Tipularia

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Membership

The Georgia Botanical Society is open to all persons interested in the botany of Georgia. Annual dues: student, $10 (electronic newsletter only); individual, $25 (electronic), $35 (printed newsletter); family/group, $30 (electronic), $40 (printed newsletter). Send address and check payable to Georgia Botanical Society to JoAnne Romfh (115 Farmdale, Roswell, GA 30075). You can join online at http://www.gabotsoc.org/?page_id=7423. Members receive *Tipularia* without extra charge. Persons wishing only to receive the magazine may become *Tipularia* associates for $10 per year. Single copies, when available, may be ordered from Richard Ware (2 Idlewood Court NW, Rome, Georgia 30165–1210), (1991 and before, $6; 1992 and after, $10).

Editorial information

Tipularia strives to combine the scientific authority of a botanical journal with the readability of a magazine. Some articles are assigned; unsolicited manuscripts are welcomed for consideration. *Tipularia* is unable to pay for articles or art, but there is no charge for publication of them.

Cover

Asclepias purpurascens (Purple Milkweed) by Richard & Teresa Ware


photo by Jim Drake

In Memorium

Thomas S. Patrick

December 5, 1944–August 22, 2019

Those of us in the botanical/conservation community considered Tom Patrick, a state and regional treasure! His knowledge of the plants of Georgia (especially *Trilliums*) was unmatched, especially the rare plants and their habitats and locations. Tom was the contact person at the Georgia Deptartment of Natural Resources (DNR) for any information about Georgia plants and his name was known far and wide. He was the agency's first botanist, joining in 1986 what was then the Georgia Natural Heritage Inventory Program, an initiative of DNR and The Nature Conservancy. Since coming to Georgia, Tom and his associates have been responsible for the discovery and preservation of many rare plants and their habitats.

In addition to all these accomplishments, in my opinion, Tom was the most friendly, easy going, individual that I've been blessed to know. I never heard him speak ill of anyone and he seemingly had the patience of Job. Of course, he was only human and had his idiosyncrasies, that, in this case, is explained by a genius intellect.

Tom was our premiere field trip leader (and past president) for the Georgia Botanical Society since he moved to Georgia. Because of his vast knowledge, he was able to lead field trips to botanically rich locations all over the state, a delightful and superb learning experience for all participants. He was always so willing to share his knowledge and enthusiasm for botany with others. He was a mentor to me and I had the pleasure of attending many field trips led by Tom. I was lucky enough to work with, and for, him on several projects down through the years.

He was a charter member of the Tennessee Native Plant Society. Tom published numerous papers on *Trilliums* and authored studies of many other rare and endangered plant and animal habitats as well as *Protected Plants of Georgia*, a botanical standard. He worked with DNR staff and volunteers in plant rescues and plant protection. Tom worked extensively with volunteers in the Georgia Native Plant Society, Georgia Botanical Society, Great Smoky Mountain Wildflower Pilgrimage, Georgia State Parks and Historic Sites, Association of Southeastern Biologists, the Nature Conservancy, Georgia Plant Conservation Alliance, and others. Recently the Georgia Plant Conservation Alliance presented its first lifetime achievement award to Tom—an award named after him.

It goes without saying that Tom will be sorely missed by everyone who knew him or worked with him on any type of project. Perhaps the void that he left in the botanical world will eventually be filled by others.

Richard Ware

Trillium grandiflorum (Large-flowered Trillium)

Trilliums of Georgia

Reprinted from *Tipularia*, Vol. 22, 2007

Tom Patrick

Introduction

One of the most characteristic wildflowers of the deciduous forests of the southeastern United States is the trillium. In fact, Georgia has more kinds of trillium than anywhere else in the world. Current distribution patterns suggest that Grassy Mountain in Murray County, where the Blue Ridge Mountains meet the Great Valley, is the hot spot for the genus. Nine species occur on Grassy Mountain, if one includes the lower eastern slope around Lake Conasauga. In the richest coves, it is possible to find six species in the same habitat. There is also an abundance of variation within species, such as that expressed in what most consider one of the "most stable" of all trilliums, namely, the Painted Trillium (*Trillium undulatum*). Here, Painted Trilliums, found beneath mountain laurel and rhododendrons, and shoved to their southern limit during the last glacial advance 12,000 years ago, vary tremendously in coloration of the petals—some flowers are pure white, some pink, some with red veins, some with typical red blazes.

A second region of high diversity for trilliums is the Coastal Plain, especially along the Fall Line and in the ravines that drain into the Chattahoochee River to the Florida line where it joins with the Flint River to form the Apalachicola River. Several of the sessile-flowered trilliums, especially those that resemble Relict Trillium (*T. reliquum*) are most abundant in the southwest and west central Georgia area.

In Georgia, trilliums are common in the mountains, Piedmont and upper Coastal Plain. There is a huge gap in trillium distribution as one enters the longleaf pine-wiregrass and flatwoods vegetation of the outer Coastal Plain. The prevalent lightning fire history, agriculture and forestry practice (including use of prescribed fire), free-ranging livestock, and conversion of hardwoods to pine plantations, all influence present day distributions and likely eliminated trilliums even where deciduous forests still linger along major streams.

Narrowly endemic trilliums restricted to a single gorge or river drainage occur in northeast Georgia and the adjacent Carolinas. Thus, the story continues, with possible additional species yet to be described and several taxonomic issues yet to be resolved.

It is the purpose of this account to illustrate and briefly distinguish the twenty-two species of trillium documented at the present time from Georgia.

Trillium Morphology

Recognition of trillium as a distinctive group of wildflowers is a simple matter. From the growing tip of an underground horizontal stem or rhizome, a stem emerges with three leaves in a single whorl. Each leaf is identical in shape and the whorl itself is symmetrical. Only one other common wildflower genus, *Arisaema* or Jack-in-the-pulpit, has such a simple stem with a single whorl of three leaves, but its leaves and the arrangement of the whorl are asymmetrical. Trillium leaves have 3–7 parallel main veins and an irregular network of connecting smaller veins in between, creating a netted venation not often found in monocots (Figure 1).

Each stem bears but one showy, terminal flower with its parts in threes. From outside to inside the flower, first are three green sepals, then three colorful petals, six large stamens, and an ovary with three prominent stigmatic lobes.

Fig. 1. Leaf with netted venation.

Fig. 2. Stamen with pronounced beak.

The petals sometimes turn from white to pink; they wither into dark stringy remnants as they age. The stamens are important features of the trillium flower. Each stamen consists of a filament (stalk) holding up an anther (two pollen sacs on either side of a band of sterile tissue (the connective). The anther is basifixed, joined directly at the base to the filament. Sometimes the connective tissue extends beyond the pollen sacs in the form of a tiny rounded glob or a more pronounced pointed or beak-like projection, as shown in Figure 2.

The stages in the life cycle of a trillium are given in Figure 3. Although the germination time for seeds and the number of years from seed to flowering is variable, in general, seeds take one to two years to produce a mature cotyledon (seed leaf). Plants are usually five to seven years old before they flower. Curiously, trilliums of the Coastal Plain take less time to mature than trilliums found in the Appalachian Mountains. An individual can live hundreds of years, since the underground rhizome continues to produce shoots from one end, while the oldest end disintegrates. When monitoring trilliums from year to year and tracking individuals, a flowering individual may revert to a sterile phase (three leaves, no flower} or juvenile phase (one leaf). Usually such reversions are due to deer browsing, prescribed burning too late into the growing season, or unfavorable rainfall.

Evolution of Trilliums

Trilliums belong to a very old plant family not any closer to true lilies than hyacinths, greenbriers, bunchflowers, hellebores, autumn crocuses, or yuccas. Chromosomes, pollen, seeds, leaf venation, distinct sepals and petals, persistent petals, anther attachment, unique chemistry (alkaloids, anthocyanins, flavonoids with multiple sugars) and its north temperate worldwide distribution help distinguish the Trillium Family. Although no fossils exist because trillium pollen is thin-coated, students of evolution surmise that trilliums once were part of the Arcto-Tertiary flora when a continuous and similar vegetation existed from Southeast Asia across the Bering Strait into North America. Today, trilliums and their closest relatives are mostly found in the western and eastern United States, and in Southeast Asia (Kamchatka Peninsula, Japan, Korea, and southeast China to the Himalayan Mountains).

Scientists are just beginning to reconstruct plant movements over time through molecular genetics and have found migration routes from un-glaciated regions of North America back into glaciated regions since the last Ice Age. Trilliums differentiated in varying directions on either side of the ancient Appalachians and in several pockets much further southward along the major rivers of the South, such as the Chattahoochee and the Savannah, on the Coastal Plain, as well as in the mountains.

Trilliums were first placed in their own family, Trilliaceae, in 1845 by John Lindley using purely morphological characteristics. This trend was brought to perfection in the early 1900s by John K. Small, who also recognized Trilliaceae, but correctly eliminated Indian Cucum-

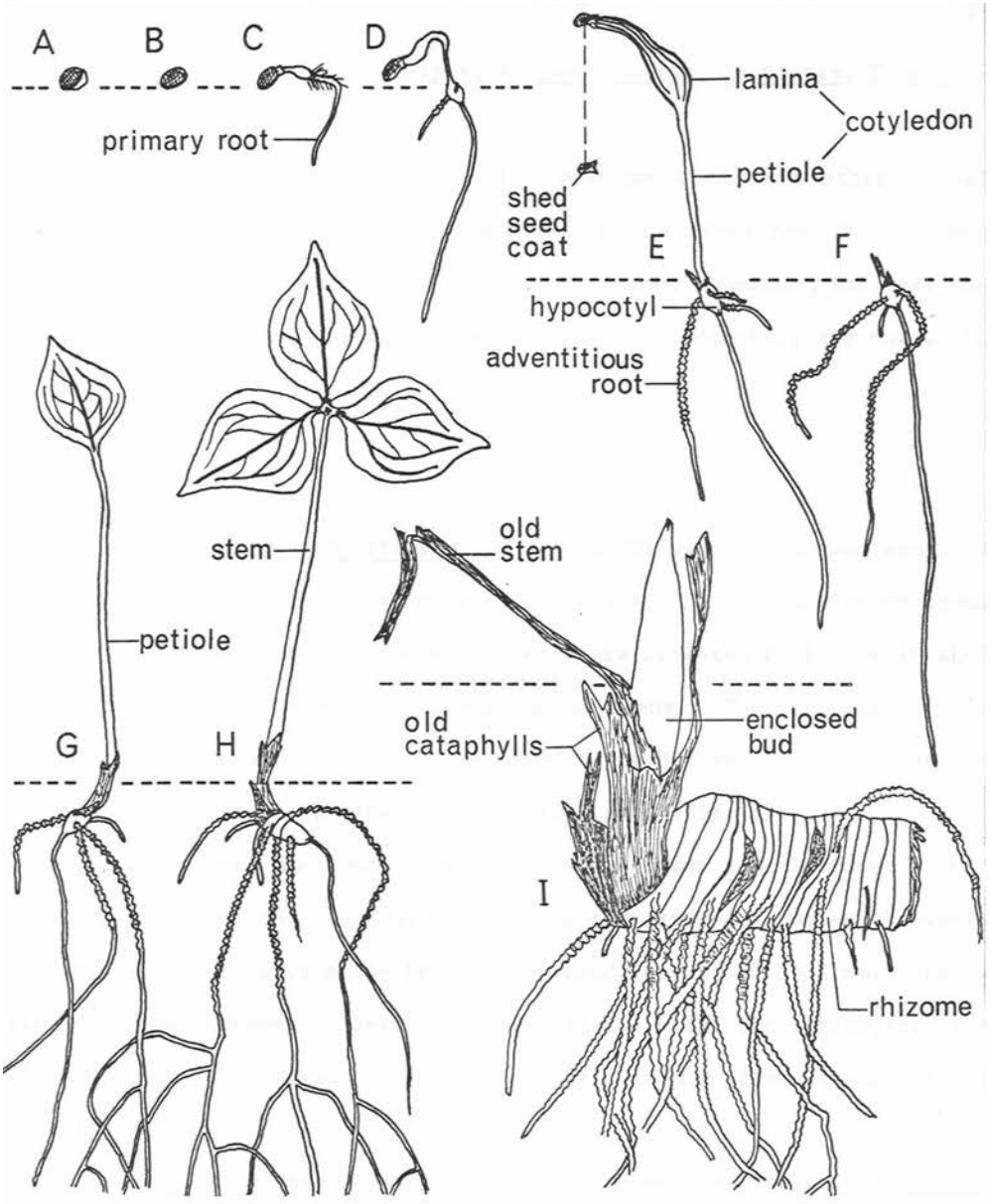

Fig. 3. Life Cycle of *Trillium grandiflorum*. A. Seed with appendage shed in midsummer. B. Seed during first winter. C. Germination the first spring. D. Seedling the second winter. E. Maturing cotyledon the second spring. F. Dormant plant the third winter. G. Single-leaved plant the third spring. H. Three-leaved plant the sixth spring. I. Dormant mature plant at about twenty-two years. Note two old stem scars on the rhizome above the mass of adventitious roots. Note old cataphylls—protective bracts that surround buds and leave circular scars on the rhizome.

ber-root, *Medeola virginiana*, from the family. Molecular evidence places trilliums closer to fly poison, bunchflower and death camus, in Melanthiaceae, than to true lilies of Liliaceae. However, to unite Trilliaceae (Trillium Family) with Melanthiaceae (Fly Poison Family) makes no practical sense. The reasons I prefer to keep trilliums in their own family include a suite of characters that when taken together easily define most of the species. The more important characters of the Trilliaceae include: distinct sepals and petals (not similar tepals); presence of plump seeds with appendages; lack of specialized nectaries (although painted trilliums have nectar guide designs); huge chromosomes based on the number five (mostly seven and smaller in fly poison types); globose pollen (others have ellipsoid pollen); fleshy capsular fruits (berry-like in painted trillium); mature plant with one set of whorled leaves; a singular flower with persistent sepals and ephemeral petals (tepals turn green in fly poison types and remain around the dry capsules that produce winged flattened seeds); presence of haustorial cotyledons.

Some Life History Attributes

The seeds of trillium are known to be dispersed by a variety of animals. Ants are the primary seed carriers. Some smaller ants feed on the fruits and fleshy appendages of the seeds, but several larger species actually carry them to nests, eat the fleshy appendage and discard the seed nearby. Yellow jackets, and other vespid wasps, are also attracted to the fruits and seeds. Wasps and ants disperse trillium seeds short distances (perhaps a few meters at best). The bright red berry of the painted trillium may be carried by birds, but this is speculation. Other dispersal agents include mammals, such as white-tailed deer and woodchucks, observed to eat fruits. Studies of deer indicate that they can effectively distribute seed of Large-flowered White Trillium (*Trillium grandiflorum*) up to three kilometers.

Seeds germinate variably and may remain dormant in a seed bank for many years if desiccated. In germination tests and in garden settings, freshly collected seeds germinate after at least ninety days of after-ripening under moist, light or dark, conditions. They germinate in nature the following spring. In Florida, this may be in December or January and in the Georgia mountains during April and early May. The primary root soon produces a tiny corm-like structure where starch is stored. The spatula-shaped single cotyledon remains suctorial with its apex embedded within the seed coat, sometimes for an entire year. Then, sometimes after another year, sometimes sooner, the cotyledon breaks from the seed coat and matures into a green spatula-shaped seed leaf in early spring. One year later, the first true leaf appears; perhaps six or seven years later, a flowering shoot is produced. All this time, secondary roots appear from the expanding corm-like structure, now properly termed a rhizome with adventitious roots. The cortex of these roots shrivels at the base, pulling the rhizome underground. Without the litter layer of the deciduous forest and accumulated other organic debris, this lengthy establishment phase would be impossible.

Stephanie Solt has made a career out of studying trillium seed germination for commercial propagation purposes. (see Solt, 2002, for pictures of fruits and seeds and further discussion).

Classification Highlights

There are twenty-two species within the state, depending upon the ultimate disposition of two newly discovered types under study. One state record trillium referred to in this document is the Louisiana Trillium (*T. ludovicianum*) [Synonym: *Trillium freemanii* in prep. (Lookout Mountain Trillium)] from Lookout Mountain in northwesternmost Georgia. Additional comments on its taxonomy are given below.

A second, more difficult, entity can be called the Amicalola Trillium. Unlike the Louisiana Trillium, this has no formal scientific name. After over five years of observation, I conclude that this entity is a rare, discontinuous, assemblage of individuals closely resembling a progenitor-like ancient species that features many primitive characters found in the *Trillium*

erectum complex. Discussed below in the classification section, this complex of species centers on trilliums like Vasey's, Sweet White, Bent Trillium, Southern Red Trillium and Southern Nodding Trillium. These trilliums have coarse-textured petals with indented, netted venation. Their petals tend to recurve or arch outward especially near the apex. They all have occasional albino forms in which the pistil (at least the ovary) is essentially white, the pollen light yellow or creamy, the stamens otherwise white and white petals often with greenish veined pattern beneath. The ability of the flower stalk to change position from horizontal to erect or from nodding to horizontal when in fruit is particularly prominent in the Amicalola trillium that resembles an "albino primitive stock" for the *Trillium erectum* complex. This entity is predominantly a white-flowered species resembling an erect-flowered Vasey's trillium with a pungent, somewhat obnoxious fragrance, paler and larger ovaries, and flowers that are held nodding below the leaves, horizontally in the plane of the leaves, or above the leaves. This entity has tentatively been called the "Amicalola" Trillium found in the Piedmont foothills into the southernmost Blue Ridge Mountains of Georgia and, possibly, extreme western South Carolina. It appears that the tendency for nodding flowers in some populations has disguised this entity, or indicates its close affinity with *Trillium vaseyi*. On the other hand—malodorous fragrance, mostly dark pinkish to whitish ovary sometimes flask-shaped, long, sometimes creamy stamens resemble *Trillium flexipes*.

Within the past half-century, many discoveries have been made within Georgia. For instance, the Dwarf Trillium (*T. pusillum*) [Synonym: *Trillium georgianum* (Georgia Dwarf Trillium)] was found for the first time in 1996. While looking for wetland mitigation sites, Brian Dickman, an environmental consultant, located dwarf trillium in a ditched swamp in Whitfield County. Trailing Trillium (*T. decumbens*) is normally found in northwest Georgia and in isolated colonies in and near the western front of the Blue Ridge, where it is found along the Conasauga and Coosawattee rivers and in the marble valleys around Tate. However, it has now been found at a Piedmont locality in Greene County and a Coastal Plain site in Houston County [recently described as a new species: *Trillium delicatum* (Ocmulgee Trillium)]. Once described as the "rarest of trilliums" by John D. Freeman, the leading trillium taxonomist until his untimely death in 1998, Relict Trillium (*T. reliquum*) continues to be found in new areas. Known from only four Georgia counties when described in 1975, relict trillium is now documented from thirteen counties and over forty sites.

Identification of Georgia's Trilliums

To identify the Georgia trilliums, first consider the two subgenera. Subgenus *Trillium* contains the wakerobins. The flowers have stalks and the leaves are solid green or blue-green. Subgenus *Phyllantherum* Rafinesque includes the toadshades. The flowers are sessile or without stalks; the leaves are mottled in different shades of green.

The Wakerobins

This includes the only trilliums found from eastern New York into New England and Canada. John Burroughs, a naturalist and contemporary of John Muir, resided in the Catskill Mountains and wrote of the red trillium found there and called them "wakerobins." This colloquialism, I believe, corresponded to the contemporaneous blooming time of red trillium with the return of the eastern robin from the South to this area. I limit the use of Wakerobin to this group of trilliums and call the sessile-flowered trilliums "toadshades."

There are three species groups within subgenus *Trillium*. This classification is a practical one, not based on molecular breakthroughs or formal names. The following remarks are written to apply to Georgia's trilliums. Lumping into groups does not infer that members of the group are closely related unless the species group is called a complex. It means only that they resemble each other, or stand alone as

Trillium erectum (Red Trillium) Alan Heilman

Trillium flexipes (Bent Trillium) Richard & Teresa Ware

distinctive on morphological grounds. Within each group, species will key out closely using easily observed field characters. Two characters, petal color and floral fragrance, tend to be too variable in some species and must be used with caution. Floral fragrance is best detected during early evening hours on a warm, sunny day when flowers are fresh or in anthesis (pollen sacs shedding pollen).

There are twelve wakerobins in Georgia informally placed in three groups as follows: Group 1: The Erectum Complex (seven species), Group 2: Species with white flowers that turn pink; pollen yellowish (four species), and Group 3: Painted Trillium; pollen whitish lavender (one species).

Group 1. The Erectum Complex

The Erectum Complex is a group of closely related problematic trilliums apparently still developing. These trilliums have coarse-textured petals that are not wavy-margined, do not change colors following pollination, and show prominent netted veins. The petals spread without overlapping at the base into a tube. The stigmas are thickened toward the base, but do not fuse into a distinct style. The fruit is a fleshy capsule, 6-winged when immature but obscurely winged when plump. Capsule color ranges from shiny black to dull purplish red.

1. *Trillium erectum* Linnaeus, Red Trillium, Stinking Benjamin, Stinking Willie, Wakerobin. Best characters: leaves rhomboid; cup and saucer flower profile with sepals and petals (the "saucer") widely spreading from base at right angles to flower stalk, the stamens and ovary ("the cup") totally exposed; stamens about as long as the ovary; ovary globose, mostly purplish black to black. Uncommon and restricted to higher elevations (above 3,500 ft.) of the Blue Ridge Mountains. Known for petal color variations from maroon to white, pale green, bronze, or yellow. Material from Southern Appalachians is somewhat smaller than northern specimens, has more spreading petals, produces shiny black fruit, and has more petal color variation. The floral fragrance is strongly fishy, similar to that of Florida Anise (*Illicium floridanum*) blossoms; sometimes described as like a "wet dog." Named by Carolus Linnaeus in 1753, based on specimens from the Catskill Mountains of New York, as well as every other trillium with stalked, erect flowers observed at that time.

2. *Trillium flexipes* Rafinesque, White Trillium, Bentstalk Trillium. Best characters: filaments shorter than creamy anthers; ovary prominent, flask-shaped, white to pink with prominent stigmas. Extremely local and rare on slopes of Cumberland Plateau in limestone areas. Appears to be west of the Appalachians in the Southeast. The orientation of the flower and fruit, always "flexed" or "bent" away from the vertical, is variable, sometimes changing during the growing season. Flowers emit a musky, unpleasant odor. Named by Constantine Rafinesque in 1840 as interpreted by Merritt Lyndon Fernald, based on material from the Cumber-

Trillium rugelii (Southern Nodding Trillium)
Hugh & Carol Nourse

Trillium simile (Sweet White Trillium) Tom Patrick

land Mountains (Wasioto Mountains) of Kentucky.

3. *Trillium rugelii* Rendle, Southern Nodding Trillium. Best characters: stamens longer than ovary; stamens bicolored with burgundy anthers and white filaments; petals strongly recurved from the base; ovary mostly white to pink. Most abundant in the Atlanta area, widely scattered northward along large streams and rivers, mostly on lower slopes and in or near floodplains. One peculiar population along Panther Creek, Stephens County bears mostly erect flowers and displays variable stamen and ovary colors. Rare, maroon-flowered forms are spectacular. For years thought to be synonymous with Northern Nodding Trillium (*Trillium cernuum*), a lanky species found in black ash-red maple bogs of northern Virginia northward and with shorter, less colorful anthers. Floral fragrance weakly like freshly caught fish or absent. Named by Alfred Rendle in 1908, based on a collection with red splotches on lower inside of the petals from Bat Cave, North Carolina by Ferdinand Rugel.

4. *Trillium simile* Gleason, Sweet White Trillium, Jeweled Trillium. Best characters: leaves broadly elliptic, sometimes overlapping; sepals and petals gradually spreading, flowers with a cup-shaped profile; petals broad enough to overlap near base; stamens much longer than ovary; ovary black to purplish black. Uncommon and found at moderate elevations (2,500 to 3,800 ft.) of the Blue Ridge Mountains, especially in the Cohutta and Southern Nantahala Wilderness Areas. This entity is highly variable in size, but is generally white-flowered and has a faint, green apple floral fragrance. Its taxonomy is confusing due to the abundance of white-flowered forms of *T. erectum*, the occasional erect-flowered individuals of *T. rugelii* and the newly defined entity referred to as "Amicalola Trillium." Named by Henry Alan Gleason in 1908, based on material from the vicinity of Pearson Falls, Tryon, North Carolina. Thought

Trillium sulcatum (Southern Red Trillium)
Hugh & Carol Nourse

Trillium vaseyi (Vasey's Trillium) Hugh & Carol Nourse

to resemble Vasey's trillium when first described because of its robust stature, long stamens, broad petals and, some thought mistakenly, nodding flowers.

5. *Trillium sulcatum* Patrick, Southern Red Trillium, Barksdale's Trillium, Rainbow Trillium. Best characters: flowers on long stalks that are more than twice as long as sepals; flower gaping in profile like a candle snuffer; petals ovate, gradually spreading, concealing the ovary from side-view; stamens longer than ovary. Rare on sandstone slopes of the Cumberland Plateau, also isolated on western face of Rich Mountain, Gilmer County. Sepals often with a tint of purple and shaped like canoes with a keel. Flowers emit a weak, fungal odor. I named this species in 1984 based on specimens from Layne Cove, Grundy County, Tennessee. Lane Barksdale was the first to recognize the entity as new to science in a 1938 monograph based on a specimen from Roaring Gap, Surry County, North Carolina. Despite his astute earlier work, recognition of Barksdale's Trillium was problematical because he failed to publish the required Latin diagnosis (a precise statement on its unique characters written in Latin) and was unaware of the mother load occurrence of the species west of the Blue Ridge Mountains.

6. *Trillium vaseyi* Harbison, Vasey's Trillium. Best Characters: long exerted stamens; nodding flowers; broadly ovate petals; funereal (like a room full of deep red roses) fragrance. Possibly extirpated on the Coastal Plain as far south as Cuthbert in Randolph County, extremely rare on the Piedmont of west central Georgia, otherwise only known from the Piedmont Foothills and the Blue Ridge. In the mountains, it prefers rhododendron thickets and hemlock forests. This trillium is last to bloom, has the largest flowers, and the most protruding stamens. Named by Thomas G. Harbison in 1902 based on specimen collected from Toccoa Falls, Stephens County by George Vasey.

7. *Trillium sp*., "Amicalola Trillium." Best characters: blooms late, with or just before Vasey's Trillium; stamens much longer than ovary, both filaments and anthers relatively long; flowers on long stalks either above or below leaves; petals usually white; ovary prominent, sometimes flask-shaped, pinkish white to reddish purple, the stigmas very pronounced and recoiled. Rare and local from Springer Mountain east to Sosebee Cove, southward into the Etowah River watershed, including slopes above the Amicalola River, into the Piedmont Foothills. This is an undescribed entity and resembles *T. vaseyi* in flower shape and tardy bloom time; *T. flexipes* in ovary characters and floral fragrance; and *T. simile* in overlapping, broadly elliptic leaves and stamen characters. This trillium may represent the relictual stock from which these other taxa evolved. It was first shown to me by Henning von Schmeling about 1992. Steve Bowling, Tom Govus, John Kiser, Jim Smith and Doug Walker revealed additional sites to me since that time. The floral

Trillium catesbaei (Catesby's Trillium)
Hugh & Carol Nourse

Trillium grandiflorum (Large-Flowered Trillium)
Richard & Teresa Ware

fragrance is obnoxious and complex, like moldy cheese, sweaty feet and old sneakers combined.

Group 2. Species with White to Pink Flowers that Deepen with Age

These are the "Trumpet Flowers" with petals loosely to tightly overlapping into a tube at base, then flaring outward like the bell of a trumpet. The stigmas are narrow, uniform in width from base to apex, and joined into a short style at the base. The pollen color ranges from pale yellow to deep yellow; the pollen falls to the inside. The petals are white, changing to pink; or sometimes pink from the start turning darker with age. The delicately textured petals have inconspicuous veins and may have wavy margins. The fruit is a fleshy capsule, from obscurely 3-winged to prominently 6-winged when mature. Capsule color ranges from white to greenish white.

8. *Trillium catesbaei* Elliott, Catesby's Trillium, Bashful Wakerobin, Rose Trillium. Best characters: leaves with small stalks, the blades broadest near the middle, the tips pointed with convex sides; flowers below leaves; sepals falcate (strongly arched), often purplish; petals strongly reflexed above the tube; anthers somewhat twisted and curved outward, the pollen deep yellow. The most widespread trillium in Georgia, absent from southeast Georgia but found in most other regions, especially in upland mixed oak-pine forests. Occasionally, flowers bloom above the leaves and entire populations may exhibit considerable variation in this character. Some forms open pink, turning darker as they age. Named by Stephen Elliott in 1812 based, in part, on an elegant drawing made by Mark Catesby.

9. *Trillium grandiflorum* (Michaux) Salisbury, Large-Flowered Trillium, White Trillium, Showy Wakerobin. Best characters: leaves without stalks, the blades broadest below the middle, the tips pointed with convex sides; flowers above leaves; sepals gradually spreading; anthers straight, pale yellow, concealing young ovary. Uncommon, local, restricted to rich coves in the Blue Ridge Mountains. Collected by André Michaux from the mountains of North Carolina in the 1790s and published in 1802.

10. *Trillium persistens* Duncan, Persistent Trillium, Edna's Trillium. Best characters: plants blooming early, as early as late February and peaking by early April; anthers pale yellow, straight, somewhat appressed against the pistil; leaves evenly tapered to a sharp point; flowers weakly trumpet shaped to merely gaping, the petals not stiffly erect at the base and often twisting independently. Mature plants persist above ground until October. Found in Tallulah Gorge, from just below the Tallulah Lake dam downstream sporadically nearly seven miles to Panther Creek, Stephens County. Officially listed as Endangered. The species usually occurs in small colonies without other trilliums, only occasionally growing with *T. catesbaei, T. discolor* or *T. cuneatum.* Named by Wilbur H. Duncan

Trillium persistens (Persistent or Edna's Trillium)
Hugh & Carol Nourse

in 1971, based on earlier Tallulah Gorge observations of vegetative material and the fortuitous discovery of fresh flowers by Edna Garst while exploring Battle Creek, South Carolina with John Garst and George Neece.

11. *Trillium pusillum* Michaux, Dwarf Trillium, Least Trillium [Synonym: *Trillium georgianum* (Georgia Dwarf Trillium)]. Best characters: entire plant less than eight inches high, usually much smaller, with narrow, blunt leaves; sepals with rounded, upturned tips; anthers pale purple between the pollen sacs. Known from only one small swampy forest near Dalton, Whitfield County. The habitat is subject to industrial development, ditching and unscrupulous collecting. The Georgia Plant Conservation Alliance is safeguarding material from the site and hopes eventually to establish new populations in the wild. This is undoubtedly Georgia's rarest trillium and may eventually be described as a distinctive variety due to its narrow leaves and the presence of stomates (appearing as small specks) on the upper surface of the leaves. The Dwarf Trillium was first collected by André Michaux from the Low Country near Charleston, South Carolina in the 1790s and published in 1802.

Group 3. Painted Trillium

This group consists of a single distinctive species. Leaves blue-green, sometimes with a coppery tint, with short leafstalks; petals delicate, wavy-margined, white with red blazes, rarely diffused pink or pure white; fading to brown

Trillium georgianum (Georgia Dwarf Trillium)
Hugh & Carol Nourse

and withering; anthers much smaller than filaments, the pollen falling outward; fruit a smooth, bright red berry. No floral fragrance detected.

12. *Trillium undulatum* Willdenow, Painted Trillium. Best characters: petals delicate, wavy, usually splotched with a red blaze or red triangular pattern on the inside base; leaves coppery green with small petioles. Uncommon, local in the Blue Ridge Mountains where it is found in mountain bogs, in moderate to high elevation chestnut oak-northern red oak forests, and in mountain laurel-rhododendron habitats. Named by Karl Willdenow in 1801 based on a collection from Quebec by Peter Kalm. Both Willdenow and Kalm were students of Linnaeus, but Linnaeus was an extreme "lumper" who regarded all trilliums with erect flowers as *T. erectum*, all trilliums with sessile flowers as *T. sessile*, and ones with nodding flowers as *T. cernuum.*

The Toadshades

These ten species have sessile flowers or flowers without stalks; the leaves are mottled with two

Trillium undulatum (Painted Trillium)
Richard & Teresa Ware

Trillium undulatum in fruit Richard & Teresa Ware

Trillium cuneatum (Sweet Betsy or Toadshade)
Hugh & Carol Nourse

to five shades of green, blue-green and/or silvery green. To assist in identification of Georgia's sessile trilliums or toadshades, three species groups are used in subgenus *Phyllantherum*. These are described below as Group 1: The Cuneatum Complex (three species); Group 2: Species with Narrowly Clawed Petals (three species); and Group 3: Species with Prominent Anther Beaks (four species).

Group 1. The Cuneatum Complex, Species with Gradually Tapered Petals and Stamens without Prominent Beaks

These are trilliums with weakly to strongly spotted or mottled leaves, flowers that are closed in side-view with petals erect and somewhat overlapping concealing inner parts, stamens that end in blunt tips (not pronounced beak-like sterile appendages), and floral fragrances that are pleasant. The petals may have narrow, evenly tapered bases (wedge-shaped or cuneate), but they are not distinctly clawed. The stamens are straight, each appressed between the ovary wings and about as long as the ovary; the ovary is broadest near the base or flask-shaped.

13. *Trillium cuneatum* Rafinesque, Sweet Betsy, Whippoorwill Flower, Purple Toadshade. Best characters: floral fragrance like spicy bananas or papayas; ovary purplish; stamens and ovary about equal in length; petals maroon, yellow, bronze, green, and usually more than one half inch wide**.** Common on the Piedmont and throughout North Georgia. Often called "sessile trillium" not to be confused with *T. sessile* found in Alabama and middle Tennessee and distinguished by anthers with beaks, stamens and ovary half as long as the petals, and floral fragrance putrefied (fetid); whereas in *T. cuneatum* anthers have no beaks, stamens and ovary

Trillium ludovicianum (Louisiana Trillium) [Synonym: *Trillium freemanii* in prep. (Lookout Mountain Trillium)] Hugh & Carol Nourse

are about a third as long as the petals, and floral fragrance is pleasant like bananas or tropical fruit mix. Named by Constantine Rafinesque in 1840 based on material from Kentucky as interpreted by John Freeman.

14. *Trillium ludovicianum* Harbison, Louisiana Trillium [Synonym: *Trillium freemanii* in prep. (Lookout Mountain Trillium)]. Best Characters: ovary purplish; stamens slightly longer than pistil; petals maroon, narrow (less than one-half inch wide); floral fragrance obnoxious, weakly fetid. Newly reported from escarpment of Cumberland Plateau on Lookout Mountain, Northwest Georgia. This species resembles Sweet Betsy (*T. cuneatum*) with an earlier bloom time, more malodorous fragrance, smaller flowers, and more strongly mottled leaves, some with a faint silvery stripe down the middle of the leaf. Although under study as possibly a new species by other researchers, I currently regard Georgia material as consistent with adjacent Tennessee populations that may be contiguous with true *T. ludovicianum* southwestward through Alabama. Plants examined in the field and in gardens are indistinguishable from published accounts of Louisiana Trillium, formerly regarded as endemic to Louisiana and Texas. Further field observations are needed on its distribution between Georgia and Louisiana. First collected in 1900 by Thomas G. Harbison from Rapides Parish, Louisiana and later published by him in 1901,

Trillium luteum (Yellow Trillium) Richard & Teresa Ware

while employed as a botanist at the Biltmore Estate. The photograph was taken in Athens in the garden of Steve Yeatts, who discovred plants on Lookout Mountain.

15. *Trillium luteum* (Muhlenberg) Harbison, Yellow Trillium. Best characters: floral fragrance weakly lemony; leaves sometimes only weakly mottled; ovary greenish white; petals yellow aging to deep yellow. Uncommon in Ridge and Valley, Piedmont Foothills, rare in Blue Ridge Mountains in areas with circumneutral soils over amphibolite or calcareous gneiss. First published as a yellow trillium found in the "Cherokee Country" of eastern Tennessee by the Reverend Henry Muhlenberg in 1810.

Group 2. Species with Narrowly Clawed Petals

These trilliums are distinguished by petals narrowed at the base, a condition known as "clawed petals" where the lower part of the petal is constricted and thicker than the upper portion. When viewed from the side, the flower

Trillium discolor (Pale Yellow Trillium) Les Saucier

Trillium lancifolium (Lanceleaf Trillium)
Richard & Teresa Ware

is open with its inner parts visible between the narrowed bases of the erect petals. This is an adaptation to attract pollinators cued by strong fragrances emitted from the fleshy base of the ovary and the accumulation of pollen found within the flower.

16. *Trillium discolor* Wray ex Hooker, Pale Yellow Trillium. Best characters: fragrance like cloves; petals with claw-like base, incurved toward the apex with a distinctive pointed tip; petal color pale yellow to almost ivory aging to lemon yellow. Found mostly on bluffs and ravines along the Tugaloo River and upper Savannah River. Recently, Doug Walker showed me a disjunct occurrence in the Tennessee River watershed near Patterson Gap, Rabun County. William Hooker described the species as new in 1831 based on specimens sent to Kew Gardens by Dr. Wray, who lived in Augusta. Several stations for this narrowly endemic trillium were inundated by the various Corps of Engineer lakes along the Savannah River north of Augusta.

17. *Trillium lancifolium* Rafinesque, Lanceleaf Trillium. Best characters: skinny, lanky habit, the leaves narrowly elliptic; sepals abruptly spreading to reflexed; petals stiffly erect, extremely narrow, their tips sometimes twisted together; stamens arched over ovary. Infrequent and widely scattered in Georgia, in all regions except the Blue Ridge Mountains and the outer Coastal Plain. Found in Oaky Woods, Houston County of central Georgia, along the Chattahoochee River in extreme southwest Georgia, below Fall Line along the Savannah River; isolated mountain slopes and low woods on the Piedmont, especially in the Tallapoosa and Coosa River watersheds; coves at base of Cumberland Plateau and lower slopes of the Ridge and Valley. Another species first published by Constantine Rafinesque in his 1840 monograph, likely based on collections seen by Rafinesque from Florida and Alabama.

18. *Trillium maculatum* Rafinesque, Spotted Trillium. Best characters: fragrance spicy with cinnamon overtones; petals rich burgundy,

Trillium maculatum (Spotted Trillium)
Hugh & Carol Nourse

Trillium decumbens (Decumbent Trillium)
Hugh & Carol Nourse

rarely pale yellow; anthers broad, flat, with small pollen sacs. The most widespread trillium on the Coastal Plain, except south of Savannah where there are no trilliums, extends into the Piedmont north of Augusta with *T. reliquum* on Savannah River bluffs. West of Macon, however, *Trillium cuneatum* replaces *T. maculatum*, as the common associate of the rarer, relict trillium on the Piedmont. This stately trillium resides in rich ravines with bluffs and lower slopes underlain by limestone, often in association with Needlepalm (*Rhapidophyllum hystrix*). Constantine Rafinesque first named this as a distinct species in 1830 based on the published work of Stephen Elliott, who had placed *T. maculatum* material within a broadly defined *T. sessile*. Rafinesque described several species based on few, if any, original observations and few characters. Most of the names Rafinesque published are ambiguous because his herbarium mostly was destroyed and his descriptions lack details. However, he was an astute observer, an infamous "splitter," and determined to place his name on anything newly discovered whether published first by others or not.

Group 3. Species with Gradually Tapered Petals and Prominent Anther Beaks

This group most closely resembles the mottled-leaved species of *Paris* found in China than any other North American trilliums. They exhibit stamens renowned for their pronounced sterile anther tips that resemble tiny "beaks. " These are prolongations of the connective tissue between the two anthers sacs; the "beaks" are more than 1 mm long and curve slightly inward. Other sessile-flowered trilliums sometimes have remnant "beaks," but these are smaller, less than 1 mm long and often resemble stub-like points. This group tends to have obnoxious floral fragrances and strong mottling in the leaves. A prominent silver stripe is often found down the center of the leaf; at least five shades of green make the leaves attractive.

19. *Trillium decumbens* Harbison, Trailing Trillium, Decumbent Trillium. Best characters: leaves strikingly mottled with large patches of

Trillium decipiens (Deceptive Trillium)
Hugh & Carol Nourse

Trillium reliquum (Relict Trillium)
Hugh & Carol Nourse

silvery green, the leaves often as broad as long, those on mature plants held at ground level; upper stems minutely hairy near top (use lens); anthers opening toward the outside and with extended beaks; petals longer than half the length of the leaves. Colonies rare in the marble region of the Piedmont Foothills and in ravines of the upper Etowah River watershed; locally abundant on limestone terraces and slopes near base of the Cumberland Plateau; amazingly disjunct on Coastal Plain in Oaky Woods, Houston County of central Georgia below Macon, and on the Piedmont along Lake Oconee, Greene County these disjunct populations have now been described as *Trillium delicatum* (Ocmulgee Trillium)]. Floral fragrance fetid. Described in 1902 by Thomas G. Harbison based on a specimen collected by Boynton in 1901 from near Collinsville, DeKalb County, Alabama.

20. *Trillium decipiens* Freeman, Chattahoochee Trillium, Deceptive Trillium. Best characters: leaves with a strong central silver stripe; petals widest above the middle, usually three or four times as long as wide. Found infrequently in rich deciduous forests along the Chattahoochee River south of Columbus. Floral fragrance like old sneakers. Named by John Freeman in 1975 from collections in Early County of plants he thought mimicked *T. underwoodii*, but had wider petals and taller stems.

21. *Trillium reliquum* Freeman, Relict Trillium. Best characters: anthers with extended beaks at least 2 or 3 mm long; petals narrowly elliptic, much shorter than half the leaf length; mature plants with leaves at ground level; stems S-shaped, smooth; leaves ovate to orbicular with central silver stripe. Infrequent on the Piedmont north of Augusta along the Savannah River, north of Macon on the Ocmulgee River, along the Flint River south and west of Thomaston, and the Chattahoochee and its tributaries north of Columbus to Mulberry Creek; on the Coastal Plain sporadically from west of Dublin, Laurens County to Macon, in

Trillium underwoodii (Underwood's Trillium)
Jim Drake

Bibb County; south along the Flint River to Montezuma, south along the Chattahoochee to Ft. Gaines and Blakely, Early County. Named by John Freeman in 1975, based on his collection from the Savanna River bluffs, north of Augusta, Columbia County in 1968. One of the earliest collections was also from this area by Albert Cuthbert in the 1890s.

22. *Trillium underwoodii* Small, Underwood's Trillium. Best characters: anthers with minute beaks; petals narrowly elliptic to elliptic; fragrance like moldy old cheese; leaves with strong central silver stripe, somewhat drooping, nearly touching ground when first coming into flower; leaves much longer than broad with a long, evenly tapered, pointed apex. Infrequent in Southwest Georgia to central inner Coastal Plain, Underwood's trillium extends eastward to limesinks near Sandersville and bluffs near the Ocmulgee River and major tributaries below Macon and Hawkinsville; then disjunct along the Withlacoochee River near Valdosta, Lowndes County area and west to the headwaters of streams flowing into the Chattahoochee. It is sparse or absent from the rich ravines close to the Chattahoochee, where it seems to be replaced by *T. decipiens* and *T. reliquum*. Lucien Underwood first collected this trillium in 1896 and began a review of sessile-flowered trilliums at the New York Botanical Garden. He was unable to complete his work and the project was continued by John Kunkel Small, who named the trillium officially in 1897. John Freeman, revered professor at Auburn University, continued revisions in sessile-flowered trilliums. He once told me his cabin home near Auburn was likely the area in which this trillium was first collected by Underwood.

A Plea for the Deciduous Forest

Most trilliums require deciduous forests in which a humus layer and leaf litter provide moisture, protection and nutrients for the establishment of seedlings. Although pines and hemlock often occur in mountain habitats with trilliums, moisture levels are higher there. In the drier and harsher environments of more southern Piedmont and Coastal Plain Georgia, build up of the topsoil with decay of basswood, maple, beech, oak, blackgum, and deciduous magnolias keeps conditions moist, non-acidic, and nutrient rich, providing seed beds for many of our spring ephemerals.

The use of prescribed fire in uplands can be overdone on hardwood slopes and bottoms. I plea for a greater appreciation of the deciduous hardwood forest, a product of over sixty million years of evolution. We must be judicious in application of fire to manipulate forest structure and more aware of the importance of forest litter to all inhabitants of the deciduous forest. In awe of nature's resiliency despite human foils, I often ponder the verse from Wendell Berry's poem, *Manifesto: The Mad Farmer Liberation Front:*

> Say that your main crop is the forest
> that you did not plant,
> that you will not live to harvest.
> Say that the leaves are harvested
> when they have rotted into the mold.
> Put your faith in the two inches of humus
> that will build under the trees
> every thousand years.

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Key to Georgia Trilliums

1. Flowers on stalks (pedicellate-flowered) arising from a whorl of three uniformly greenish leaves **2**

1. Flowers without stalks (sessile-flowered) arising directly from a whorl of three variably mottled leaves; leaves with different shades of green, weakly to strongly patterned with spots and stripes **15**

2. Flowers held about at the level of the leaves, or above leaves 7

2. Flowers clearly nodding, somewhat hidden, below leaves **3**

(NOTE: rarely, plants exhibit horizontal or erect flowers when "normally" they would be nodding; also there are two species, ***T. flexipes*** and "**Amicalola Trillium**," that may appear below the leaves in flower and above the leaves in fruit, or vice versa. To be certain you don't have one of these "oddballs" verify that other more stable key characters match your specimen. Always refer to best characters to use in the text and compare illustrations.)

3. Flowers white to pink, turning darker pink with age; petals smooth-surfaced, with wavy margins; anthers curved outward, often asymmetrically; stigmas joined into a short style . . . . . ***T. catesbaei***

3. Flowers white, maroon or otherwise, fading to brown with age; petals veiny with straight margins; anthers straight, symmetrical; stigmas widest at base, separate, without joining into a style, thus the ovary apex a shallow dimple surrounded by three style bases **4**

4. Stamens much longer than ovary, filaments about as long as ovary or longer; ovary dark purplish black, relatively small, globose . . . . . ***T. vaseyi***

4. Stamens as long as or slightly longer than ovary, filaments about half as long as ovary; ovary more or less flask-shaped, usually white, dull red or with pinkish tones, relatively large and conspicuous **5**

5. Stamens bicolored with anthers burgundy and filaments white; petals strongly recurved from the base like a Turkscap Lily; pedicels 1–1.5 X length of sepals, somewhat recurved, normally below the leaves, when above, the flower facing downward; plants frequent on low elevation montane and Piedmont toe slopes and floodplains; floral fragrance weak, inoffensive, like fish oil . . . . . ***T. rugelii***

5. Stamens otherwise, if bicolored, then with anthers yellow, creamy or light maroon, robust, longer than filaments and filaments purplish or white; petals spreading outward gradually from the base, sometimes recurved toward the apex; plants rare, narrowly restricted, found on limestone terraces, montane boulder-fields, steep cove hardwood slopes, Piedmont foothill slopes; floral fragrance strong, offensive, like moldy cheese **6**

6. Stamens about as long as ovary or slightly longer; the filaments short, about one third the length of the anthers or less, half as long as the ovary or less; pollen creamy to pale yellow; filaments and anthers white, anthers at least in part somewhat appressed against the ovary; plants of the Cumberland Plateau escarpment in clayey soils derived from limestone . . . . . ***T. flexipes***

6. Stamens far exceeding ovary height; filaments about half the length of the anthers; pollen creamy, yellow, or pale grayish purple; anthers and filaments also variable in color, mostly white, occasionally with purplish coloration; the anthers mostly longer than the ovary and not appressed against the ovary; plants of central Blue Ridge and adjacent Piedmont foothills in deep, loamy, rocky soils derived from amphibolite gneiss, or other metamorphosed granitic bedrock. . . . . **Amicalola Trillium**

7. Petals white with a red blaze near the base; anthers much shorter than filaments, the pollen sacs shedding pollen toward the outside; leaves bluish green to bronzy green, distinctly petiolate; ovary without wings; fruit a red berry . . . . . ***T. undulatum***

7. Petals and anthers otherwise; leaves green, slightly petiolate or not; ovary with 3–6 wings; fruit a fleshy capsule, opening irregularly from the base. **8**

8. Petals with conspicuous netted veins, margins not wavy; flower center with stamens surrounding a prominent ovary; petals white, maroon or otherwise, fading to brown; ovary white, pink, purple, black or any-

thing in between with 6 wings; stigmas thicker near the base, distinct, not fused into a style, tip of ovary exposed, depressed in fruit **11**

8. Petals delicate, sometimes wavy-margined; flower center with stamens obscuring the deeply set ovary; petals white to pink, turning darker pink; ovary white to greenish white with 3–6 wings; stigmas evenly thickened, relatively thin, united at the base into a short style, tip of ovary with a small beak in fruit. **9**

9. Leaves less than two inches wide, lanceolate, narrowly ovate to ovate, the tips either rounded or evenly tapered to a point; stem slightly angled (roll gently between fingers); petals not overlapping at base, held somewhat agape or barely spreading to fully open in side profile. **10**

9. Leaves usually more than two inches wide, elliptic, the tips pinched into a strongly acuminate apex; stems round; petals overlapping at base forming a tube and resembling a trumpet in profile . . . . . ***T. grandiflorum***

10. Sepals rounded at apex, the margin upturned, the width nearly as broad as petals; leaves rounded at the apex, less than one inch wide; stamens with a weak purplish color between the anthers sacs . ***T. pusillum***

10. Sepals pointed, the width much less than the petals; leaves evenly tapered to a point (acute apex) more than one inch wide; stamens white to cream between the anther sacs . . . . . ***T. persistens***

11. Ovary flask-shaped, broadest near base, prominent and protruding, usually white to pinkish, sometimes purplish black; petals usually white to creamy white, with maroon forms occasional. **12**

(NOTE: The following two species have unusually variable flower positions ranging from below to above the leaves, sometimes reversing when in fruit, sometimes nearly horizontal.)

11. Ovary globose, widest near middle, not prominently protruding, hidden partially by the anthers, black to purplish back; petals white, maroon, yellowish or otherwise **13**

12. Stamens about as long as ovary or slightly longer; the filaments much shorter than the anthers (less than one third the length of the anthers) and half as long as the ovary or less; pollen creamy to pale yellow; filaments and anthers white, somewhat appressed against the ovary; plants of the Cumberland Plateau escarpment in clayey soils derived from limestone. . . . . ***T. flexipes***

12. Stamens far exceeding ovary height; with longer filaments; pollen creamy, yellow or pale grayish purple; anthers and filaments also variable in color, mostly white, occasionally with purplish coloration; the anthers not appressed against the ovary; plants of central Blue Ridge and adjacent Piedmont foothills in deep, loamy, rocky soils derived from amphibolite gneiss, or other metamorphosed granitic bedrock . . . . . ***Amicalola Trillium***

13. Petals lanceolate to narrowly ovate, spreading from the base exposing ovary in side view; leaves often rhombic; pedicels relatively short, the sepals 0.5–0.8 X length of pedicel . . . . . ***T. erectum***

13. Petals ovate to broadly ovate, forming more of a cup-shaped base, concealing ovary in side view; leaves elliptic-obovate, overlapping in robust specimens; sepals variable, often less than 0.5 X length of pedicel **14**

14. Sepals often suffused with purple, 0.2–0.4 X length of pedicel; stamens 0.9–1.6 X height of pistil; petals apically recurved, appearing barely longer than sepals . . . . . ***T. sulcatum***

14. Sepals green, 0.4–0.7 X length of pedicel; stamens 1.2–1.8 X pistil height; petals not apically recurved, much longer than sepals . . . . . ***T. simile***

15. Leaves variously mottled with weak to strong splotches, rarely with a weak silvery streak down the middle; anthers with or without very short (less than width of stamen) beaks (prolonged sterile tips); floral fragrance obnoxious, from stale cheese to weakly fetid, to pleasant, rather spicy, or lemony **19**

15. Leaves attractively mottled with prominent silver pattern or distinct stripes down the middle and splotches of 4 or 5 shades of green; thers with prominent beaks (prolonged sterile tips); floral fragrance obnoxious, from strongly musty like old sneakers or stale cheese to fetid. **16**

16. Flowering stem erect; leaves narrowly elliptic to broadly ovate, long-tapered toward the straight or convex (pinched in) tip **18**

16. Flowering stem somewhat trailing, S-shaped, bent near the base, becoming upright near the whorl of leaves so that the plant rests on or near the ground; leaves ovate to round, blunt at the tips **17**

17. Flowers relatively large, 2 or 3 or more inches long, about half as long as subtending leaves or longer; stamens with pollen sacs opening to the outside; uppermost stem fuzzy with tiny hairs . . ***T. decumbens***

17. Flowers relatively small, usually under 2 inches long, less than half as long as the subtending leaves; stamens with pollen sacs opening to the inside; uppermost stem smooth . . . . . ***T. reliquum***

18. Petals narrowly to broadly elliptic, broadest near the middle; leaves somewhat drooping, stems relatively short with leaves less than twice as long as the mature stem; fragrance weakly fetid or like old cheese; plants of the central, southcentral and southwestern Coastal Plain . . . . . ***T. underwoodii***

18. Petals weakly obovate, tending to be broadest above the middle; leaves horizontal, stems relatively long with leaves at least twice as long as the mature stem; floral fragrance like old sneakers; plants of the southwestern Coastal Plain in ravines along the Chattahoochee River. . . . . ***T. decipiens***

19. Leaves narrowly elliptic, relatively blunt, much longer than broad, weakly mottled in 2 or 3 shades of green; sepals horizontal to bent downward; petals long, narrow, twisted, clawed at base; stamens blackish maroon, curved inward . . . . . ***T. lancifolium***

19. Leaves broader, often nearly as broad as long, the tips prominent, sharply pointed or acuminate (pinched in with convex sides), the mottling highly variable; either the petals or the stamens or both different than the above **20**

20. Petals ivory to pale yellow, broadest near the tip, the tip pronounced as a tiny stub (this visible as a projection at the top of a flower bud), conspicuously clawed at the base; stamens dark purple, curved inward, visible in side view; floral fragrance spicy like cloves . . . . . ***T. discolor***

20. Petals different; stamens variable in color, straight against the ovary; floral fragrance fruity like lemons, bananas or weakly fetid **21**

21. Floral fragrance somewhat like lemons, often strongly so; flowers without purple coloration when young, the petals yellow, aging darker yellow, the stamens pale, the pollen sacs facing inward, the ovary also pale . . . . . ***T. luteum***

21. Floral fragrance a different mixture, fruity to weakly fetid; flowers with some purplish coloration . . . **22**

22. Petals weakly to strongly clawed at base, at least narrowly tapered so that in side view the stamens are partially exposed to pollinators; stamens primitive, the pollen sacs much smaller than the broadly flattened connective tissue . . . . . ***T. maculatum***

22. Petals narrowly tapered at base to broader, but in side view the stamens are concealed forcing pollinators (other than thrips and tiny beetles that crawl between petals) to reach the inside from the top; stamens advanced, the pollen sacs as prominent as the connective tissue between them **23**

23. Floral fragrance fruity, mostly like bananas, sometimes over-ripened ones with a spicier, more pungent, less pleasing aroma; stamens as long as ovary and stigmatic lobes combined; petals more than one half inch wide, elliptic, the broader ones often partially overlapping . . . . . ***T. cuneatum***

23. Floral fragrance weakly fetid, obnoxious; stamens longer than ovary and stigmatic lobes combined; petals less than one half inch wide, narrowly elliptic to oblong, the broader ones barely touching . . . . . ***T. ludovicianum***

Safeguarding Georgia's Critically Imperiled Milkweed Species

(*Asclepias pedicellata, A. purpurascens, A. rubra, A. incarnata* ssp. *incarnata*)

Emma Neigel
Atlanta Botanical Garden

Plant diversity loss facilitated by globalization has instigated habitat loss, fragmentation and degradation, and the introduction of invasive species.[1] To fight the loss of plant biodiversity we need to protect the species we have left. The milkweed family, Asclepiadaceae, is characterized by milky-sap that deters predators from feeding on it and is a long-lived perennial. One predator, the monarch caterpillar, has evolved to feed on the milkweed leaves that are its sole food source. Four critically imperiled (S1) milkweed (*Asclepias*) species are found in Georgia: Savanna Milkweed (*Asclepias pedicellata*), Purple Milkweed (*Asclepias purpurascens*), Red Milkweed (*Asclepias rubra*), and Swamp Milkweed (*Asclepias incarnata ssp. incarnata*). The Atlanta Botanical Garden (ABG) Conservation and Research department, along with other conservation partners, recognized the importance of safeguarding these four species in ex-situ collections, helping to ensure that the biodiversity of these rare Georgia milkweeds is preserved.

In 2020, with the aid of the Georgia Botanical Society's Marie Mellinger field botany research grant, ABG's Conservation and Research department monitored known populations and collected seed both for ex situ living and seed banked collections. I led the project with the Conservation and Research team, which indluded Lila Uzzell (previous ABG field biologist) and Jason Ligon (Micropropagation Laboratory and Seed Bank Coordinator) to collect seed and monitor wild populations with conservation partners throughout Georgia, June–October 2020.

1A. *Asclepias purpurascens* (Purple Milkweed) Conservation Safeguarding Nursery Henning Von Schmeling Grown

Trip #1: Purple Milkweed (*Asclepias purpurascens*), Northwest Georgia

The first critically imperiled milkweed species we visited was the beautiful Purple Milkweed (*A. purpurascens*) which blooms late May to early June and occurs in the calcium-rich soils of the northwestern Georgia prairies and Coosa River Valley. Our team consisted of Jason Ligon, Henning von Schmeling (milkweed ex-

1B. *A. purpurascens* bagged seedpod Berry College

pert), Richard Ware (Georgia BOTSOC), and myself. Unfortunately, we missed the flowering window but still visited the known sites with permission from Berry College. Luckily for monitoring purposes, the plants provided evidence that they had flowered or not based on their terminal stem condition, so we were still able to monitor the sites for a total plant count and estimate how many plants had flowered. None of the known sites had any evidence of pollination. There were no signs of seedpod development, possibly due to the fact the canopy was shading out light and not providing other nectar flowers to draw in pollinators. Henning suspects some of the populations may be clonal. When we seemed to be at a loss finding any seedpods on the Berry College campus I spotted a beautiful Michigan Lily (*Lilium michiganense*) in bloom and upon closer inspection of the lily found milkweeds nearby, which were unrecorded occurrences. At first glance, it appeared to be Common Milkweed (*Asclepias syriaca*) but as we went to visit the next site, Henning recalled how the seedpods would be spiky, not smooth, if it was common milkweed. Thanks to Henning's

2. *Asclepias incarnata ssp. incarnata* (Swamp Milkweed) Alan Cressler

milkweed expertise, we were able to identify the new occurrences as Purple Milkweed and bag the developing seedpods for later collection. I returned that August to collect the pods we had bagged and successfully collected more than **70 seeds** from one of the pods, which are now safely deposited in ABG's Conservation Seed Bank! This was a significant find, given it was the only Purple Milkweed pod found at any of the known sites this summer. The other sites we visited were located just off Berry College campus and were roadside and powerline right-of-ways. One roadside population had been sprayed and the emerging plants had been deformed due to the herbicide. I contacted the local county public works department and arranged for "NO SPRAY" signs to be installed for 2021 to prevent further damage to the plants. The powerline right-of-way population did not have any flowering plants but cages were already installed thanks to Henning's efforts to protect the plants from both herbivory and spraying.

Based on the lack of pollinated plants and limited range, the Purple Milkweed populations in Georgia need special attention to ensure their populations are represented in safeguarding collections through future seed collection and monitoring trips.

Trip #2: Swamp Milkweed (*Asclepias incarnata* ssp. *incarnata*), Northwest GA

Perhaps the rarest milkweed in Georgia, the Swamp Milkweed (ssp. *incarnata*), has been discovered at a sole location. As suggested by

3A. *Asclepias rubra* (Red Milkweed)
Conservation Safeguarding Nursery

3B. *A. rubra* seed fluff

its common name, Swamp Milkweed occurs in swampy wetland areas in north Georgia and blooms into mid-July. Discovered by botanical photographer Alan Cressler and identified by Henning on Cressler's Flickr account, this subspecies could be easily mistaken for its popular counterpart, subspecies *pulchra*. Unlike subspecies *pulchra* (meaning pubescent), this subspecies has smooth leaves with no pubescence. I went out with Alan Cressler to revisit this population in 2020. While six plants had been noted in 2017, we only found one plant in bloom and observed low reproductive potential based on the abortive state of the flowers. Alan noted that in previous years the site conditions were considerably wetter and had waist-deep water versus 2020's much drier conditions with sections no more than ankle-deep. Other notable plants at this site included the beautiful Fringeless Purple Orchid (*Platanthera peramoena*). Unfortunately, no Swamp Milkweed seed was collected in 2020 but Henning has plants in cultivation from 2018 taken from maternal cuttings. A re-visit to this site is crucial in future years to try and collect seed.

Trip #3: Red Milkweed (*Asclepias rubra*), Central-South Georgia

The Red Milkweed (*A. rubra*), which is deceivingly more pink than red, can be found in wetland areas in partial shade to full sun, and blooms throughout the summer. This species has several populations in central to south Georgia, including populations located on protected land. Working together with Bryn Pipes of the Nature Conservancy (TNC), we made multiple collection trips to TNC protected properties, as well as a private land-owner property and power line right-of-ways.

The first TNC property we visited is a swampy wetland site known for its floating hybrid Pitcher Plants (*Sarracenia psittacina* x *rubra*). I had previously visited this site in summer 2019 with Henning, Alan Cressler, and Noah Yawn, so I was familiar with where the milkweeds were found. The difference on this trip? I was without a kayak this time and it is highly desirable to have a kayak for this site as it is a creek that is a drainage of the Apalachicola-Chattahoochee-Flint River (ACF) Basin. To

4. *Asclepias pedicellata* (Savanna Milkweed)
Matthew Stoddard

5. *Lilium michiganense* (Michigan Lily) Berry College

avoid swimming across the creek and crawling on hands and knees through the muck, we used a TNC access road to enter from the opposite side of the river. Along the road, we noted some Gopher Tortoise dens and enjoyed the bumpy ride down to the creek. Lila Uzzell and I were able to mark several plants with ID tags similar to those used to mark trees. These tags come into play for maternal tracking so we can associate an ID number unique to each plant from which we collect seed. The seed is marked with the ID number in its own envelope and then assigned a lab number once it makes its way to the Conservation Micropropagation and Seed Bank laboratories in Atlanta. We initially marked plants and bagged any ripening seedpods in late summer (late July-August) and returned mid-fall (October) to collect seed. When we returned for the second visit, we wisely brought waders and were ready to wade to the floating masses where these plants occur. Bryn also collected seed from the seedpods we bagged that were not quite ripe when we visited, illustrating the immense benefit of working with partners.

The second TNC property had a sole plant in flower when we visited it and the site was mostly overgrown with rivercane. Bryn mentioned TNC's plans to get fire into the area, promoting a more open-growth environment for the plants to thrive in, but burning logistics would be tricky due to the close proximity to the highway and smoke potential. Ideally, this site would be revisited post-fire after the plants have a chance to regain their territory.

The private property also only had a sole plant in bloom and even though we marked the plant to re-visit and collect seed from it, it did not develop a pod. It is likely more plants may be present on this private property but a boat or kayak would be optimal to explore more as the plant we found occurred just off the water's edge on a floating island mass. *Note to self: make sure your rubber boots do not have any holes before plunging into the sphagnum moss!

The southernmost Red Milkweed population occurs on a Georgia Power right-of-way. Jim Ozier, Georgia Power biologist, accompanied the ABG team. We found many plants in flower but only one seed pod, which was of colossal size and deemed the 'Big Daddy." My biggest regret of the field season was not bagging this seedpod for when we returned to collect, the pod was nowhere to be found. We returned two additional times to try and find it but had no luck relocating it. I assume charismatic megafauna may have grazed it, AKA Deer! A field lesson I learned is to always mark plants you mean to return to with flagging. Even with a GPS point, dense vegetation and other nearby stems can make it impossible to locate that spe-

cific plant. I did take three cuttings from this site as an alternative to getting seed, due to the population currently having no representation in the Conservation Safeguarding Nursery. One of three cuttings survived and is rooting in the ABG Atlanta greenhouses under the care of David Ruland, ABG greenhouse manager.

Trip #4: Savanna Milkweed (*Asclepias pedicellata*), Coastal Georgia

Savanna Milkweed (*A. pedicellata*) is an inconspicuous, chartreuse-flowered milkweed that occurs on coastal Georgia's barrier islands and in pinewood flatwoods habitat. It flowers early to late summer. Easily overlooked because of its natural camouflaging color, its rarity may simply be because the plants have not been noticed. Over a three day coastal excursion with Georgia DNR wildlife technician Matthew Stoddard, we monitored and documented multiple previously un-inventoried coastal sites and collected hundreds of seeds. Thanks to Matthew's botanical expertise, we were able to visit the Guale Preserve managed by St. Simons Land Trust and Crooked River State Park, where he had discovered new populations while hiking.

At the Guale Preserve *alone* we were able to collect over **300** maternal-line tracked seeds while following the 10% rule for best seed collection practices. This rule states that no more than 10% of seed is collected from a single population based on CPC guidelines (Center for Plant Conservation) derived from Menges et al. (2004).[2]

At Crooked River State Park, we worked with Tracy Worsham, the state park naturalist. Tracy was unaware of the natural population of Savanna Milkweed so it was great to introduce her to a rare species that was right under the state park's nose, growing along their nature trails. She had been trying to establish the species from nursery-sourced seed in their pollinator area without much success, so I think it was a relief to us all to find local seed on the property. Overall, the future for this species seems bright and seed collections were successful from all the sites we visited. I think the continued partnership with DNR will enable ABG to continue maternal-line seed collections from these populations well into the future.

6. Undescribed *Clematis sp.* Berry College

What's Next?

The seeds collected during the 2020 field season have undergone germination trials with 100% germination success. Seeds that germinate in the trials are to be grown-out and eventually planted in raised safeguarding beds at the ABG Conservation Safeguarding Nursery. **Over 40** maternal-tracked seed collections were established between *A. purpurascens*, *A. rubra*, and *A. pedicellata*. No seeds were collected from *A. incarnata* ssp. *incarnata*. Approximately, **700 seeds** were collected in the 2020 field season from the three species. A huge thank-you to all our partners and individuals involved in this project and to the Georgia Botanical Society for making my dream of being involved with a milkweed conservation project come true!

Did you know?

To check the ripeness of a milkweed seedpod you can gently crack open the suture (seedpod seam) and 'peek' to see if the seeds are brown or still green. If the pod is still milky and green

inside it is not ready. If it is dry and the seeds are brown it is ready. You can also secure a fine-mesh bag around the pod if the seeds are unripe to prevent seeds from escaping, as they are similar to dandelions fluffs and will readily wind-disperse when they open.

The fluff from the milkweed seeds, which aids in air dispersal of the seeds, was used as filling in life preservers for soldiers during World War II.

Monarch caterpillars can sequester more than 0.25 mg of cardenolides from the milkweed sap, which is the same amount given to heart patients in the hospital, even though a Monarch weighs on average less than one gram and a human is 2.5 million times that.[3]

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Assessing Effectiveness of *Laricobius nigrinus* in the Control of *Adelges tsugae* on the Eastern Hemlock (*Tsuga canadensis*)

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Stacie James
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Eastern Hemlock is a keystone species in Georgia. Loss of this native tree will have lasting and deleterious impacts on the watersheds in which they are found. Any improvement in reducing mortality from Hemlock Wooly Adelgid (HWA) and improving tree health will have a positive impact on riparian habitats in which these trees dominate. Multiple species, aquatic and terrestrial, plant and animal, are directly or indirectly dependent upon hemlock.

The introduced Hemlock Wooly Adelgid (*Adelges tsugae*) has been influential in the decline of Eastern Hemlock (*Tsuga canadensis*) since its first recorded presence in Virginia in the 1950s (Havill et al. 2011, Souto et al. 1996). Efforts to decrease the impact of this pest have included the release of laboratory reared predatory beetles of the genus *Laricobius* (Coleoptera: Derodontidae) (Mooneyham et al. 2016). At the University of North Georgia Ecological Protection Laboratory, we rear *Laricobius nigrinus* (Ln) for the control of HWA. On average, in Virginia, an adult female Ln can consume 9 adult adelgids/day (Lamb et al. 2002). A larva in Georgia must consume between 220–250 HWA eggs to complete its development (McDonald, personal communication). Releasing large numbers of egg producing Ln females is therefore one of several methods for biological control of HWA. Briefly, we purchase wild collected adults in late winter when they are active. Then, in the lab, we maintain colonies of beetles in growth chambers so we can provide precise environmental control and supply them with food (adelgids) to promote egg production. Beetle eggs are laid singly on the woolly ovisacs of HWA. Twigs with eggs are transferred to rearing cages where the eggs hatch and the larvae are provided with fresh HWA-infested foliage twice a week. When ready to pupate, larvae drop to the cage bottom and our student technicians collect them for transfer to soil boxes where they ultimately pupate. The lab maintains the soil boxes throughout the sum-

Eastern Hemlock (*Tsuga canadensis*) infested with Hemlock Wooly Adelgid (*Adelges tsugae*).
Alan Cressler

Eastern Hemlock (*Tsuga canadensis*) infested with Hemlock Wooly Adelgid (*Adelges tsugae*).
Alan Cressler

mer, monitoring temperature and humidity. In the fall (November in Georgia), adults emerge from soil boxes. Some of these adults are kept in the laboratory to augment breeding stocks. The remaining adults that emerged from the soil boxes are released into the field when HWA sistens, a stage in the life cycle of HWA, break dormancy and begin their egg production. HWA dormancy break is weather dependent and in Georgia can occur any time between October and December. Adult beetles lay eggs for the duration of HWA winter activity and die in the spring or early summer.

At the University of Georgia, Ln have a 33% adult emergence success from soil boxes when reared in a lab setting (Zhang, personal communication). Soil moisture does not affect the duration of adult aestivation in boxes but it does affect survival (Lamb et al. 2007). Once they emerge from soil boxes, a captive adult Ln can lay ~100 eggs (Zilahi-Balogh et al. 2003) over a ~13 week period versus 28 eggs in the field (Lamb et al. 2002).

Eastern Hemlock (*Tsuga canadensis*) infested with Hemlock Wooly Adelgid (*Adelges tsugae*).
Alan Cressler

Multiple laboratories located in the eastern US are dedicated to rearing predators of HWA. Much of the field research on the effectiveness of these predators is regional and study results may not be applicable to Georgia. We hoped that our study could assist the three laboratories releasing beetles in the state in determining the most efficacious methodology for HWA control. In addition, we expected the results of this study to have bearing on releases performed in other parts of the US where Ln is utilized for biological control. Our Marie Mellinger Grant proposal addressed a significant concern regarding the effectiveness of Ln in the control of HWA on Eastern Hemlock: With the large mortality in the lab associated with rearing Ln to the adult stage and the decreased fecundity of adults in the wild, are we reducing Ln predation effectiveness by releasing beetles in the fall versus releasing Ln eggs in the late winter/spring? Basically, we wished to investigate the effectiveness of Ln as a biological control agent when released as eggs rather than as adults.

Under permit that allows us to perform releases and research, we selected understory hemlock saplings along Boggs Creek in the Chattahoochee National Forest with adequate new growth and HWA infestation. We surveyed each tree for percent of new growth, HWA density, crown density, and foliage transparency. Twelve of these trees were selected for the study based upon uniformity of the parameters de-

Study trees being treated with *Laricobius nigrinus* (Ln) covered with netting (tents).

termined by the aforementioned survey results. Study trees were covered with netting (tents) that was secured at the ground on February 23rd, 2021. Data loggers to record soil moisture, soil temperature and air temperature were deployed with each study tree.

Adult Ln were purchased in late winter/early spring 2020 from a recognized provider and maintained as described above, producing egg-laying adults in the fall. When the adults emerged, they were sexed and separated into five groups of eight individuals with an equal sex ratio (4 female: 4 male). Beetles were maintained in the laboratory until the sistens broke dormancy in the field in March and began egg production. Once the sistens broke dormancy, we released the beetles into the tents covering the previously identified trees. Two trees without beetles served as a control. We assumed that each female would produce 25 eggs over her lifetime so each enclosure would have a total of 100 eggs over the duration of the study.

Adult Ln were purchased in late winter/early spring 2021 from the same provider used in 2020. Twenty unsexed adult Ln were bred in the laboratory in oviposition jars with 12 six-inch branches of HWA infected eastern hemlock. After one week, adult Ln were removed and an egg count for the branches was performed under magnification.

Lab-collected eggs on twigs were then transferred to the selected trees at a rate of 100 eggs

Study tree being treated with *Laricobius nigrinus* (Ln) covered with netting (tents).

per tree. Egg placement in the field occurred on March 9, 2021. A March release allowed us to target the same sisten generation as was done with the adult beetle releases (the fall 2020-spring 2021 generation). We completed all data collection on HWA numbers in April.

Unfortunately, the spring deluges, with a 27-year water level high at Boggs Creek, negatively impacted our study. We can only speculate just how bad the flood was in our study site, which was located in the flood plain. Once we were able to access the area again, which had been closed by the National Forest Service, it was obvious several of our tented trees had been inundated. Since it was too late in the season to identify new trees and start over, we allowed the experiment to continue until the HWA life stage dictated an end to the study.

Initially, while counting HWA density, we were pleased to see that it had decreased considerably from the initiation of the experiment regardless of whether we released adult beetles or their eggs. The data analysis confirmed that there was no significant difference between

biological control methods. But, there was also no difference between our treatments and the controls. Sadly, we will never know what happened… did the floods kill the HWA and our Ln? Fortunately for us, the supplies we purchased from the Marie Mellinger Grant will allow us to repeat this study in the future and, weather permitting, we will get results that will better guide our continuing efforts to control HWA on our iconic hemlocks!

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Survey of Rare Plants in a Calcareous Flatwoods Community in Northwest Georgia

John Patten Moss
Photographs by Richard and Teresa Ware

Situated in the topographically and botanically diverse Ridge and Valley region of northwestern Georgia, the 27,000-acre Berry College campus harbors numerous rare and unusual plant communities, including Montane Longleaf Forests and Woodlands, Wet Prairie patches, Dry-Mesic Prairies and Woodlands, and Calcareous Flatwoods (Edwards et. al. 2013). The most extensive of these communities, Calcareous Flatwoods, is the subject of this article.

So named due to the calcium-rich limestone bedrock that underlies the relatively flat soil surface, Calcareous Flatwoods were once a relatively widespread natural community type along the Conasauga, Coosawattee, Oostanaula, and Coosa rivers in northwest Georgia and northeast Alabama. Conversion to agriculture, pine plantations, and development has reduced this once common natural community to a handful of known sites throughout the region (Govus 2009). NatureServe* ranks the Flatwoods as "globally imperiled." Calcareous Flatwoods

Podophyllum peltatum (May-apple)

are remarkable in many respects, and they are unrivaled as deciduous forest communities in their potential for rare species and plant diversity (Govus and Pyne 2003). According to BotSoc member and experienced field botanist Tom Govus, Berry College harbors some of the best known remaining examples of flatwoods. Throughout the rest of this article, we will refer to this community as simply "Flatwoods."

Several key species are indicators of the Flatwoods: *Quercus pagoda* (Cherrybark Oak), *Q. shumardii* (Shumard Oak), *Cornus stricta* (Southern Swamp Dogwood), *Podophyllum peltatum* (Mayapple), and *Hymenocallis occidentalis* (Woodland Spiderlily). There is a notably high diversity of trees with *Q. phellos* (Willow Oak), Shumard Oak, Cherrybark Oak, and

*NatureServe, Inc. is a non-profit organization based in Arlington County, Virginia, that is the definitive source for information on rare and endangered species and ecosystems in the Americas. https://www.natureserve.org/

Hymenocallis occidentalis (Woodland Spiderlily)

Clematis fremontii (Fremont's Leatherflower)

Celtis laevigata (Sugarberry) usually the dominant species. The shrub layer is similarly diverse and dominated by calcium-loving species. The high diversity of plants in Flatwoods results partially from the presence of micro-habitats—slight variations in the ground surface that allow plants adapted to both moist and wet soils to flourish (Edwards et. al. 2013, Govus and Pyne 2003).

The presence of numerous rare species underscores the uniqueness of the Flatwoods. Soil conditions—high levels of calcium and variable soil moisture—most likely explain the presence of such unusual and unexpected species. Some Flatwoods species, referred to as "disjuncts," are separated by hundreds of miles from other populations; *Clematis fremontii* (Fremont's Leatherflower) and *Carya myristiciformis* (Nutmeg Hickory) are such disjuncts. Other species are endemics—found nowhere else in the world except these Flatwoods, including federally and/or state listed *Clematis socialis* (Alabama Leatherflower), and *Trillium georgianum* (Georgia Dwarf Trillium). Other rare calciphiles include *Asclepias purpurascens* (Purple Milkweed), *Prenanthes barbata* (Barbed Rattlesnake Root), and *Aureolaria patula* (Spreading Yellow Foxglove).

Our study sought to shed some light on the environmental conditions of rare species in the Flatwoods by studying their occurrence on the Berry College campus. We hoped to gather data on rare species that would indicate whether these plants prefer the micro-habitats they occupy or whether they have retreated there as their preferred habitats were destroyed. Considering the rare and declining nature of Flatwoods, we hoped to produce data that could guide wise habitat management practices.

Methods

Much of Berry College's campus south of Lavender Mountain is characterized by nearly flat, limestone-based soils, and by extensive forested areas of both naturally revegetating and planted trees, primarily *Pinus taeda* (Loblolly Pine). Due to time constraints, we needed to select a study area that could be reasonably surveyed within the growing season of May–August 2018. We identified a 588-acre (238-hectare) plot of land that appeared to have the typical soils and plants of Flatwoods, was surrounded by known populations of rare species, and included both natural and planted pine areas.

We assembled our target list of twelve rare species by referring to literature on Calcareous Flatwoods and by consulting with regional experts (Table 1). Literature sources included Chafin 2007, Edwards at al. 2013, Govus 2009, Govus and Pyne 2003, Ware 2009, as well as expert advice from local botanists Thomas Govus, Mincy Moffett, Henning von Schmeling, and Richard Ware (pers. comm.).

We surveyed our study area using two long-recognized field ecology methods: transect sampling and random quadrats. A transect is a

Carya myristiciformis (Nutmeg Hickory)

Nabalus barbatus (Barbed Rattlesnake-root)

Clematis socialis (Alabama Leatherflower)

Trillium georgianum (Georgia Least Trillium)

Asclepias purpurascens (Purple Milkweed)

Aureolaria patula (Cumberland Oak-leech)

Table 1. List of target species, conservation status, and locations found in this study.

Species	USDA PLANTS Code	Global Rank[1]	State Rank[2]	At Berry?	At LDCNA?
Asclepias hirtella (Pennell) Woodson	ASHI	G5	S2	Yes (main study plot)	
Asclepias purpurascens Georgi	ASPU2	G5	S1	Yes (outside study plot)	Yes
Aureolaria patula (Chapm.) Pennell	AUPA	G3	S1		
Carya myristiciformis Nutt.	CAMY1	G4	S1	Yes (outside study plot)	
Clematis fremontii W.A. Weber	CLFR	G5	S1	Y (outside study plot)	Y (outplanting)
Clematis socialis Kral	CLSO3	G1	S1		Yes
Helianthus verticillatus Small	HEVE3	G1Q	S1		
Jamesianthus alabamensis S.F. Blake & Sherff	JAAL	G3	S1		
Lilium michiganense Farw.	LIMI9	G5	S1		Yes
Marshallia mohrii Beadle & F.E. Boynton	MAMO3	G3	S2	Yes (main study plot)	
Nabalus barbatus (Torr. & A.Gray) A. Heller = *Prenanthes barbata* (Torr. & A. Gray) Milstead	PRBA	G3	S2		Yes
Packera crawfordii A.M. Mahoney & R. Kowal[3] = *Packera paupercula* (Michx.) Á. Löve & D. Löve	PAPA20	G5	S1Q	Yes (outside study plot)	Yes

[1]G1 Critically imperiled; G1Q Critically imperiled, questionable taxonomy; G3 Vulnerable; G4 Apparently Secure; G5 Secure

[2] S1 Critically imperiled in state because of extreme rarity (5 or fewer occurrences); S1Q Critically imperiled, questionable taxonomy; S2 Imperiled in state because of rarity (6 to 20 occurrences)

[3]See Kowal et al., 2016.

straight line laid out across a study area, along which observations are made or measurements taken. We established 32 north-south transects along which we walked and visually scanned about 50 feet on either side, looking for our target species. Additionally, we randomly distributed plots (quadrats) across the study area where we took soil samples and made fish-eye photographs of the tree canopy. Full-color, fish-eye (hemispherical) photographs were taken at each sample point in order to determine the amount of sunlight penetrating the tree canopy and reaching the forest floor. We also visited nine other sites outside of the main study plot that were known to support our target rare species and took soil samples and fish-eye photos at each of these sites.

Soil samples from our main study plot were sent to the Soil, Plant, and Water Lab at the University of Georgia, where they were ana-

Asclepias hirtella (Prairie Milkweed)

Marshallia mohrii (Coosa Barbara's-buttons)

lyzed for pH, lime buffer capacity, calcium, potassium, magnesium, manganese, phosphorous, and zinc. The soil samples from the nine sites outside of the main study plot were analyzed for an additional set of soil variables, including cadmium, chromium, copper, iron, molybdenum, sodium, nickel, lead, nitrate, and ammonium.

Results and Discussion

We were surprised to encounter only two out of the 12 target species within the study area: *Asclepias hirtella* (Prairie Milkweed) and *Marshallia mohrii* (Mohr's Barbara's Buttons). Voucher specimens of these two species were deposited in the Berry College Herbarium. The other rare, target species were seen outside but not within our main study plot. This suggests that they were not simply missed in our survey. One or more factors such as soil saturation, soil compaction, leaf and needle litter, density of other vegetation, and land use history may have played a part in determining these species' absence from our study area.

Our soil analyses also produced unexpected results, most notably in terms of soil pH and calcium concentrations. Soils that occur over limestone, which consists mainly of calcium carbonate, are typically high in calcium and have a relatively high pH, either neutral or basic. (Neutral soils have a pH of 6–7, and basic soils have a pH from 7–10). However, the pH values for our soil samples were acidic across the board, ranging from 4.91 to 4.45. In a nearby botanically significant site known as Martha's Meadow, calcium concentrations were nearly an order of magnitude higher than the average concentration within our study area and the soils there have a neutral pH. There are at least two potential explanations for our unusual soil results. It is possible that we did not sample deeply enough to reach the zone where the limestone bedrock influences pH and calcium. Also, pH and calcium concentration are influenced by vegetation cover and the accumulation of fallen leaves and pine needles; these may have acidified the soils in our study area and lowered their pH.

One factor in particular is likely to play an all-important role in determining the vegetation in the flatwoods: that is the impact of fire and other natural disturbances on thinning the tree canopy. Although our study made no attempt to measure disturbance, we did measure, with fish-eye photography, the amount of sunlight that penetrated the tree canopy and reached the forest floor. We found that Prairie

Packera crawfordii (Crawford's Ragwort)

Milkweed strongly favored sites where much sunlight reached the forest floor. The literature indicates other rare flatwoods species also prefer high light conditions. For example, all currently known populations of Alabama Leather Flower occur near disturbed right-of-ways, signaling a preference for open woodland conditions influenced by frequent fires (Govus 2009). Likewise, Fremont's Leather Flower exhibits a similar preference for open habitats (Montgomery and Shaw 2012).

Our study has implications for the preservation and management of Flatwoods and for the direction of future studies. Management techniques, especially the use of prescribed fire, will thin the tree canopy and increase the amount of sunlight that reaches the forest floor, thus providing optimal conditions for the rare species found in Flatwoods. Other management strategies that limit logging, grazing, and indiscriminate herbicide usage (Govus and Pyne 2003, Govus 2009, Montgomery and Shaw 2012) will also help to ensure the continued existence of these fascinating rare species. The atypical results of our soil study suggest that there are other factors besides soil chemistry creating favorable habitat for rare species in the Flatwoods. The Flatwoods offer further potential for investigations into the little known physical and biological components of this unique plant community.

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Adaptations of Dune Plants Growing on a Georgia Barrier Island

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Introduction

Barrier islands are found on approximately 15% of the world's shorelines with some of the most extensive chains located along the Atlantic and Gulf Coasts of North America. In particular, 85% of the East and Gulf Coasts of the United States contain barrier islands. Historically, ecologists have recognized the dynamic nature of the barrier island environment, describing it as being physically controlled. Abiotic factors such as high substrate surface temperatures, low water-holding capacity, sand movement, salt aerosols, high solar irradiance, and storms that result in salt water overwash have been implicated in controlling plant distribution patterns. As a result, only a relatively small suite of plant species has been documented to inhabit the barrier island ecosystems of the southeastern United States.

Habitats that typically comprise an undeveloped (or relatively undeveloped) Georgia barrier island include the upper beach, primary dune, interdune meadow, shrub zone, and maritime forest (Figures 1, 2, and 3). Three species that are abundant in the primary dunes of Georgia are *Ipomoea brasiliensis* (Railroad Vine), *Croton punctatus* (Beach Tea), and *Hydrocotyle bonariensis* (Dune Pennywort). The purpose of

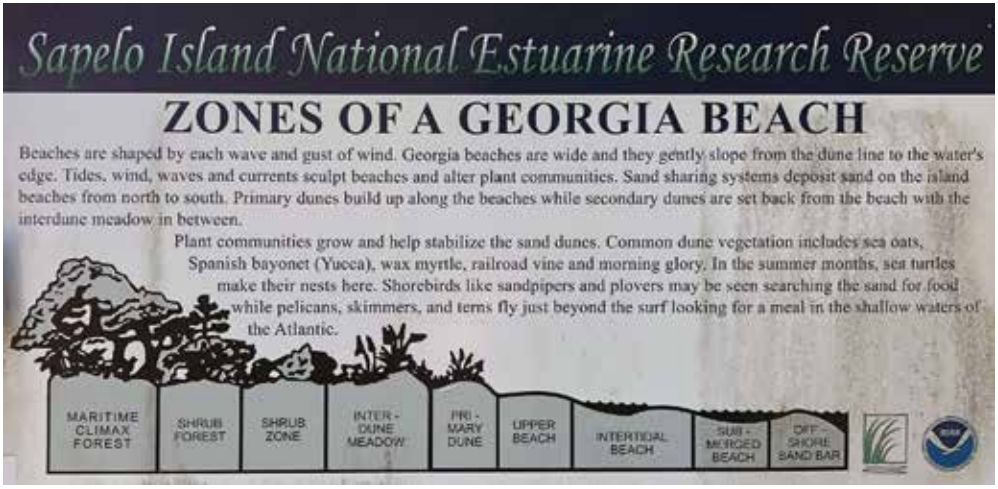

Figure 1. Zones of a Georgia beach.

Figure 2. Front of dune Sapelo Island, Georgia.

Figure 3. Interdune meadow Sapelo Island, Georgia.

this research was to address how these plants survive and apparently thrive in the harsh, transient, and dynamic barrier island environment by examining leaf anatomy, morphology, and water potential. Specifically, leaf size, leaf thickness, stomatal frequency, internal leaf anatomy, and xylem water potential in relation to location within the dune system were examined for each species.

Site description

The study was conducted on Sapelo Island during the summer of 2020. Sapelo is a barrier island approximately 18 km long and 5.5 km wide located in McIntosh County about mid-way along the Georgia coast. Geologically, Sapelo is mostly of Pleistocene origin (approximately 35,000 to 40,000 years old) with several Holocene deposits (approximately 4,000 to 5,000 years old) welded to the older island. These younger, welded areas include Cabretta Beach and Nanny Goat Beach which served as specific sites for this study.

Species descriptions

Ipomoea brasiliensis is a perennial that inhabits tropical and subtropical coastlines. The plant is commonly found just above the high tide line but has also been documented in interdune meadows and upland regions. *I. brasiliensis* grows from a central region outward by rooting at nodes along buried runners creating long line of emergent leaves and inflorescences that give the plant its common name of Railroad Vine (Figure 4). The leaves of this species can be up to 14 cm in length and 12 cm in width. Railroad Vine begins flowering in May, completing seed-set by September. As the season progresses, *I. brasiliensis* can grow into a large mass of vegetation that often overtakes competing dune species. The species produces latex as a defense against herbivores.

Croton punctatus is a perennial shrub that grows to one meter in height typically surviving for up to three years. The species ranges from Florida to North Carolina as well as along the Gulf Coast. The erect stems are orange to tan in color and support slightly succulent leaves that are alternately arranged (Figure 5). *C. punctatus* typically begins flowering in May, completing seed-set in November. The plant can be found throughout the dune and interdune habitats of Georgia barrier islands.

Hydrocotyle bonariensis is a perennial rhizomatous species that ranges from Virginia to Chile and is commonly found across a wide range of habitats on southeastern barrier islands. Each *H. bonariensis* rhizome is composed of multiple segments originating at nodes. Segments are composed of roots, one leaf and possibly an inflorescence (Figure 6). Leaves vary in width from 4 to 12 cm and senesce in winter with rhizomes persisting underground until the next growing season. Inflorescences are compound umbels that commonly flower from June–September producing seeds from July–October.

Figure 4. *Ipomoea brasiliensis* (Railroad Vine) growing on Sapelo Island, Georgia.

Figure 5. *Croton punctatus* (Beach Tea) growing on Sapelo Island, Georgia.

Figure 6. *Hydrocotyle bonariensis* (Dune Pennywort) growing on Sapelo Island, Georgia.

Methods

Leaf area

To determine average leaf area of *I. brasiliensis*, sixty leaves were randomly collected from runners of multiple individuals growing on the front of dunes and sixty leaves from the central region of multiple individuals growing on the back of dunes. To determine average leaf area of *C. punctatus* and *H. bonariensis*, sixty leaves were randomly collected from plants growing on the front of dunes and sixty leaves from plants growing on the back of dunes. All leaves were stored on ice and transported to Middle Georgia State University for measurement. In the laboratory, the long and short leaf axes were measured to the nearest mm. Total leaf area was determined by inputting the leaf axes measurements into the formula of an ellipse.

Stomatal frequency

Stomatal frequency of *I. brasiliensis* was measured by randomly selecting ten leaves from runners of different individual plants growing on the front of dunes and ten leaves from the central region of individual plants growing on the back of dunes. Stomatal frequency of *H. bonariensis* was determined by randomly selecting ten leaves from plants growing on the front of dunes and ten leaves from plants growing on the back of dunes. All leaves were stored on ice and transported to Middle Georgia State University for measurement. An epidermal peel of both the upper (adaxial) and lower (abaxial) leaf surface was made. Stomatal counts were conducted by observing peels under a dissecting light microscope. Stomatal counts of *C. punctatus* could not be made due to the presence of a protective trichome layer on both leaf surfaces.

Internal leaf anatomy

Internal leaf anatomy of *I. brasiliensis* was determined by randomly selecting ten leaves from runners of individual plants growing on the front of dunes and ten leaves from the central region of individual plants growing on the back of dunes. Internal leaf anatomy of both *C. punctatus* and *H. bonariensis* was determined by randomly selecting ten leaves from plants growing on the front of dunes and ten leaves from plants growing on the back of dunes. All leaves were

stored on ice and transported to Middle Georgia State University for measurement. Leaves were sectioned with a hand-held microtome and observed using a compound light microscope with a digital camera attached.

Water potential

Xylem water potential measurements were taken for *C. punctatus* and *H. bonariensis* approximately every two hours from 8:00 AM until 7:00 PM on July 21, 2020. Five randomly selected leaves of individuals of each species growing on the front of the dune were placed in a pressure chamber to determine xylem water potential. Leaves from the front of the dune were selected because previous field measurements indicated that the highest sand and leaf temperatures were experienced in this habitat. Water potential for *I. brasiliensis* was not assessed due to the presence of latex that fouled the pressure chamber. However, the water potential of another dune associate, *Iva imbricata* (Dune Marsh-elder), was measured to serve as a reference.

Results

Leaf area

Leaves of *I. brasiliensis* runners growing on the front of dunes were smaller than leaves growing near the central region of the plant on the back of dunes. Leaves of *C. punctatus and H. bonariensis* growing on the front of dunes were also smaller than those growing on the back of dunes.

Stomatal frequency

Stomata were more abundant on the upper leaf surface as compared to the lower leaf surface of *I. brasiliensis* runners growing on the front of dunes. Stomata were also more abundant on the upper surface as compared to the lower surface of *I. brasiliensis* leaves growing near the central region of the plant on the back of dunes. Stomata were essentially evenly distributed on the upper and lower leaf surfaces of *H. bonariensis* plants growing on the front of dunes. Stomata were also evenly distributed on the upper and lower leaf surfaces of *H. bonariensis* plants growing on the back of dunes.

Internal leaf anatomy

The internal leaf anatomy of *I. brasiliensis*, *C. punctatus*, and *H. bonariensis* was equifacial, meaning a mirror image of tissue layers existed above and below a central midline. In all three species, leaves growing on the front of dunes were thicker than leaves growing on the back of dunes.

Water potential

Water potential measurements for *C. punctatus* and *H. bonariensis* were high and stable throughout the day, indicating that the plants were not water stressed. Water potential measurements for *I. imbricata* were appreciably lower than those for *C. punctatus* and *H. bonariensis*. Water potential measurements for *I. imbricata* did become low enough in the late afternoon to indicate that the plant experienced water stress.

Discussion

All three species, *I. brasiliensis*, *C. punctatus*, and *H. bonariensis* had smaller and thicker leaves when growing on the front of the dune as compared to larger and thinner leaves when growing on the back of the dune. This is an example of classic phenotypic plasticity as it relates to sun and shade leaves. *Phenotypic plasticity* refers to some of the changes in an organism's behavior, morphology and physiology in response to a unique environment. Although the backdune area of Sapelo Island cannot be considered a completely shaded habitat, percent cover of vegetation does increase from approximately 10% in the front of the dune to approximately 60% in the back of the dune. Measurements taken during this study indicated that leaves growing on the back of dunes received approximately 70% less light than did leaves growing on the front of dunes. Additionally, sand surface temperatures were approximately 15 degrees cooler

on the back of the dune as compared to the front of the dune. These differences indicate that leaves growing on the front of dunes can experience a very different microhabitat than leaves growing on the back of dunes.

A typical unifacial leaf (for example *Quercus alba*, White Oak) has stomata located primarily on the lower surface (hypostomatous). Internal anatomy is unifacial, meaning there are different tissue layers above and below a central midline. This stomatal distribution pattern and internal anatomy indicates that the leaf processes light almost exclusively from the upper surface. Indeed, this is how leaf anatomy (form) is related to photosynthesis (function) in almost all introductory biology textbooks. However, there are many different light environments in the natural world besides those experienced in a temperate oak forest. Case in point is the dune environment of Georgia barrier islands. Leaves that grow both on the front of dunes and on the back of dunes process the majority of light via their upper surfaces. However, due to the high albedo (the amount of solar radiation reflected from an object or surface, usually expressed as a percentage) of sand, as much as 40% of incident sunlight on the front of dunes and 27% on the back of dunes is reflected to the lower leaf surface and subsequently processed for photosynthesis. The amphistomatous distribution pattern (stomata on both leaf surfaces) and equifacial internal leaf anatomy of *I. brasiliensis*, *C. punctatus*, and *H. bonariensis* support the idea that leaves of these plants growing both on the front of dunes and back of dunes are subjected to significant sunlight from above and below. Although not specifically measured in this study, it is logical to expect that appreciable amounts of photosynthesis occurs in cells of both the upper and lower portions of the leaf.

Some researchers have concluded that dunes plants are often water stressed and that low water availability can affect species distribution, growth, and reproduction. Other researchers, in contrast, determined that the dune plants they measured were not water stressed. Still other researchers have stated that whether dune plants are water stressed or not depends upon the microenvironment in which they live. Some attention has been given to leaf anatomy, morphology, growth form, and life history trait characteristics that might be considered adaptations to water stress in the dune environment. In the present study, water potential of plants growing in the hottest and driest part of the system, the front of dunes, was measured. Neither *C. punctatus* nor *H. bonariensis* experienced water stress during the measurement period whereas the dune associate, *I. imbricata*, did experience afternoon water stress. *Croton punctatus* may be able to avoid water stress due to the succulence of its leaves, presence of trichomes on both leaf surfaces that retard water loss, and deep root architecture that taps the water table. Previous studies have demonstrated the ability of *H. bonariensis* to translocate water from low areas in the dunes (near the water table) to the leading edge of growth in drier areas. It appears that the morphology (clonal) growth pattern of *H. bonariensis* affords it a ready supply of water within the dune system.

Conclusions

In conclusion, *Ipomoea brasiliensis*, *Croton punctatus*, and *Hydrocotyle bonariensis* demonstrate phenotypic plasticity in leaf size and thickness depending upon location (front of dune or back of dune) within the barrier island system of Sapelo Island, Georgia. All leaves, regardless of location, were equifacial and amphistomatous indicating that light was processed through both the upper and lower surfaces. Neither *C. punctatus* nor *H. bonariensis* experienced water stress during a typical hot, dry day in mid-summer. Each species has a variety of anatomical, morphological, and growth form characteristics that may serve as adaptations to conserve water. This study has provided evidence and possible explanations to why *I. brasiliensis*, *C. punctatus*, and *H. bonariensis* are abundant and thriving in the dune environment of Sapelo Island, Georgia.

Acknowledgements

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Contributors

Michael Bodri is a Professor of Biology and the Director of the University of North Georgia (UNG) Environmental Leadership Center (ELC). His background is in entomology and botany, with a particular interest in carnivorous plants. As Director of the ELC, his primary objectives other than assuring the smooth operation of the ELC, are fostering public engagement and encouraging students to pursue careers or graduate studies that have an environmental emphasis.

Micah Burks currently works as a quality control laboratory technician with BASF. She received her Bachelor of Science in Biology from Middle Georgia State University (MGA) in December 2020. While at MGA, Micah studied changes in leaf anatomy and morphology of coastal plant species growing on southeastern dune systems. Micah intends to continue her plant research by pursuing a Masters degree in Integrated Plant Sciences at the University of Georgia.

Tom Hancock is an Assistant Professor of Biology at Middle Georgia State University in Macon. He teaches ecology, marine biology, evolution, environmental science, invertebrate zoology, introductory biology, and research methods. Tom received his B.S. in biology from University of North Carolina Charlotte, M.S. in marine biology from UNC Wilmington, and Ph.D. in biology from Wake Forest University. His research interests include barrier island ecology, coastal plant biology, and oyster spat settlement dynamics.

Stacie James, a UNG alumna, worked for the Department of Natural Resources at Smithgall Woods and was later employed at a private company performing R&D for the Department of Defense. She is currently Program Coordinator for the ELC. In this role, Stacie is responsible for the oversight of the UNG water lab and predatory beetle lab, where she enjoys mentoring students in developing their environmental monitoring skills and engaging them in research.

John Patten Moss hails from the Sandhills of Augusta, Georgia. While attending Berry College, he developed an interest in the calcareous flatwoods and other exceptional plant communities on campus and elsewhere in Floyd County. After researching Berry Collegeís flatwoods, he graduated in 2019 and has since moved on to work field seasons at the Jones Center at Ichauway and on a prescribed fire crew based in the western Fall Line of Georgia. He hopes to explore the BotSoc world and meet other lovers of plants in the field.

Emma Neigel is a conservation horticulturist who graduated with her B.S. and M.S. in Horticulture from Mississippi State University where she attended on a full-ride Track and Field scholarship. In between degrees, she was a horticultural intern at the National Tropical Botanical Garden (NTBG) in Hawaii, which sparked her interest into the world of conservation. Her Master's thesis project, "Mapping potential habitat for Butterfly Weed (*Asclepias tuberosa*) in Mississippi using GIS," started her love affair for milkweeds. Growing up she loved to help her mother in the garden and worked at a greenhouse throughout high school. She worked as the ABG Conservation Safeguarding Nursery coordinator from 2018-2021 and is now pursuing her PhD in Biosystems and Biodiversity at University of Lethbridge in Alberta, Canada. Originally from Athabasca, Alberta, she will be returning home after ten years in

the southeastern United States and working in southern Ontario doing rare plant translocation experiments. She will miss attending Georgia Plant Conservation Alliance (GPCA) meetings and all the diverse plants and people who are rooted in Georgia!

The late **Tom Patrick** grew up in the Finger Lakes Region of upstate New York. He graduated from the College of Environmental Science and Forestry at Syracuse University and received a Master of Science in Botany degree from Cornell University. He also earned the Specialist in Education degree from Peabody College for Teachers at Vanderbilt University and worked for ten years on a doctorate at the University of Tennessee, lacking only a final copy of his dissertation in order to graduate. In 1986 he was chosen as botanist by the Georgia Department of Natural Resources. His specialties included rare plant surveys, trilliums, orchids, and the management of botanically significant natural areas, including pitcherplant bogs and blackland prairies. His family includes wife Bretta Perkins, and two sons, Andy and Ben.

Joseph Watson is an Emergency Room Technician at Atrium Health Navicent in Macon, Georgia. He received a Bachelor of Science in Biology from Middle Georgia State University (MGA) in December 2020. Joseph participated in various research projects during his time at MGA which included barrier island ecology, coastal plant biology, and oyster spat settlement dynamics under the direction of Thomas Hancock. Joseph's research primarily focused on *Hydrocotyle bonariensis*, *Ipomoea brasiliensis*, and *Croton punctatus*. He intends to begin a Physician Assistant Program in 2022.

Asclepias purpurascens (Purple Milkweed)

Hymenocallis occidentalis (Woodland Spiderlily)

Lilium michiganense (Michigan Lily)

Nabalus barbatus (Barbed Rattlesnake-root)

Trillium georgianum (Georgia Least Trillium)

Photography by Richard and Teresa Ware