Natural History of Torreya taxifolia

• USDA: Fire Effects Information System (FEIS) SPECIES: Torreya taxifolia

1993, USDA, is the most detailed and referenced source of what was known about the species up to that date; the list of references is long and particularly useful

• iNaturalist: Florida Torreya

(good overview, and with 66 references, both old and recent)



ABOVE LEFT: **The largest Florida Torreyas are those planted hundreds of miles north of Florida**, as long ago as a century. This Torreya was planted ca. 1950 in **Gladwyne**, **Pennsylvania** in a full-sun setting.

ABOVE RIGHT: Planted as a potted seedling in 2008 by Torreya Guardians in a <u>subcanopy habitat of western North</u> <u>Carolina</u>, this Torreya shows the typical growth form of whorled branches with a single dominant leader.



ABOVE LEFT: A fleshy sarcotesta surrounds the single large seed of Florida Torreya, Torreya taxifolia

ABOVE RIGHT: Connie Barlow with (then) **STATE CHAMPION** *Torreya californica* near Santa Cruz CA, 2005.

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Florida Torreya is a stranded "Glacial Relict"

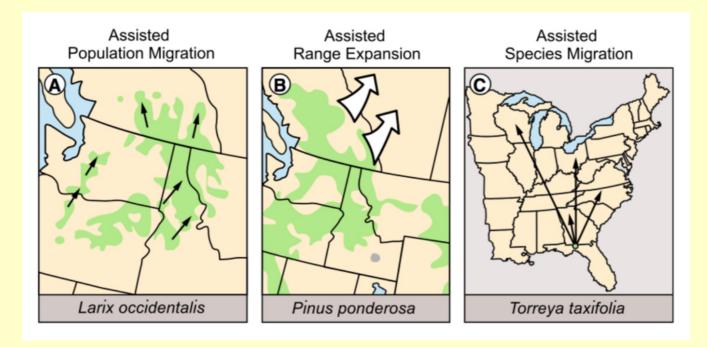
Since the early 1900s, a number of botanical publications have categorized Florida torreya as a "glacial relict".

• Visit the <u>Classic papers</u> section of this webpage for excerpts of and links to papers characterizing *Torreya taxifolia* as a glacial relict. For more links and interpretations see the **Paleoecology webpage** on this website.

By definition, a glacial relict has been stranded at a site it had retreated to during the peak glacial episode some 20,000 years ago. But for some reason or another (geographic barrier, extinction of its coevolved animal disperser, and others) the relict plant was unable to retrace its route to where it would have prevailed during a previous climate similar to our warm Holocene.

Continued **anthropogenic warming** puts a glacial relict at even greater risk of extinction — unless humans assist the species in migrating poleward. <u>"Assisted migration"</u> of Florida Torreya is the grounding purpose of the citizen group Torreya Guardians. (See the <u>Wikipedia page on Torreya Guardians</u>.)

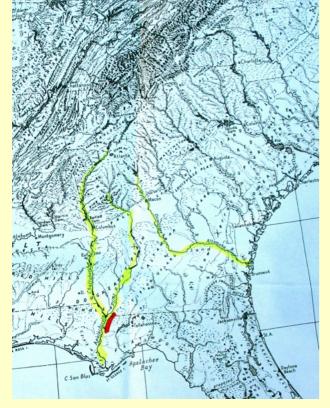
Connie Barlow, founder of Torreya Guardians, visited the sister species, Torreya californica in 2005 with the goal of acquiring a sense of the climate, habitat, and community plant preferences of the California torreya. This experience documented (via photographs) the mountain habitat preferences and plant associates of the California species. In turn, this field experience offered clues for ensuring success in helping the stranded "Florida" member of this genus move poleward. Notably, there was now a basis for selecting appropriate microsite habitats, as well as the broad latitudinal choices for "assisted species migration" (see image below) into the southern Appalachian Mountains and points even northward.



Genus Torreya is a mountain species in all locations except the small endemic range of Florida Torreya. That Florida torreya exists as a remnant population in a <u>well-known "peak glacial refuge"</u> is an indicator that **its pre-glacial native range was the Appalachian Mountains** (at least the southern portions).

The thesis is that *T. taxifolia* (along with many other plants) migrated to Florida as the Ice Ages set in, but has been unsuccessful in this current interglacial (and possibly in the previous interglacials, too) in returning to the Appalachians from its "pocket refuge" in Florida. Its sudden failure to thrive and reproduce in its localized Florida habitat beginning in the 1950s supports this thesis, as does the fact that all other species of genus *Torreya* — in California, Korea, Japan, and China — live in mountain habitats.

• **RIVER FLOAT HYPOTHESIS:** Torreya Guardians has long been aware that harvested seeds come in two varieties: floaters and sinkers.

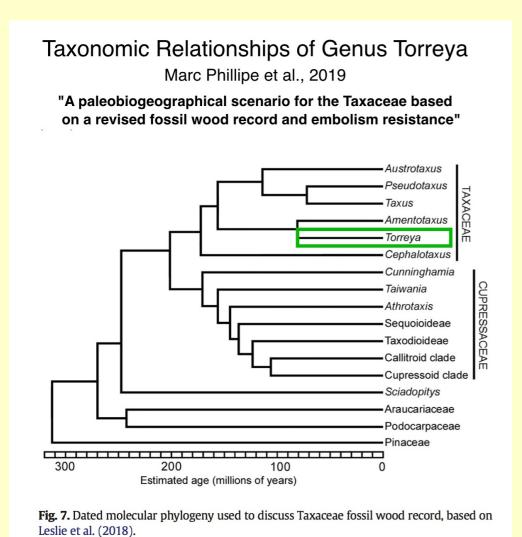


In November 2015 <u>Clint Bancroft</u> conducted an experiment in germination capacity of the 91 floater seeds v. 59 sinkers in a batch of 150 total seeds (fleshy covering removed). May of 2017 he reported results: that the floaters germinated in at least as well as the sinkers."

This result supported the "river float hypothesis":

Torreya migrated from the southern Appalachians to its peak glacial refuge in Florida by way of floating through the Chattahoochee / Apalachicola river system. As climate warmed, a reverse float trip was, of course, impossible.

MAP: The orange patch marks the bounds of Florida torreya's endemic range along the Appalachicola River.



Genus *Torreya* is a primitive member of the yew family (Taxaceae). Six species of this genus are known worldwide: 3 in **China**, one in **Japan and Korea**, one in **California**, and one in the **Florida** panhandle.

The Florida species is by far the most imperiled and is the subject of our concern.

"Comparisons of rbcl chloroplast DNA sequences involving T. californica, T. grandis, T. jackii, T. nucifera, and T. taxifolia indicated that Florida torreya is very distinct from other species, and is most closely related to T. californica and T. grandis (Price 1999).

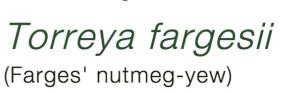
In addition, the DNA sequences suggested that the closest generic relative is the Asian Amentotaxus." — "Torreya taxifolia 5-year review" (by US Fish & Wildlife Service)

Other Species of Genus Torreya

T. nucifera T. grandis T. fargesii T. jackii T. californica T. taxifolia









*Click on your approximate section of the country to see a detailed map.

USDA Zone: 7 (0 to 10 F / -12.2 to -17.8 C) Horticultural Status: Established Origin: Genera species

Growth Shape: Broad Upright or Oval

Origin: Genera species

Growth Shape: Broad Upright or Oval

Torreya jackii (Jack's nutmeg-yew)



*Click on your approximate section of the country to see a detailed map.

USDA Zone: 8 (10 to 20 F / -6.7 to -12.2 C) Horticultural Status: RHS Accepted Genus

Origin: Genera species

Growth Shape: Broad Upright or Oval

Torreya californica

Origin: Genera species

(California nutmeg-yew)

USDA Zone: 8 (10 to 20 F / -6.7 to -12.2 C)

Horticultural Status: RHS Accepted Genus

Growth Shape: Broad Upright or Oval



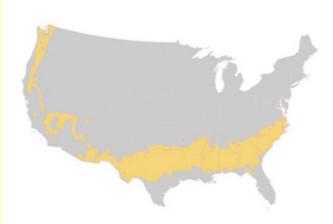
*Click on your approximate section of the country to see a detailed map.

USDA Zone: 7 (0 to 10 F / -12.2 to -17.8 C) Horticultural Status: RHS Accepted Genus Origin: Genera species

Growth Shape: Conical (Pyramidal)

Torreya taxifolia

(Florida nutmeg-yew)



*Click on your approximate section of the country to see a detailed map.

USDA Zone: 8 (10 to 20 F / -6.7 to -12.2 C) Horticultural Status: RHS Accepted Genus

Origin: Genera species

Growth Shape: Conical (Pyramidal)

The above fact sheets, by American Conifer Society, contain the above maps of where the native ranges of each species would transcribe onto the USDA plant zones — which are determined only by "annual extreme minimum temperature" and thus have nothing to do with high-temperature limits, rainfall limits, or effects of competitive exclusion in natural settings. More problematic is that the presumed physiological limits of each species is based on its current native range — and thus Florida Torreya as a "glacial relict" is inappropriately depicted as having a range for horticultural plantings far southward of what the actual **Historic Groves** have established as locales for species success. Notice, too, how far north T. nucifera would reside; in fact, that species has long been planted in botanical gardens of northern states.

The Missouri Botanical Garden stewards *Torreya taxifolia*. Its species-specific <u>Plant Finder</u> page reads, "Native to USDA **Zone 8, but probably winter hardy to Zone 5....** Some mature trees which have been planted outside the native range of this tree have grown well. Trees within the native range are under attack from a fungal blight (perhaps a species of Fusarium) which threatens to drive this tree to extinction."

Note: The **T. nucifera** page above characterizes this species as having an ability that Torreya Guardians documented with our T. taxifolia: "It is a subdioecious plant, with individual trees producing either mostly male or mostly female cones, but usually with at least some cones of the other sex present.

LEFT: Harvesting the seeds of *Torreya grandis* in China.

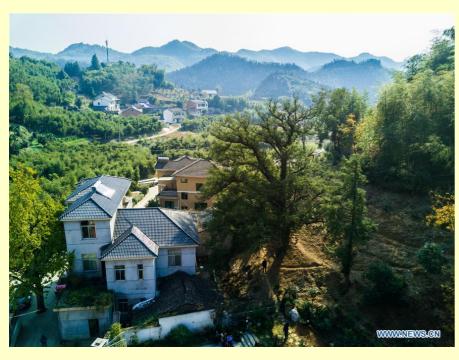
• 3-minute Chinese VIDEO on the processing and harvesting of *Torreya grandis* seeds.

Editor's note: Because the seeds are harvested green



and when oblong, it is possible that harvesting prematuration ensures that the shell beneath the fleshy sarcotesta remains tender enough to chew. The shell hardens in fully mature seeds, whose fleshy sarcotesta turns a purple and orange color.

A webpage presents **the uses and food-processing of Torreya nucifera** in Japan.





ABOVE LEFT: A big Chinese torreya tree is seen at Huaqiao Village of Banqiao Township of Hangzhou City, east China's Zhejiang Province, Nov. 3, 2017. There are more than 300,000 torreya trees in Banqiao Township and planting of the nutritious torreya has increased local growers' income. (Xinhua/Xu Yu)

ABOVE RIGHT: Farmers hold hands around a thousand-year old Chinese torreya tree in Zhaojia Town of Zhuji City, east of China's Zhejiang Province, Nov. 7, 2017. Zhuji City is a major producer of Chinese torreya with the total output reaching over 2,500 tons in 2016.

Torreya nucifera thrives in horticultural plantings of NE USA







Notice in the maps above that Torreya nucifera is the Asian species with the most northern range.





Specimens a century or more old are thriving in New England arboretums.

Photos here are all of a single specimen at <u>Highland Park, Rochester NY</u>, which was designed by Frederick Law Olmsted.

Close-up of branchlet tip shows buds of female cones in May 2022, which will not mature until autumn of 2023.

Photos courtesy of Fred Bess.

Female and Male Reproductive Structures





ABOVE: Connie Barlow took these photos while visiting the *Torreya taxifolia* collection at the Atlanta Botanical Garden in December 2007. The bulky, squarish FEMALE CONE buds (LEFT) are always few in number and near the branchlet tip. The MALE CONES (RIGHT) will produce pollen in the spring, and they are always more numerous and stretch a good distance along the underside of a branchlet.







ABOVE LEFT: vegetative buds.

ABOVE RIGHT: male pollen-producing buds. (photos by Fred Bess, spring 2016)

LEFT: The male structures release pollen sequentially over an extended period — which could be a crucial adaptation for this species that generally has only male or female structures per each tree. (photo by Clint Bancroft)

COMPARISON of Torreya species branchlets



Above photos by Connie Barlow:

LEFT: Cox Arboretum, Canton GA, elevation 1200 feet, NW Georgia, March 2019 RIGHT: Yosemite National Park, California, May 2005 (full report)

CAUTIONARY NOTE: Barlow's experience onsite with live specimens (horticulture and wild in USA) suggests to her that **the branchlet forms vary more widely within a Torreya species than between them**. Even the same genotype will express differently, depending on habitat conditions (especially thrival and access to sunlight).

A **1998 monograph on FAMILY TAXACEAE** confirms that species within each of the genera (especially genus *Taxus*) can be notoriously difficult to distinguish by form — even among the distinct "species" located on different continents. Thus, in utilizing the genus Torreya key in the monograph, one should be careful. The full pdf is downloadable as linked: "Taxaceae: The Genera and Cultivated Species, by Edward A. Cope, 1998, *Botanical Review*.

Genus Torreya: a classic examples of the <u>Arcto-Tertiary Geoflora</u>, in which highly disjunct sister species are located in extremely disjunct locales in temperate zones of the Northern Hemisphere. A 2001 paper by Donoghue et al., published in *International Journal of Plant Science*, attempted to track the speciation and intercontinental migration pathways of seven genera, one of which is *Torreya*. See <u>"Phylogenetic Patterns in Northern Hemisphere Plant Geography"</u> for details. Clearly, any attempt to understand the ecological and micro-site preferences of Florida Torreya in order to ensure its recovery from the brink of extinction should not be limited to the current climate and ecological conditions in its tiny refuge in northern Florida. Nor should recovery, therefore, focus on habitat alterations in Florida nor genetic manipulations under the presumption that Holocene native range is the only acceptable range worth striving for.

... The Japanese Walnut is very like the American Butternut, while, rather curiously, the Japanese Thuja [red cedar] and the two Chamaecyparis, the Piceas [spruce] and Abies [fir], resemble species of Pacific North America, a region whose flora has little affinity with that of eastern Asia. Torreya is common to the two regions; in America it is one of the most local of all our trees, while in Japan it is abundant in the mountainous regions of the central and southern parts of the empire. — "Notes on the Forest Flora of Japan", by C.S. Sargent, 2000, Arnoldia.

Another helpful paper for understanding **paleogeography of Family Taxaceae** back to the Jurassic and the **adaptive value** of the family's subcanopy character (including desication resistance) see this 2019 review paper: "A paleobiogeographical scenario for the Taxaceae based on a revised fossil wood record and embolism resistance".

This paper indicates that, given the high Arctic range of this ancient plant family during the peak Eocene warming, it makes sense to attempt "assisted migration" for genus Torreya as far north as this genus can survive, subcanopy, today.

- ... Taxaceae are considered monophyletic, splitting from the sister-group, the Cupressaceae, during the Late Triassic or earliest Jurassic. Cephalotaxus branched during the Early to Middle Jurassic and the division between the two remaining clades of Taxaceae occurred during the Middle to Late Jurassic, one clade containing Torreya and Amentotaxus, the other Austrotaxus, Pseudotaxus and Taxus (Cheng et al., 2000; Renner, 2009; Leslie et al., 2018).... According to the phylogeny of Fig. 7 (based on Leslie et al., 2018) the stem group of the most embolism-resistant genus of Taxaceae, Cephalotaxus, evolved at the end of the Early Jurassic and the crown group in the late Cenozoic. So the highly resistant wood may have evolved any time in this period. Thus, the Cretaceous record is entirely consistent with late evolution of resistance.
- ... A striking feature is that by the Early Cretaceous the record of Taxaceae fossil foliage record is centered on much higher paleolatitudes. Although there are putative records from Belgium (Alvin, 1960), UK (Watson et al., 2001) and North Carolina (Berry, 1910), the strongholds are at higher paleolatitudes than any presumed Jurassic records of the family: Greenland (Heer, 1883), Siberia (Krassilov, 1976; Samylina, 1988; Golovneva, 1994; Bugdaeva et al., 2006), Spitzbergen (Bose and Manum, 1990), northeastern China (Xu et al., 2015). There is thus a similar northward shift for both leaf and reproductive organ record and wood record during the Jurassic-Cretaceous interval. This shift is concomitant with abietinean TRP becoming dominant in wood. By the Cenozoic the Taxaceae were widespread over high latitude regions of the Northern Hemisphere, with fossil foliage records in North America (e.g. Kvacek and Rember, 2007), Europe (e.g. Givulescu, 1973; Ferguson, 1978; Ferguson et al., 1978; Kvacek, 1986; Spjut, 2007; Macovei, 2013) and Asia (Xu et al., 2015).

... The Late Jurassic, during which this split might have taken place (Fig. 7), is well known as a time of global drying of

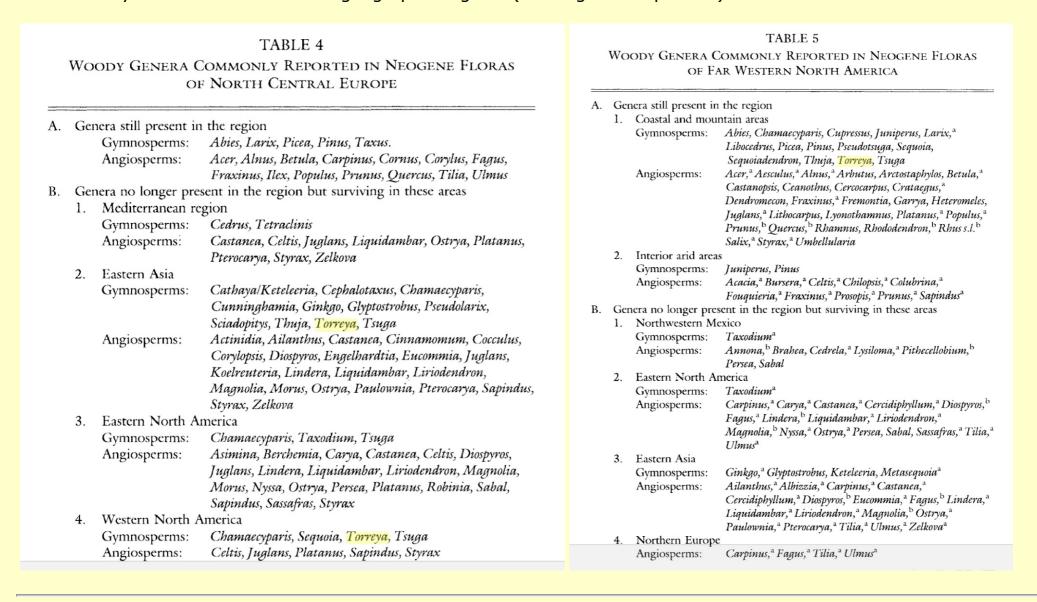
Northern Hemisphere climates. Taxaceae have probably been through several ecological bottlenecks during the Jurassic, which selected embolism-resistant taxa. This resistance was maintained when they acquired their typical wood, i.e. Taxaceoxylon features. This genus first appeared during the Early Cretaceous, a time when it was to be found in eastern continental Eurasia only, at relatively high paleolatitudes. This area is known to have been relatively dry at that time (Oh et al., 2011), with strongly influences of continental drought and the existence of an eastern coastal Cordillera. No Araucariaceae-like woods (i.e. genus Agathoxylon) are reported from this area at that time, while this type of wood was otherwise so common worldwide, possibly because of continental drought. Later, during the Late Cretaceous, at a time when North America and Western Europe climates became more continental (Wolfe and Upchurch Jr, 1987), Taxaceoxylon spread to these two areas. It persisted there through the Cenozoic, and until now, with modern Taxaceae spanning most of the temperate boreal area, except for the high latitudes that were probably their Cretaceous cradle.

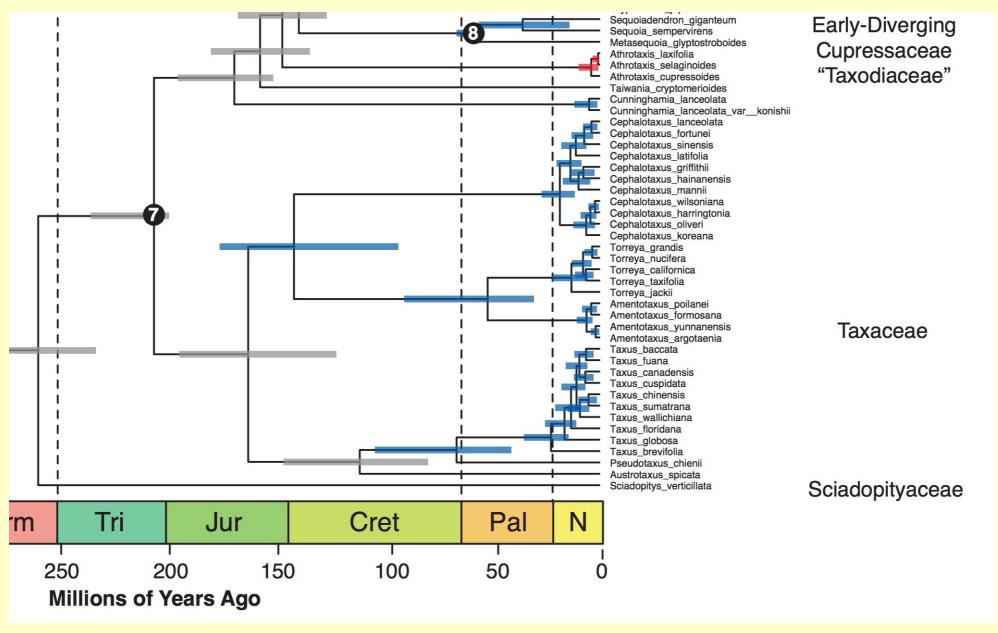
.... The high resistance to embolism is interesting because extant Taxaceae are rather mesophytic trees and shrubs, which may also be the case for most of their Cenozoic ancestors (Ferguson et al., 1978). However, this is in line with other physiological adaptations to drought observed in the Taxaceae (Hoffman et al., 1999; Feucht et al., 2012). Extant Taxaceae trees and shrubs are all shade tolerant. Their resistance to drought, together with their shade tolerance strategy, might have allowed Taxaceae to establish under angiosperm-dominated canopies.



Plate 7. 1-10. Torreya sp.; 1. Leaf, adaxial side, specimen MNHN20077; 2. Leaf, abaxial side with two narrow stomatal bands, specimen MNHN20074; 3. Leafy axis, specimen MNHN20342; 4. Leafy axis, specimen MNHN20343a; 5. Leafy axis with terminal bud, specimen MNHN20340; 6. Leafy axis with terminal bud, specimen MNHN20341b; 7. Leafy axis, specimen UCMP202020 (6004); 8. Leafy axis, detail, specimen UCMP202020 (6004); 9. Leafy axis, specimen UCMP202021 (n.n. MAT 434); 10. Leafy axis, specimen UCMP202022 (5858)

Notice Torreya in the following two lists, which appeared in the 1988 book by Jonathan D. Sauer, *Plant Migrations: The Dynamics of Geographic Patterning in Seed Plant Species*. **Europe and California lost the most tree species** of the warmer geoflora during the Plio-Pleistone. **East Asia retained the most, with eastern North America coming in second place.** Genus Torreya survived in 3 of the 4 geographic regions (missing in Europe now).





SOURCE: <u>Appendix</u> to <u>"Hemisphere-scale differences in conifer evolutionary dynamics"</u>, by Andrew B. Leslie et al., 2010, Proceedings of the National Academy of Sciences.

• CENTER FOR PLANT CONSERVATION description of the **PALEOGEOGRPAHY of GENUS TORREYA**:

"The taxon is an extremely rare conifer that once towered fifty feet above the forested ravines of the Apalachicola drainage system in northern Florida (Godfrey 1968, Foote and Jones 1994). An ancient genus of at least 160 million years old in age, species in the genus Torreya were widely distributed across the northern hemisphere during the Jurassic and Pliocene periods. Named for John Torrey, one of America's most distinguished botanists (1796–1783), this is one of the rarest native trees in the USA. Within its very limited range, it has become nearly extinct. There are no large trees left in its native habitats. What survives are a few scattered young saplings or suckers from root systems and bases of destroyed plants." [webpage accessed June 2021]

Florida Torreya is a subcanopy species

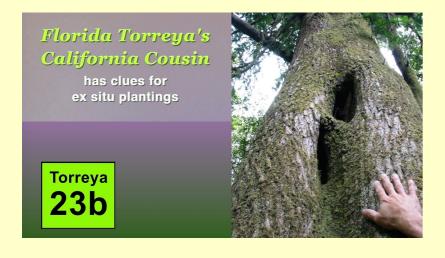
- Excerpt from the **1986** "Florida Torreya Recovery Plan", U.S. Fish & Wildlife Service:
 - "... The Florida torreya is an understory tree of mature beech-magnolia-pine forests (hammocks) (Harper 1914). The canopy trees are mostly deciduous, but evergreen hardwoods [Southern Magnolia] and conifers are also fairly common. These areas have diffuse sunlight in summer, and a relatively open canopy in winter (Kurz 1938b, Brock 1983).... Other species of *Torreya* appear to have similar habitat requirements (Burke 1975). *Torreya californica* is found 'on moist, shaded slopes and along water courses' (Abrams 1940) [see also <u>California Torreya webpage</u>.] *Torreya nucifera* is an understory element of beech forests in Japan (Ishizuka 1974). *Torreya grandis* occurs in mixed forests of southeastern China (Lee 1973). Fossils of the genus occur in assemblages of other species indicative of mesophytic forests (Knowlton 1919, Leopold and Macginitie 1972, Raven and Axelrod 1978)..."
 - "... Growth following germination is slow. Eight to 12-year-old torreya trees are generally 6-8 feet tall. They become sexually mature when 10 feet or taller (Bowden 1981). Under optimal conditions, growth continues after maturation, attaining heights of 60 feet (Reinsmith 1934). The largest existing tree is one that was moved to **Norlina**, **North Carolina** in 1840. It is 45 feet tall with a basal diameter of 34 inches (Turnage 1983)." [Note: It was growing in full sunlight and later declined, being delisted as "national champion" of its species in 2016.]





PHOTOS: Left was the **Norlina NC Tree** in 1975; growth form in full sun. Right is the largest of the 3 original plantings at **Caroline Dormon Nature Preserve** in central Louisiana; growth form beneath a deciduous canopy.

Learn about Florida Torreya by studying CALIFORNIA TORREYA



In 2005, Connie Barlow visited **4 forested regions in California where** *Torreya californica* could be found growing in the wild. Her aim was to experience and photo-record observations of the trees and their surrounds such that volunteer planters of the Torreya species native to the eastern USA (along with professionals in charge of this endangered species' recovery) could discern habitat preferences of the genus and thus pinpoint similar environments in eastern states for planting seeds and seedlings. *Read Connie's 2005 observational notes at: Photo-essays of California Torreyas*.

VIDEO Part 1 (25 minutes) • Part 2 (27 minutes)

Note by Connie Barlow: Two early contributors to professional field studies of *Torreya taxifolia*, Mark Schwartz and Sharon Hermann, published in 1999 a paper on their study of *Torreya californica* in the field: "Is Slow Growth of the Endangered Torreya taxifolia (Arn.) Normal?", Journal of the Torrey Botanical Society. Their final paragraph:

In aggregate, the results of this work suggest that the observed low growth rates of T. taxifolia might not be indicative of disease-induced stress. The similarity between T. taxifolia and T. californica growth rates and patterns is consistent with the hypothesis that T. taxifolia is growing normally within its environment. The infrequent expansion of terminal buds may simply be the way that these trees naturally grow in low light environments. Evidence of suppression and release growth pattern in tree rings, along with a preliminary observation that trees in high light environments grow more frequently than those in low light, support the hypothesis that growth in T. taxifolia is light limited. Given the continued lack of an identified primary disease agent, we recommend pursuing further tests of the light limitation hypothesis, and management to increase light levels above extant trees in the wild.

Barlow adds: This is a helpful paper. My own natural history observations in 2005 (at a greater number and diversity of sites than the quantitatively driven experimental approach undertaken by Schwartz and Hermann) would add two interpretations:

- (1) Genus Torreya evolved as a subcanopy species (as are other members of the yew family). With the assistance of mycorrhizae it is capable of living a very long time in a seemingly stunted state, until a canopy offers an opportunity for a vertical growth spurt and also for seed production on any of the branches that can directly access sufficient sunlight.
- (2) With the rare exception of <u>the immense Torreya trees found along Scott's Creek north of Santa Cruz</u> (the grand size of which may be attributed to the fact that the canopy redwoods were cut for timber in the early 20th century, thus releasing a population of subcanopy Torreyas to grow tall and to seed), **Torreya seems to do best on extremely steep slopes**, where the usual canopy giants (Coast Redwoods and Douglas-fir) cannot competitively prevail and thus are not found.

Why MOUNTAIN HABITATS sustain genus Torreya during CLIMATE CHANGE

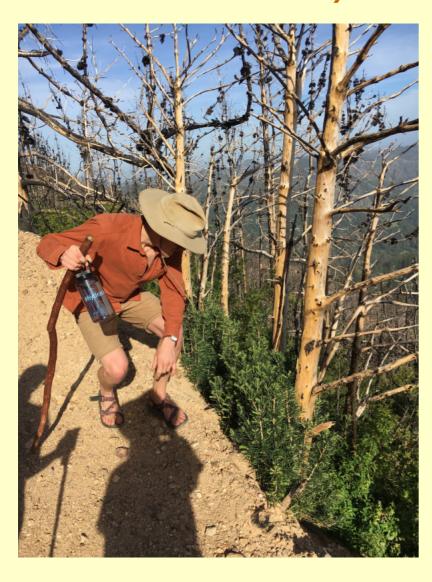
Direct access to mountains (along with Torreya's capacity to resprout new stems from its epicormic base, and its multi-year span of seed dormancy prior to germination) is **the most plausible explanation for how this slow-to-disperse, ancient genus has managed to survive for more than 100 million years**. This is likely the reason that the California, Japanese, Korean, and Chinese species of *Torreya* are not endangered — but the species in flatland Florida is critically endangered.

Consider: California torreya is reported in the literature as "rare, though locally abundant," and this was Barlow's experience, too, in her California fieldwork of 2005. It is "locally abundant" because, during this interglacial episode, it has been able to compensate for rises in temperature by moving relatively short distances upslope or laterally into north-facing slopes or the cool depths of ravines. Its large seed, however, may be the reason that it is "rare". A large seed cannot waft on a breeze from one favorable habitat to the next. Rather, Torreya depends on squirrels to distribute its seed and thus to carry out the shifts in range (in contrast to other conifers, such as Douglas-fir and Redwood, whose seeds are easily airborne).

Possibly tortoises and other reptilian or avian animals that are now extinct played important roles distributing Torreya seeds in the Northern Hemisphere for millions of years prior to the end-Pleistocene extinctions. However, today squirrels (and humans) are the only seed carriers who remain.

• Consult "Move Torreya taxifolia North Now, by Connie Barlow and Paul Martin, 2004, which offers several such paleoecological hypotheses.

California fires show Torreya californica resprouting basals





PHOTOS ABOVE: APRIL 2019 - Zach St. George sent 4 photos of multi-age California Torreyas he saw during a hike in Stevenson State Park (northwest mountains of Napa Valley, north of San Francisco, Coast Range). He wrote:

"We walked through a large area that had burned recently. It was a crown fire, and all of the mature trees (mostly pine) were dead. A few oaks / tanoaks survived. But I noticed a bunch of torreyas coppicing around some dead trunks. They were far



bigger than the seedling pines that surrounded them, although I suspect the pines will catch up quickly."

Notice the yellow color of the Torreya standing trunks, after its bark had burnt and fallen fallen off. **Torreya's remarkable survival capacities** (the genus originated in the Jurassic) owe in part to its ability to prolifically sprout new stems from its root crown after the main stem is injured or killed.

PHOTO LEFT: MAY 2022 - Don Thomas sent several photos of his visit to the Swanton RR site area of the massive CZU Fire that began August 2020.

Notice how the **basal sprouts can achieve a lot of photosynthesis** — **crucial for the individual to keep its roots alive**. Eventually, just a few of the basals will begin to rapidly grow tall, while the remaining continue to photosynthesize, so long as sunlight penetrates to their spot near the ground.

Genus Torreya joins the elder genus Ginkgo and the younger Sequoia (but not Sequoiadendron) in the ability to resprout basals after the death of the main stem. Might this be a key feature enabling these genera to survive the End Cretaceous and other lesser extinctions?

CALIFORNIA TORREYA INFORMATION helpful for understanding Florida Torreya: <u>USFS "Fire Effects" species page on Torreya californica</u> contains useful information.

EXTRACT: Male California nutmeg bear their microsporophylls within strobili. In contrast, the ovules of female trees are not contained within strobili but are solitary [16]. Male strobili begin growth the year prior to flowering, while females trees develop ovules in one growing season [21]. Torreyas are wind pollinated [16]. Male trees must normally be within 75 to 90 feet (23-27 m) of female trees in order to effect pollination [24]. Seed production is erratic. Good seed crops may be followed by crop failure the following year [10]. Seeds mature in 2 years [19]. Being heavy, seeds usually fall near the parent plant; wind dissemination is rare [17]. Seed predation by Steller's and scrub jay is high [10]. Seeds require a 9- to 12-month stratification period before germination [21]. In one study, seeds stratified for 3 months before planting took an additional 9 months to germinate under greenhouse conditions. Ninety-two percent of seedlings germinated at that time. [15]. Temperature regimes during the stratification period were not noted. Seeds sometimes germinate without stratification but do so slowly [21].

Growth of trees in the understory is slow [10]. Sudworth [24] reported trees from 4 to 8 inches (10-20 cm) in diameter were 60 to 110 years of age, while those from 12 to 18 inches (30-46 cm) in diameter were 170 to 265 years old. The growth rate needs further study, however, as rates of over 1 foot (30 cm) per year have been reported in cultivars [3]. Preliminary data obtained from tree-ring counts of saplings on the El Dorado National Forest shows some trees attained heights of 4.8 feet (1.5 m) in 28 years [10].

California nutmeg sprouts from the roots, root crown, and bole following damage to aboveground portions of the tree [3,10,19]. Some nutmegs **reproduce by layering** [21], but the layering capacity of California nutmeg is unknown.

Note by Barlow: Resprouting from root crown and bole: yes. But I dispute for Torreya (and genus Sequoia of Coast Redwood) the prevalent statement that "roots" (hence, outward from the main stem) also can sprout new main stems.

SUCCESSIONAL STATUS: California nutmeg is **very shade tolerant** [9] and is found in late seral and climax communities [3]. Following disturbance such as fire or logging, sprouts growing from surviving perennating buds appear in initial communities [10].

Adaptive value of multi-year, variable-span SEED DORMANCY

Torreya Guardians volunteers have been contributing to the understanding of the complex seed dormancy of this endangered tree. Research scholarship (table below) confirms that **Torreya genus** — **along with the entire taxonomic plant family it**

is part of (Taxaceae) — utilizes an ancient mode of seed dormancy and germination triggers that, while preventing fast action, has certainly helped this genus survive brief episodes of climate mayhem that would have been very difficult for plants that lacked these features. The dormancy type is called "Morphophysiolgical Dormancy" (MPD).

Five Types of Seed Dormancy

Source: "Dormancy and germination: Making every seed count in restoration"

Olga Kildesheva et al., 2020, Restoration Ecology

	Seed Dormancy Class	Seed Characteristics	Examples of Plant Families Containing Species With a Known Seed Dormancy Class
	Nondormancy (ND)	Seeds imbibe water and germinate readily (within 4 weeks) over the widest range of environmental conditions possible for the species	Amaranthaceae, Asteraceae, Begoniaceae, Brassicaceae, Bromeliaceae, Dipterocarpaceae, Fagaceae, Lauraceae, Pinaceae, Rubiaceae, Velloziaceae, Xyridaceae
1	Physiological dormancy (PD)	Seeds imbibe water and possess fully developed embryos with a low growth potential, sometimes in combination with a mechanical constraint from the seed/fruit covering layers	Aceraceae, Amaranthaceae, Asteraceae, Balsaminaceae, Brassicaceae, Byblidaceae, Caryophyllaceae, Commelinaceae, Cucurbitaceae, Cupressaceae, Dioncophyllaceae, Droseraceae, Drosophyllaceae, Ephedraceae, Ericaceae, Euphorbiaceae, Fagaceae, Iridaceae, Lamiaceae, Lauraceae, Lentibulariaceae, Melastomataceae, Myrtaceae, Nymphaceae, Oleaceae, Pinaceae, Plantaginaceae, Poaceae, Rosaceae, Rubiaceae, Rutaceae, Sapindaceae, Solanaceae, Ulmaceae, Urticaceae, Violaceae, Vitaceae
2	Physical dormancy (PY)	The seed or fruit coat is impermeable (preventing the uptake of water)	Anacardiaceae, Biebersteiniaceae, Bixaceae, Cannaceae, Cistaceae, Convolvulaceae, Cucurbitaceae, Dipterocarpaceae, Fabaceae, Geraniaceae, Lauraceae, Malvaceae, Nelumbonaceae, Rhamnaceae, Sapindaceae, Sarcolaenaceae, Sphaerosepalaceae, Surianaceae
3	Combinational dormancy (PY + PD)	The seed or fruit coat is impermeable (preventing the uptake of water) and seed embryos are physiologically dormant	Anacardiaceae, Fabaceae, Geraniaceae, Rhamnaceae, Sapindaceae
4	Morphological dormancy (MD)	Seeds readily imbibe water; however, embryos are underdeveloped but differentiated and require time to grow before germination	Annonaceae, Apiaceae, Arecaceae, Aristolochiaceae, Campanulaceae, Caprifoliaceae, Cycaceae, Gentianaceae, Iridaceae, Lentibulariaceae, Papaveraceae, Ranunculaceae, Rubiaceae, Sarraceniaceae, Vitaceae
5	Morphophysiological dormancy (MPD)	Seeds readily imbibe water but have embryos that are underdeveloped and/or undifferentiated and physiologically dormant	Allicaceae, Annonaceae, Apiaceae, Araliaceae, Ericaceae, Gentianiaceae, Ginkgoaceae, Lentibulariaceae, Liliaceae, Magnoliaceae, Papaveraceae, Primulaceae, Ranunculaceae, Taxaceae, Zamiaceae

Helpful RESEARCH PAPERS: Excerpts and Links

• <u>"Dormancy and germination: Making every seed count in restoration"</u>, 2020, Olga Kildisheva et al., *Restoration Ecology*:

"Worldwide, 50-90% of wild plants produce seeds that are dormant upon maturity, with the specific dormancy traits contingent on factors including environmental conditions, geographic distribution, growth form, and genetics.... Seed dormancy is an evolutionary adaptation that can benefit long-term survival under intact natural conditions.... The ability to define the seed dormancy class is the first step in determining the most effective means of dormancy alleviation and should be considered foundational knowledge for all restoration practitioners working with native seeds."

"... Seeds with morphophysiological dormancy (MPD) have underdeveloped (or undifferentiated) embryos that are also physiologically dormant, and require an environmental signal to stimulate embryo growth as a precursor to final development. MPD is a complex dormancy class, further subdivided into nine levels on the basis of the environmental conditions required for embryo growth. The additional physiological component to dormancy means that radicle emergence requires significantly more time than that of seeds with MD alone...."

- "Underdeveloped embryos and kinds of dormancy in seeds of two gymnosperms: Podocarpus costalis and Nageia nagi (Podocarpaceae)", 2013, Shun-Ying Chen et al., Seed Science Research.
 - "... In one classical view of extant gymnosperms, there are three classes, Ginkgoopsida, Cycadopsida and Pinopsida (Meyen, 1984). Among the nine families in Pinopsida, only Podocarpaceae and Taxaceae are reported to have underdeveloped embryos. Detailed studies have shown that seeds of species in Taxaceae have an underdeveloped embryo, and deep simple MPD has been documented in seeds of Cephalotaxus wilsoniana and various Taxus species...."
- <u>"Deep simple morphophysiological dormancy in seeds of the basal taxad Cephalotaxus"</u>, 2011, Chia Ju Yang et al., Seed Science Research.
 - "... MPD is divided into nine levels of dormancy: non-deep simple, intermediate simple, deep simple, deep simple epicotyl, non-deep simple epicotyl, deep simple double, non-deep complex, intermediate complex and deep complex. All five classes of dormancy occur in seeds of angiosperms, but only PD, MD and MPD occur in those of gymnosperms (Baskin and Baskin,

1998).

Within the gymnosperms, underdeveloped embryos, and thus MD and/or MPD, occur in Cycadales, Ginkgoales and some conifers. However, not all families of conifers have been studied in detail, e.g. the monogeneric family Cephalotaxaceae sensu stricto, which is the subject of this study.... Warm, cold and warm plus cold stratification are known to play an important role in breaking MD, MPD or PD in seeds of both angiosperms and gymnosperms.

- ... Cephalotaxus species grow in shady to semi-shady sites but tolerate full sun and are resistant to diseases and insect attack, making them desirable as ornamentals. The genus was introduced to Europe, North America, and Australia in the 1800s for use in landscaping. In nurseries, most Cephalotaxus plants are propagated by the stem-cutting technique. Rooted cuttings from the top of the tree grow upward (orthotropic), but those from lateral shoots grow prostrate (plagiotropic).
- ... Fossils of Cephalotaxus have been found in the Miocene in North America; in the Eocene, Oligocene, Miocene and Pliocene in Europe and as far back as the Eocene in Asia, where it is still extant.
- ... To determine the critical embryo length for radicle emergence, seeds for which the seed coat had split but none of the radicle had emerged were excised and measured, i.e. the embryo had grown to its maximum length, and the next phase of growth would be radicle emergence.
- ... Warm stratification for less than 36 weeks and/or cold stratification for less than 8 weeks decreased seed germination percentages.... The slow germination of seeds during 98 weeks at 15/6C suggests that the warm stratification requirements for germination were being fulfilled at 15 degrees C and the cold stratification requirements at 6 degrees C.
- ... Since (1) the underdeveloped linear embryo in *Cephalotaxus wilsoniana* seeds increased in length by 120% before radicle emergence occurred, and (2) many months of exposure to simulated habitat temperature regimes were required for germination, we conclude that seeds have both morphological and physiological dormancy, i.e. morphophysiological dormancy (MPD).
- ... Embryos only grew at 20/10C and 25/15C if seeds previously had received a long period of warm stratification followed by cold stratification and then moved to warm again. Seeds of *C. wilsoniana* do not have epicotyl MPD because at the simulated spring temperature regime (20/10C) there was only a short delay of 2 weeks between time of radicle and shoot emergence.
- ... The only sequence of temperature regimes that resulted in embryo growth and germination was warm-to-cold-to-warm, leading to the conclusion that the seeds have deep simple MPD. In deep simple MPD, the breaking of physiological dormancy (PD) occurs in two steps, which we can designate as PD-1 and PD-2. PD-1 is broken by warm stratification and PD-2 by cold stratification.
- ... In seeds with deep simple MPD, **embryo growth occurs at non-cold-stratifying temperatures**. However, there is variation among species with regard to timing of embryo growth, germination, and the breaking of PD-1 and PD-2. In *Taxus mairei*, embryo growth occurs while PD-1 is being broken; in *Jeffersonia diphylla*, embryo growth occurs after PD-1 is broken; and in *Cephalotaxus wilsoniana*, embryo growth does not occur until after both PD-1 and PD-2 are broken.
- ... The ecological significance of deep simple MPD in seeds of *C. wilsoniana* is that seeds matured and dispersed in late November through December can not germinate the following spring. To germinate in the field, seeds must receive warm stratification (summer), cold stratification (winter) and warm stratification (spring). For seeds in the warm-to-cold-to-warm temperature sequence, embryo growth occurred in the final warm incubation, and then seeds germinated soon after the embryo grew.
- ... For another collection of *Cephalotaxus wilsoniana* seeds harvested at the same location in 2007 and incubated at 20/10, 25/15 and 30/20C, only 5% of the seeds had germinated after 2 years. However, when these seeds were moist cold-stratified at 5C for 12 weeks and then re-incubated at 20/10, 25/15 and 30/20C, 88, 83 and 13% of them germinated, respectively (C.T. Chien, unpublished data).

IMPLICATIONS FOR TORREYA: To maximize full germination potential from any seed source, winter stratification must entail temperatures lower than 10 degrees C. In the above report, 5 degrees C was the lowest stratification temperature that was tested. *Excerpts continue* ...

... Cephalotaxus is basal in the taxad clade, which includes Taxus, Pseudotaxus, Austrotaxus, Torreya, Amentotaxus and Cephalotaxus (Cheng et al., 2000). Within the taxad clade, at least Amentotaxus (Li, 2000), Torreya (Martin, 1946; Weng, 2000) and Taxus (Chien et al., 1998; Wang, 2000), along with Cephalotaxus, have underdeveloped embryos and thus either MD or MPD.

Within the taxad clade, the level of MPD is known in Taxus baccata (Devillez, 1978), T. brevifolia, T. cuspidata (Nikolaeva et al., 1985) and T. mairei (Chien et al., 1998), and all of them have deep simple MPD.



In addition, according to Nikolaeva et al. (1985) seeds of Torreya californica and Torreya grandis have a combination of dormancy types, the former species mechanical dormancy combined with non-deep simple MPD and the later species mechanical dormancy combined with MD.

Baskin and Baskin (1998) have argued that mechanical dormancy is a part of PD, and Nikolaeva (2004) agreed. In which case, T. californica would have non-deep simple MPD and T. grandis some unidentified level of MPD. Further studies are needed in the taxad clade to work out the relationships between deep simple MPD in the basal genus Cephalotaxus and the kind of dormancy in the higher taxa within the clade.

PHOTO ABOVE: Torreya germinated seed with radicle, epicotyl, and shoot. Photo by Connie Barlow, June 2015.

PHOTOS BELOW: Germination sequence: crack, germination, radicle 4 days additional growth. Photo by Connie Barlow, June 2015.







• <u>"A framework for the interpretation of temperature effects on dormancy and germination in seed populations showing dormancy"</u>, 2015, Diego Batlla and Roberto Benech-Arnold, *Seed Science Research*:

EDITOR'S SUMMARY: This is a highly technical paper that explores the role of temperature (and sometimes light) FLUCTUATIONS in triggering a shift to the next stage in the germination sequence. Of importance for propagating Torreya is the likelihood that, unlike experimental lab conditions, dormant seeds in the natural world will inevitably experience FLUCTUATIONS in temperature that can greatly alter the timing and sometimes percentages of success. One implication is that "winter" cycles that entail one or more significant warm spells alternating with near-freezing episodes in the soil surroundings of seeds might create enough of a warm-cold-warm-cold-warm cycle to prompt some seeds (especially if shallow planted) to germinate at least a radicle (if not also a shoot) in the first spring or summer — which is otherwise highly unusual:

"Fluctuating temperature effects can be interpreted as a [dormancy breaking] factor, the dose of which terminates dormancy in a certain fraction of the seed population."

Seed dormancy affects seed-planting practices

The extended dormancy of Torreya seeds makes them especially valued by RODENTS.

Consider: Because WHITE OAK tree species bear seeds that germinate a radicle almost immediately after dropping from the tree in autumn, they are of little value to squirrels in their quest to bury seeds for later consumption. In contrast **RED and BLACK OAK tree species produce acorns that do not germinate until spring** — so squirrels are eager to collect, disperse, and bury these acorns for consumption throughout the winter.

TORREYA is even more valuable because squirrels can depend upon these seeds not only during the winter but equally as a

food source throughout the spring, summer, and usually a second winter, too, before germination degrades the seed's food value (radicles tend to be inedible). A helpful paper on this topic of squirrel seed preferences is:

• <u>"The Proximate Basis of the Oak Dispersal Syndrome: Detection of Seed Dormancy by Rodents"</u>, 2001, by Michael A. Steele et al., *Integrative and Comparative Biology* Torreya Guardians have experienced the skills and determination of rodent seed predators the hard way: Outdoor cages and wire mesh must be installed perfectly (below ground as well as above) to keep both arboreal and burrowing rodents from raiding the seeds.

Among the Torreya Guardians who have tried **direct planting into forest soil, nearly all seeds usually disappeared** — until we discovered solutions. Seeds must be **planted deep enough (4+ inches) to escape olfactory detection** or covered over by a rock that a squirrel cannot move.

As to burrowing rodents (voles and chipmunks), it has proven important to learn which elements visible on the ground surface attract the burrowers (such as tangles of fallen branches or near logs). Our best advice (as of 2022) is to avoid such debris. Also important is to plunge a kitchen knife into the soil of a prospective site as a final test; it is easy to sense a burrow when the knife penetrates one.



Visit a photo-rich, lengthy webpage on this website to see numerous examples of success and failure in Torreya Guardians attempts in <u>"Free-Planting Torreya Seeds"</u> directly into forest soil.

The fact that **each seed needs to remain undetected for at least 18 months**, makes the odds of escaping rodent seed predators even less in our favor. Nevertheless, there are substantial benefits to planting seeds directly into forest soil, rather than beginning with germinating and growing seedlings in pots. Like other ancient plants (and many modern taxa, too) **Genus Torreya relies upon arbuscular mychorrizal fungi** to not only assist nutrient transfer but in order to develop any root hairs at all):

"Mycorrhizal networks are important for seedling establishment in perennial vegetation. The fact that seedlings that germinate in perennial communities, with existing mycelial networks, often become quickly colonized by mycorrhizal fungi (e.g. within 3 to 6 days after seedling emergence) is probably very important because small seedlings then have immediate access to a low-cost 'nutrient adsorption machine', provided and maintained by the surrounding vegetation." — Marcel Van der Heijden et al., "Mycorrhizal Ecology and Evolution: The past, the present and the future", 2015, New Phytologist

<u>FRED BESS is a Torreya planter in Cleveland, OHIO</u>. February 2016 he reported, "I have gotten **almost 100%** germination on **150 seeds from the 2014 crop**. As of now there are only 13 seeds that have not sprouted. It would seem they germinate better after double stratification [2 winters]....



Photo by Fred Bess, February 2016 (Torreya Guardian, Cleveland Ohio)

"When they arrived I put them into a 1-gallon ziplock bag with about 4 cups of slightly damp peat/soil mixture and placed it under the bench in my greenhouse (temperature rarely dips below freezing there).

"I checked the bag beginning Spring 2015 weekly and removed any that germinated, then resealed the bag and placed it back under the bench.

I hadn't looked at the bag since about Thanksgiving 2015. To my surprise, today (February 6, 2016) I found that all but 13 of the rest of the seeds have germinated. Most are just showing the radicle; a few have sprouted significantly."



Fallen seeds are fair game for squirrels. But squirrels cannot raid seeds still hanging from a tree-form of Torreya, which is the growth form arising from seeds.

Squirrels are repulsed because torreya leaves are too prickly, and the seeds are borne too far out on slim, dangling branches for any squirrel to access.

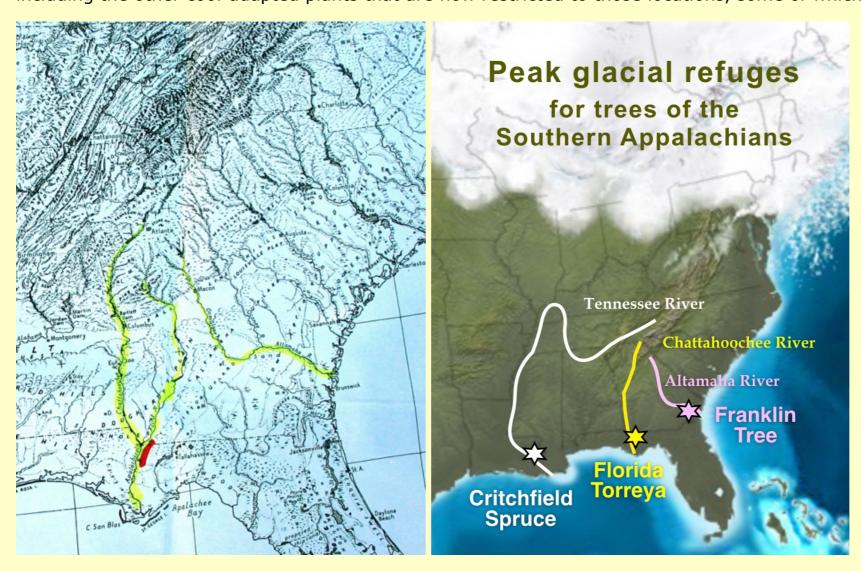
LEFT: <u>A. J. Bullard</u> with his Torreya taxifolia in Mt. Olive NC

TORREYA SEEDS CANNOT BE STORED. **Torreya's seed is recalcitrant and cannot be stored** except via cryo-preservation following laboratory manipulation of tissue culture via "somatic embryogenesis". The thousands of seeds currently being produced ex situ must therefore be used for plantings or will be lost. They cannot be inexpensively stored. In 2018, a paper published in *Nature Plants* confirmed that a large proportion of plants (especially endangered plants and notably trees) have recalcitrant seeds that cannot be stored: "Seed banking not an option for many threatened plants".

Assisted migration northward is a proven success

Florida Torreya is an evergreen conifer tree historically found only along a 65 kilometer stretch of the **Apalachicola River** of northern Florida and the adjacent sliver of southern Georgia. It favors the cool and shady ravines, known as "steepheads," that dissect the high bluffs of the river's east shore. Despite its current extreme endemism, the species was once a prominent midand under-story member of its forest community, which includes an odd mix of northern and southern species: towering beech and hickory next to tall evergreen magnolia, and surrounded by stubby needle palm.

The **Northwest Florida Environmental Conservancy** has information on <u>the unique steephead habitats</u> in their region, including the other cool-adapted plants that are now restricted to those locations, some of which are threatened or endangered.



LEFT: "Historically native" range of *Torreya taxifolia* (along Apalachicola River), marked by orange.

RIGHT: Connie Barlow made this image to mark the 3 primary river systems by which floating seeds could swiftly travel southward — and the primary "left behind" tree species associated with each. (Consider that floating is no dispersal method for heading upstream.) Critchfield Spruce went extinct. Franklin Tree (Franklinia) was seen and named by the earliest botanists, who carried its seed back to their home in Philadelphia and planted it there. But the tree was never again seen in its discovery site near the mouth of the Altamaha River.

A recent attempt by **The Nature Conservancy** to restore horticulturally grown Franklin seeds in New England to its peak glacial refuge **ended in failure**. (This story is reported in "Have Tree Will Travel, by Kevan Williams, Sept 2014, Landscape Architecture Magazine.)



Florida Torreya survived the Holocene warming in its peak glacial reserve in the Florida portion the Chattahoochee River system.

But human-caused additional warming made it vulnerable to a number of diseases in its peak glacial refuge, such that it pretty much stopped producing seeds in its historically native range in Florida by the 1960s.

Fortunately, Torreya Guardians <u>achieved seed production beginning in 2017</u> at one of its "assisted migration" plantings in Ohio:

PHOTO: Fred Bess in Cleveland, Ohio, shows some seeds ripening (October 2018) in his Florida Torreya orchard.

• Below is how the <u>1986 recovery plan for Torreya taxifolia</u> (its first) speaks of Florida Torreya's distribution. This plan is online and contains more background information than do the recovery plan <u>updates of 2010 and 2020</u>.

The Florida torreya ranges primarily along the east side of the Apalachicola River from near Bristol, Liberty County, Florida northward through Gadsden County and across the state line into southernmost Decatur County, Georgia (Figure 1). Trees have been found as much as eight miles east of the river. In Florida, portions of the habitat have been preserved in The Nature Conservancy's Apalachicola Bluffs and Ravines Preserve, in Torreya State Park, and in Chattahoochee city parks. In Georgia, the tree is present on land owned by the U.S. Army Corps of Engineers at Lake Seminole, Decatur County (Kurz 1938b, Savage 1983a, Butler 1981). Torreya taxifolia is most abundant in the Rock Creek drainage of Torreya State Park (Southeastern Wildlife Services, Inc. 1982). One small population of torreya is on the west side of the river at Dog Pond in Jackson County, Florida (Kurz 1938a, Milstead 1978). The Nature Conservancy is working to preserve this site, which is a beech-magnolia forest.

• <u>"Anachronistic Fruits and the Ghosts Who Haunt Them</u>, by Connie Barlow, 2001, *Arnoldia* pp. 14-21. (Also via <u>Researchgate</u>.)

BARLOW WRITES: "Arnoldia editor Peter del Tredici asked me to write this article, which focuses far more on the fruit characteristics and paleohistory of genus Torrreya than does the 2004 paper by Barlow and Martin, "Bring Torreya taxifolia North Now" — which is the most cited. The last section of this article, pages 19-21, present an exclusive focus on torreya."

EXCERPTS: "... The proximate cause of Torreya taxifolia's imminent extinction, and thus the cause that gets all the attention, is disease. Some thirty pathogens are known to infest it, but no single disease seems to be the culprit.... The genus Torreya was once distributed throughout the Northern Hemisphere. Range fragmentation has created distinct species in eastern China, patches of the Coast Range and the Sierras of California, and the Apalachicola of Florida. During the coldest times of the



Volume 61 • **Number 2** • **200**?

Arnoldia (ISSN 004–2633; USPS 866–100) is published quarterly by the Arnold Arboretum of Harvard University. Second-class postage paid at Boston, Massachusetts.

Anachronistic Fruits and the Ghosts Who Haunt Them

Connie Barlow

hirteen thousand years ago, the Age of Great Mammals came crashing to a close in the Western Hemisphere. Lost were the giants of the elephant clan: the mammoths, mastodons, and gomphotheres, which had maintained a presence in North America for twenty million years. The native horses, a tall camel, and all but one species of pronghorn—each group from a lineage thought to have originated in North America—vanished from the plains. Gone, too, were the strange beasts that had evolved in



Reunited: osage orange and mastodon. Shown here is surely the first time in thirteen thousand years that the fruit of osage orange. Maclura pomifera, has touched a molar of its missing partner in evolution, Mammut americanum.

South America during millions of years of continental isolation: ground sloths as massive as elephants, hippo-like toxodons, and lumbering,

Pleistocene, the Apalachicola, with its moderate climate and rich soils, was a refuge for the trees and forbs that now enrich the Cove Hardwood forest of Great Smoky Mountains National Park, 375 miles (600 km) to the north. After the ice retreated, most of the plants hitched rides from wind and animals and moved back north to their pre-glacial home. Torreya seems to have been left behind.... Global or regional extinction of an animal partner (or partners) may be the root cause of the tree's current distress. Torreya is probably not ideally suited for the warmth and humidity of today's Apalachicola region. It wants to head north, but it hasn't found a vehicle....

"... Squirrels that fed on torreya seeds on the east side of the river would be unable to carry them across water to the west side, and if the rich soils of the Apalachicola are isolated from rich soils to the north by a barrier of sandy soils, then the squirrels would also be unable to disperse the seeds farther north. Squirrels may thus be a disperser, but they apparently are not the right disperser for helping this tree reclaim its pre-glacial range. This explanation would account for the seemingly paradoxical fact that until the 1950s, Florida torreya was the seventh most abundant tree species in an astonishingly small patch of 'native' habitat.

"Perhaps the best evidence that Florida torreya may be suffering from an inability to track climate change is that before the blight took hold, this tree was planted hundreds of miles north of its Florida habitat in the mountains of North Carolina, near Asheville. There, on the Biltmore Estate, the torreyas are thriving, and the females produce abundant seeds. 'Flower beds often abound with seedlings planted by squirrels,'reports Bill Alexander, landscape historian at the Biltmore. During his 23 years there, Alexander has watched the torreyas stand up well to a five-year drought. And in the winter of 1985 the thermometer plunged to minus-20 degrees Fahrenheit, yet 'our trees smiled right through,' he told me.

"For a number of years, Alexander had been thinking that 'Florida' torreya really belonged back in North Carolina. So he was delighted to hear of the lost disperser theory. A megafaunal ghost? If so, the ghost may well be a large extinct tortoise, I suggested, as reptiles are far more tolerant of plant terpenes than are mammals, and as the thin 'shell' protecting the large single seed of this conifer offers scant protection against molars.

"One must not, however, ponder the plight of the Florida torreya in isolation from its sister species. In contrast to Torreya taxifolia, California's torreya (Torreya californica) is maintaining its population, as are the several Asian species of Torreya — all of which bear nearly identical propagules. Nevertheless, all occupy restricted geographic ranges. What if the entire genus lost its key dispersers and now depends on the local activities of squirrels? Bill Alexander and I easily came up with two plausible explanations for the differences in endangerment, based strictly on geographic differences. In eastern North America, the climatic effects of the Ice Sheet reached much farther south than was the case in either western North America or eastern Asia, forcing the Appalachian species to take refuge at a lower latitude. Perhaps even more significant is that latitudinal migration was the only option for Florida torreya as the climate warmed. In contrast, torreya species in California and in Asia could head upslope. These torreyas are native to mountainous regions, where altitudinal gain facilitated by nothing more than squirrels could help the trees keep pace with a warming climate.

"Such unsubstantiated and untested leaps of speculation are normally not well received within the scientific community — but these are not normal times. Without some drastic breakthrough in the management of Florida's wild population of torreya trees, Torreya taxifolia will, within fifty years, almost surely be extinct outside of botanical gardens. Perhaps it is time to help this torreya gain rootholds of wild populations in the mountains of North Carolina.

"Such is not, alas, how things are done with endangered species — the exception being the recent return of the California condor to its Pleistocene home near the Grand Canyon. Native territory is regarded as the last best place to be. But what is 'native'? How far might we justifiably reach back in time for a benchmark? In a study of endangered species published in 2000, Rob Channell and Mark Lomolino concluded that 'most species examined persist in the periphery of their historical geographic ranges.' If habitat at the periphery of historical range is adequate but not ideal, then the last place a troubled species is found may not, in fact, be the best place to assist its recovery.

"Transplantation across great distances is an uncommon and controversial technique for biodiversity conservation today. But as the greenhouse effect ratchets up temperatures and reroutes rainfall, and as botanical preserves become even more isolated islands in a sea of human development, long-distance transplantation will become the norm. If gardening a few local patches of endangered plants is tough today, it's going to get a lot tougher when, like it or not, we become gardeners of the planet [citation Daniel Janzen, 1998, "Gardenification of wildland nature and the human footprint".] Helping plants track climate change from one patch of habitat to another will be a routine tactic for conserving biodiversity decades hence. Is it too early to begin now with Florida torreya?"

Gopher Tortoise testing of Torreya seed dispersal

Summary by Connie Barlow, July 2020:

2015 EXPERIMENT LAUNCHED by Jason Richardson, PhD Student, Department of Integrative Biology, University of South

Florida. Feb 3, 2015, Jason Richardson wrote to Lee Barnes:

... I would like a pack of seeds. I assume Connie or Jack had me added to this list. If you are unfamiliar, I am a PhD student at the University of South Florida. For my dissertation, I am examining the effects gopher tortoises have on plant community composition, and also how they affect germination of seeds in their diet. I am particularly interested in how they may enhance germination of rare and endangered plant seeds, and if they may be used in conservation efforts for such plants, and thus I emailed the Torreya Guardians about obtaining seeds." February 9: "I will be quantitatively testing germination rate and percentage as well as qualitatively examining the seed coat structure via electron microscopy. These two methods will be done both for ingested and non ingested seeds. I had not considered the stratification effects, could I get a pack of 20 of both stratified and non? More is always better for statistical analyses, but I think this will be a good start to see where it leads."

Note by Barlow: Lee Barnes sent Jason **seeds from the 2014 harvest**, but they were already cleaned of the fleshy covering that would be what tortoises are interested in. Jack Johnston sent **seeds with green flesh in 2015**.

2020 REPORT OF RESULTS by Jason Richardson via email to Connie Barlow. July 21, 2020, Jason Richardson wrote to Connie Barlow:

"Seeds were unable to be consumed by gopher tortoises (too large). Any possible chelonian seed disperser is probably extinct. Seeds were fed to a sulcata tortoise at Zoo Tampa. Some were crushed but we did manage to collect a good number of them passed seemingly intact. I unfortunately had no germination success for these seeds, nor for the unpassed seeds. I have since graduated and am no longer working in science. If you are interested I can give you some other researchers who may be interested in trying to replicate or further this work."

Supplemental information by Connie Barlow: (1) Because Torreya seeds usually require 2 winters of cold stratification before germinating, it is possible that less time and/or insufficient cold were available for study prior to the need to publish results. (2) Richardson's PhD thesis can be found in full here; torreya seed experiments are not mentioned in it, however, "Seeds from the two fleshy-fruited species, O. humifosa and P. angustifolia, germinated in significantly greater proportions and faster after gut passage than seeds that did not pass through the gut." (3) Wikipedia entry on Sulcata Tortoise: "The African spurred tortoise (Centrochelys sulcata), also called the sulcata tortoise, is a species of tortoise, which inhabits the southern edge of the Sahara desert, in Africa. It is the third-largest species of tortoise in the world, the largest species of mainland tortoise, and the only extant species in the genus Centrochelys."

- <u>The Florida Torreya and the Atlanta Botanical Garden</u>, by David Ruland, in *Conifer Quarterly*, pp. 10-14 (2007). *Note:* As of 2019, David Ruland is Greenhouse Manager for Atlanta Botanical Garden.
 - ... According to fossil records, the Florida torreya is estimated to be over 165 million years old. Like many other conifers with such an impressive age, it was once scattered throughout the northern hemisphere. Scientists theorize the species was driven south by glaciers that once covered the northern latitudes. When the glaciers retreated, the Florida torreya was left isolated in small microhabitats of the southeastern United States, where it thrived for thousands of years.
 - ... Many of the original Arnold Arboretum cuttings have matured into cone and seed producing trees [at Atlanta Botanical Garden] that, in total, form **over 500 viable seeds per year on average**. These plants are grown in the ABG "seed orchard" and propagales produced from these seeds have been used to facilitate the next phase in the recovery of this species.
 - ... In 2002 ABG initiated a collaborative project with Florida State Park Service that involved reintroduction of seedlings into ravines at Torreya State Park (TSP), where *Torreya taxifolia* has been extirpated.... Great efforts are made to ensure that introduced plants are not planted in ravines where existing plants occur. The plants are bare-rooted prior to placing in the native soil. Four treatments are used on the outplanting: fungicide, fertilizer only, fertilizer and lime, and control. These experimental transplants will help determine the optimal treatment, if any, that is needed for future success reintroducing this species. A total of 200 seedlings have been outplanted in TSP and the survival rates so far are encouraging.
 - ... Despite the successes of the conservation program, the Florida torreya faces a long road ahead to recovery. Even if wild populations were capable of producing viable seed, the Florida torreya would seem incapable of expanding its limited range due to a lack of a natural dispersal agent. The aforementioned squirrel has proven to be capable of seed dispersal but almost certainly is not the original prime disperser. It was most likely a large extinct animal, although speculation on such matters in the plant world is endless.
 - ... The concern over the Florida torreya's inability to reclaim its former habitats has given rise to a movement among conservationists called "assisted migration." The basic idea is to see populations of *T. taxifolia* moved further north into more hospitable climates. It would be encouraged to integrate naturally, thereby securing the tree in the wild again. *Torreya taxifolia* does thrive in areas such as Asheville, North Carolina and even much further north. Indeed, as is the case with many types of plants, the cool night / warm day temperature differential would seem to be conducive to a healthier tree. The Atlanta Botanical Garden is not a proponent of such measures. It is prudent to establish safe-guarded populations in cooler climates within the confines of cultivated or human disturbed areas, not in pristine natural habitats. Therefore these plants can be further evaluated in a botanical garden setting and seed development encouraged without creating further ecological disturbance.

The Florida torreya is a glacial relic, seemingly stranded in an increasingly hostile niche without any natural means of escape or survival. This tree would certainly be doomed without the intercession of concerned individuals and institutions....

• October 2019 / Connie Barlow / VIDEO by Tallahassee Public TV station on Hurricane Michael Damage

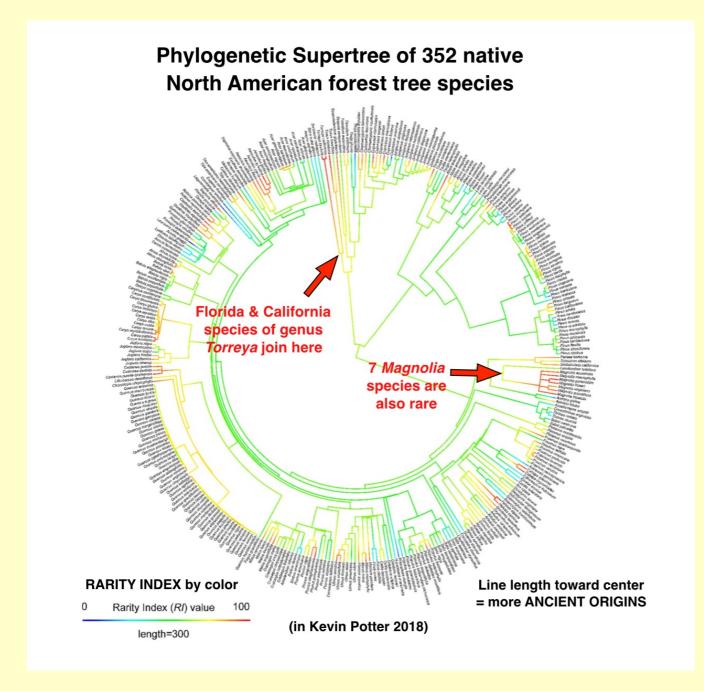
Six-minute video titled <u>Torreya State Park After Hurricane Michael: One Year Later</u> was produced by WFSU, the public TV station affiliated with Florida State University in Tallahassee. The video begins with a look at the two unlikely survivors of the hurricane where the entrance road ends in a parking lot. Both Gregory House and a planted little grove of torreya trees at the lawn edge survived, the tall trees fallen all around them.

For viewers and readers familiar with the paleoecological foundation undergirding the drive for "assisted migration" poleward of the glacial relict Torreya tree, the video offers a few hints of the steephead ravine ecosystem similarities in the park to habitats now found in the southern Appalachians. The actions of Torreya Guardians are of course not mentioned. But the accompanying essay does say this:



"In the 1950s, a fungal blight wiped out a population of about 600,000 Torreya taxifolia in the region. The Florida Park Service, Nature Conservancy, and the Atlanta Botanical Garden have been working to revive the Florida torreya, a species whose future may lie in its likely ancestral home of North Carolina, where planted trees have thrived disease free."

• August 2019 / Connie Barlow / 2018 paper ranks genus *Torreya* as both very rare and ancient



Kevin M. Potter, Dept. Forestry and Environmental Resources of North Carolina State University, published a paper in the May 2018 online issue of the journal *Biological Conservation*:

"Do United States protected areas effectively conserve forest tree rarity and evolutionary distinctiveness?"

Connie Barlow added red type and arrows to the original figure, left.

Notice that the sister species in Florida and California of genus *Torreya* are among the rarest of 352 tree species native to North America.

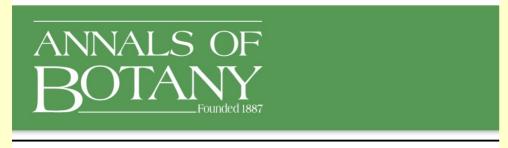
These two Torreya species also are among the most ancient tree lineages.

Together, rarity and age of origin call out for the highest levels of conservation attention.

May 2019 / Connie Barlow / New paper useful for understanding male/female flexibility in Torreya

During our site visit to the <u>mature Florida Torreya trees in Louisiana</u>, our guides recounted their experience with the largest specimen beginning as male and then starting to produce some female buds on various branches — culminating in seeds that fell and germinated beneath the parent tree. A <u>2019 paper on Striped Maple of eastern North America</u> (a subcanopy species, just as is Torreya) can help us understand how to observe and possibly predict an individual's ability and propensity to begin producing seeds. Access <u>full text</u>.

EXCERPTS: "... Male-dominated sex ratios occurred consistently across study sites and the 4 years that sex expression was monitored. Approximately one-third of trees [studied as single branches cut and grown in a lab conditions] changed during any 2-year period. The five most common transitions were, in descending order of frequency: from non-reproductive to male, male to full or partial female flowering, female to dead, and from partial to full female flowering...."



Time for a change: patterns of sex expression, health and mortality in a sex-changing tree

Jennifer Blake-Mahmud ™, Lena Struwe

Annals of Botany, mcz037, https://doi.org/10.1093/aob/mcz037

Published: 22 April 2019 Article history ▼

"... We have shown that in the sexually plastic tree *Acer pensylvanicum* a variety of factors influence expressed sex. Chief among them are previous sex and the health of an individual. Although the general theory regarding ESD in dioecious plants has indicated that females are often found in relatively better condition and at larger sizes, we find the opposite pattern in this species.... We show that mortality is disproportionately high in females...."

The Strange Mix of Vegetation Along the Apalachicola River





LEFT: hickory trunk in front of evergreen magnolia canopy, with trunk of American Beech at center.

RIGHT: Several shrubby palm species beneath a large beech in Florida's Torreya State Park, along the Apalachicola River. The botanical mix in the "steephead ravines" in this park is a treasure because the same site served, just 18,000 years ago, as a crucial "pocket reserve" in which the botanical richness of today's southern and central Appalachians took refuge at the peak of the last glacial advance.



Glacial Stragglers

More from Alex Eilts

Autoplay next video

VIDEO: "Glacial Stragglers": Here the Apalachicola is presented as a peak glacial refuge.

FLORIDA ANISE is featured as a species that didn't get very far north post-glacial (timecode 12:48).

FLORIDA YEW (13:50) and FLORIDA TORREYA (14:25) are featured as species that were entirely left behind. (Scientifically, "glacial relicts".)

Quote by Alex Eilts: "Ironically, they are now trapped in the same place that sheltered them in the past. But now as the the climate warms, their refuge — turned prison — may lead to their extinction."

Note: Mark Gelbart hypothesizes that Mastodons, rather than tortoises (or squirrels) were the dispersers of Torreya taxifolia during the Pleistocene. See also his blog contending that Torreya is missing its megafaunal disperser. In the latter blogpost, Gelbart draws from a 1978 book by Charles Wharton, The Natural Environments of Georgia, in which the Torreya's very limited habitat in Florida is described as "torreya ravines." Associated plants are listed:

"The dominant trees in a torreya ravine are red maple, southern sugar maple, beech, magnolia, basswood, elm, torreya, and sabal palm. Most of these species have northern affinities and are more commonly found in Appalachian cove forests. Other plants found in torreya ravines also represent species of northern affinities such as strawberry bush, hydrangea, and redbud. Wharton found torreya growing with beech, sourwood, and plum in the Faceville Ravine on the Flint River."

ASSOCIATED SPECIES: "Florida torreya is not included among the forest cover types established by the Society of American Foresters but is commonly known to be among the oak-gum-cypress or oak-pine types. In 1919, it made up about 4 percent of the forest along the Apalachicola River. The most commonly associated species are beech (Fagus grandifolia), yellow-poplar (Liriodendron tulipifera), American holly (Ilex opaca), Florida maple (Acer barbatum), loblolly pine (Pinus taeda), spruce pine (P. glabra), white oak (Quercus alba), eastern hophornbeam (Ostrya virginiana), and sweetgum (Liquidambar styraciflua). Shrubs and lianas associated with Florida torreya are poison-ivy (Toxicodendron radicans), greenbriar (Smilax spp.), crossvine (Bignonia

capreolata), yaupon (Ilex vomitoria), Florida yew (Taxus floridana), blackberry and dewberry (Rubus spp.). Forbs, grasses, and sedges include sedges (Carex spp.), panic grass (Panicum spp.), partridgeberry (Mitchella repens), little sweet Betsy (Trillium cuneatum), giant cane (Arundinaria gigantea), and American climbing fern (Lygodium palmatum)." — <u>Silvics Manual, Volume 1:</u> <u>Conifers</u> (Click on Florida Torreya).

• VIDEO: Site Visits to Florida's Endangered Torreya and Yew Trees



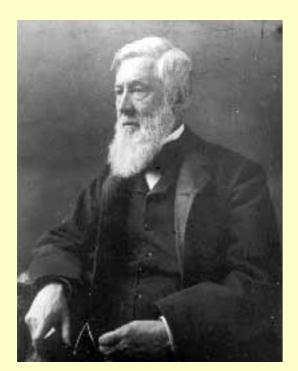
Connie Barlow presents 15 years of baseline photos and videos she recorded of Torreya taxifolia and Taxus floridana in their historically native range in Torreya State Park in northern Florida. Photos of spectacular California Torreya trees, recorded by Barlow in 2005, show the potential for Florida Torreya recovery efforts to strive for. Fred Bess shows (in 2014 video) 2 Asian conifers (Cephalotaxus and Cunninghamia) used in landscaping that are Torreya look-alikes. Paleoecological evidence that Florida's Torreya was "left behind" in its peak glacial refuge supports "assisted migration" actions.

63 minutes - assembled & published, January 2016

• Learn why T. tax is at the brink of EXTINCTION.

Classic Writings on Florida Torreya

In the spring of **1875**, distinguished Harvard botanist **Asa Gray** embarked upon a trip to the panhandle of Florida, to "make a pious pilgrimage to the secluded native haunts of that rarest of trees, the Torreya taxifolia". The trees observed by Gray grew up to a meter in circumference and were as much as 20 meters tall.



A PILGRIMAGE TO TORREYA.1

ORDERED to go south until I should meet the tardy spring and summer, I was expected to follow the beaten track to east Florida. But I wished rather to avoid the crowd of invalids and pleasure travelers, and turned my attention in preference to western Florida, determined that, if possible, I would make a pious pilgrimage to the secluded native haunts of that rarest of trees, the *Torreya taxifolia*.

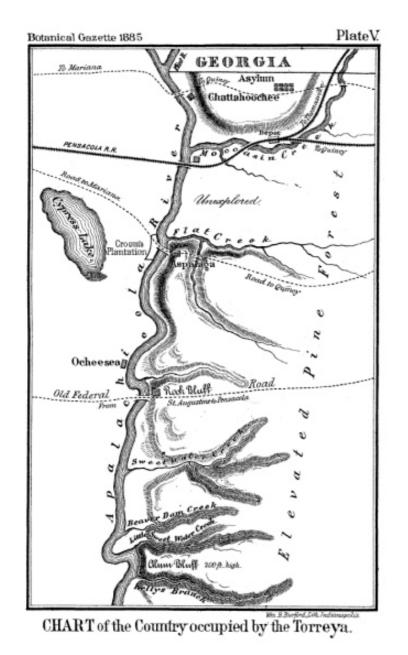
"... One young tree, brought or sent by Mr. Croom himself, has been kept alive at New York [Central Park] — showing **its aptitude for a colder climate than that of which it is a native** — and has been more or less multiplied by cuttings..."

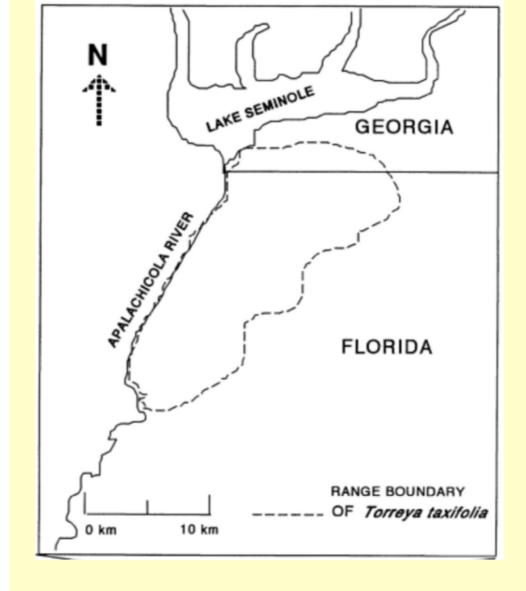
EXCERPTS FROM "A PIOUS PILGRIMAGE":

"... The people of the district knew it by the name of 'Stinking Cedar' or 'Savine' — the unsavory adjective referring to a peculiar unpleasant smell which the wounded bark exhales. The timber is valued for fence-posts and the like, and is said to be as durable as red cedar. I may add that, in consequence of the stir we made about it, the people are learning to call it Torreya. They are proud of having a tree which, as they have rightly been told, grows nowhere else in the world...

"The largest [Torreya] tree I saw grew near the bottom of a deep ravine; its trunk just above the base measured almost four feet in circumference, and was proportionally tall. But it was dominated by the noblest Magnolia grandiflora I ever set eyes on, with trunk seven and a half feet in girth.... Seedlings and young trees are not uncommon, and some old stumps were sprouting from the base, in the manner of the California Redwood...."

A.W. Chapman's Torreya Experience, 1885





LEFT: Map published in 1885 of Torreya's native range, in report by A.W. Chapman

RIGHT: Map of 20th century range of *Torreya taxifolia*, from "Defining Indigenous Species: An Introduction" by Mark W. Schwartz, chapter in *Assessment and Management of Plant Invasions*, 1997.

Online access to **Chapman's report** in the April 1885 Botanical Gazette:

Torreya taxifolia "occupies a narrow strip of land extending along the east bank of the Apalachicola River from Chattahooche on the north to Alum Bluff on the south, a distance of about twenty miles, and forming a continuous forest, but in detached and often widely separated clumps or groves, generally mingled with, or overshadowed by, magnolia, oaks, and other native trees. . . It is a wild, hilly region, abounding in rocky cliffs and deep sandy ravines ("spring-heads") and unlike in scenery and vegetation any other part of the low country known to me. To these cliffs, and to the precipitous sides of the ravines, the tree appears to be exclusively confined; for it is never seen in the low ground along the river, nor on the elevated plateau east of it, nor, indeed, on level ground anywhere. Hence, although the suggestion may appear a startling one, were the trees of the whole region growing side by side in one body, I estimate that an area of a few hundred acres would suffice to contain all of them.

... But its chief value is due to the **remarkable durability of its wood when exposed to the vicissitudes of climate**; for it is credibly reported that some fences constructed of it sixty years ago still remain in sound condition. In consequence of this peculiarity it is now extensively employed by the inhabitants of the surrounding country for posts, shingles, and other exposed constructions. In view of these facts, **the future of our Torreya is a matter calculated to excite very grave apprehensions**. A tree possessed of such valuable qualities, occupying an area so limited in extent, and in the midst of a population where the old rule of "Let him take who has the power, And let him keep who can" has unlimited sway, is destined, it is to be feared, to ultimate extinction.

Let us indulge the hope that the interest which is beginning to be manifested in regard to the preservation of our forests generally, may result in measures statutory or otherwise for its preservation.

1890 Editorial Reports Common Name Switch to Torrey-Tree

MAY 7, 1890 issue of Garden and Forest, page 222 excerpt:

"...Trees, which are usually of importance to man or sufficiently conspicuous to attract his attention, obtain naturally **local vernacular names** before science imposes others on them, and the common names once engrafted on a language, almost always hold their own among the people of the country where the trees are found. It was a matter, therefore, of much interest and some surprise to hear recently, in western Florida, the *Torreya taxifolia*, one of the rarest of all our trees, spoken of generally as the **'Torrey-tree'**; and to find that Stinking Cedar, the unattractive name by which this tree was first known to the inhabitants of western Florida, was gradually being replaced by that of on of the Nestors of American botany.

The reason for this change is found perhaps in the fact that this tree, from its rarity, the interest attached to the geographical distribution of the small genus to which it belongs, and the reverence which his successors have always felt for the name of **John Torrey**, has several times been visited in its remote and isolated stations on the banks of the Appalachicola by men of science from distant parts of the country. When the people of the region, therefore, found that men of mature years

and apparently in the enjoyment of all their faculties had journeyed thousands of miles merely to look at a tree which they had always considered as valuable only because it furnished indestructible material for fence posts, their own interest and curiosity became aroused; and therefore hearing these eccentric strangers talking always about Torrey and Torreya, the name has gradually become fixed, and now 'Torrey-tree' may often be heard in at least two or three counties of west Florida."

EDITOR'S NOTE: This 1905 publication contains the first suggestion that Torreya's preferred habitat lies northward of its endemic Florida range. Access online the entire report.

NUMBER 3 VOLUME XXXIX

BOTANICAL GAZETTE

MARCH, 1905

GAMETOPHYTES AND EMBRYO OF TORREYA TAXI-FOLIA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXIX.

JOHN M. COULTER and W. J. G. LAND.

(WITH PLATES A, I, II, III)

Torreya taxifolia Arnott¹ occurs in a narrow belt along the eastern side of the Apalachicola River, extending from the southern boundary of Georgia for about thirty miles southward (1). In April 1904 this region was visited by H. C. Cowles of this laboratory, among whose notes the following are of interest in this connection:

My visit was to the northernmost colony, west of Chattahoochee village, and close to the Georgia line. The distribution lines on Chapman's map (1) would lead one to suppose that the tree is xerophytic and frequents the steep and dry eastern bluffs. I was much surprised to find that it was confined (in the Chattahoochee station at least) to the extremely mesophytic slopes of ravines, growing exclusively in the shade of trees, and in places that are continually moist, preferably on slopes facing north. The northern and southern known limits of the tree are only about thirty miles apart, and the east-west range is much less. Furthermore, on account of the great economic value of the wood, and the familiarity of the tree to all the inhabitants of the region, the likelihood of finding other areas is very slight.

It is associated with a remarkable and somewhat extensive group of northern mesophytic plants, and the conclusion is irresistible that Torreya is a northern plant of the most pronounced mesophytic tendencies, and to be associated with

¹ Unfortunately, Torreya was used at least three times as a generic name, in as many families, before 1838, the date of the publication of Torreya Arnott. Hence Arnott's genus has been replaced by Tumion Raf., and our species becomes Tumion taxifolia Greene. In the present paper, however, the more familiar name is used for onvenience.

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such forms as the beech-maple-hemlock forms of our northern woods, our most

MARCH

mesophytic type of association. Probably it never becomes a large tree, although farmers always cut the trees as soon as they become at all usable. Rarely were any found over 30cm in diameter or more than 9 to 12m high. It has remarkable capacity for vegetative reproduction, almost equaling the redwood in this respect. Many suckers issue from cut stumps, and even from fallen trunks; even rotten stumps show vigorous suckers, and it seems to be as tenacious of life as the poplar. Staminate trees appear to be the more numerous; however, when in blossom they are far more conspicuous than are the pistillate trees, and the conclusion as to proportion may not hold.

Note that in this **1905** report, the author posits that

"It is associated with a remarkable and somewhat extensive group of northern mesophytic plants, and the conclusion is irresistible that Torreya is a northern plant of the most pronounced mesophytic tendencies, and to be associated with such forms as the beech-maplehemlock forms of our northern woods, our most mesophytic type of association."



ABOVE RIGHT: In 2013 AJ Bullard demonstrated on his Torreya taxifolia tree in Mt. Olive North Carolina that this species actually will produce both female cones (top branchlet) and male cones (middle branchlet) on a single individual. Lower left branchlet shows vegetative buds. This condition is termed **subdioecious**, and it is documented in the Japanese Torreya.

In an email to Lee Barnes on 9/29/16 Frank Callahan wrote of his mature Florida Torreya trees in Medford OR: "Both of these trees exhibit male and female 'flowers', which is unusual for this taxon." A 1904 issue of The New Phytologist provided strong evidence of male and female reproductive specimens on the same individual of *Torreya californica*:

THE PHYTOLOGIST. Vol. 3. Nos. 6 & 7. JULY 27TH, 1904.

SPORE FORMATION IN TORREYA CALIFORNICA. By Agnes Robertson, B.Sc.

... The tree of Torreya califoniica at Orton Longueville bears both staminate cones and ovules. Mr. Harding has kindly given me the following account of their distribution. " The ovules and staminate flowers are not confined to one side of the tree, but for some years I have noticed that the ovules are more abundant on the side facing the north, also a sprinkling of male that side as well; but the male is certainly more abundant (four times as many) on the south side. There are less (about half as many) ovules on the south side."

The above paper is very detailed re reproductive structures and timing of development. Here are a few extracts of note:

The genus Torreya now consists of four species of restricted distribution, inhabiting respectively Japan, China, Florida, and California. In Cretaceous times it was much more widely spread, being also recorded from Greenland, France, Bohemia, and other districts. Such a history suggests that the genus, which has been comparatively little studied, is an old one, and might be expected to shew primitive characters.

... The peculiar ruminated endosperm of the seed in its second year of development has been described by Professor F. W. Oliver in this journal and he has drawn attention to its similarity to that of certain paleozoic forms. The vascular anatomy of the seeds, which is unique and isolated among recent plants, and also presents analogies with fossil types, has been discussed by the same author in a paper published in the Annals of Botany in 1903' and based on a lecture delivered before Section K of the British Association at the Belfast Meeting in 1902. These topics will be dealt with in greater detail in a future memoir. A further contribution to our knowledge of the plant was made by Mrs. A. G. Tansley (Miss Edith Chick), who published an account of the structure of the seedlings in the NEW PHVTOLOGIST for May 1902 (Vol. 11. p. 83). The young plants shewed some strikingly primitive characters; centripetal wood was found in the cotyledons, which were lobed and adhered together like those of Ginkgo and the Cycads...

may remain dormant for a long time. For instance on one branch gathered this summer no cones had been developed on the parts of the axis corresponding to the years 1904, 1903 and 1902, while a considerable crop of cones occured on the 1901 wood. On another branch ripe cones were found on the 1903 and 1902 wood. At the base of the cone there are a variable number of pairs of decussating bracts. These get more scarious and filmy as we pass up the axis, and one or more of the uppermost pairs have fimbriated margins. During the winter which precedes their ripening season the young cones are completely ensheathed in their bracts, and it is not till the following spring that the bracts separate at the tip and disclose the sporophylls (Figs. 1, 2, 3). ... In dividing into two cells whilst still enclosed in the pollen-sac the pollen-grains of Torreya agree with those of Cephalotaxus and differ from those of Taxus...

The **ovules** of *Torreya californica* occur on the shoots of the current year, especially near the base.... [after the winter] Before the end of April the integument has over-topped the nucellus and the arillus has begun to appear... At **the time of pollination**, **three or four weeks later, a drop of liquid exudes from the micropyle**, and in this the pollen grains are caught....

"A Remarkable Colony of Northern Plants
Along the Apalachicola River, Florida, and Its
Significance"

by H. C. Cowles, **1905**

Report of the Eighth International Geographic Congress Held in the United States

KEY SECTION:

A REMARKABLE COLONY OF NORTHERN PLANTS ALONG THE APALACHICOLA RIVER, FLORIDA, AND ITS SIGNIFICANCE

By H. C. COWLES, University of Chicago

[Abstract.]

The topography of Florida in the neighborhood of the Apalachicola River is in striking contrast to the level areas in other parts of Florida and the adjoining States. There are high river bluffs and deep ravines with steep slopes. In these ravines, and especially on the northwardfacing slopes, is to be found a mesophytic association of plants that is abundant far to the north, but which reaches its southern limit here. Among the plants of this association are beech, maple (Acer floridanum), Mitchella, Hepatica, Sanguinaria, Epigæa, Anemonella, and many other species that dominate in mesophytic northern woods. In this association one finds two of our most notable endemic plants-Torreya and Croomia. It seems likely, then, that we should regard Torreya taxifolia as a northern mesophytic left stranded to-day only in Florida. It presumably is one of the plants that failed to follow up the last retreat of the Pleistocene ice, and is preserved here perhaps because of exceptionally favorable topographic conditions. These facts may help to determine the nature of the pre-Glacial climates, since Torreya was then a widespread form.

DISCUSSION

Dr. J. W. Spencer called attention to the canyons incising the submarine continental border as evidence of a great elevation during part of the Pleistocene period, which would favor the migration of northern plants to Florida, and, other things being equal, the remaining of the plants is an additional suggestion of the correctness of the hypothesis of the late elevations shown by the canyons.

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In this association one finds two of our most notable endemic plants — Torreya and Croomia. It seems likely, then that we should regard Torreya taxifolia as a northern mesophytic left stranded to-day only in Florida.

It presumably is one of the plants that **failed to follow up the last retreat of the Pleistocene ice**, and is preserved here perhaps because of exceptionally favorable topographic conditions.

Another archival piece: Frank Thone contributed a short section on "The Apalachicola River endemics" in the 1926 edition of Naturalist's Guide to the Ameericas:

"There is a colony of *Torreya taxifolia*, together with a number of other endemic and disjunct species along the bluffs of the Apalachicola River between Chattahoochee and Bristol. Are well drained, but at the same time thoroughly moist, because of the abundant seepage water and the low evaporation rates that prevail. Magnolia occurs among the trees, and scrub palmettos in the undergrowth are plentiful. *Torreya* grows all over the slopes of the ravines, from stream-bank to rim, wherever there is any shade. It is mostly an undergrowth tree, seldom reaching a height of more than 20 or 25 ft. or a trunk diameter of more than 6 in."



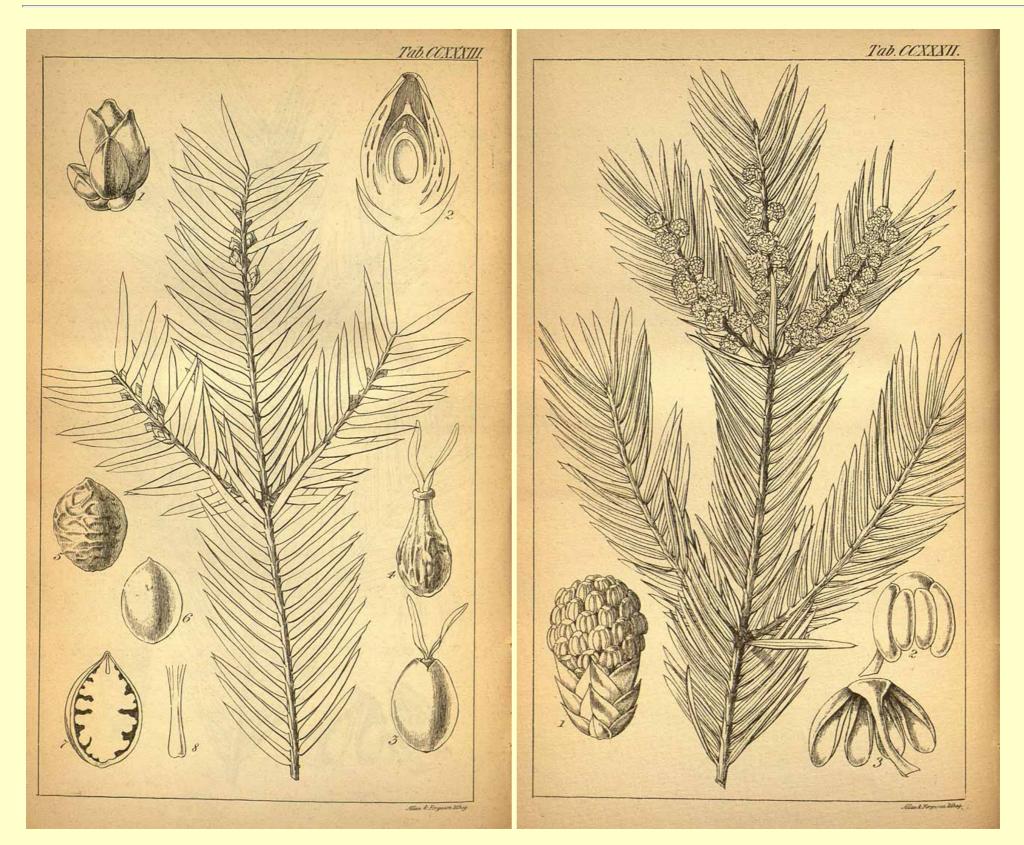
<u>Lee Barnes</u>, one of the founding Torreya Guardians (and a native North Carolinian), measures the growth of "Thoreau" T. taxifolia tree, four years after it was <u>planted at Corneille Bryan Native Plant Garden</u>, in Junaluska NC. (photo by Connie Barlow, May 2012). In spring of 2014, Lee rediscovered in his archives a paper he wrote for a graduate course in horticultural science in 1983. You can access a pdf of that paper: "Morphology of Torreya taxifolia".

In 2013, Torreya Guardians began trying to learn how best to encourage **symbiotic fungi (mycorrhizae)** to grow amidst Torreya's roots in our plantings, so Lee's 1983 observation is prescient: "Seedlings produce extensive root systems before much top growth. Also, numerous individuals have noted that Torreya spp. grow naturally slow. It has also been observed that **many species with thick roots grow slowly unless inoculated with mycorrhizae**. Currently, investigations are underway to determine if mycorrhizal inoculation will increase the growth rate of rooted cuttings and micropropagated plants." (p. 12)

Note: Four unpublished papers by Lee Barnes and his doctoral dissertation are in the "Literature cited" list of the **1986** "Florida Torreya Recovery Plan.



The Encyclopedia of Life online has a lot of **photos of genus Torreya** — especially the one Californian and several Asian native species. For example, the photo left of **ripe seeds of California Torreya** confirms that this sister species has the same seed shape and color as Torreya Guardians have documented of North Carolina plantings of the Florida Torreya. (If you click on the "original" link associated with each photo, you will sometimes find not only the original photo but detailed information on date and place.)



ABOVE: Click on images for links to these Torreya taxifolia archive pages of Hooker's Icones Plantarum, 1840.

In 2020 the **New York Botanical Garden reported archival research in collating the communications between Croom and Torrey** on the initial botanical recognition in Florida of this species as a new-to-science genus. Clips of the correspondence appear in this very helpful report: <u>"The Case of the Florida Nutmeg: Empowering Research on Endangered Plants"</u>, by Grace Constantino.

Environmental Status of the Stinking Cedar, Torreya taxifolia

RICHARD STALTER

Environmental Studies Program

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STEVE DIAL

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Torreya taxifolia Arn. is one of the rarest of Florida's trees. Its common name, stinking cedar, is derived from the disagreeable odor given off when the tree, its bark, branches, or leaves are bruised. Torreya was discovered by H. B. Croom near the Aspalaga Crossing on the Apalachicola River in 1833. Torreya occurs naturally in three counties in Florida: Gadsden, Liberty, and Jackson, and at one station in southern Decatur County, Georgia, just north of the city of Chattahoochee, Florida. The natural habitat of Torreya is limestone bluffs on the eastern banks of the Apalachicola River and its tributaries from Chatahoochee, south to Torreya State Park. One population of Torreya exists approximately twelve kilometers west of the Apalachicola River in the vicinity of Dog Pond, a small pond, near a much larger pond, Ocheesee Pond.

The objectives of the present study are: (1) locating populations or individuals of extant Torreyas in their natural range; (2) outlining methods which if followed may preserve *Torreya* in ravines and on limestone bluffs of the Apalachicola River and its tributaries, at Maclay State Gardens, and at Torreya State Park.

Three trips were made to the Apalachicola River in May 1980, January 1981, and July 1981 to locate populations of Torreya, Sites in extreme southern Georgia and bluffs along the Apalachicola River and its tributaries in northwestern Florida were examined to locate Torreya. These sites were: (1) Chattahoochee Nature Park, Chattahoochee, Jackson County. One Torreya approximately 0.3 meters tall was observed here. (2) Woods at the terminus of Satsuma Road West, Chattahoochee, Jackson County. Torreya was observed growing on moderate slopes of the woods associated with Pinus glabra, Fagus grandifolia, and Acer floridana. Several dead Torreyas, 4-8 meters tall, were mute evidence of the blight's effect. These and a dozen living Torreyas were within 200 meters of the road. (3) Florida 269 at Flat Creek, Gadsden Co., Florida. Four Torreyas were located within 10 to 50 meters of Flat Creek, 200 to 500 meters north of Florida 269; one plant, 1 meter tall, was located on the south side of the creek within 150 meters of the road. (4) Torreya State Park, Liberty County. Torreyas used to grow naturally in this park which was established as a Torreya preserve. Several planted specimens are located on the lawn in front of the Gregory House. Additional cultivated specimens are planted in the nearby woods. The planted Torreyas are approximately 2.5 meters tall and are badly infected with a fungal infection. Noel Wamer and I observed 20 smaller Torreyas south of the Gregory House on river bluffs overlooking the Apalachicola River. These Torreyas are on the sides of steep ravines. Taxus floridana, a plant that somewhat resembles Torreya, thrives here. (5) Aspalaga Landing, Gadsden County. We searched and found approximately 20 Torreyas on the limestone banks of a small tributary creek of the Apalachicola River near Aspalaga Landing. Several dead Torreyas, that may have been 7 to 10 meters tall while living, were observed in varying stages of decay. Here and in the other sites where Torreya grows, they were observed to be associated with Pinus glabra, Acer floridana, Fagus grandifolia, Ulmus sp., Magnolia grandiflora, and other species. (6) Ocheesee Pond, Jackson County. The tallest (2.3 meters) native Torreyas occur at Ocheesee Pond, located 11 kilometers west of the Apalachicola River. All of the largest trees were badly infected with blight. The population numbered one dozen individuals. (7) Maclay Gardens, Tallahassee, Leon County. Several dozen Torreyas are growing here and all are badly infected by blight. The largest Torreya is 10 meters tall and has a DBH of 0.25 meters. One of the Torreyas here produces seed. The work of a concerned horticulturist, Bob Bowden, resulted in the germination of 28 of 35 seeds collected in 1980. (8) Decatur County, Georgia. One small population of 24 Torreyas exists on the banks of a steep ravine just south of Lake Seminole. These trees were observed in the second ravine south of the Resource Manager's Office, approximately 0.8 kilometers north of Chattahoochee, Florida, perhaps 100 meters from the Georgia-Florida border. Several additional Torreyas were observed just south of the Georgia-Florida border. These ranged in size from 0.3 to 1.2 meters tall.

Torreya taxifolia has been planted in at least three locations in Georgia. Two mature Torreyas are located on Front Avenue in Columbus, Georgia's historic district. A dozen planted Torreyas are growing at Callaway Gardens, Georgia. These are males, fungus free, and range from 0.2 meters to 3.2 meters tall. Mr. Burl Turnage, Albany, Georgia, propagates Torreyas from cuttings, and distributes them throughout the United States (Butler 1981). Fourteen healthy trees ranging from 6 to 10 meters in height are thriving at the Biltmore Gardens, Asheville, North Carolina. These Torreyas produce seed and several seedlings have been observed near the parent trees (Timothy Dunford, pers. comm.). A male and female tree are thriving at the Brooklyn Botanical Gardens, New York. Two other Torreyas are growing at Planting Fields Aboretum, near Oyster Bay, New York. Additional trees may be growing on the estates of wealthy individuals along the eastern United States.

In March 1962, Drs. Godfrey and Kurz noticed that population of *Torreya* on the east side of the Apalachicola River at Aspalaga Landing and Rock Bluff were decimated by a fungal infection. Alfieri et al. (1967) identified the fungi responsible for the stem and needle blight of *Torreya* to be *Physalospora* and *Macrophora*. However, these investigators did not determine how the fungal agents act to cause the blight.

At the present time there may be only 100 native Torreyas (1,5 to 2.0 meters tall) left in the wild. These trees, like their extinct predecessors, will most surely succumb to the blight. Some living Torreyas may send up root sprouts, as *Castanea* does. Unless measures to control the blight are undertaken to preserve *Torreya* in its natural range, the taxon is doomed for extinction. The authors suggest several measures to preserve the species: (1) First, disease-free Torreyas along the Apalachicola River should be identified. (2) The conditions necessary for the fungal agent(s) to cause the infection should be determined.

Alfieri et al. (1967) found that Maneb fungicide at the concentration of 1.5 lb/100 gal applied at weekly intervals resulted in "very good control" of the fungal agents, *Physalospora* and *Macrophora*, after 9 weeks of treatment. *Torreya* trees at Maclay treated in this manner "showed marked improvement and recovery" and produced new growth "showing little or no infection." Trees at Maclay State Gardens and "accessible" trees in the wild should be treated in the aforementioned manner to control the

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"Environmental Status of the Stinking Cedar, Torreya taxifolia", by Richard Stalter and Steve Dial, 1984, Bartonia 50: 40-42.

TORREYA TAXIFOLIA-Stinking Yew; Savin.

A very rare evergreen tree, resembling the yew, growing in the north-

According to Dr. Torrey it is a tree from 6 to 18 inches in diameter and 20 to 40 feet high, with numerous spreading branches, having an appearance at a distance not unlike the hemlock (*Tsuga Canadensis*). The wood is said to be rather light, not very close grained, of a yellowish-white color, or in old trees of a reddish color like that of red

It has a strong and peculiar odor, especially when bruised or burnt, and hence it is frequently called in the country where it grows, stinking cedar; it makes excellent fence rails and is not liable to the attacks of insects. A blood-red turpentine, of a pasty consistence, flows sparingly from the bark, which is soluble in alcohol, forming a deep, clear solution, and when heated evolves a very powerful terebinthinous, but unpleasant odor.

According to Dr. A. W. Chapman it is found on the calcareous hills along the east bank of the Appalachee River, near the confluence of the Flint and Chattahoochee, and also on the banks of the Aspalaga River in the same district.

The foliage is much like that of the yew, but the leaves are broader and marked with two longitudinal lines. They are two-ranked on the branchlets, about 1 inch long, and one line wide, of a light green color, very rigid, and with a stiff sharp point.

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The male and female flowers are borne on different trees. The male ones are in small roundish clusters in the axils of the leaves near the ends of the branches. The female or fertile flowers are solitary near the end of the twigs, very small at first but ripening into an oval, drupelike fruit 1 inch or more long, with a tough, rather leathery exterior, next to which is a thin hard shell, and occupied by a seed similar in shape to a nutmeg, and, like that, mottled within.

It is a singular fact that this tree is nowhere else found than in the few localities above named, and even there is in danger of extinction. It belongs to an order of which there are but three other species known to exist, of which one is in California and two in Japan. It is believed to be a remnant of an early flora, when a more intimate land connection existed between the eastern and western continents.

tion existed between the eastern and western continents. Plate IV.
Mr. A. H. Curtis, of Jacksonville, Fla., has recently investigated the
locality of this tree, and he gives the following account of it:

Leaving the State of Georgia either by the Chattahoochee or Flint Rivers, we find ourselves on a turbid, rapid river composed of their combined waters and named the Appalachicola. Behind us, like a large island, rises the wall of verdure which recently separated these waters. The western bank is steep and of uniform height. A shady road follows the bank a mile or two, and affords a most beautiful drive. This road leads from Marianna and other settlements to a ferry. At the eastern end of the ferry is a yellow bluff, on which stands the ferryman's house. Here also is a steamboat landing for Chattahoochee, a village situated a mile or more from the river. Following the road leading eastward we cross about half a mile of wooded river bottom, under the shade of grand black oaks, water-oaks, sycamores, and cottonwoods. After crossing this bottom we commence the ascent of a long and tiresome hill. After traversing a poor gullied pine wood we find ourselves at the summit of the hill. Here there is as great a change of scene as if we had been transferred suddenly from the wild country of Eastern Tennessee to the wide-spreading cotton fields of Middle Alabama. In the foreground of the scene is the little village of Chattahoochee, and about a mile beyond are the old United States arsenal buildings, now used as an insane asylum. In the center of the village we find the house of Dr. Scull, who owns all the country we have passed through and much besides, a thousand acres or more, much of it being heavily timbered. From the doctor we obtain instructions for finding and permission to cut what he calls savin, which my axman calls stinking cedar, the same being called by botanists Torreya taxifolia. Taking a northwestern course from the town, after passing through a dense woodland we find near the base of a steep rocky hillside the object of our search. There can be no mistaking the trees, for they are very different from anything we ever saw before—somewhat like the spruces and firs, more like the yew, yet very different. The leaves of the Torreya are about an inch in length, dark, shiny, rigid, and very sharp-pointed. They are borne in flat sprays, the lower branches nearly touching the ground. The fruit or nut of the tree is still more remarkable. It is about an inch in length, and resembles a green plum both in color and form. It is simply a naked seed, without a vestige of cone or other envelope. In this respect the Torreya and Taxus (yew) differ from our other conifers, and constitute a distinct tribe. The tree is pyramidal in form, of somber appearance, and appears strangely out of place in this latitude among oaks, beeches, and poplars. No doubt the Torreya is a relic of a past epoch, when it may have had a wide range at the time when the elephant and mastodon were denizens of this country.

In wood and bark the Torreya resembles the cypress—still more the firs. The wood is extremely durable, almost imperishable. Dr. Scull showed me Torreya posts which had been in the ground sixty years and were still quite sound. The wood, especially when freshly cut, emits a strong and offensive odor; probably this is also offensive to the "tooth of time." Most of the best Torreyas have been cut for post timber. About a mile south of the first locality I found another growth of these trees. Ten miles farther south there is a larger quantity, near the landing called Aspalaga, and it is also found on Sweetwater Creek, ten or fifteen miles farther down the river. Possibly it may grow in other spots, but I have no knowledge of its occurrence except at these three places near the eastern bank of the Appalachicola River.

1890 ATTEMPT TO REPLACE COMMON NAME "STINKING CEDAR" WITH "TORREY TREE"

Title: Garden and forest. / Volume 3, Issue 115 [an electronic version]

May 7, 1890 · Page 222

It is a matter of rare occurrence that names of botanists, often associated in scientific language with the names of trees, gain any real foothold in popular language. Magnolia, a name which commemorates the scientific labors of Pierre Magnol, a French botanist of two centuries ago, is a conspicuous exception in this country, and our great evergreen Magnolia is only known to the people living in those parts of the southern states where it grows as "Magnolia." The name of David Douglas is occasionally associated in British Columbia with the Fir-tree which he discovered, but "Douglas Spruce" can hardly be said to have established itself very firmly or very generally yet in the language of the people of any part of western America. Cases are less rare where the names of scientific worthies, perpetuated in the names of plants other than trees, are in common use; but trees, which are usually of importance to man or sufficiently conspicuous to attract his attention, obtain naturally local vernacular names before science imposes others on them, and the common names once engrafted on a language, almost always hold their own among the people of the country where the trees are found.

It was a matter, therefore, of much interest and some surprise to hear recently, in western Florida, the Torreya taxifolia, one of the rarest of all our trees, spoken of generally as the "Torrey-tree"; and to find that Stinking Cedar, the unattractive name by which this tree was first known to the inhabitants of western Florida, was gradually being replaced by that of one of the Nestors of American botany. The reason for this change is found perhaps in the fact that this tree, from its rarity, the interest attached to the geographical distribution of the small genus to which it belongs, and the reverence which his successors have always felt for the name of John Torrey, has several times been visited in its remote and isolated stations on the banks of the Appalachicola by men of science from distant parts of the country. When the people of the region, therefore, found that men of mature years and apparently in the enjoyment of all their faculties had journeyed thousands of miles merely to look at a tree which they had always considered as valuable only because it furnished indestructible material for fence posts, their own interest and curiosity became aroused; and therefore hearing these eccentric strangers talking always about Torrey and Torreya, the name has gradually become fixed, and now "Torrey-tree" may often be heard in at least two or three counties of west Florida.

The Apalachicola River endemics

There is a colony of Torreya taxifolia, together with a number of other endemic and disjunct species along the bluffs of the Apalachicola River between Chattahoochee and Bristol. Are well drained, but at the same time thoroughly moist, because of the abundant seepage water and the low evaporation rates that prevail. Magnolia occurs among the trees and scrub palmettos in the undergrowth, are plentiful.

Torreya grows all over the slopes of the ravines, from stream-bank to rim, wherever there is any shade. It is mostly an undergrowth tree, seldom reaching a height of more than 20 or 25 ft. or a trunk diameter of more than 6 in.—Frank Thone.

Apalachicola River Endemics

Section of *Naturalist's Guide to the Americas*, 1926, Ecological Society of America.

Many years ago, Arnott published in Taylor's Annals of Natural History a description of a new genus, established on one of the beautiful Conifers of Florida, and gave it the name of Torreya. The Florida species is Torreya taxifolia. Since then there have been added to the genus Torreya nucifera from the island of Japan, Torreya Californica from the Pacific coast, and possibly another from Northern China, T. grandis. While we are glad that a so fine and widely spread genus should bear the name of our friend, we regret that Arnott had not been more happy in his choice of a term to designate our native species. Although a native of Florida, it is hardy on this island, and even as far north as Fishkill, on the Hudson. It holds its bright foliage through the cold and snows of winter, and its presence here suggests thoughts of more genial climes and seasons. Had Arnott possessed the power of prophecy, he surely would have written Torreya sempervirens; for does not he whose name it bears disregard the frosts of time? Does not his presence always bring genial summer, and show us that years bring no winter to the heart which has not lost the freshness of youth, but in which love-love to man and to God-reigns supreme? Long after the flowers shall have bloomed above us all, future botanists will carry on the work he has so nobly helped. Those yet unborn will wander by the Southern rivers, visit the mountains of far-off Japan, or climb our own grand Sierra Nevada in search of the Torreya, and his name will be remembered as long as there shall be botany and botanists. But these can only talk of him whom it is our privilege to know, to honor, and to love, and whose presence we now greet with the already too long-delayed sentiment: Long life, health, happiness, and every blessing to our honored guest, Doctor John TORREY.

This card designated the seat to he eccupied at the table, on the evening of the 20th December 1867. TORREYA The badge which I wore in my button hole, at the supper given to Inc. John Torrey, at the Astor House, N.Y. by the Botanical Club. The Relames.

<u>celebration of career of John</u> <u>Torrey</u>

The American Naturalist

p. 45

1867

"John Torrey: A Biographical Notice by Asa Gray

American Journal of Science and Arts 1873.

EXCERPT ON DISCOVERIES OF 4 TORREYA SPECIES:

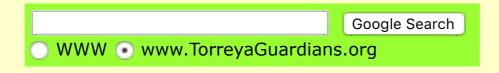
"... Almost in his youth a genus was dedicated to him by his correspondent, Sprengel: this proved to be a Clerodendron, misunderstood. A second, proposed by Rafinesque, was founded on an artificial dismemberment of Cyperus. The ground was clear, therefore, when, thirty or forty years ago, a new and remarkable evergreen tree was discovered in our own Southern States, which it was at once determined should bear Dr. Torrey's name. More recently a congener was found in the noble forests of California. Another species had already been recognized in Japan, and lately a fourth in the mountains of Northern China. All four of them have been introduced and are greatly prized as ornamental trees in Europe. So that, all round the world, Torreya taxifolia, Torreya California, Torreya nucifera, and Torreya grandis as well as his own important contributions to botany, of which they are a memorial — should keep our associate's memory as green as their own perpetual verdure."

IMAGE LEFT APPEARS ON THIS SAME DIGITAL PAGE OF THE HARVARD ARCHIVE (above).



Click above for a **2-minute video of Torreya State Park** in n. Florida.

• 1983 paper with map of inventory of Florida Torreya wild populations in southern-most Georgia: <u>"A Georgia Station for Torreya Taxifolia arn. Survives"</u>, by Thomas Savage, 1983, *Florida Scientist*.



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Could Torreya Take the Place of Eastern Hemlock?

Annotated List of Papers/Reports Online re Assisted Migration