Co., Georgia, 18 Jun 2011. Photo: Alan Cressler.

The New York Fern is easily recognized by fronds that taper sharply at both the tip and the base (Fig. 360). A familiar mnemonic—"New Yorkers burn their candles at both ends"—reflects this distinctive shape. The specific epithet *noveboracensis* derives from *Nova Eboracum*, the Latin name for New York, though scholars debate whether Linnaeus based it on specimens from New York or from Canada (Dunbar 1989). In the field, this fern thrives in moist, shaded woodlands, often forming extensive colonies that carpet the forest floor (Fig. 361).

Figure 361. *Amauropelta noveboracensis*, Fayette Co., Pennsylvania, 19 Jun 2023. Photo: Noah Yawn.

Gardeners value the New York Fern for its graceful fronds and woodland charm, often cultivating it in lightly shaded forests or spacious landscapes where it forms lush green colonies that enrich the landscape. Its long-creeping rhizomes, however, allow it to spread aggressively, and in smaller gardens it can become invasive. Homeowners should manage the fern's growth regularly to keep it from overwhelming neighboring plantings. With mindful care, the New York Fern thrives as a striking, harmonious feature that enhances the beauty of the garden (Mickel 1994).

2. CHRISTELLA H. Léveillé 1915 {kris-TELL-uh}
[Named for Hermann Heinrich Christ, 1833-1933, Swiss pteridologist]

1. Christella dentata (Forssk.) Brownsey & Jermy {toothed} — DOWNY MAIDEN FERN; SOFT FERN; DOWNY SHIELD FERN; TAPERING TRI-VEIN FERN (Fig. 362). [*Cyclosorus dentatus* (Forssk.) Ching; *Dryopteris dentata* (Forssk.) C. Chr.; *Thelypteris dentata* (Forssk.) E.P. St. John]

Figure 362. *Christella dentata*, Calhoun Co., Alabama, 13 Mar 2023. Photos: Dan Spaulding.

Plants terrestrial or epipetric; evergreen to semi-evergreen. Disturbed woods, streambanks, ditches, roadsides, masonry of brick walls, and cracks in the concrete of wells or bridges. Sporulates May–December; rare in northern Alabama; uncommon in the Coastal Plain (Fig. 363). Native to tropical and subtropical regions of Asia and Africa, this species has been introduced into the southeastern United States, the West Indies, Mexico, and southward into South America (Smith 1993d).

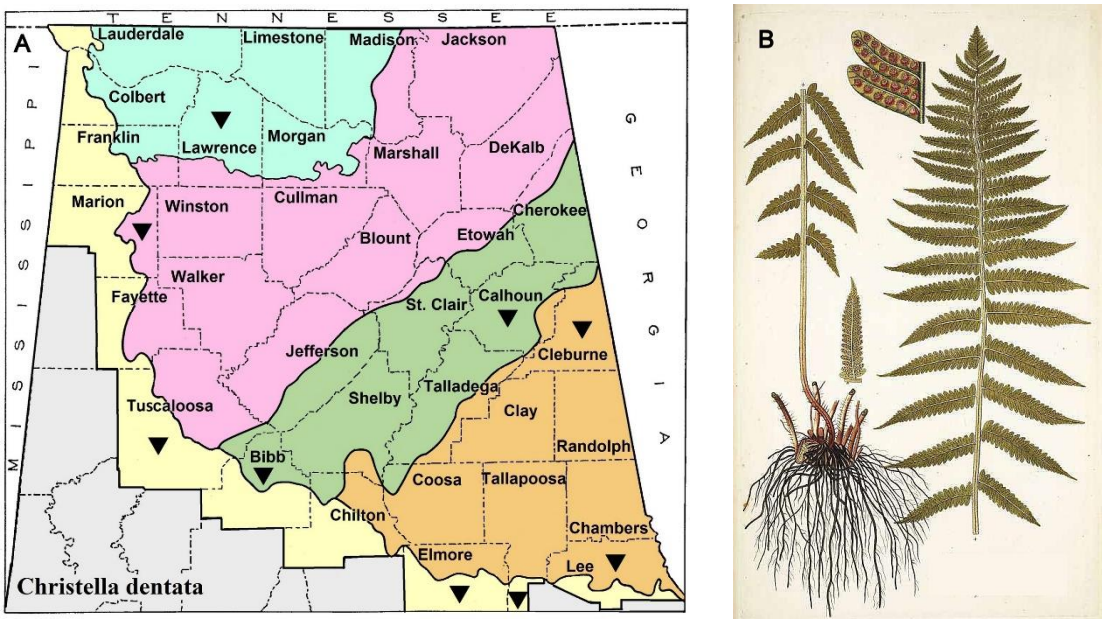


Figure 363. *Christella dentata*. **A.** Distribution map. **B.** Illustration: Franz Bauer, 1786.

Christella dentata thrives in disturbed habitats (Fig. 364a). Many of its common names emphasize the distinctive downy hairs covering the rachis and the abaxial surface of the costae (leaflet midveins). These dense, short hairs give the fronds a soft, velvety texture (Fig. 364b). Key diagnostic features of the Downy Maiden Fern include: 1) uniformly short pubescence, 2) purplish leaf stalks, 3) typically more than two pairs of reduced basal pinnae, and 4) basal veins from adjacent pinnae lobes that merge below the sinus to form a single excurrent vein extending to the sinus. The vernacular name "tapering tri-vein fern" refers to the united veins and the tapered base of the leaf blade.

Figure 364. *Christella dentata*, Elmore Co., Alabama, 17 Apr 2024. Photos: Dan Spaulding.

The Variable Maiden Fern, *Christella hispidula* (Decne.) Holttum, a native of the southeastern Coastal Plain, closely resembles *C. dentata*. Both species share the diagnostic feature of basal veins that unite to form a single excurrent vein running to the sinus between lobes (Fig. 365). In *C. hispidula*, however, the venation is often inconsistent, sometimes even within the same frond—hence its common name. Some basal veins unite, while others remain separate and merely converge at the sinus. The excurrent veins are shorter in *C. hispidula*, measuring less than 2 mm, while those of *C. dentata* exceed 2 mm (Fig. 365). Other distinguishing traits of *C. hispidula* include hairs of mixed lengths, a straw-colored petiole, and blades with fewer than three basal pairs of slightly reduced pinnae (Smith 1993d). The Widespread Maiden Fern, *Pelazoneuron kunthii*, may also be confused with these species, but its basal veins of adjacent pinnae remain entirely separate, never forming excurrent veins (Fig. 365).

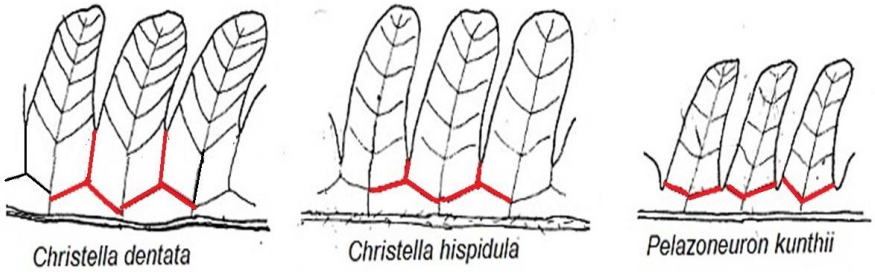
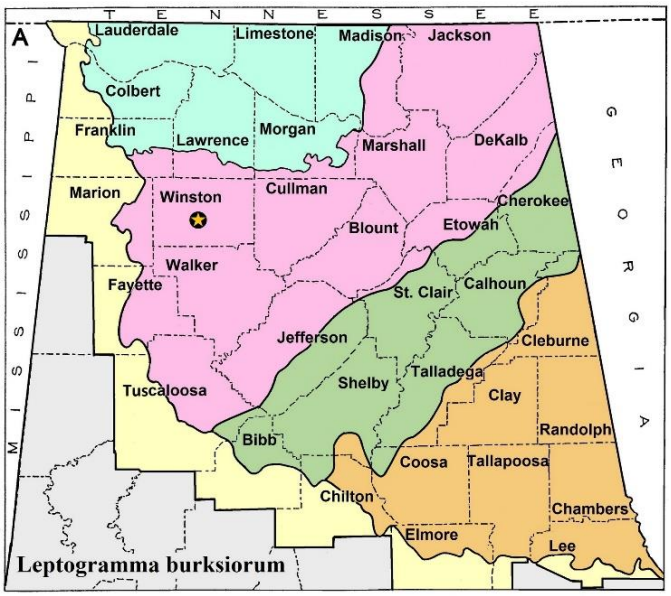


Figure 365. Comparisons of basal veins between segment lobes of *Christella dentata*, *Christella hispidula*, and *Pelazoneuron kunthii* (Nelson 2000).

3. LEPTOGRAMMA J. Smith 1842 {lep-toh-GRAM-uh}
[Greek *leptos*, slender, and *gramme*, line; sori are slender and linear]

1. Leptogramma burksiorum (J.E. Watkins & Farrar) Y.H. Chang & L.Y. Kuo {in honor Mary Ivy Burks (1920–2007), Alabama conservationist} — ALABAMA STREAK-SORUS FERN (Fig. 366). [*Leptogramma pilosa* (M. Martens & Galeotti) Underw. var. *alabamensis* (Crawford) Wherry; *Stegnogramma burksiorum* (J.E. Watkins & Farrar) Weakley; *Stegnogramma pilosa* (M. Martens & Galeotti) K. Iwats. var. *alabamensis* (Crawford) K. Iwats; *Thelypteris burksiorum* J.E. Watkins & Farrar; *Thelypteris pilosa* (M. Martens & Galeotti) Crawford var. *alabamensis* Crawford]

Figure 366. *Leptogramma burksiorum*, Winston Co., Alabama, 24 Sep 2022. Photos: Noah Yawn.



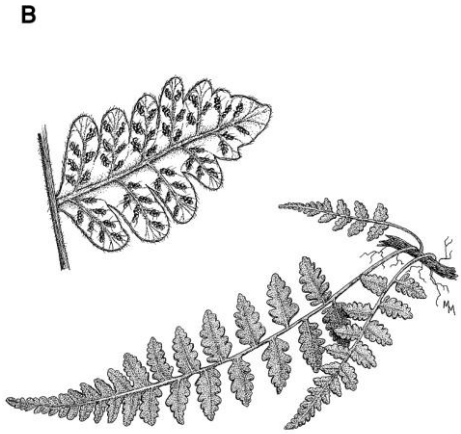


Figure 367. *Leptogramma burksiorum.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 2000.

Plants epipetric; evergreen. Moist sandstone grottoes, rockhouses, and overhangs in river gorges. Sporulates year-round; very rare in the Warrior Basin District of the Cumberland Plateau (Fig. 367). Narrow endemic of northern Alabama (Winston County). The U.S. Fish and Wildlife Service lists *Leptogramma burksiorum* as federally threatened (Gunn 1996), and the Alabama Natural Heritage Program (2023) ranks it as critically imperiled (S1) within the state.

The Alabama streak-sorus fern (*Leptogramma burksiorum*) ranks among the rarest ferns in the world, restricted to sandstone rock shelters in Winston County, Alabama (Fig. 368). University of Alabama student Lloyd C. Crawford and his professor, Alton M. Harvill, discovered it on October 15, 1949, along the Sipsey Fork of the Black Warrior River. Experts noted its close resemblance to a Mexican species, and in 1951, Crawford formally described the Alabama plant as *Thelypteris pilosa* var. *alabamensis* (Crawford 1951). Wherry (1964) later transferred the taxon to *Leptogramma*, emphasizing its elongated sori, which distinguished it from the more typical round or oblong sori of *Thelypteris*. This distinctive feature gave rise to the common name "streak-sorus" (Fig. 369). Subsequent authors (Lellinger 1985; Smith 1993d), however, regarded it as merely a disjunct variety of Mexican populations of *T. pilosa*, now recognized as *Leptogramma pilosa*.

Figure 368. *Leptogramma burksiorum*, Winston Co., Alabama, 4 Sep 2009. Photo: Alan Cressler.

The completion of the L. M. Smith Dam by Alabama Power in 1961 posed a significant threat to the fern's habitat, located just a few miles upstream from the dam. The project raised the water level of Smith Lake within the Sipsey Gorge, necessitating the construction of a new U.S. Highway 278 bridge. Construction crews destroyed the fern's habitat when they leveled the sandstone cliffs to build the new bridge. Despite extensive searches, the fern remained elusive, leading many to conclude that it might have gone extinct (Dean 1969).

A significant rediscovery occurred in 1975 when Birmingham gardener Louise "Weesie" Smith (Fig. 370a) informed Auburn University botanist John Freeman about sightings of the Alabama Streak-Sorus Fern near its type locality. Acting on this lead, John Short found the fern beneath an overhanging cliff where Alabama Highway 33 crosses the Sipsey Fork (Short & Freeman 1978). Following this discovery, Scott Gunn and researchers from the Alabama Natural Heritage Program documented approximately 17 separate occurrences along an estimated 4.25-mile stretch of the Sipsey Fork in Winston County (Gunn 1996).

Figure 369. *Leptogramma burksiorum*, Winston Co., Alabama, 24 Sep 2022. Photo: Noah Yawn.

In the early 21st century, Eddie Watkins and Don Farrar (2002) reevaluated the relationship between the Alabama streak-sorus fern and its Mexican relatives. They concluded that Alabama plants were distinct enough to merit recognition as a separate species, which they named *Thelypteris burksiorum*. Watkins and Farrar (2005) suggested that it likely represents a tropical relic of the Tertiary Period (65.5–2.6 million years ago), predating Pleistocene glaciations, rather than the result of long-distance dispersal. As the genus *Thelypteris* underwent subdivision, Weakley et al. (2011) reassigned this species to *Stegnogramma*, but later analyses placed it back in *Leptogramma* (Kuo et al. 2019).

Figure 370. A. Louise "Weesie" Smith (1927–2016). Photo: Michael Hayman. **B.** Mary Ivy Burks with her husband, Robert. **C.** Blanche Evans Dean (1892–1974). <https://encyclopediaofalabama.org/article/mary-ivy-burks/>

Watkins and Farrar (2002) named their new species in honor of Mary Burks (Fig. 370b) in recognition of her dedication to preserving the Sipsey Wilderness and the Bankhead National Forest. Burks collaborated closely with Blanche Dean (Fig. 370c), a highly respected author, teacher, and self-taught Alabama botanist. Inspired by Dean's deep passion for nature, Burks often joined her in exploring the wild landscapes of Bankhead National Forest. Their shared commitment to conservation led to the founding of the Alabama Conservancy in 1967, with Burks serving as its first president.

Although geologically part of the Warrior Basin, the Sipsey Fork drainage stands apart as a refuge of distinctive habitats and flora. Much of the basin consists of shale hills capped by sandstone outcrops and interbedded with coal seams, where decades of strip mining have scarred the landscape. In these areas, the Pottsville Formation occurs in thick layers that extend deep underground. By contrast, in the Sipsey Fork region, the Pottsville is thinner, reduced to a continuous layer of sandstone over a narrow band of shale, all resting on older limestone, notably lacking extensive coal deposits. Where streams cut through the resistant sandstone, they rapidly erode the softer underlying rocks, carving narrow gorges with steep walls and dramatic overhangs.

These sandstone gorges in the Cumberland Plateau generate cool, moist microclimates that support forest communities uncommon elsewhere in Alabama. Often described as hemlock–hardwood ravine forests, they resemble the vegetation of the higher Appalachians and cooler northern latitudes. In Alabama, this community occurs only in the Sipsey Fork drainage and in the Jackson County Mountains District in the northeast, with a wide intervening gap where it is absent.

Figure 371. *Leptogramma burksiorum* habitat, Winston Co., Alabama, 24 Sep 2022. Photo: Noah Yawn.

The ravines also shelter plants of tropical or subtropical affinity, creating a rare overlap of floras (Fig. 371). These include the Alabama Streak-Sorus Fern (*Leptogramma burksiorum*), Peters' Filmy Fern (*Didymoglossum petersii*), the Appalachian Filmy Fern (*Vandenboschia boschiana*), and the Appalachian Shoestring Fern (*Vittaria appalachiana*), which exists only in its gametophyte stage and never develops sporophytes. This unique combination of northern relicts and tropical elements makes the Sipsey Fork drainage one of the most ecologically distinctive regions in Alabama.

The conservation value of this landscape is profound. Situated within the William B. Bankhead National Forest and permanently protected in the Sipsey Wilderness, the drainage safeguards rare endemics, fragile filmy ferns, and ancient hemlock groves. In a basin otherwise transformed by coal mining and land conversion, the Sipsey Fork region remains a refuge of exceptional ecological and evolutionary significance.

4. MACROTHELYPTERIS (H. Itô) Ching 1963 {mak-roh-thel-LIP-ter-iss}
[Greek *makros*, large, and the genus *Thelypteris*; a big maiden fern]

1. Macrothelypteris torresiana (Gaudich.) Ching {for Luís de Torres of the Mariana Islands and governor of Guam in the early 19th Century} — MARIANA MAIDEN FERN; FALSE MAIDEN FERN (Fig. 372). [*Thelypteris torresiana* (Gaudich.) Alston]

Figure 372. *Macrothelypteris torresiana*, Cleburne Co., Alabama, 7 Aug 2021. Photos: Dan Spaulding.

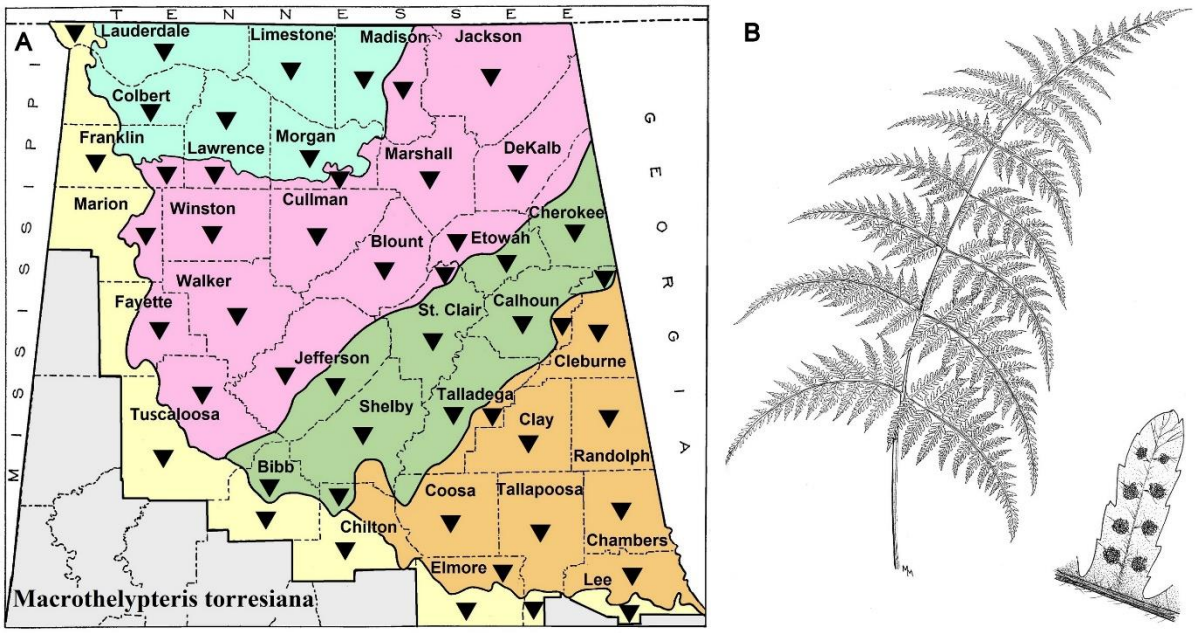


Figure 373. *Macrothelypteris torresiana*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 2000.

Plants terrestrial; deciduous. Wooded streambanks, floodplains, moist forests, roadbanks, roadside ditches, under highway bridges, and other disturbed areas. Sporulates June–November; frequent in northern Alabama; common in the Coastal Plain (Fig. 373). Native to tropical and subtropical regions of Asia and Africa, this species has been introduced into the southeastern United States, the West Indies, Mexico, and southward into South America (Smith 1993b).

Figure 374. *Macrothelypteris torresiana*, Winston Co., Alabama, 13 Jun 2024. Photos: Dan Spaulding.

Once regarded as rare, *Macrothelypteris torresiana* has spread rapidly and has become abundant throughout much of its introduced range. In 1904, American botanist Alvah A. Eaton made the first U.S. collection in Seminole County, Florida, noting that it had escaped cultivation. Following this initial record, botanists found the fern in other Florida counties, and by 1948, Lloyd Crawford recorded it in Conecuh County, Alabama (Leonard 1972). During the early 1960s, it advanced into the southeastern Coastal Plain and has continued to expand northward (Wyatt 2020).

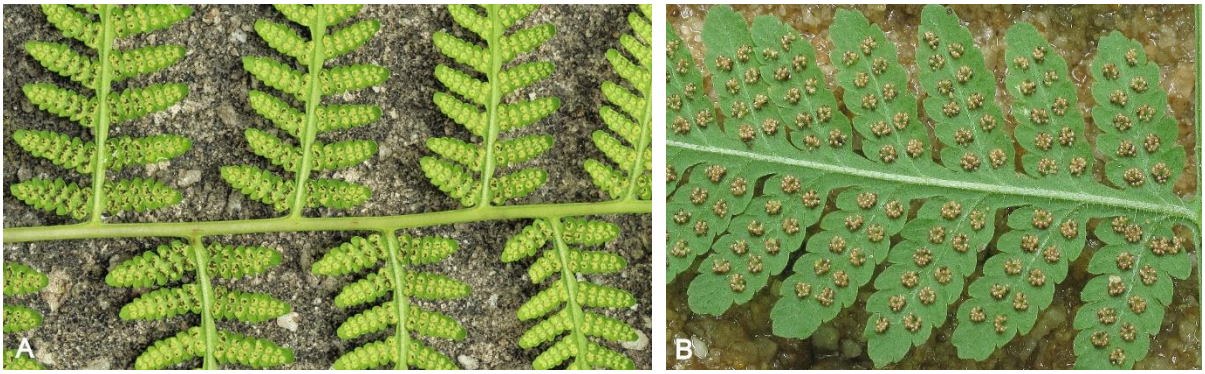


Figure 375. *Macrothelypteris torresiana.* **A.** Rachis not grooved on abaxial surface, Bartow Co., Georgia, 24 Jul 2021. **B.** Round sori with small indusia, Pike Co., Georgia, 16 Sep 2011. Photos: Alan Cressler.

The Mariana Maiden Fern has become one of the most widespread naturalized ferns in the Southeast. It differs from other members of its family by its large, broadly triangular fronds, which are bipinnate to tripinnate (Fig. 374). Key identifying features include the absence of a groove on the undersurface of the pinna midribs and round sori with inconspicuous indusia (Fig. 375). This adaptable species thrives in disturbed areas but has also spread into natural habitats, where it can displace native vegetation. Despite its availability in some plant nurseries, this fern is an invasive exotic, and gardeners should avoid using it in their landscapes to prevent further ecological disruption.

5. PELAZONEURON (Holttum) A.R. Smith & S.E. Fawcett 2021{peh-lah-zoh-NYOO-ron}
[Greek *pele*, dark, *zone*, belt, and *neuron*, vein; possibly alluding to the petiole's dark base]

1. Pelazoneuron kunthii (Desv.) A.R. Sm. & S.E. Fawc. {for Karl Sigismund Kunth, 1788–1850, a German botanist} —WIDESPREAD MAIDEN FERN; SOUTHERN SHIELD FERN; SOUTHERN MAIDEN FERN; KUNTH'S MAIDEN FERN (Fig. 376). [*Christella normalis* (C. Chr.) Holttum; *Cyclosorus kunthii* (Desv.) Christenh.; *Thelypteris kunthii* (Desv.) C.V. Morton; *Thelypteris normalis* (C. Chr.) Moxley]

Figure 376. *Pelazoneuron kunthii*, Cleburne Co., Alabama, 1 Sep 2024. Photos: Dan Spaulding.

Plants terrestrial; deciduous. Streambanks, swamp margins, forested floodplains, suburban woods, moist roadbanks, under bridges, roadside ditches, limestone bluffs, ravines, and sinks. Sporulates May–October; Uncommon in northern Alabama; frequent in the Coastal Plain (Fig. 377). This species ranges in the southeastern USA from Virginia to Arkansas, south to eastern Texas, and Florida (Kartesz 2025); also in the West Indies, Mexico, Central America, and northern South America (Smith 1993d).

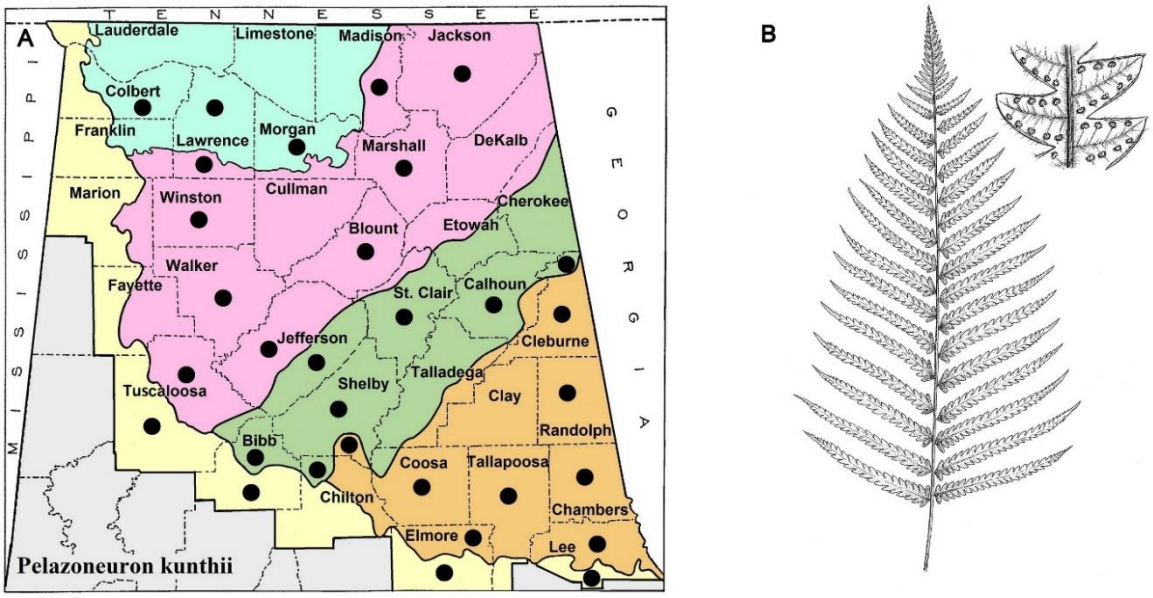


Figure 377. *Pelazoneuron kunthii.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 2000.

Figure 378. *Pelazoneuron kunthii.* **A.** Roadside ditch in full sun, Cleburne Co., Alabama, 1 Sep 2024. **B.** Drainage ditch in disturbed woods, Shelby Co., Alabama, 6 Jul 2023. Photos: Dan Spaulding.

Pelazoneuron kunthii is a hardy, adaptable native fern that thrives in southern gardens. Its lush, arching fronds create a natural woodland aesthetic, making it an excellent choice for shaded borders. Resilient to heat and humidity, it requires little maintenance in southeastern landscapes (Olsen 2007). However, this species can spread aggressively, forming large colonies that may overrun garden spaces if not managed. Despite its vigor, it remains one of the most attractive and desirable ferns for cultivation. Its expanding range likely reflects escapes from cultivation, as it now frequently appears in disturbed habitats across northern Alabama (Fig. 378).

Botanists often confuse the native Widespread Maiden Fern (*Pelazoneuron kunthii*) with the exotic Downy Maiden Fern (*Christella dentata*) due to the similarity of their fronds. However, careful examination of the basal veins between the pinnae lobes allows for clear differentiation. In *P. kunthii*, the basal veins remain free and do not converge below the sinus, while in *C. dentata*, the veins unite to form a single excurrent vein extending into the sinus between the lobes (Fig. 378).

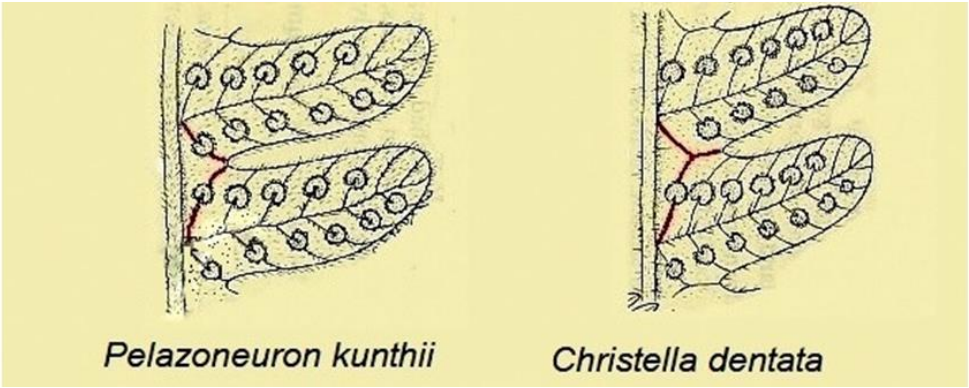


Figure 379. Basal veins (in red) between segment lobes of *Pelazoneuron kunthii* and *Christella dentata*, Illustration: Jane W. Roller, 1972.

The Ovate Maiden Fern (*Pelazoneuron ovatum*), a close relative, occurs on Alabama's Coastal Plain (Fig. 380). Jim Allison (1996) reported it from the Ketona Glades of Bibb County, but John Short later annotated the collection as *P. kunthii*. Several subtle characters distinguish these two species. *Pelazoneuron ovatum* has smooth veins on the upper leaf surface and lacks glands on its fronds, whereas *P. kunthii* bears at least a few stout hairs along the veins and typically has stalked glands. Their leaf shape also differs: *P. ovatum* has mostly ovate blades, while *P. kunthii* has primarily lanceolate ones. In both species, the basal veins from adjacent lobes remain free, contrasting with the Downy Maiden Fern (*Christella dentata*), where they unite below the sinus to form a single excurrent vein.

Figure 380. *Pelazoneuron ovatum*. **A.** Illustration by Marion Montgomery, 2000. **B.** Photograph by Alan Cressler, Sumter County, Florida, 19 July 2009.

6. PHEGOPTERIS (C. Presl) Fée 1852 {fee-GOP-ter-iss}
[Greek *phegos*, beech, and *pteris*, fern; some in this genus grow under beech trees]

1. Leaf blade lanceolate, widest near the middle and tapering at both ends; primary leaf segments alternate; rhizome short and erect; plants often growing on rock .....***Phegopteris decursive-pinnata***
1. Leaf blade broadly triangular, widest at or near the base; primary leaf segments opposite; rhizome long-creeping; plants terrestrial .....***Phegopteris hexagonoptera***

1. Phegopteris decursive-pinnata (H.C. Hall) Fée {running down stem, feather-like; winged rachis} — JAPANESE BEECH FERN; WINGED BEECH FERN (Fig. 381). [*Thelypteris decursive-pinnata* (H.C. Hall) Ching]

Figure 381. *Phegopteris decursive-pinnata*, Cleburne Co., Alabama, 30 Aug 2023. Photos: Dan Spaulding.

Plants epipetric or terrestrial; deciduous. Crevices in cliffs along drainages and moist soil of rocky banks. Sporulates June–October; very rare in northern Alabama (Fig. 382). Native to China, Japan, Korea, Taiwan, and Vietnam (Fujiwara et al. 2021); introduced and naturalized in the southeastern USA, with records extending north to Delaware and Pennsylvania (iNaturalist 2024).

Gardeners value the Japanese Beech Fern (*Phegopteris decursive-pinnata*) for its striking upright, sword-shaped fronds and ease of cultivation. In its native Asian range, it typically grows in moist, shaded soils but also thrives on walls and rocks (Mickel 1994). In 2010, James A. Peck of the University of Arkansas documented the first occurrence of *P. decursive-pinnata* outside cultivation in the United States, finding it on sandstone rocks around an artificial pool in Garland County, Arkansas (Peck 2011). Four years later, Richard and Nancy Cobb discovered a second U.S. population on Mount Cheaha in Cleburne County, Alabama, where it grew in rock crevices along a cliff face within the spray zone of a small waterfall (Florez-Parra & Keener 2016). Since then, naturalists have reported additional populations in other counties of Alabama's Cumberland Plateau.

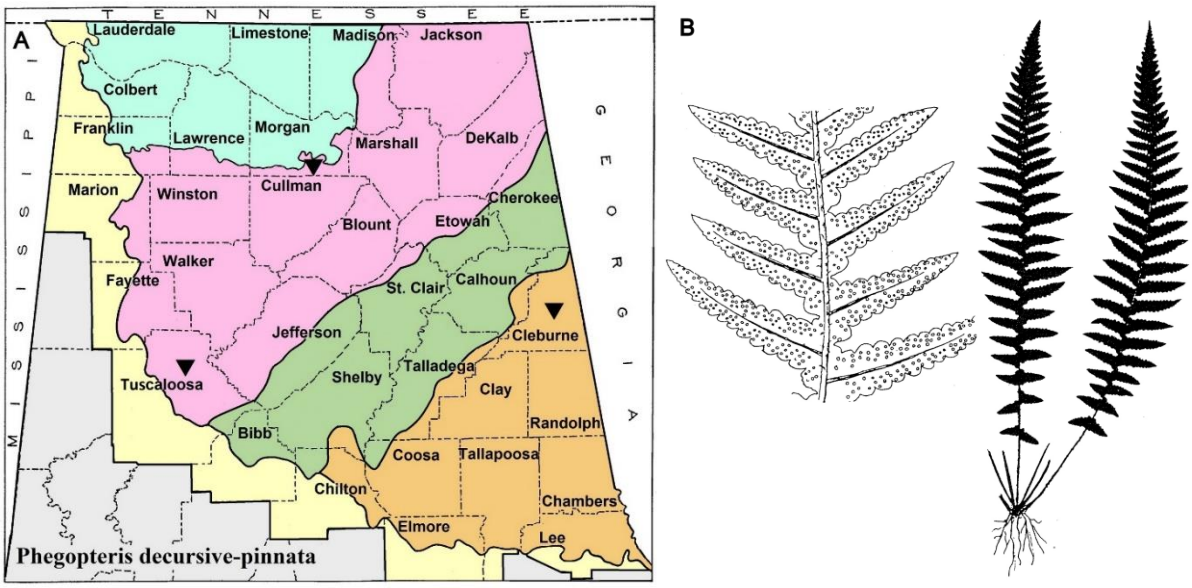


Figure 382. *Phegopteris decursive-pinnata*. **A.** Distribution map. **B.** Illustration: Barbara Joe Hoshizaki, 2001.

Figure 383. *Phegopteris decursive-pinnata*, Cleburne Co., Alabama, 28 Aug 2022. Photo: Noah Yawn.

Both *Phegopteris decursive-pinnata* and *P. hexagonoptera* have a winged rachis, but *P. decursive-pinnata* stands out with its lance-shaped frond, widest at the middle and tapering at both ends, with alternately arranged pinnae (Fig. 383). Some botanists speculate that U.S. specimens identified as *P. decursive-pinnata* might represent *P. taiwaniana* (Sessa 2024). While these two species share many morphological traits (Fig. 384a), *P. taiwaniana* has evergreen fronds and grows strictly in soil, whereas *P. decursive-pinnata* has deciduous fronds that die back in winter (Fig. 384b) and can grow on both rocks and soil (Fujiwara et al. 2021).

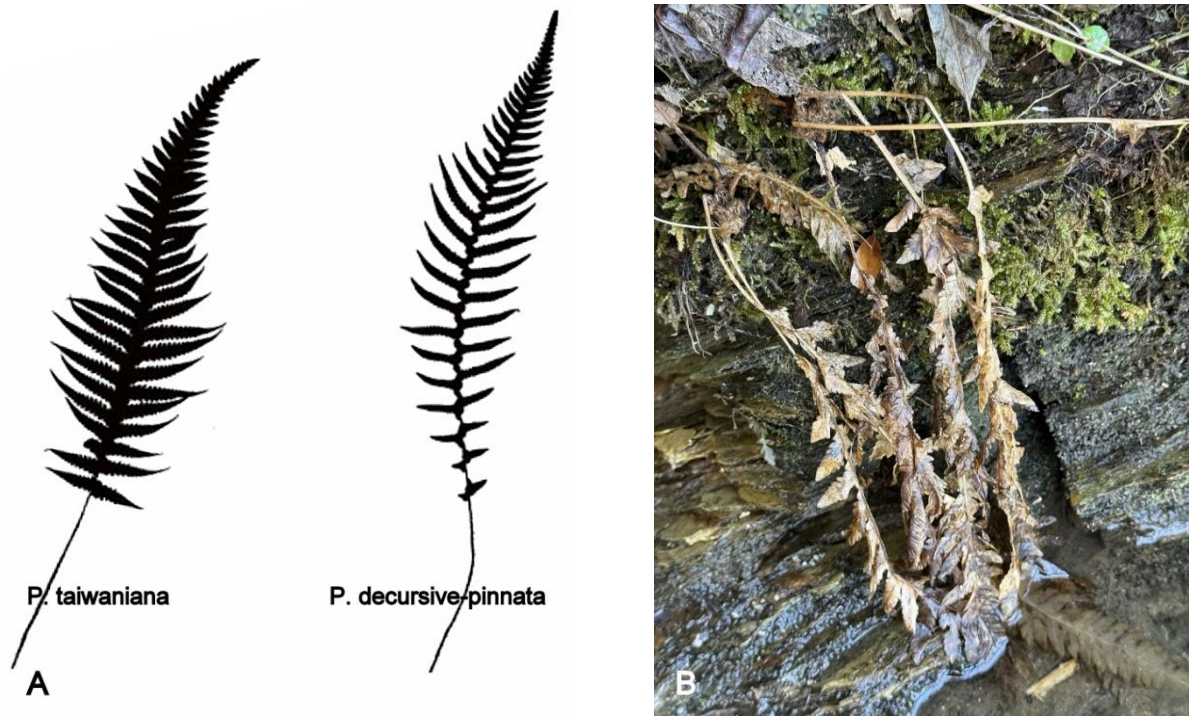


Figure 384. A. Comparison of *Phegopteris taiwaniana* and *P. decursive-pinnata* fronds (Fujiwara et al. 2021). **B.** *P. decursive-pinnata* in winter, Cleburne Co., Alabama, 19 Jan 2024. Photo: Dan Spaulding.

2. Phegopteris hexagonoptera (Michx.) Fée {six-angled wing}— BROAD BEECH FERN; SOUTHERN BEECH FERN (Fig. 385). [*Dryopteris hexagonoptera* (Michx.) C. Chr.; *Thelypteris hexagonoptera* (Michx.) Weath.]

Figure 385. *Phegopteris hexagonoptera*, Winston Co., Alabama, 13 Jun 2024. Photos: Dan Spaulding.

Plants terrestrial; deciduous. Mesic hardwood forests, sloped woods, shaded streambanks, and rich woods. Sporulates April–August; frequent in northern Alabama; uncommon in the Coastal Plain (Fig. 386). This species is native to eastern North America, ranging from Maine and southern Quebec to Michigan, south to East Texas and Florida (Smith 1993c).

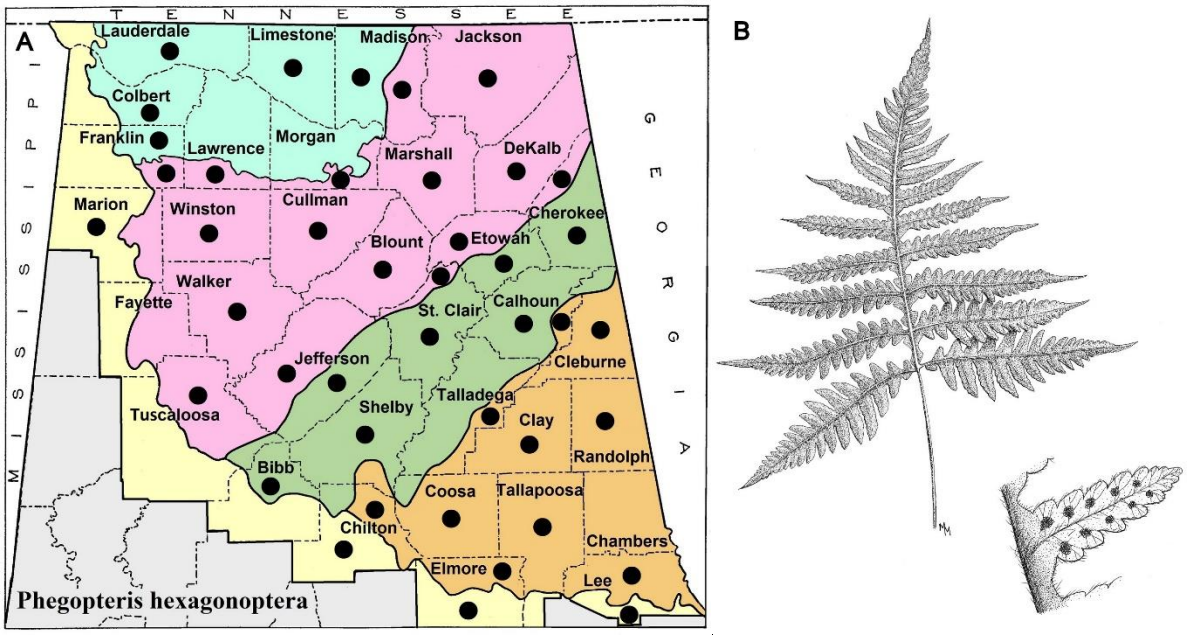


Figure 386. *Phegopteris hexagonoptera.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 2000.

Figure 387. *Phegopteris hexagonoptera*, Talladega Co., Alabama, 4 Jul 2024. Photo: Dan Spaulding.

Figure 388. *Phegopteris hexagonoptera*, Erie Co., Pennsylvania, 3 Aug 2023. Photo: Noah Yawn.

The Broad Beech Fern (*Phegopteris hexagonoptera*) thrives in moist deciduous forests, often forming extensive colonies through its long, creeping rhizomes (Fig. 387). Its broadly triangular, bipinnatifid fronds make it easy to recognize. A notable feature of this species is its winged rachis (Fig. 388), which gives the fern a distinctive appearance and inspired its Latin name. The specific epithet *hexagonoptera*, from the Greek *hexagonos* ("six-angled") and *pteron* ("wing"), refers to the angular wings on the rachis, while the common name alludes to the fern's distinctive frond shape and habitat. When crushed, the fronds release a characteristic "ferny" scent from tiny glands scattered across the blade (Clute 1901).

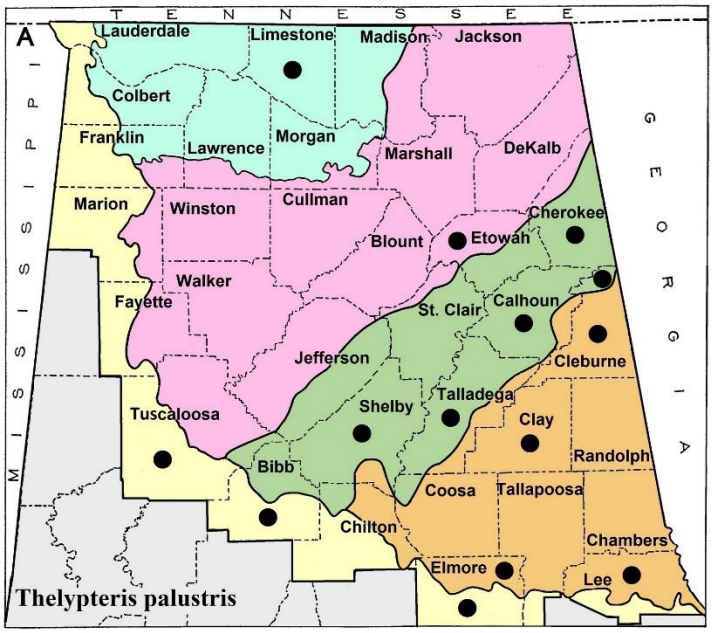
7. **THELYPTERIS** Schmidel 1763 {thuh-LIP-ter-iss}

[Greek *thelys*, female, and *pteris*, fern; old Greek name for a delicate fern]

1. Thelypteris palustris Schott {of marshes} var. **pubescens** (G. Lawson) Fernald {hairy} — EASTERN MARSH FERN; MEADOW FERN; SNUFF-BOX FERN; AMERICAN MARSH FERN (Fig. 389). [*Dryopteris thelypteris* (L.) A. Gray var. *pubescens* (Lawson) A.R. Prince ex Weatherby]

Plants terrestrial; deciduous. Marshes, swamps, bogs, wet ditches, riverbanks, wet woods, and lake shores. Sporulates June–October; rare in northern Alabama; uncommon in the Coastal Plain (Fig. 390). Ranging in eastern North America from Newfoundland to Ontario, south to East Texas and Florida; also in the West Indies, Bermuda, Cuba, and Mexico (Smith 1993d).

Figure 389. *Thelypteris palustris*, Shelby Co., Alabama, 12 May 2023. Photo: Susan DeMonia Grantham.



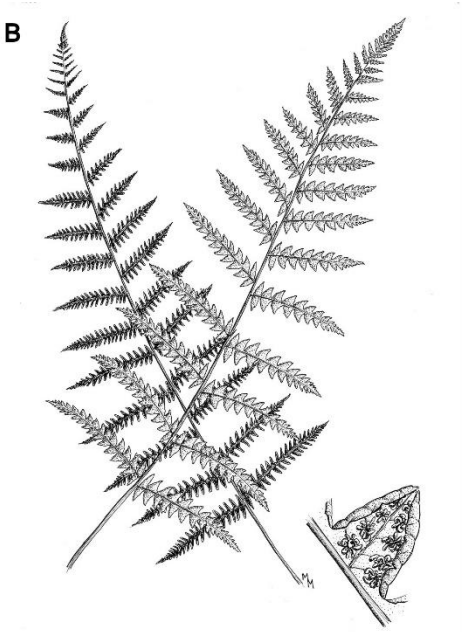


Figure 390. *Thelypteris palustris.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 2000.

Figure 391. *Thelypteris palustris*. **A.** Sterile frond, Elmore Co., Alabama, 17 Apr 2024. Photo: Dan Spaulding. **B.** Fertile frond, Macon County, North Carolina, 13 Sep 2009. Photo: Alan Cressler.

Thelypteris palustris is a widespread species with two recognized varieties. All North American specimens belong to *T. palustris* var. *pubescens*, while the type variety, *T. palustris* var. *palustris*, is native to Eurasia (Smith 1993d). The primary distinction between these varieties is the presence of hairs on the fronds, a characteristic that gives *T. palustris* var. *pubescens* its name (Fig. 391a). The fern's scientific and common names reflect its preference for wet habitats. George Tilton (1923) noted that the colloquial name "snuff-box fern" refers to a distinctive feature of the fertile fronds—their curled-in leaf margins resemble a snuff box (Fig. 391b).

Figure 392. *Thelypteris palustris*. **A**–**B.** Weeks Bay, Baldwin Co., Alabama, 21 Apr 2011. Photos: Wayne Barger. **C.** Illustration of forked lateral veins on sterile frond (Nelson 2000).

The Marsh Fern bears a long petiole, often exceeding the length of the blade (Fig. 392a). This trait prompted American naturalist Frances Parsons (1899) to remark, "The lowest pinnae are set so high on the long slender stem as to give the fern the appearance of trying to keep dry, daintily holding its skirts out of the mud." Another key character is the forked lateral veins, especially conspicuous on sterile fronds (Fig. 392b–c). These Y-shaped veins readily separate it from similar-looking species.

23. DRYOPTERIDACEAE (Wood Fern Family) – in Polypodiales

1. Leaves 1-pinnate; pinnae toothed, shallowly lobed, or undulate.

    2. Larger pinnae usually more than 1.5 cm wide; venation reticulate (veins connected in a net-like pattern forming 2 or more rows of areoles)..... ***Cyrtomium***
    2. Larger pinnae usually less than 1.5 cm wide; venation free (veins dichotomously branching, not forming areoles).

        3. Pinnae with well-developed basal lobes, margins with bristle-tipped teeth; petiole and rachis bearing tan to brown scales ..... ***Polystichum***
        3. Pinnae lacking basal lobes, margins shallowly lobed or coarsely toothed, without bristle-tipped teeth; petiole and rachis bearing blackish scales ..... ***Dryopteris***

1. Leaves pinnate-pinnatifid, bipinnate or tripinnate; pinnae deeply lobed or divided, with ultimate segments often toothed or lobed.

    4. Blades about as long as wide, pentagonal in outline, abruptly tapering toward the apex; leaves often variegated with yellow-green bands along the midveins .....***Arachniodes***
    4. Blades at least 1.5 times as long as wide, lanceolate, oblong, ovate, or triangular in outline, gradually tapering toward the apex; leaves rarely variegated.

        5. Leaf segments with blackish midveins, tips mucronate (ending in a short, bristle-like point); petiole scales ciliate; indusia round, centrally attached..... ***Polystichum***
        5. Leaf segments with greenish midveins, tips not mucronate, often toothed; petiole scales not ciliate; indusia kidney-shaped, laterally attached at the sinus..... ***Dryopteris***

1. ARACHNIODES Blume 1828 {uh-RAK-nee-oh-deez}

[Greek *arachnion*, spider's web; alluding to the spidery appearance of the sporangia]

1. Arachniodes simplicior (Makino) Ohwi {simpler, unbranched} — EAST INDIAN HOLLY FERN; VARIEGATED SHIELD FERN; SIMPLER FALSE HOLLY FERN (Fig. 393).

Plants terrestrial; evergreen. Streambanks, alluvial forests, and moist suburban woods. Sporulates year-round; rare throughout Alabama (Fig. 394). Native to China and Japan; naturalized in the southeastern USA (Kartesz 2025).

Gardeners prize the East Indian Holly Fern (*Arachniodes simplicior*) for its bold coloration and dependable performance in shaded landscapes. Its arching, glossy fronds are deep green with striking yellow-green stripes flanking each midrib, creating vivid contrast and textural appeal. This fern thrives in partial to full shade, where filtered light enhances its color without causing the leaves to burn or fade. It prefers loamy, well-drained soil enriched with organic matter and performs best with consistent moisture that avoids waterlogging. Landscapers often use *A. simplicior* to add a lush, tropical element to shaded beds, woodland gardens, or containers. In mild climates, it retains its vibrant foliage year-round, offering lasting visual interest (Jones 1987).

Figure 393. *Arachniodes simplicior*, Jefferson Co., Alabama, 17 Nov 2024. Photo: Reed Craft.

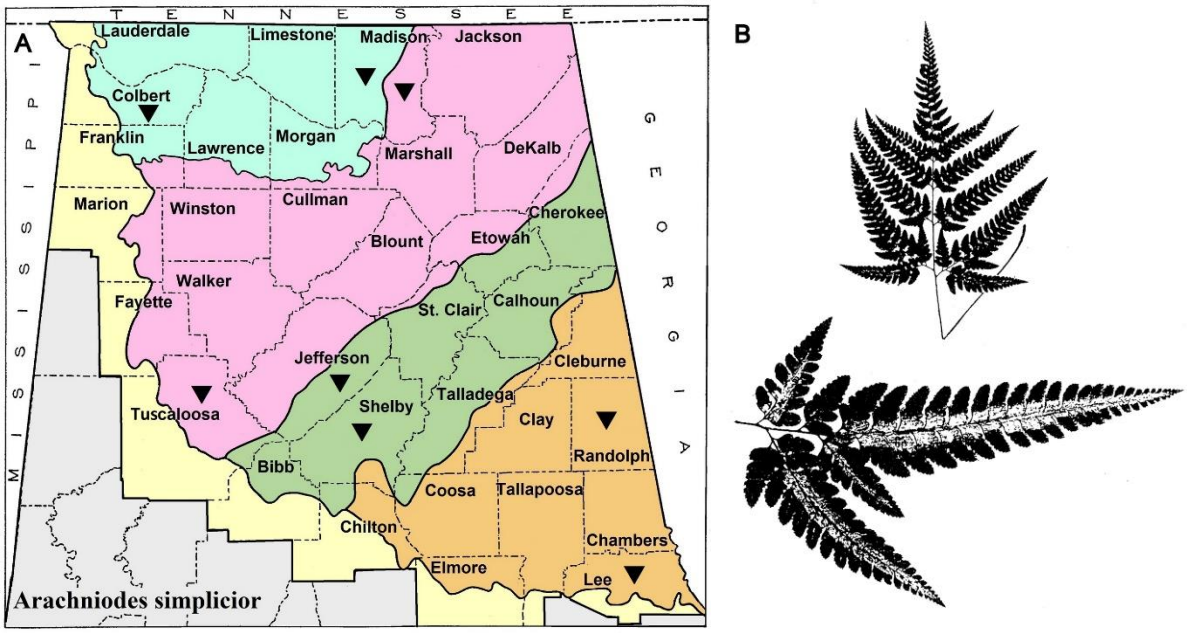


Figure 394. *Arachniodes simplicior*. **A.** Distribution map. **B.** Illustration: Barbara Joe Hoshizaki, 2001.

Figure 395. *Arachniodes simplicior*. **A.** Streambank, Colbert Co., Alabama, 27 Mar 2012. Photo: Wayne Barger. **B.** Sori, herbarium specimen (AMAL), *Barger SP#422*, Colbert Co., Alabama, 27 Mar 2012.

In 1980, Judith Gordon, a professor at Augusta University, first documented *Arachniodes simplicior* escaping cultivation in North America. She discovered about 100 plants along a tributary of the Savannah River in North Augusta, South Carolina. Based on their slow growth, she estimated the population to be 20–25 years old and likely established from wind-dispersed spores (Gordon 1981). For nearly three decades this was the only known naturalized population, until 2008 when Theo Witsell of the Arkansas Natural Heritage Commission observed the species on a drainage bank in Little Rock (Peck 2011; Smith 1993a). In 2012, Wayne Barger and Brian Holt collected the first Alabama record of the East Indian Holly Fern in Colbert County (Fig. 395). Since then, botanists have documented additional populations in Alabama, Florida, and Georgia (Hansen 2025; Wyatt & Harris 2022).

2. CYRTOMIUM C. Presl 1836 {sir-TOH-mee-um}

[Greek *kyroma*, arch; alluding to its arching fronds]

1. Pinnae margins entire (lacking teeth) or coarsely toothed, not finely serrate; blades thick and leathery, upper surface dark green and glossy ..... ***Cyrtomium falcatum***
1. Pinnae margins finely serrate, with small, sharp teeth; blades papery to thinly leathery, upper surface usually pale green and dull .....***Cyrtomium fortunei***

1. Cyrtomium falcatum (L. f.) C. Presl {sickle-shape; pinnae} — JAPANESE HOLLY FERN; HOUSE HOLLY FERN; ASIAN NET-VEIN HOLLY FERN; JAPANESE NET-VEIN HOLLY FERN (Fig. 396).

Plants terrestrial or epipetric; evergreen. Old mortar of brick walls, disturbed woods along drainages, cracks in old concrete buildings, crevices of rocky cliffs, under highway bridges, suburban woods, and old brick piles. Sporulates year-round; rare in Alabama (Fig. 397). Native to East Asia; naturalized in North America, chiefly in the southeastern United States and California, and also in Europe (Smith 1993a).

Figure 396. *Cyrtomium falcatum*, Madison Co., Alabama, 29 Mar 2024. Photos: Steve Threlkeld.

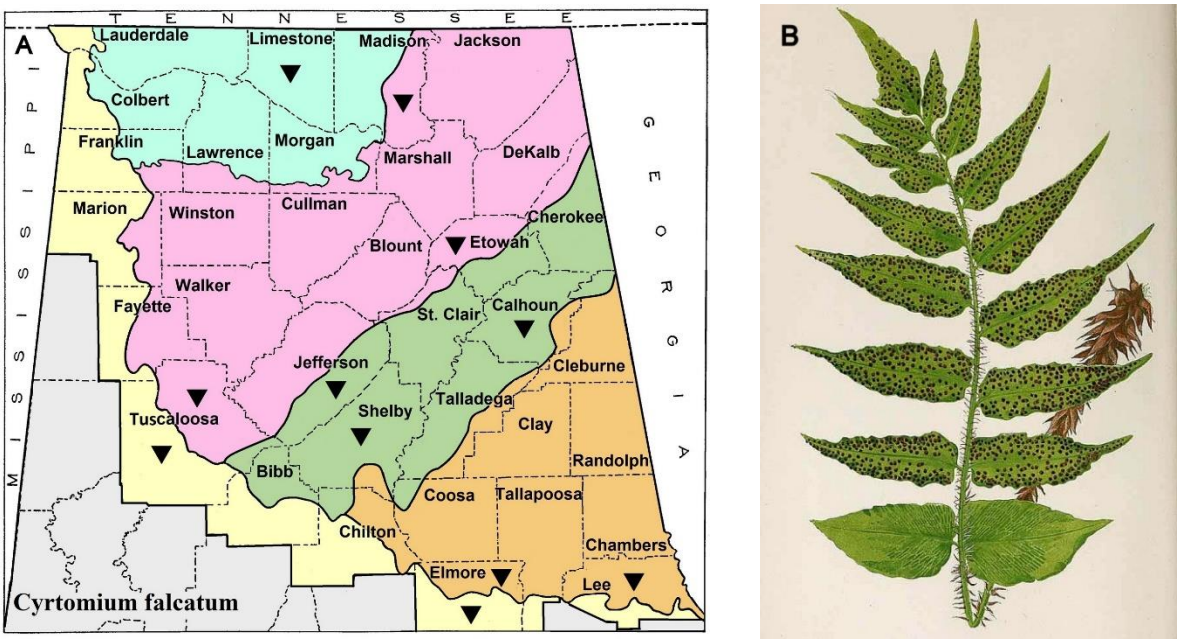


Figure 397. *Cyrtomium falcatum*. **A.** Distribution map. **B.** Illustration: Alfred Frost Lyndon, 1839.

The Japanese Holly Fern (*Cyrtomium falcatum*) is a popular evergreen species widely cultivated in the southeastern and southwestern United States (Mickel 1994). Its arching fronds form a distinctive, vase-like crown with glossy, dark green leaflets that are dull beneath (Fig. 398). This fern thrives in shaded to partially shaded environments, making it well-suited for woodland gardens, shaded borders, or containers on patios and porches. It is especially valued for its drought tolerance once established and its resistance to pests and diseases—qualities that make it a low-maintenance choice for gardeners. In its native range across southeastern Asia, *Cyrtomium falcatum* occupies many habitats, from forest floors in mountainous regions to stone walls in urban areas (Olsen 2007).

Figure 398. *Cyrtomium falcatum*. **A.** Disturbed woods, Calhoun Co., Alabama, 6 Apr 2021. **B.** Sloss Furnaces National Historic Landmark, Jefferson Co., Alabama, 1 Aug 2024. Photos: Dan Spaulding.

One of the earliest North American records of *Cyrtomium falcatum* is a 1907 specimen from Montgomery County, Alabama (Keener et al. 2025). In 1918, Edward W. Graves recorded the species growing on a brick wall in Mobile County (Graves 1919). John K. Small, in *Ferns of the Southeastern United States* (1938), later noted it as an escape in Florida, citing a 1923 collection from an old wall in St. Augustine. Introduced through horticulture and widely cultivated, the Japanese Holly Fern has since spread from gardens and become naturalized in scattered sites across the southeastern United States (Smith 1993a).

2. Cyrtomium fortunei J. Sm. {for Robert Fortune,1812–1880, Scottish horticulturist} — FORTUNE'S HOLLY FERN; FORTUNE'S NET-VEIN HOLLY FERN (Fig. 399).

Plants terrestrial or epipetric, evergreen. Rocky bluffs, alluvial woods, walls of sinkholes, rocky streambanks, old mortar of brick walls, and calcareous woods. Sporulates year-round; rare in Alabama (Fig. 400). Native to southeast China; naturalized in Europe and in North America, chiefly the southeastern USA and Oregon (Yatskievych 1993).

Fortune's Holly Fern is the hardiest *Cyrtomium* in cultivation. It is capable of thriving as far north as New England. Its resilience and attractive foliage make it a favorite among gardeners seeking to add evergreen texture to shaded areas (Mickel 1994). This fern's specific epithet and common name commemorate Robert Fortune, a Scottish plant hunter who collected the species in southeast China in 1845. After introducing this fern as an ornamental plant in Japan, he later sent a specimen to the Royal Botanic Gardens in London, where botanist John Smith formally described it in 1866 (Wyatt 2020).

Figure 399. *Cyrtomium fortunei*, Jefferson Co., Alabama, 26 Oct 2024. Photos: Dan Spaulding.

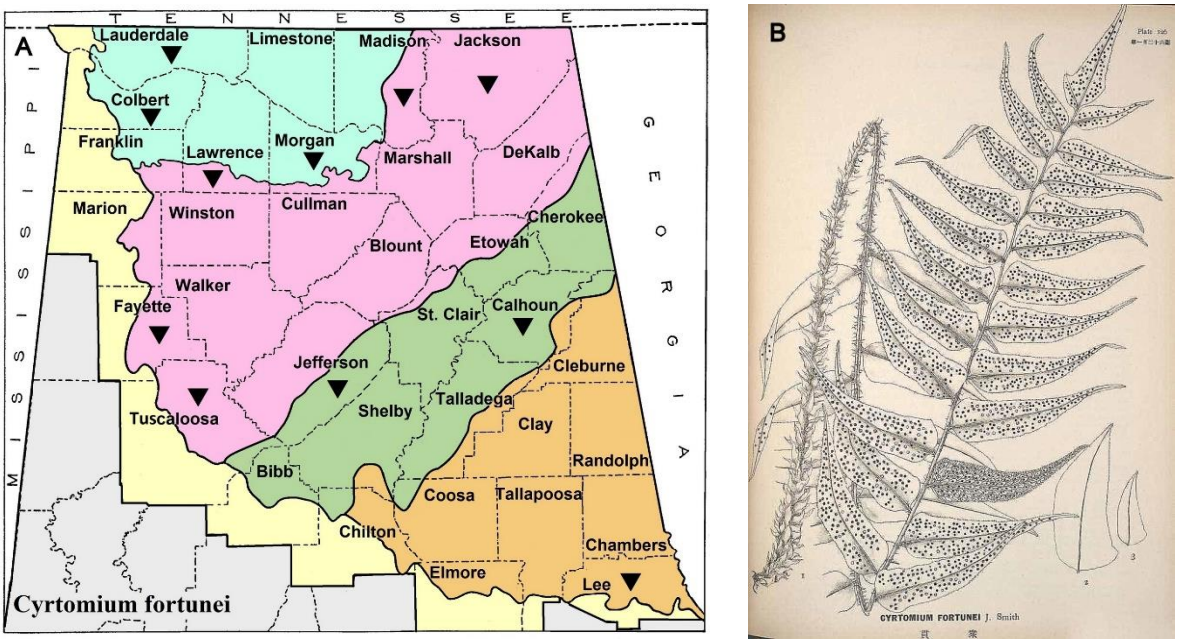


Figure 400. *Cyrtomium fortunei.* **A.** Distribution map. **B.** Illustration: Chengru Feng, 1935.

In 1973, while a student at the College of Charleston, John MacDougal discovered the first known naturalized population of *Cyrtomium fortunei* in North America. He found the ferns growing on a moist, north-facing brick wall in a Charleston cemetery. When he revisited the site in 1975, he collected specimens and noted that the population had increased to about 70 plants (MacDougal 1976). After this initial report, botanists documented the species as established in Georgia, Louisiana, Mississippi, and Oregon (Yatskievych 1993), indicating that the fern had spread more widely than first recognized. In 2002, David Whetstone of Jacksonville State University made the first collection of *C. fortunei* in Alabama from a disturbed ravine in Birmingham.

Figure 401. *Cyrtomium fortunei*, Lawrence Co., Alabama, 26 Nov 2022. Photo: Kevin England.

Cyrtomium fortunei closely resembles *C. falcatum*, but several key features distinguish the two. The most noticeable difference lies in leaflet texture and color: *C. fortunei* has thin, papery leaflets with a pale green upper surface, while *C. falcatum* bears thick, leathery leaflets that are dark green and glossy. Additionally, *C. fortunei* typically has narrower leaflets (1–2 cm wide) with finely serrated margins, in contrast to the broader, often coarsely toothed margins of *C. falcatum*. It also tends to produce more pinnae per frond, although leaflet count varies in both species and is not a reliable diagnostic trait. Both species often occur in disturbed habitats and may invade natural areas (Fig. 401).

3. **DRYOPTERIS** Adanson 1763 {dry-OP-ter-iss}

[Greek, *drys*, tree, and *pteris*, fern; an allusion to their woodland habitat]

1. Leaves 1-pinnate; pinnae shallowly lobed or coarsely toothed; rachis bearing numerous linear black scales with fimbriate margins ..... ***Dryopteris hangchowensis***
1. Leaves pinnate-pinnatifid, bipinnate to tripinnate; pinnae deeply lobed or divided, usually toothed; rachis with scattered to numerous linear or triangular light tan, brown, or blackish scales with entire margins.

    2. Leaves bipinnate-pinnatifid to tripinnate; blade surfaces with glandular hairs, at least along pinna midribs.

        3. Leaves tripinnate (at least lower pinnae), uppermost pinnae usually bipinnate-pinnatifid; marginal teeth with acuminate tips; spores normal, fertile..... ***Dryopteris intermedia***
        3. Leaves bipinnate-pinnatifid throughout; marginal teeth with acute tips; spores shrunken, infertile ..... ***Dryopteris ×cressleri***

    2. Leaves pinnate-pinnatifid or bipinnate; blade surfaces lacking glandular hairs.

        4. Sori marginal, located at the margins of leaf segments; indusia thick and swollen; scales at the petiole base uniformly light brown..... ***Dryopteris marginalis***

4. Sori medial or submedial, located between segment margins and midrib; indusia thin and flat; scales at petiole base bicolored, with a dark central band and light brown margins.

    5. Rachis and undersurface of costae (midribs of pinnae) with dark, bullate (blistered) scales often with tail-like tips; leaves remaining upright in winter; new fronds usually a reddish-coppery color; young indusia with reddish centers ..... ***Dryopteris erythrosora***
    5. Rachis and undersides of costae with flat tan scales; leaves reclining on the ground in winter; new fronds light green; young indusia with dark brown centers.

        6. Fronds monomorphic, fertile and sterile pinnae similar; blade base slightly tapering or not at all, lower pinna pairs nearly equal in length to those above; spores normal, fertile .....***Dryopteris celsa***
        6. Fronds subdimorphic, fertile pinnae narrower and more contracted than sterile ones; blade base distinctly tapering, usually with at least the lower two or three pinna pairs much shorter than those above; spores shrunken, infertile..... ***Dryopteris australis***

1. Dryopteris australis (Wherry) Small {southern} — DIXIE WOOD FERN; SOUTHERN WOOD FERN; WHERRY'S FERN (Fig. 402). [*Dryopteris clintoniana* (D.C. Eaton) Dowell var. *australis* Wherry]

Figure 402. *Dryopteris australis*, Cleburne Co., Alabama, 25 Jun 2024. Photos: Dan Spaulding.

Plants terrestrial; evergreen. Swamp margins, alluvial forests, shaded marshes, and mesic woods. Sporulates June–September; very rare in the Ridge & Valley, Piedmont, and Coastal Plain (Fig. 403). Widely scattered in the southeastern USA, from Maryland south to Georgia, west to Arkansas and Louisiana (Kartesz 2025). The Alabama Natural Heritage Program (2006) once tracked *Dryopteris australis* but later removed it from consideration because of its hybrid origin. We recommend reinstating it as critically imperiled (S1) within the state.

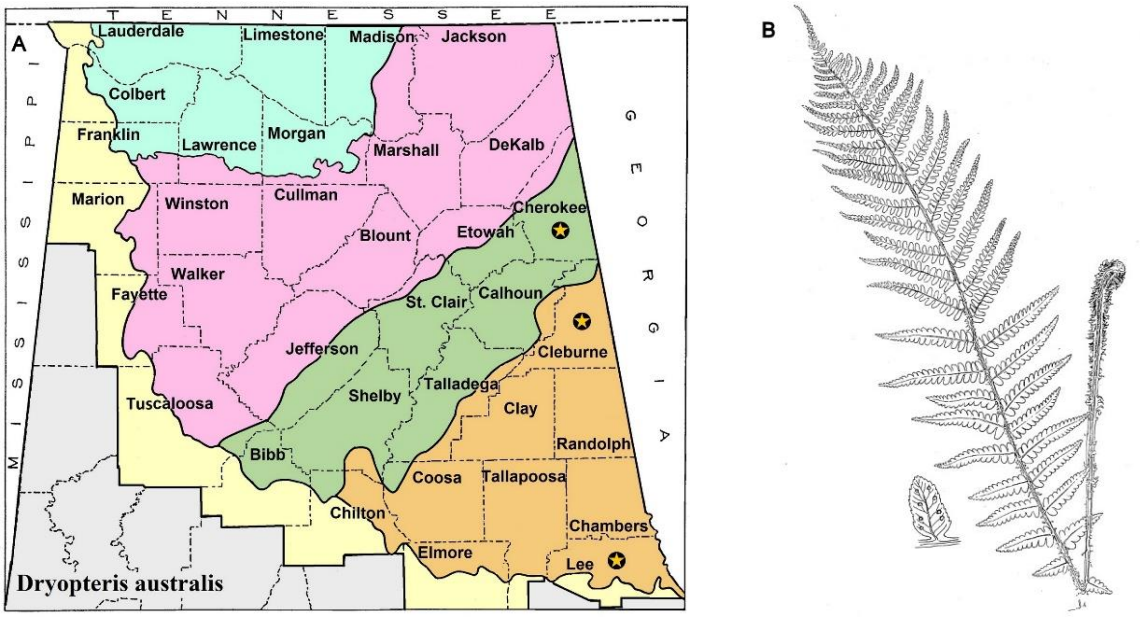


Figure 403. *Dryopteris australis.* **A.** Distribution map. **B.** Illustration: Forrest Bonner (Dean 1969).

The history of the Dixie Wood Fern dates back to 1895, when botanist Samuel Tracy of the University of Missouri discovered an unusual wood fern in Lee County, Alabama (Wherry 1937b). Shortly thereafter, Lucien Underwood, then a professor at Alabama Polytechnic Institute in Auburn, became aware of Tracy's find. In May 1896, Underwood collected specimens from the site and initially identified them as the Florida Wood Fern, *Dryopteris floridana* (Hook.) Kuntze [= *D. ludoviciana*]. He later reconsidered this identification and annotated his specimens as a new species, *D. alabamensis*, although he never formally published the name (Fig. 404a). On July 9, 1900, Charles Pollard and William Maxon of the U.S. National Museum visited the site and made additional collections, but they were also uncertain of the fern's identity (Fig. 404b). In *Plant Life of Alabama*, Mohr (1901) followed earlier identifications and listed the plant as *D. floridana*.

Figure 404. Historic herbarium specimens of *Dryopteris australis.* **A.** Sterile frond (NYBG), *Underwood s.n.*, Lee Co., Alabama, May 1896. **B.** Fertile frond, *Pollard & Maxon 45* (US), Lee Co., Alabama, 9 Jul 1900. **C.** Fertile frond (US - isotype), *Wherry s.n.*, Cherokee Co., Alabama, 1 Jun 1927.

Nearly three decades later, on June 1, 1927, botanists Edgar T. Wherry and Harry Trudell discovered a colony of the fern while camping in Cherokee County, Alabama (Fig. 404c). To their surprise, it was thriving in wet woods near their campsite. Although it resembled Clinton's Wood Fern (*Dryopteris clintoniana*), they noted several distinguishing features that set it apart from the more northern species (Wherry 1937b). Initially, Wherry identified the Cherokee County plant as *D. floridana* [= *D. ludoviciana*], albeit with some uncertainty. Following further study, Wherry (1937b) formally described it as *D. clintoniana* var. *australis*, noting its similarity to earlier collections from Lee County (Fig. 405). However, the Cherokee County site represents the type locality. Small (1938), in *Ferns of the Southeastern States*, elevated Wherry's variety to species rank and published the name *Dryopteris australis*.

Figure 405. *Dryopteris australis*, Lee Co., Alabama, 14 Apr 2023. Photo: Noah Yawn.

Wherry (1961) later suggested that the abnormal spores produced in the sori of *Dryopteris australis* (Fig. 406) indicated a hybrid origin. Walker (1962) confirmed this through cytological studies, showing that *D. australis* is a triploid hybrid backcross between the Log Fern (*D. celsa*) and the Florida Wood Fern (*D. ludoviciana* (Kunze) Small). Notably, *D. australis* often occurs in habitats where one or both parents are absent, sometimes even beyond their known ranges. Yawn et al. (2024) advocate recognizing *D. australis* as a distinct species rather than a hybrid, citing its ability to form large, self-sustaining colonies independent of either parent. Wagner and Musselman (1982) proposed that such populations may originate vegetatively or from unreduced "giant spores," which germinate into gametophytes and produce sterile, triploid sporophytes through apogamy—thus bypassing fertilization entirely.

Figure 406. *Dryopteris australis* sori, Cleburne Co., Alabama, 25 Jun 2024. Photo: Dan Spaulding.

The Dixie Wood Fern (*Dryopteris australis*) exhibits hybrid vigor due to its origins, resulting in a plant larger than either parent species, *D. celsa* or *D. ludoviciana* (F.S. Wagner & Musselman 1982). Despite its greater size, *D. australis* (Fig. 407a) more closely resembles the Florida Wood Fern (*D. ludoviciana*, Fig. 407b), which is endemic to the southeastern Coastal Plain. Both species share characteristics such as reduced basal leaflets and fertile fronds with contracted fertile lobes. However, *D. ludoviciana* bears narrower fertile leaflets with more widely spaced lobes and markedly reduced lower pinnae. By contrast, the Log Fern (*D. celsa*, Fig. 407c) has fertile pinnae that closely resemble its sterile ones and leaf blades that taper only slightly at the base.

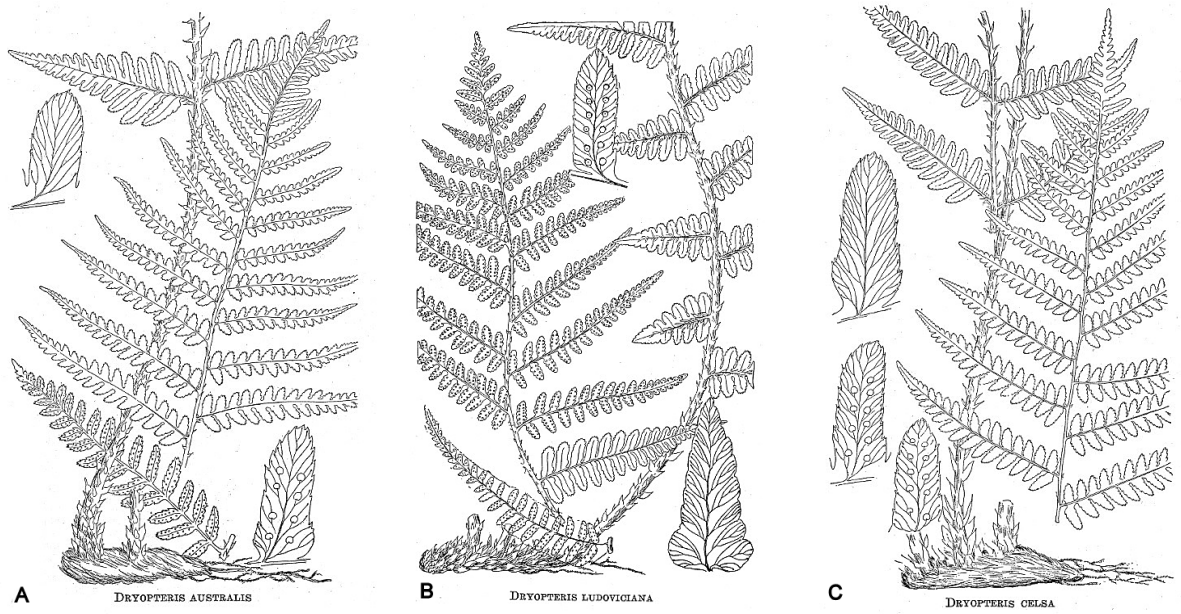


Figure 407. Comparisons of three related wood ferns. **A.** *Dryopteris australis*. **B.** *Dryopteris ludoviciana*. **C.** *Dryopteris celsa*. Illustrations by Ruth Sinclair George (Small 1938).

2. Dryopteris celsa (Wm. Palmer) Knowlt., T.S. Palmer, & Pollard ex Small {high} — LOG FERN (Fig. 408). [*Dryopteris atropalustris* Small; *Dryopteris goldieana* (Hook. ex Goldie) A. Gray subsp. *celsa* Wm. Palmer]

Figure 408. *Dryopteris celsa*, Fulton Co., Georgia, 19 May 2017. Photo: Alan Cressler.

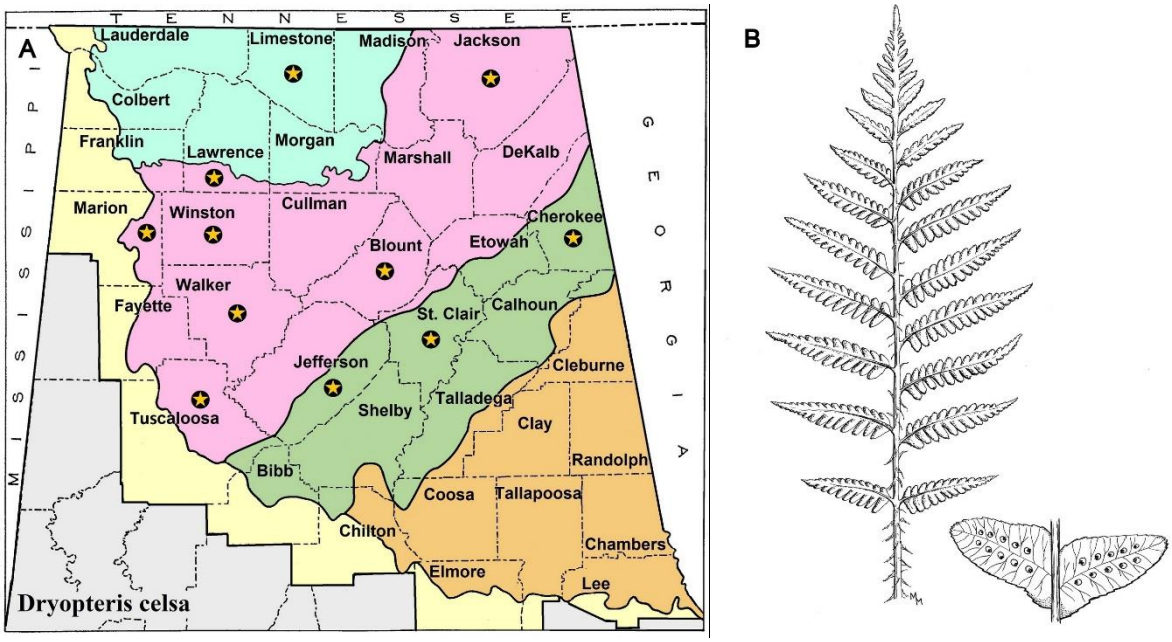


Figure 409. *Dryopteris celsa.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Plants terrestrial; evergreen. Seepage slopes, alluvial forests, moist calcareous woods, swamps, and bogs. Sporulates June–September; very rare in the Highland Rim; rare in the Cumberland Plateau, Ridge & Valley, and Coastal Plain (Fig. 409). Scattered in the eastern USA, from New York to Illinois, south to Georgia, and west to Arkansas and East Texas (Kartesz 2025). The Alabama Natural Heritage Program (2023) ranks *Dryopteris celsa* as imperiled (S2) within the state.

American naturalist William Palmer discovered the Log Fern on June 8, 1899, in the Great Dismal Swamp of Virginia. He classified it as *Dryopteris goldieana* subsp. *celsa*, noting its structural similarity to Goldie's Wood Fern (*D. goldieana*) but distinguishing it by its more upright habit and longer, narrower fronds. Palmer coined the common name "Log Fern" after observing it growing on moss-covered stumps and fallen logs rather than directly on the swamp floor (Fig. 410). To reflect this preference for elevated microhabitats, he chose the subspecific epithet *celsa*, meaning "high" or "exalted" (Palmer 1899). Later, Small (1938) recognized the Log Fern as a full species in *Ferns of the Southeastern States*.

Figure 410. *Dryopteris celsa*, King and Queen Co., Virginia, 28 Jun 2024. Photo: Anne Parker.

Log Fern originated as a fertile allotetraploid through hybridization between *D. goldieana* and *D. ludoviciana* (Florida Wood Fern). This hybrid carries four sets of chromosomes—two from each parent—which enables it to reproduce sexually, unlike many sterile hybrids (Werth 1991). Although the modern ranges of its parent species no longer overlap in the southeastern United States, paleobotanical evidence suggests that past climatic shifts and glacial movements brought them into contact, allowing hybridization to occur and giving rise to *D. celsa* (Sessa et al. 2012).

Two closely related wood ferns in Alabama—*Dryopteris australis* (Dixie Wood Fern) and *D. ludoviciana* (Florida Wood Fern)—differ from *D. celsa* in several key traits. Both *D. ludoviciana* and *D. australis* typically have basal leaflets that taper more abruptly than those of *D. celsa* and bear fertile pinnae that are narrower than the sterile ones. In these two species, fertile pinnae usually occur only in the upper portion of the blade, whereas *D. celsa* generally produces them on at least half the blade (Fig. 411). This distinction, however, is not always consistent, since *D. celsa* may sometimes develop sori only on the upper pinnae. Leaf dentition can also aid identification, though it is variable: *D. ludoviciana* often has small triangular teeth, *D. celsa* usually shows sharply pointed, frequently curved teeth, and *D. australis* tends to be intermediate. Because tooth shape varies within and among these species, this character should not be used as the sole basis for identification.

Figure 411. *Dryopteris celsa*. **A.** Bankhead National Forest, Lawrence Co., Alabama, 10 Jun 2024. Photo: James Eddie Watkins. **B.** Erie Co., Pennsylvania, 6 Jul 2023. Photo: Noah Yawn.

Blanche Dean (1969) and later authors, including Short and Spaulding (2012), reported *Dryopteris goldieana* from Alabama, but subsequent annotations have reidentified those specimens as *D. celsa*. Several characters can reliably separate the two species: (1) *D. celsa* usually has lanceolate blades that taper gradually toward both tip and base, whereas *D. goldieana* has oblong blades that taper sharply at the tip and only slightly, if at all, at the base; (2) the sori of *D. celsa* are situated about midway between the midrib and margin, while in *D. goldieana* they occur nearer the midrib; and (3) basal petiole scales of *D. celsa* are medium to dark brown with a narrow black central band, whereas those of *D. goldieana* are dark brown to nearly black with a narrow pale margin. These traits consistently distinguish the two taxa in field and herbarium material.

3. Dryopteris ×cressleri Yawn, ined. {for Alan Cressler} — CRESSLER'S WOOD FERN (Fig. 412).

Figure 412. *Dryopteris ×cressleri*, Jackson Co., Alabama, 22 May 2021. Photo: Alan Cressler.

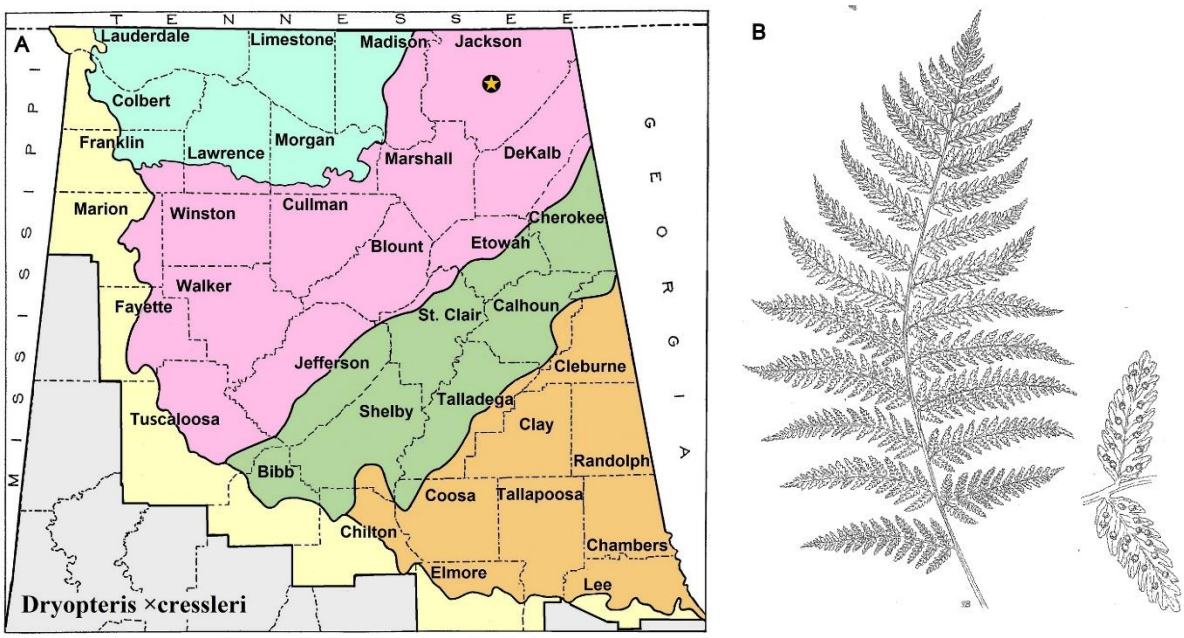


Figure 413. *Dryopteris ×cressleri.* **A.** Distribution map. **B.** Illustration: Sue Blackshear, 2012.

Plants epipetric; evergreen. On rocks in forests. Sterile hybrid [*Dryopteris intermedia* × *marginalis*], spores abortive; very rare in the Jackson County District of the Cumberland Plateau (Fig. 413). Widely scattered in eastern North America, restricted to localities where the two parent species co-occur (Montgomery & Wagner 1993). Although the Alabama Natural Heritage Program does not currently track this hybrid, we recommend listing it as critically imperiled (S1) in the state.

Figure 414. Noah Yawn with *Dryopteris* ×*cressleri* and its two parents, *D. marginalis* and *D. intermedia*. Jackson County, Alabama, 22 May 2021. Photo: Alan Cressler.

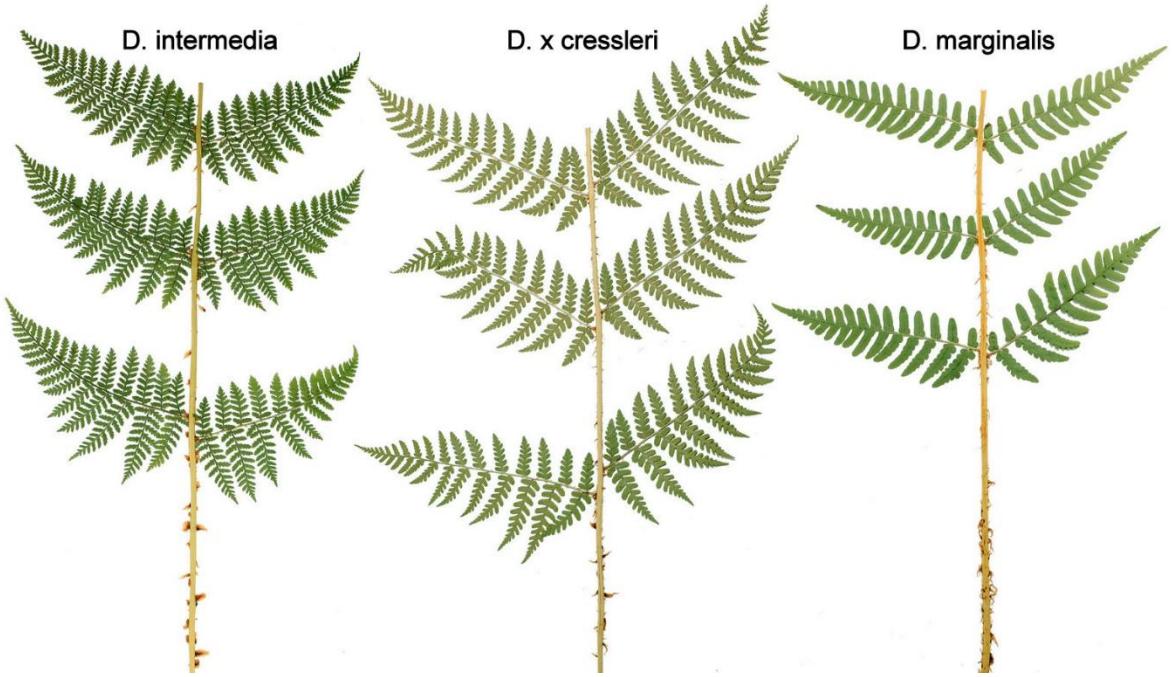


Figure 415. *Dryopteris* ×*cressleri* with its parents, Jackson Co., Alabama, 23 Jun 2024. Photo: Noah Yawn.

Ralph C. Benedict (1909) was the first to describe the sterile hybrid between *Dryopteris intermedia* (Intermediate Wood Fern) and *D. marginalis* (Marginal Shield Fern). On June 21, 1981, Alan Cressler discovered this hybrid in Jackson County, Alabama, growing on a moss-covered limestone boulder near a cave entrance, with both parent species present nearby (Fig. 414). The plant had a multi-crowned rhizome nearly two feet long, suggesting considerable age. Over four decades later, Noah Yawn is honoring Cressler's discovery by formally naming the hybrid *Dryopteris ×cressleri* (Yawn & Spaulding in prep.).

On July 3, 1984, John Short made the first collection of this hybrid in Alabama. He initially visited the site to observe the Single-Sorus Spleenwort (*Asplenium monanthes*) but unexpectedly found the hybrid *Dryopteris* thriving on a boulder by the cave. Earlier that day, Short had joined Murray Evans, a University of Tennessee professor, and David Webb, a TVA botanist, on a field trip in Jackson County to study the Hart's-Tongue Fern. After learning about the rare spleenwort from Dr. Evans, Short stopped by the cave on his way home and documented both species.

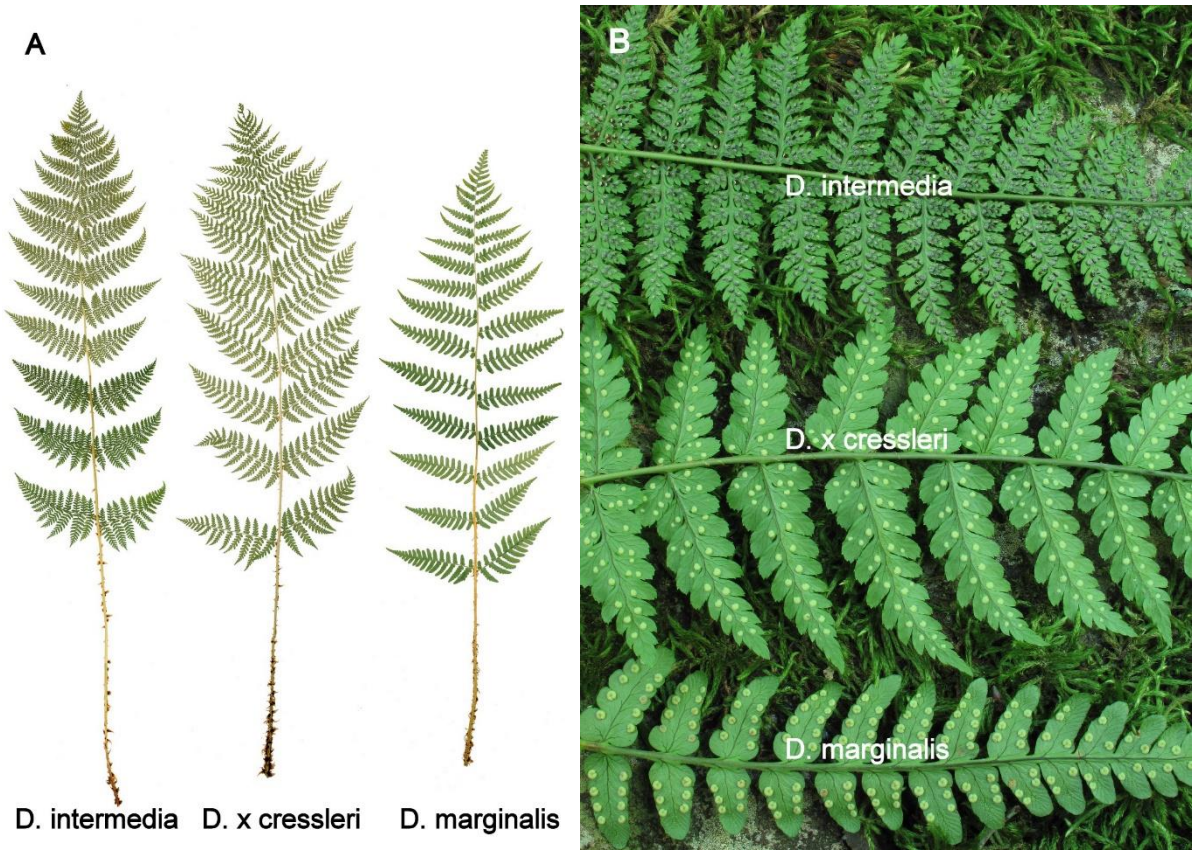


Figure 416. *Dryopteris ×cressleri* and its parents. **A.** Jackson Co., Alabama, 23 Jun 2024. Photo: Noah Yawn. **B.** Jackson Co., Alabama, 20 Jun 2009. Photo: Alan Cressler.

Dryopteris ×cressleri is a striking fern that showcases hybrid vigor, combining robust growth with a distinctive appearance. While typically more vigorous than its parent species—*Dryopteris intermedia* and *Dryopteris marginalis*—this hybrid displays intermediate traits that reflect its mixed heritage (Fig. 415). However, its unique features are distinct enough to distinguish it from either parent species. Defining characteristics of Cressler's Wood Fern include 1) sparsely glandular fronds, particularly along the midrib; 2) bipinnate-pinnatifid blades; 3) leaf segments with acute marginal teeth; and 4) sori positioned closer to the margin than to the midvein (Fig. 416).

4. Dryopteris erythrosora (D.C. Eaton) Kuntze {red sorus} — AUTUMN FERN; JAPANESE RED SHIELD FERN (Fig. 417).

Figure 417. *Dryopteris erythrosora*, Cleburne Co., Alabama, 12 Apr 2025. Photos: Dan Spaulding.

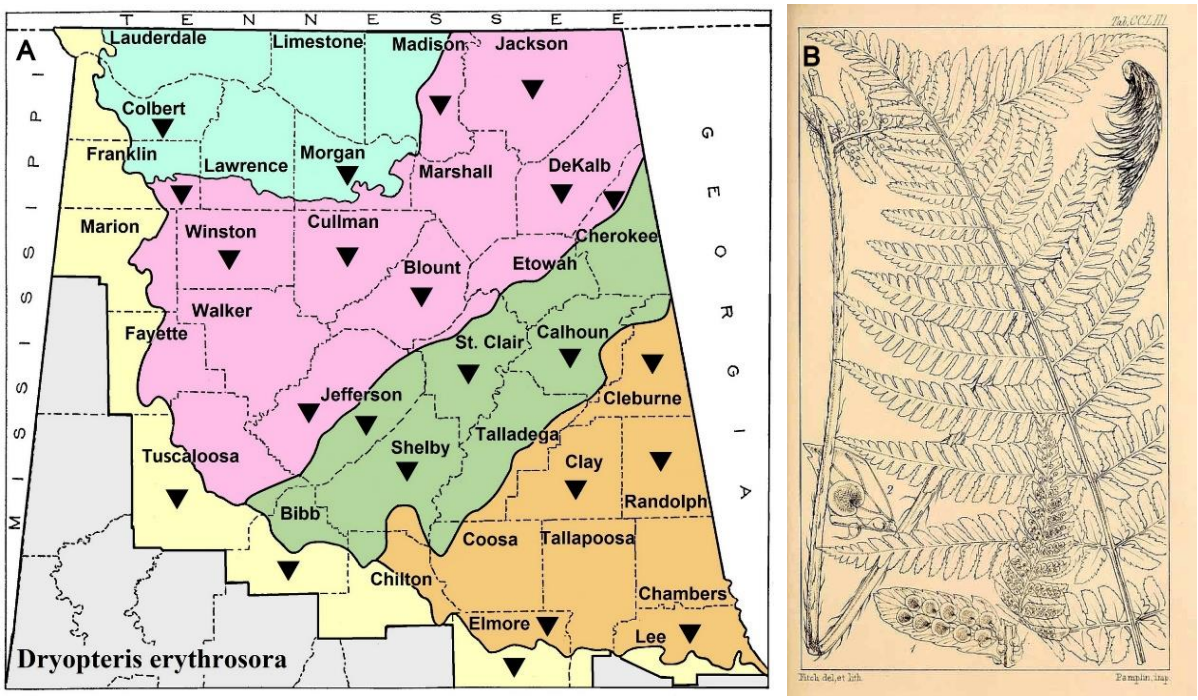


Figure 418. *Dryopteris erythrosora*. **A.** Distribution map. **B.** Illustration: Walter Hood Fitch, 1862.

Plants terrestrial or epipetric; evergreen. Woods, shaded streambanks, rocky buffs, lake banks, roadbanks, and other disturbed sites. Sporulates year-round; uncommon throughout Alabama (Fig. 418). Native to Japan, China, and Korea, this species has escaped from cultivation and naturalized in the southeastern USA (Shugang & Barrington 2013).

The Autumn Fern (*Dryopteris erythrosora*) is a popular landscaping plant in the southeastern United States, valued for its lustrous evergreen foliage and minimal maintenance needs. It is widely available in nurseries, and gardeners frequently grow it for its ornamental appeal. Its most striking feature is the bronze-colored flush of new growth, with young fronds emerging copper-pink before maturing to a deep, glossy green by early summer (Fig. 419a). Mature fronds remain erect and vibrant through winter, providing year-round interest in the garden (Mickel 1994). A distinctive trait is the bright red indusia covering the developing sori, a vivid contrast against the foliage. Botanists distinguish this species from similar-looking ferns by its dark, blister-like scales on the rachis and along the midveins on the undersides of the pinnae (Fig. 419b).

Figure 419. *Dryopteris erythrosora*, Cleburne Co., Alabama. **A.** Red sori on young fronds, 12 Apr 2025. **B.** Older frond with blister-like scales still present on the pinna midribs, 2 Feb 2025. Photos: Dan Spaulding.

In *Ferns of Alabama*, Short and Spaulding (2012) omitted *Dryopteris erythrosora* from their treatment. However, while the book was in press, Dan Spaulding collected naturalized specimens of this species in Calhoun County on March 3, 2012, and later in Shelby County in January 2013. Natural Heritage botanist Theo Witsell recorded the first naturalized occurrence of *D. erythrosora* in North America in 2007 in Hot Springs County, Arkansas (Simpson et al. 2008). Since then, Umstead and Diggs (2018) have reported its aggressive spread in the southeastern United States, highlighting its potential as an invasive species. Wyatt (2020) identifies two factors that may contribute to Autumn Fern's widespread establishment: its popularity as an ornamental plant, with countless specimens installed in landscapes across the Southeast, and its hardiness across most of the United States.

5. Dryopteris hangchowensis Ching {for Hangzhou or Hangchow, a city in China} — HANGCHOW WOOD FERN; HANGZHOU WOOD FERN; CHINESE WOOD FERN (Fig. 420).

Figure 420. *Dryopteris hangchowensis*, Lee Co., Alabama, 14 Aug 2020. Photos: Wayne Barger.

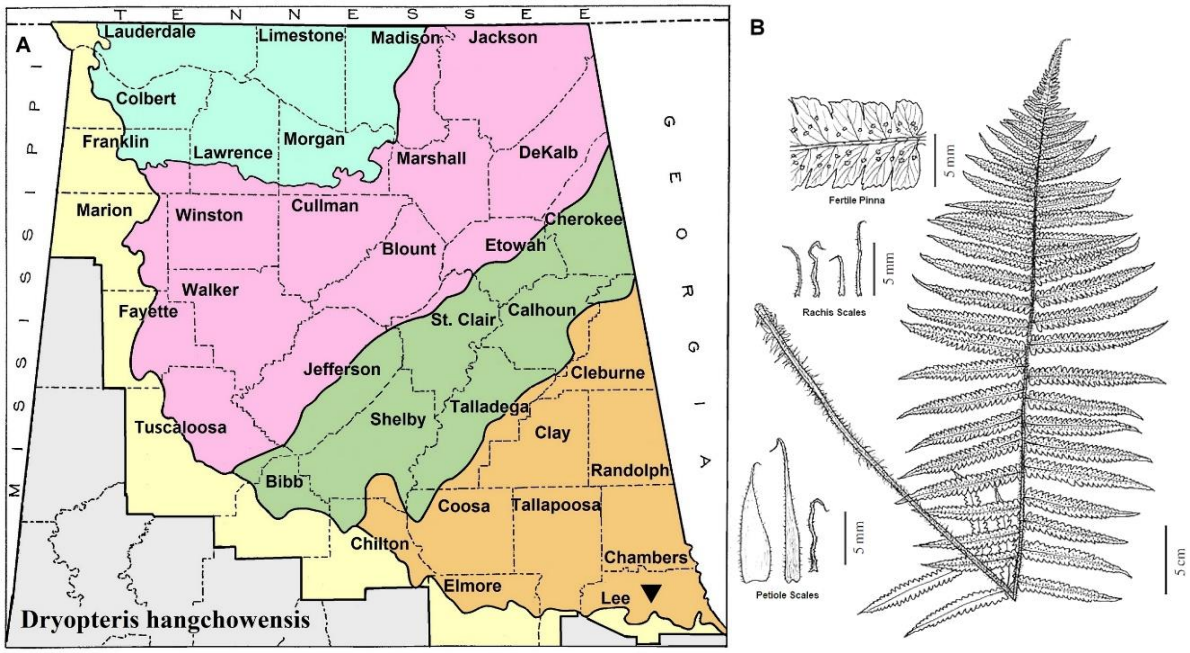


Figure 421. *Dryopteris hangchowensis.* **A.** Distribution map. **B.** Illustration from Lee et al. 2013.

Plants terrestrial; evergreen. Moist mixed woods, somewhat disturbed. Sporulates year-round; very rare in the Piedmont of Alabama (Fig. 421). Native to the forested mountains of Korea, Japan, southeastern China, and Taiwan (Lee et al. 2013); documented in North America as naturalized only in Alabama and Georgia, though possibly occurring elsewhere.

On June 28, 2020, Wayne and Priscilla Barger discovered an unidentified fern in a disturbed mixed pine-hardwood habitat near a birdwatching trail in Opelika, Alabama (Fig. 422a). They observed a small population of over a dozen individuals at the site, with no evidence of nearby plantings. Initially, Wayne Barger tentatively identified the fern as the Shaggy Wood Fern, *Dryopteris cycadina* (Franch. & Sav.) C. Chr., a species commonly grown in the southeastern United States. However, uncertain about this identification, he sent specimens to three pteridologists—Chris Fraser-Jenkins, Alan Smith, and George Yatskievych—who identified it as *D. hangchowensis*, the Hangzhou Wood Fern (Fig. 422b). This collection represents the first documented occurrence of the species in North America (Yawn et al. 2024).

Figure 422. *Dryopteris hangchowensis*. **A.** Habitat, Lee Co., Alabama, 14 Aug 2020. Photo: Wayne Barger. **B.** Herbarium specimen (TEX), *Barger & Barger SP#5219*, Lee Co., Alabama, 28 June 2022.

Dryopteris hangchowensis closely resembles *D. cycadina*, as both species have pinnate fronds covered with black ciliate scales (Fig. 423). However, Wu et al. (2013) differentiate the two by the arrangement of sori along the costa (midvein) of each leaflet: *D. hangchowensis* primarily forms two irregular rows of sori, while *D. cycadina* usually has more than three scattered rows along each side. Leaf blade morphology also sets them apart. In *D. cycadina*, the blades gradually narrow at the base, with the lowest pinnae distinctly shorter than the ones above. In contrast, the leaf blades of *D. hangchowensis* are relatively broad at the base, with the lower pinnae nearly equal to or slightly shorter than those above.

Figure 423. A. *Dryopteris cycadina*, cultivated at BBG, Jefferson Co., Alabama, 8 May 2024. Photo: Dan Spaulding. **B.** *Dryopteris hangchowensis*, Lee Co., Alabama, 14 Aug 2020. Photo: Wayne Barger.

Figure 424. *Dryopteris cycadina*, cultivated, Jefferson Co., Alabama, 8 May 2024. Photos: Dan Spaulding.

The origin of *Dryopteris hangchowensis* in Alabama remains a mystery, as there is little evidence to explain its presence. It seems unlikely that spores traveled vast distances across the ocean to establish this species. Hoshizaki and Wilson (1999) excluded *D. hangchowensis* from their list of *Dryopteris* species cultivated in the United States. One plausible explanation is that a garden center may have sold this fern under the mistaken identity of *D. cycadina*, a more widely recognized and commonly available species. The Shaggy Wood Fern, *D. cycadina* (Fig. 424), is popular among gardeners for its symmetrical, fountain-like arrangement of fronds and striking black, shaggy scales adorning its stems (Olsen 2007).

6. Dryopteris intermedia (Muhl. ex Willd.) A. Gray {intermediate} — INTERMEDIATE WOOD FERN; FANCY FERN; EVERGREEN WOOD FERN; GLANDULAR WOOD FERN (Fig. 425). [*Dryopteris austriaca* (Jacq.) Woyn. ex Schinz & Thell. var. *intermedia* (Muhl. ex Willd.) C.V. Morton; *Dryopteris spinulosa* (O.F. Müll.) Watt var. *intermedia* (Muhl. ex Willd.) Underw.]

Figure 425. *Dryopteris intermedia*, Winston Co., Alabama, 13 Jun 2024. Photo: Dan Spaulding.

Plants terrestrial or on rock in thin soil; evergreen. Rocky woods, cliffs, cool ravines, and cove forests. Sporulates May–September; rare in the Cumberland Plateau (Fig. 426). This species occurs in eastern North America from Newfoundland to Ontario and Minnesota, south to northern Alabama, and Georgia (Montgomery & Wagner 1993).

The Intermediate Fern, often called "fancy fern," is prized for its delicate, lacy fronds, which lend an intricate, ornamental appeal. This aesthetic quality makes it popular for cold-temperate gardens (Olsen 2007). Historically, florists collected *Dryopteris intermedia* for decorative purposes, especially valuing its evergreen leaves for floral arrangements and wreaths (Clute 1901; Dean 1969). During the 19th-century "fern craze," or pteridomania, excessive harvesting of wild ferns sometimes threatened native populations. Although commercial fern harvesting has declined, florists now primarily rely on cultivated sources rather than wild plants (Whittingham 2012).

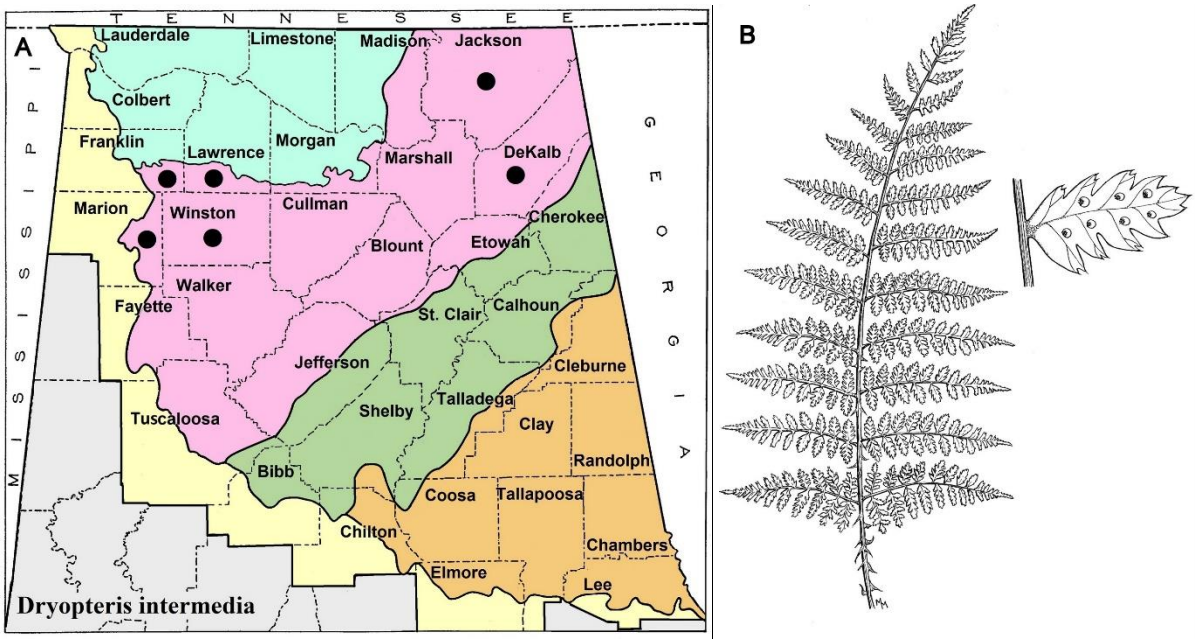


Figure 426. *Dryopteris intermedia*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 427. *Dryopteris intermedia*, Towns Co., Georgia, 17 May 2009. Photo: Alan Cressler.

Dryopteris intermedia has finely divided leaf blades, spiny-toothed margins, and glandular fronds (Fig. 427). In young plants, the undersides of the fronds are so sticky with glands that they often adhere to the drying papers used in pressing specimens (Clute 1901). The common name "intermediate fern" reflects its morphology, which falls between that of two close relatives: the Mountain Wood Fern, *D. campyloptera* (Kunze) Clarkson, and the Spinulose Wood Fern, *D. carthusiana* (Vill.) H.P. Fuchs (Britton 1961). Dean (1969) included these two northern species in her book *Ferns of Alabama*, but no verified collections exist from the state.

7. Dryopteris marginalis (L.) A. Gray {marginal} — MARGINAL SHIELD FERN; MARGINAL WOOD FERN; LEATHER WOOD FERN (Fig. 428).

Figure 428. *Dryopteris marginalis*, Etowah Co., Alabama, 17 Sep 2024. Photo: Dan Spaulding.

Plants epipetric or terrestrial; evergreen. Rocky, sloped woods, rock outcrops, cliffs, and rocky forests. Sporulates May–September; uncommon in the Highland Rim and Piedmont; frequent in the Cumberland Plateau and Ridge & Valley; rare in the Coastal Plain (Fig. 429). This species occurs in eastern North America from Newfoundland to southern Ontario, south to eastern Oklahoma, and through the Appalachians to northern Georgia and Alabama (Montgomery & Wagner 1993).

The Marginal Shield Fern (*Dryopteris marginalis*) thrives in rocky woodlands, adapting to both alkaline and acidic substrates, including limestone and sandstone. Its specific epithet and the first part of its common name refer to the sori positioned along the margins of the leaf segments (Fig. 430). While members of this genus are commonly known as wood ferns—reflecting their typical woodland habitats—they are also called shield ferns, a reference to the distinctive, shield-like indusia that cover their sori. In *D. marginalis*, these indusia are especially thick and kidney-shaped at maturity. The combination of leathery, gray-green fronds, swollen marginal sori, and uniformly light brown scales at the base of the petioles (Fig. 431) makes this species readily identifiable in the field.

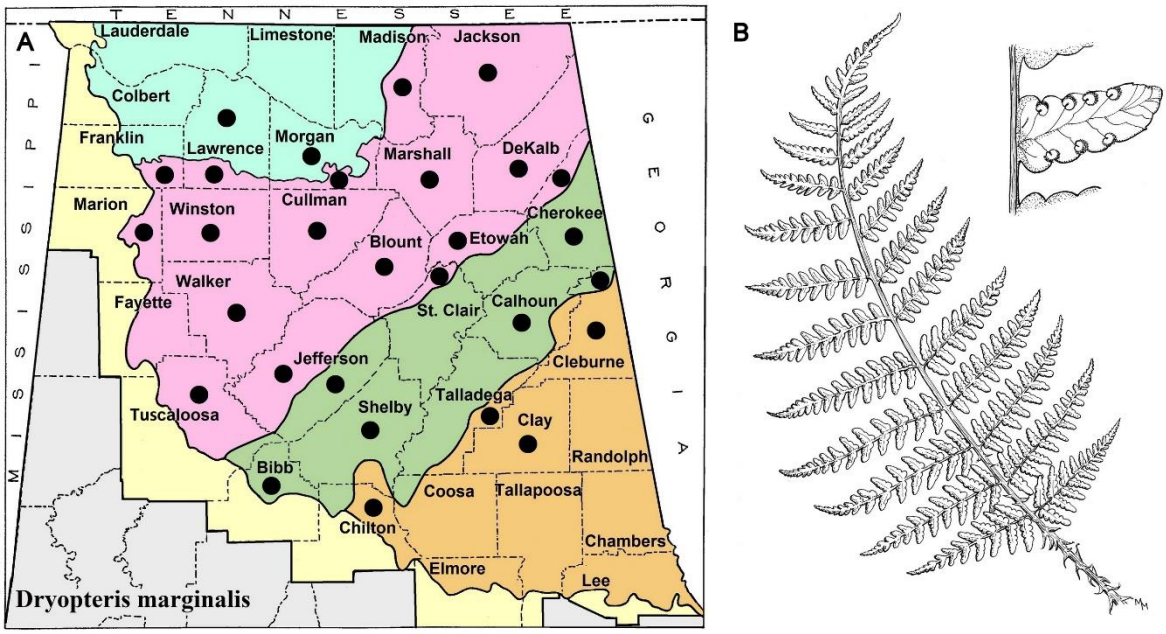


Figure 429. *Dryopteris intermedia*. **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 430. *Dryopteris marginalis* sori, Jackson Co., Alabama, 21 Jun 2006. Photo: Wayne Barger.

Figure 431. *Dryopteris marginalis* scales, Rabun Co., Georgia, 1 May 2016. Photo: Alan Cressler.

4. Polystichum Roth 1800 {poh-LISS-tik-um}
[Greek, *poly*, many, *stichos*, rows; alluding to the sori on each pinna]

1. Leaves 1-pinnate; fertile pinnae restricted to the blade apex and strongly contracted; sori continuous, nearly covering the entire lower surface of pinnae.....***Polystichum acrostichoides***
1. Leaves 1-pinnate-pinnatifid to 2-pinnate; fertile pinnae not contracted; sori separate, and scattered across the lower surface of pinnae ..... ***Polystichum tsus-simense***

1. Polystichum acrostichoides (Michx.) Schott {like *Acrostichum*; the leather fern} — CHRISTMAS FERN; DAGGER FERN (Fig. 432).

Plants terrestrial or occasionally in thin soil over rock; evergreen. Forests, wooded slopes, ravines, and bottomlands. Sporulates June–November; common throughout Alabama (Fig. 433). Common throughout eastern North America from Nova Scotia to Ontario, south to East Texas and Florida; also in Mexico; naturalized in Europe (D.H. Wagner 1993).

The Christmas Fern (*Polystichum acrostichoides*) is one of Alabama's most common and recognizable ferns, thriving in a wide range of forested habitats throughout the state. Its evergreen fronds persist through winter, creating a striking contrast against the muted browns and grays of dormant forests. These fronds often exhibit a unique seasonal adaptation: they stand upright during summer and lie flat on the ground in colder months. Its winter posture serves two vital purposes. First, it traps moisture beneath the leaves, reducing water loss. Second, it raises leaf temperatures on sunny days, optimizing conditions for photosynthesis. By maintaining temperatures closer to the optimal range for photosynthetic activity, these adaptations allow the fern to flourish even in freezing conditions (Forget et al. 2018).

Figure 432. *Polystichum acrostichoides*, Cleburne Co., Alabama, 29 Apr 2023. Photo: Dan Spaulding.

The Christmas Fern produces dimorphic fronds, with two distinct leaf forms (Fig. 434a). Sterile fronds are shorter and broader than fertile fronds, which are taller, narrower, and taper near the tip, where the contracted upper leaflets bear spores. The sporangia are confluent, covering nearly the entire undersurfaces of the fertile segments (Fig. 435). Some individuals show natural variation, developing curled, ruffled, or deeply divided leaflets (Fig. 434b), but the typical form remains the most widespread (Clute 1961).

Gardeners prize the Christmas Fern for its resilience, versatility, and ornamental appeal. It transplants easily and thrives in shaded woodland gardens, serving as a lush ground cover or an elegant accent plant in the landscape. The fern's ability to stabilize soil makes it an excellent choice for planting on slopes to prevent erosion. Many also grow it indoors as a houseplant, where its vibrant green fronds add natural beauty to interior spaces (Mickel 1994; Olsen 2007).

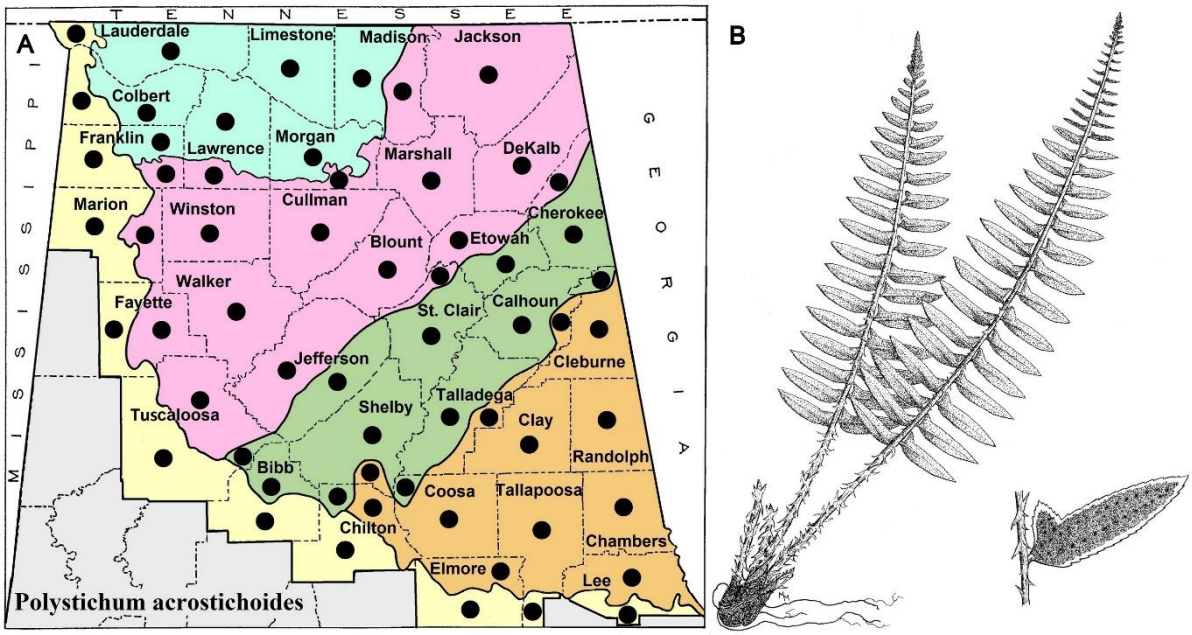


Figure 433. *Polystichum acrostichoides.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 434. *Polystichum acrostichoides*. **A.** Sterile and fertile fronds, Calhoun Co., Alabama, 17 April 2025. Photo: Dan Spaulding. **B.** Ruffled form, Floyd Co., Georgia, 27 May 2011. Photo: Alan Cressler.

Figure 435. *Polystichum acrostichoides*. **A.** Young fertile pinnae, Calhoun Co., Alabama, 17 April 2025. Photo: Dan Spaulding. **B.** Mature fertile pinnae, Winston Co., Alabama, 10 Jun 2018. Photo: Kevin England. **C.** Old fertile pinnae, Calhoun Co., Alabama, 9 Nov 2024. Photo: Savannah Spaulding.

The name "Christmas fern" reflects its seasonal association, as its evergreen fronds remain vibrant through the holiday season. This characteristic made it a popular choice for Christmas decorations such as wreaths, garlands, and other festive arrangements (Clute 1901). The fern earned its common name from early New England settlers who harvested it for use in Christmas decorations (Mickel 1994). Its distinctive leaflets, characterized by a basal lobe, resemble a Christmas stocking or Santa's sleigh (Fig. 436), providing a memorable visual cue that serves as a mnemonic for the common name (Dunbar 1998).

Figure 436. *Polystichum acrostichoides*, Calhoun Co., Alabama, 9 Nov 2024. Photo: Savannah Spaulding.

The Cherokee recognized the medicinal value of *Polystichum acrostichoides* and used its rhizome in a variety of traditional remedies. They brewed decoctions to treat rheumatism and to induce vomiting, and prepared infusions to ease chills, fevers, stomachaches, and bowel complaints. For toothaches, they created a mixed herbal preparation that combined the rhizome with other medicinal plants. Beyond its medicinal roles, the Cherokee also harvested the young fiddleheads in spring as a nutritious seasonal food (Moerman 1998).

2. Polystichum tsus-simense (Hook.) J. Sm. {from Tsushima, an island in the Korea Strait} — KOREAN ROCK FERN; TSUS-SIMA HOLLY FERN (Fig. 437). [*Polystichum luctuosum* (Kunze) T. Moore; *Polystichum tsus-simense* var. *mayebarae* (Tagawa) Sa. Kurata]

Figure 437. *Polystichum tsus-simense*, Jefferson Co., Alabama, 18 Jan 2003. Photo: Vitaly Charny.

Plants terrestrial or epiphytic; evergreen. Rocky woods, crevices in rocks, cracks in masonry, and other disturbed sites. Sporulates June–November; very rare in northern Alabama (Fig. 438). Native to Korea, Japan, China, Taiwan, Vietnam, India, and South Africa (Zhang & Barrington 2013). Naturalized in the southeastern USA and documented from Alabama, Arkansas, Florida, Georgia, Louisiana, Tennessee, Kentucky, and North Carolina (iNaturalist 2025; Kartesz 2025).

The Korean Rock Fern (*Polystichum tsus-simense*) is an evergreen species with glossy, dark green leaves marked by black midveins with segments tipped with short, bristle-like points (Fig. 439). This species thrives in moist, well-drained soils and prefers partial to full shade. Well-suited for shaded garden beds, rock gardens, and container plantings, it is hardy in USDA zones 6 through 9. Due to its attractive foliage and low maintenance requirements, it has become a popular ornamental in temperate regions (Mickel 1994).

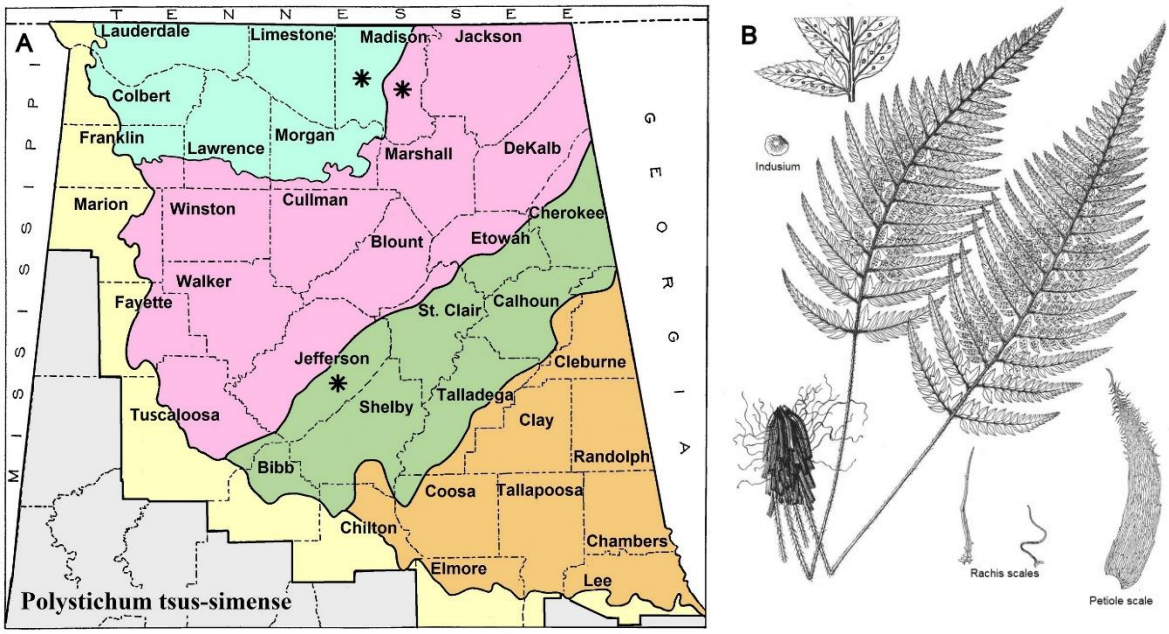


Figure 438. *Polystichum tsus-simense.* **A.** Distribution map. **B.** Illustration: Ren-Chang Ching, 1958.

Figure 439. *Polystichum tsus-simense,* mixed woods in a nature preserve, Madison Co., Alabama, 14 May 2023. Photo: @andreusviridis, iNaturalist observation.

Naturalists have documented *Polystichum tsus-simense* escaping cultivation in the southern United States. In 2010, James Peck (2011) reported the species from three counties in Arkansas. Decades earlier, in 1942, botanist T.C. Sidney collected it from a gully in a pine forest in Saint Tammany Parish, Louisiana—likely the earliest known record of its establishment in the region. In 2003, physicist and nature photographer Vitaly Charny observed a population in rocky woods along a lakeshore in Jefferson County, Alabama (Fig. 437). Although Peck emphasized that the fern's slow growth reduces the risk of invasive spread, its persistence in natural habitats warrants continued monitoring to determine whether it is truly naturalized or merely a casual waif. Most occurrences are associated with urban areas, often in rocky habitats (Fig. 440) or disturbed sites (Fig. 441).

Figure 440. *Polystichum tsus-simense*, rocky woods in a nature preserve near Atlanta, DeKalb Co., Georgia, 9 Mar 2016. Photos: Erik Danielsen

Figure 441. *Polystichum tsus-simense*, Alamance Co., North Carolina, 1 Jan 2025. Photo: Ethan Pitts.

24. **POLYPODIACEAE** (Polypody Family) – in Polypodiales

1. Lower surface of leaf blade densely scaly with scurfy, dark-centered scales; leaves gray-green; lobe margins entire; rhizome 1–2 mm in diameter ..... ***Pleopeltis***
1. Lower surface of leaf blade glabrous, lacking scales; leaves green; lobe margins usually crenulate or denticulate (minutely toothed), rarely entire; rhizome 3–6 mm in diameter ..... ***Polypodium***

1. **Pleopeltis** Humboldt & Bonpland ex Willdenow 1810 {plee-oh-PELL-tiss}

[Greek, *pleos*, many, and *pelte*, shield; alluding to the abundant scales covering lower leaf surfaces]

1. Pleopeltis michauxiana (Weath.) Hickey & Sprunt {for André Michaux, 1746–1802} — RESURRECTION FERN; SCALY POLYPODY; TREE POLYPODY; GRAY POLYPODY (Fig. 442). [*Marginaria polypodioides* (L.) Tidestr.; *Pleopeltis polypodioides* (L.) E.G. Andrews & Windham var. *michauxiana* (Weath.) E.G. Andrews & Windham; *Polypodium polypodioides* (L.) Watt var. *michauxianum* Weath.]

Figure 442. *Pleopeltis michauxiana*, Cleburne Co., Alabama, 4 May 2024. Photos: Dan Spaulding.

Plants epiphytic or epipetric; evergreen. On oaks and other hardwood trees with rough bark, occasionally growing on rocks or old buildings. Sporulates May–November; common throughout Alabama (Fig. 443). Occurs chiefly in the southern section of the eastern USA, from Virginia to southwestern Kansas, south to East Texas and Florida; also in Mexico and Central America (Andrews & Windham 1993).

The Resurrection Fern is among the most common ferns in Alabama, flourishing on mature hardwood trees with deeply furrowed bark and often on their broad, spreading limbs. As an epiphyte (Fig. 444a), it anchors its rhizomes into the bark of its host tree, relying entirely on the tree for physical support, not nutrients. This fern is a familiar sight in residential neighborhoods, parks, and along city streets. In addition, it is also epipetric (Fig. 444b), growing on rocks and even within the cracks of old brick buildings.

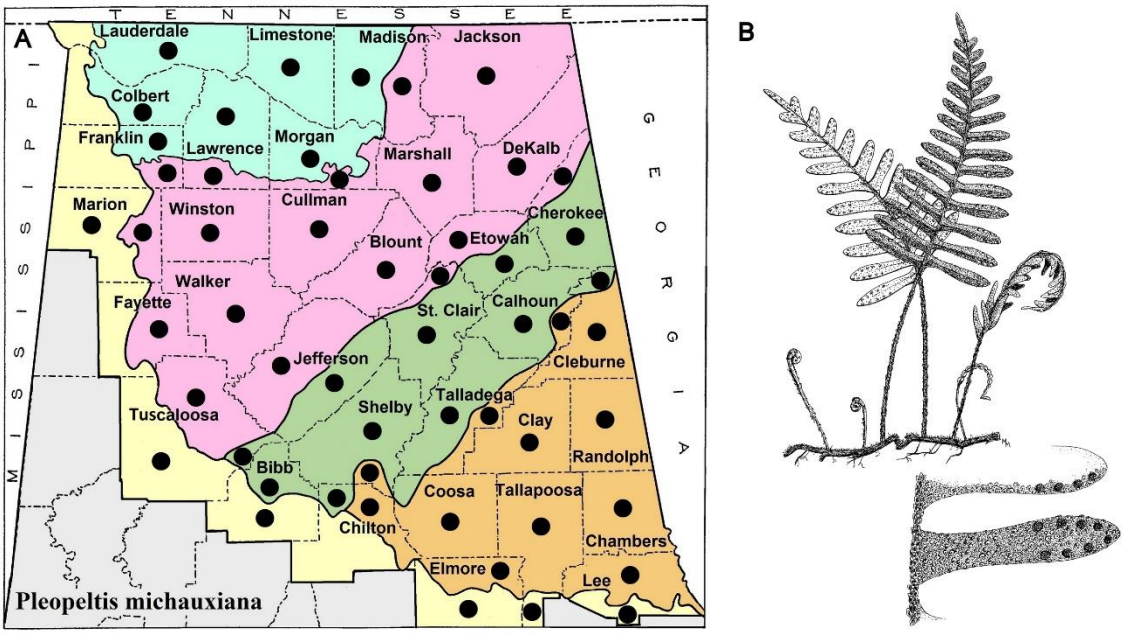


Figure 443. *Pleopeltis michauxiana.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Figure 444. *Pleopeltis michauxiana*. **A.** Epiphytic, Calhoun Co., Alabama, 27 Mar 2023. **B**. Epipetric, Blount Co., Alabama, 13 Dec 2024. Photos: Dan Spaulding.

During drought, fronds of the Resurrection Fern desiccate and curl, giving the appearance that they are dead (Fig. 445a). After rainfall, they rapidly absorb moisture, unfurl, and regain their healthy green color—an impressive transformation that inspired the fern's common name. Surprisingly, this curling behavior does not reduce water loss. Instead, the fern exposes the scaly undersides of its fronds, where stomata that regulate transpiration are concentrated. Although one might expect the plant to protect these surfaces, Pessin (1924) demonstrated that the curling helps trap raindrops, enhancing the fern's ability to rehydrate efficiently. Shield-shaped scales that densely cover the lower frond surfaces (Fig. 445b) further aid in capturing even the slightest traces of moisture. This adaptation enables the fern to survive in habitats where water availability is sporadic. Its alternate name, "scaly polypody," refers to these distinctive scales and reflects its former placement in the genus *Polypodium*.

Figure 445. *Pleopeltis michauxiana*. **A.** Dry fronds, Calhoun Co., Alabama, 9 Nov 2024. Photo: Savannah Spaulding. **B.** Scales on undersurface of leaf, Blount Co., Alabama, 13 Dec 2024. Photo: Dan Spaulding.

Harvard botanist Charles Weatherby (1939) named this taxon in honor of André Michaux, the French naturalist known for his extensive North American plant collections. Weatherby originally classified it as a variety of the Tropical Resurrection Fern (*Polypodium polypodioides*) based on the absence of scales on the upper leaf surfaces. Windham (1993b) later transferred the North American taxa in the scaly *Polypodium* group to *Pleopeltis*. Otto et al. (2009) reinforced this move by presenting compelling morphological, chemical, and molecular evidence to support the separation. Building on these findings, Susan Sprunt (2010) elevated all previously recognized varieties to species rank in her monograph on the *Pleopeltis polypodioides* complex.

Native Americans used Resurrection Fern for various medicinal purposes. They applied a topical ointment made from heated stems and leaves to treat sores and ulcers. For headaches, tribe members drank an infusion made from the fronds, which acted as an analgesic, relieving pain. The leaves were also brewed into tea and used as a mouthwash to ease sore mouths, thrush, and bleeding gums. In addition, they ingested a decoction of the leaves to treat dizziness and vertigo (Foster & Duke 1990; Moerman 1998).

1. Polypodium Linnaeus 1753 {polly-POH-dee-um}
[Greek, *poly*, and *podion*, many feet; alluding to numerous knoblike traces of leaf stalks on rhizome]

1. Polypodium virginianum L. {Virginian; first discovered} — ROCK POLYPODY; ROCKCAP FERN; (Fig. 446). [*Polypodium vulgare* L. var. *virginianum* (L.) Eaton]

Figure 446. *Polypodium virginianum*, Cherokee Co., Georgia, 9 Aug 2009. Photos: Alan Cressler.

Plants epipetric; evergreen. Grows on moist, shaded rocks and cliff ledges, usually on acidic rocks like sandstone. Sporulates June–November; uncommon in the Cumberland Plateau; rare in the upper Piedmont (Fig. 447). This species is native to eastern North America from Newfoundland to the Northwest Territories, south to Arkansas, and northern Georgia (Haufler et al. 1993b).

Historically, botanists often treated the North American *Polypodium virginianum* (Rock Polypody) and the Eurasian *P. vulgare* (Common Polypody) as a single polymorphic species within the *P. vulgare* complex (Haufler et al. 1995). Cytogenetic studies by Manton (1947, 1951), however, established them as distinct species. Further investigations by Manton and her student Molly Shivas (1953) initially identified two cytological forms within the *P. virginianum* subgroup in eastern North America: a diploid (2n) and a tetraploid (4n). Manton (1957) later argued that the diploid represents the ancestral species, while the tetraploid arose through hybridization between two diploid progenitors. Although she described only two cytotypes, she suspected the existence of a third, since one of the diploid parents remained unidentified and likely represented a distinct species.

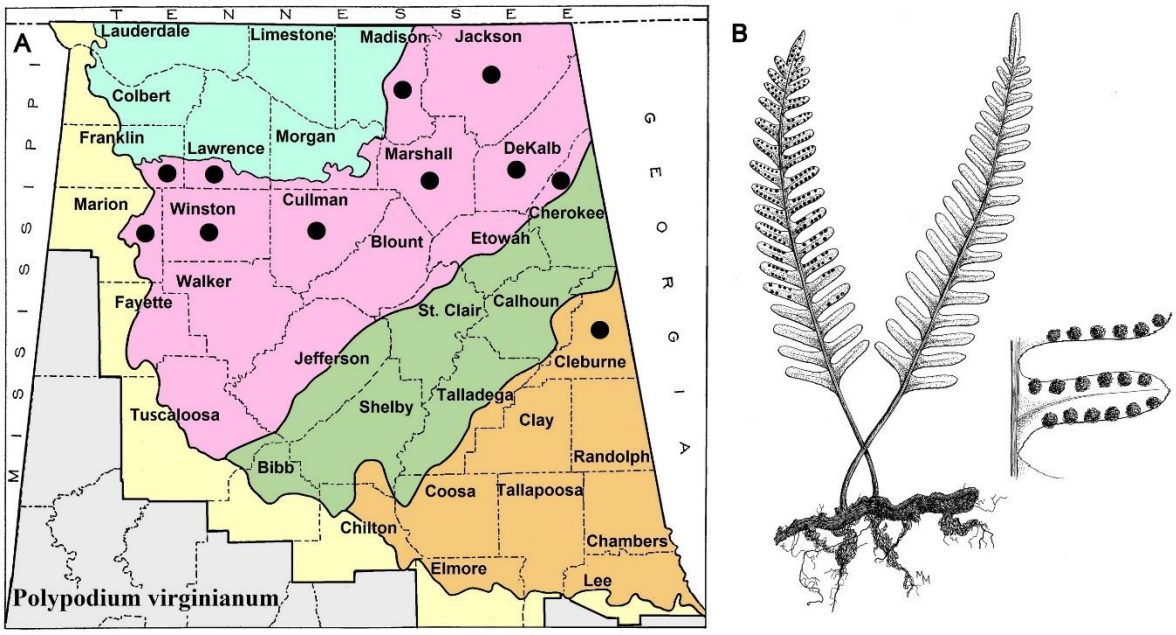


Figure 447. *Polypodium virginianum.* **A.** Distribution map. **B.** Illustration: Marion Montgomery, 1999.

Later research confirmed Manton's hypothesis and clarified the taxonomy of the *P. virginianum* complex. Pteridologists now recognize the three cytotypes as distinct species (Haufler et al. 1993b). Cranfill and Britton (1983) identified the tetraploid *P. virginianum* as the type specimen, and Haufler and Wang (1991) later confirmed it arose through hybridization between *P. appalachianum* Haufler & Windham (Appalachian Polypody) and *P. sibiricum* Sipliv. (Siberian Polypody). Chromosome doubling in the sterile hybrid ancestor enabled regular pairing during meiosis, restoring fertility. Significantly, *P. sibiricum*—a circumpolar species—proved to be the once-unknown progenitor that Manton had anticipated.

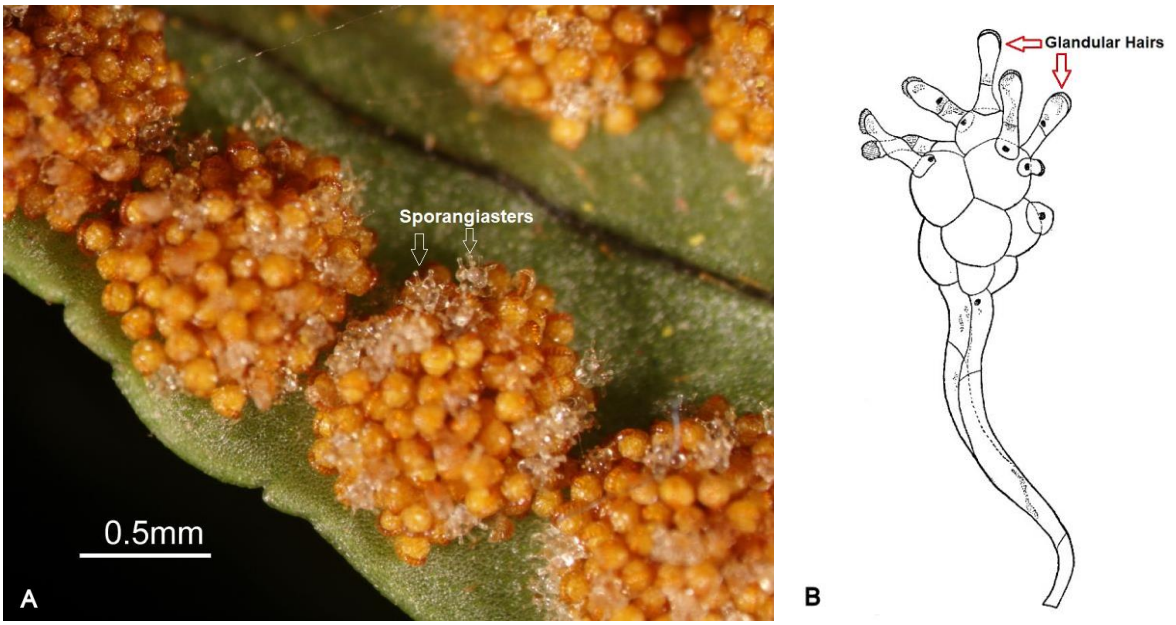


Figure 448. *Polypodium virginianum* sporangiasters. **A.** Sori on the underside of leaf segment composed of sporangia (the orange structures) and sporangiasters (the whitish structures), Westchester Co., New York, 23 Sept 2007. Photo: Robbin Moran. **B.** Illustration of a sporangiaster (Martens 1943).

Polypodium appalachianum and *P. virginianum* differ morphologically in several key traits. The leaf blades of *P. appalachianum* are elongate-triangular, usually widest at or near the base, averaging 5.8 cm wide, with sharply pointed segments (Fig. 449). Its rhizome and petiole scales are uniformly golden brown. In contrast, *P. virginianum* bears oblong to narrowly lanceolate blades, widest near the middle, averaging 4.5 cm wide, with more rounded segment tips. Its scales are bicolored—brown along the margins with a darker central stripe. Another diagnostic feature lies in the number of sporangiasters per sorus: *P. appalachianum* typically has more than 40, while *P. virginianum* has fewer (Fig. 448a). These sporangiasters—specialized, glandular, knob-tipped stalks—are consistently associated with the sporangia in both species (Fig. 448b).

Haufler and Windham (1991) reported the range of *Polypodium appalachianum* (the diploid element of the *P. virginianum* complex) from southeastern Canada southward along the Appalachian Mountains to Georgia and Alabama. However, we have excluded this species from our flora due to a lack of verified specimens. The senior author examined a collection annotated as *P. appalachianum* from Pisgah Gorge in Jackson County (*Kral 40803*, 28 Aug 1970) but determined it to be *P. virginianum*. Unverified online herbarium records list *P. appalachianum* from Franklin (US, *Harper 3402*, 17 June 1935), Lawrence (UT, *Schell s.n.*, 10 June 1983), and Winston (US, *Mohr s.n.*, 20 July 1887) counties in the Bankhead National Forest, all of which require confirmation.

Figure 449. *Polypodium appalachianum*, Polk Co., Tennessee, 9 Apr 2023. Photos: Nate Parrish.

The species within the *Polypodium vulgare* complex have long played a significant role in traditional medicine. Herbalists brewed potent teas from the rhizomes, which served as effective purgatives for expelling worms. The tea acted as a tonic, laxative, and expectorant in milder concentrations. Practitioners also recommended the fern as a remedy for various ailments, including coughs, hoarseness, consumption, loss of appetite, fever, and jaundice (Dunbar 1989). Indigenous peoples of North America used the ferns in their healing practices. They prepared a decoction of the rhizome to ease stomach pain, chewed the "root" to soothe sore throats, and made poultices to treat swellings, cuts, and wounds (Moerman 1998). Beyond its medicinal uses, manufacturers burned the plant to produce potash-rich ashes, an essential ingredient in glassmaking (Abbe 1981).

Figure 450. *Polypodium virginianum*, Lawrence Co., Alabama, 12 Sep 2022. Photo: Kevin England.

The Resurrection Fern (*Pleopeltis michauxiana*) closely resembles the Rock Polypody (*Polypodium virginianum*) but differs in several diagnostic characters. *Pleopeltis michauxiana* bears gray-green leaves with entire (untoothed) lobe margins and lower surfaces densely covered in scurfy, dark-centered scales. In contrast, *Polypodium virginianum* has green leaves with toothed lobe margins near the tip, and its blade undersurface lacks scales (Fig. 450). The rhizomes also differ: those of *Pleopeltis* are slender, only 1–2 mm in diameter, while those of *Polypodium* are more robust, 3–6 mm thick. Among these features, the presence or absence of scales on the blade undersurface provides the most reliable distinction between the two species.

PHYSIOGRAPHY AND PHYTOGEOGRAPHY OF ALABAMA

Alabama's landscapes are strikingly diverse, influenced by geology, climate, and geography—all of which determine the distribution of plants, including ferns and lycophytes. Many species are restricted to specific rock types or soils, or persist only under narrow combinations of light, moisture, and temperature. Some flourish in shaded ravines with constant seepage, while others cling to exposed cliffs or thin calcareous soils over bedrock. These close dependencies underscore the importance of phytogeography—how geology and climate shape patterns of biodiversity—and physiography—the landforms that constitute the physical foundation for plant geography.

Spanning nearly five degrees of latitude, from the Gulf of Mexico to the Tennessee border, Alabama lies in a transitional zone where the Appalachian plateaus and mountains reach their southern limits before dipping beneath the softer sediments of the Coastal Plain. This meeting of ancient uplands and comparatively young deposits creates sharp contrasts in terrain, soil, and hydrology, producing a remarkable range of environments within a relatively small geographic area. As a result, Alabama supports exceptional habitat diversity and notable botanical richness.

The state's complex geology shapes its floristic variety. Rock formations differ widely in age, composition, acidity, alkalinity, and resistance to erosion, generating many soil types. Over geologic time, uplift, folding, and erosion carved Alabama into a mosaic of ridges, valleys, and plains. Rugged topography provides microhabitats that shelter relict or narrowly adapted plant taxa. Because geology and landform exert such a substantial influence, vegetation follows distinct regional patterns, and scientists have developed multiple classification systems.

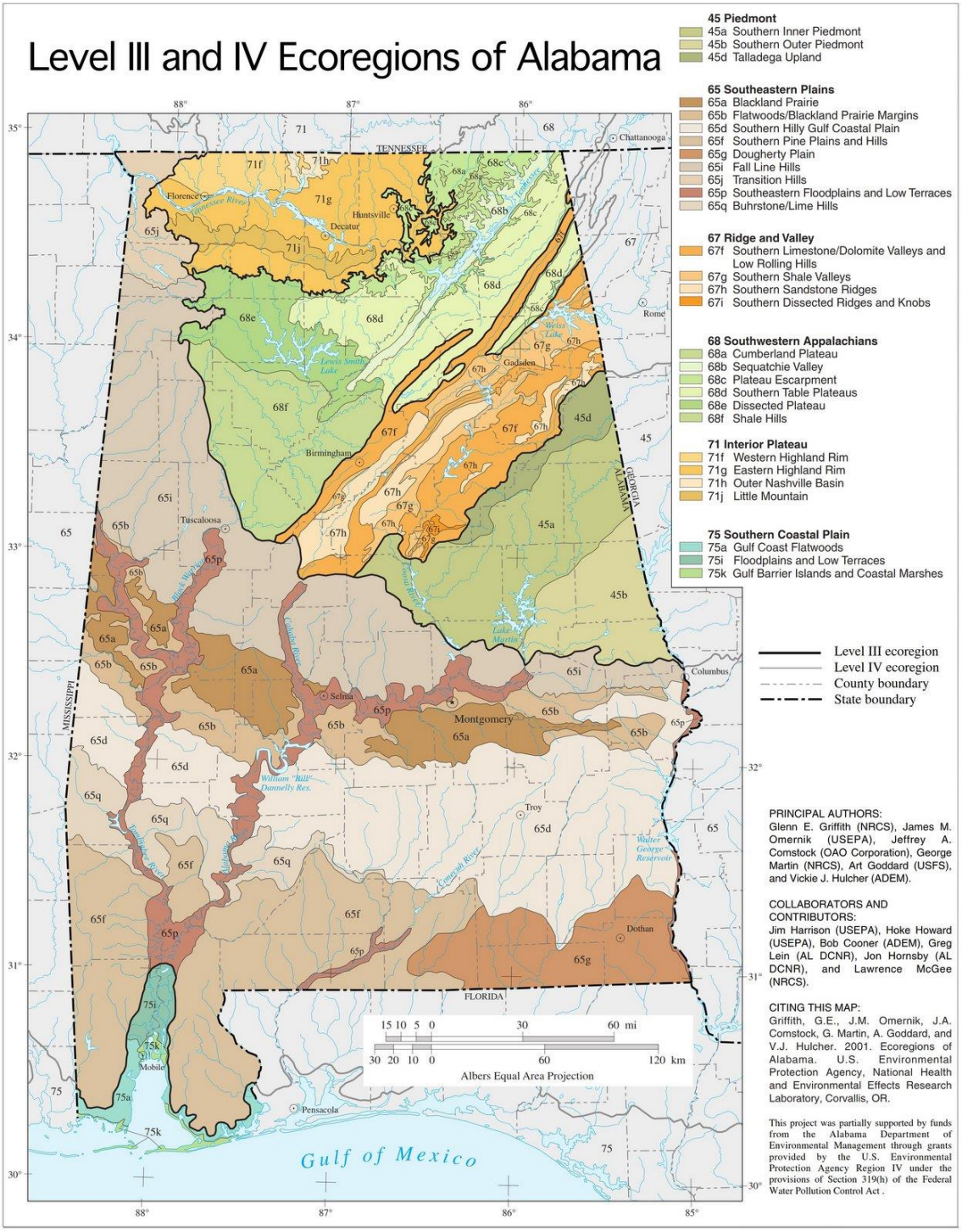


Figure 451. Map of Level III and IV ecoregions of Alabama (Griffith et al. 2001).

One widely applied framework is the U.S. Environmental Protection Agency's hierarchical ecoregion system (Griffith et al. 2001), which organizes landscapes into four nested levels reflecting differences in geology, soils, climate, vegetation, and hydrology. At the broadest scale, Level I delineates continental biomes such as the Eastern Temperate Forests, Great Plains, and North American Deserts. Level II further subdivides these into regional units, while Level III identifies ecoregions at the state or multi-state scale, which conservationists and resource managers find especially useful. Level IV provides the most detailed classification, distinguishing ecologically uniform areas that capture fine-scale habitat variation. Alabama contains six Level III ecoregions—Interior Plateau, Southwestern Appalachians, Ridge and Valley, Piedmont, Southeastern Plains, and Southern Coastal Plain—and ecologists classify these into 30 Level IV units (Fig. 451).

Geologists have traditionally divided Alabama into five physiographic regions (Fig. 12): the Highland Rim, Cumberland Plateau, Ridge and Valley, Piedmont, and Coastal Plain, further subdivided into 28 districts (Butts 1926; Fenneman 1938; Johnson 1930). However, biological writers such as Robert Mount (1975) and John Short (1978) emphasized that, in terms of plant and animal distributions, the state's highest ridges resemble the Blue Ridge more than the Piedmont or Ridge and Valley. Building on this perspective, Short and Spaulding (2012) argued that these ridges are not a disjunct fragment of the Blue Ridge Province but instead form a distinct physiographic unit, the Appalachian Ridges. This region encompasses the Talladega–Horseblock–Rattlesnake Mountains, crowned by Mt. Cheaha (734 m / 2,407 ft), and the Weisner Ridges, which extend into the Ridge and Valley and include Dugger Mountain (652 m / 2,140 ft), Alabama's second-highest peak. Both are underlain by quartzite, a metamorphic sandstone whose hardness and resistance to weathering account for their prominent elevations. Collectively, they stand apart geologically and floristically from the surrounding highlands.

From north to south, Alabama's upland provinces rest upon resistant Paleozoic rock deposited more than 250 million years ago. In contrast, younger, more erodible sediments form the Coastal Plain, the oldest dating to the Late Cretaceous, less than 100 million years ago. These deposits become progressively younger and less consolidated toward the Gulf, where they remain loose and unconsolidated at the shoreline. The 'hard-rock' provinces thus stand in marked contrast to the softer, weakly lithified strata of the Coastal Plain.

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Special thanks go to Alan Cressler (Fig. 452) for generously contributing his remarkable photographs, which have greatly enhanced the impact of this publication. His extraordinary ability to capture the beauty and intricacy of ferns has brought these plants to life for both scientific audiences and the general public. Beyond his photography, Alan's keen field observations have led to the first documented occurrences of several fern species in Alabama—contributions that have significantly expanded our knowledge of the state's flora. His dedication to exploration and documentation is deeply appreciated.

Figure 452. Alan Cressler on a hillside of trout-lilies, 5 May 2018. On a long day trip to the Blue Ridge Parkway in western North Carolina with good friends Jim Fowler and Steve Bowling. Photo: Jim Fowler.

We gratefully acknowledge our esteemed coauthor, John W. "Jack" Short (Fig. 453). Since the 1970s, John's unwavering dedication and tireless efforts have significantly advanced the understanding of Alabama's fern flora (Short 1978). His unparalleled field expertise, meticulous documentation, and steadfast commitment to botanical exploration have enriched the region's scientific record and set a high standard for future research. His work has been instrumental in building a comprehensive foundation for studying ferns in Alabama, providing inspiration and guidance for generations of botanists, ecologists, and naturalists.

Figure 453. John "Jack" Short collecting *Dendrolycopodium obscurum* near Flat Rock, Jackson Co, Alabama, 7 Sept 2001. On a field excursion with Dan Spaulding to see the rare ferns at Guess Creek Cave.

Figure 454. Jacksonville State University Herbarium, 9 April 1997. Photo 1: Warren "Herb" Wagner, Florence Wagner, Dan Spaulding, and Hayes Jackson. Photo 2: David Whetstone and Herb Wagner.

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Figure 455F Photo 1: Mark Ballard and Dan Spaulding, Upson Co., Georgia, 10 Oct 1992. Photo 2: John MacDonald, Dan Spaulding, and Bob Kral, flora checklist meeting, University of Alabama, 3 January 2002.

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