

TAXONOMY OF *TIARELLA* (SAXIFRAGACEAE) IN THE EASTERN USA

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ABSTRACT

Tiarella in the eastern USA is recognized as comprising 5 species: (1) *Tiarella cordifolia* L., non-stoloniferous, on the eastern seaboard from Maryland to Georgia; (2) ***Tiarella stolonifera* Nesom, sp. nov.**, widespread from Michigan into the northeastern USA and adjacent Canada and south into Kentucky, Tennessee, and montane Virginia and North Carolina — previously misinterpreted as the typical Linnaean element; (3) ***Tiarella austrina* (Lakela) Nesom, comb. et stat. nov.**, stoloniferous, narrowly endemic to North Carolina, South Carolina, Georgia, and Tennessee, with a small cluster of disjunct populations in northern Alabama and adjacent Tennessee; (4) *Tiarella wherryi* Lakela, non-stoloniferous, southern Kentucky to Tennessee, Georgia, and Alabama; and (5) ***Tiarella nautila* Nesom, sp. nov.**, non-stoloniferous, narrowly endemic to northern Georgia and adjacent North Carolina and Tennessee. Included are summaries of formal taxonomy, photos of types and representative collections, field photos, a key to species, distribution maps, discussions of variation, and phylogenetic hypotheses. An epitype is designated for *T. cordifolia*. *Tiarella macrophylla* is lectotypified to place it as a synonym of *Heuchera villosa*.

Plants identified as *Tiarella cordifolia* L. sensu lato occur widely over the eastern USA and closely adjacent southeastern Canada. Views on *Tiarella* taxonomy in this region have included recognition of one, two, or three species, some with formal variants at infraspecific rank (Lakela 1937; Wherry 1940, 1949; Fernald 1943, 1950; Radford et al. 1968; Spongberg 1972). Soltis & Bohm (1984), Gleason & Cronquist (1991), Jog (2009), and Weakley (2020) have recognized only a single species *T. cordifolia* L., without infraspecific taxa. Taxonomy of these plants is presented here, with observations on biology and morphological variation.

A significant problem in reaching a meaningful taxonomy of eastern USA *Tiarella* has been ambiguous knowledge of stolon production — a collection from a population of stoloniferous plants sometimes does not include stolons. Student collectors have often overlooked this biological feature and even experienced ones may miss it. In this study, I made field observations (May 4-6, May 28-30, 2021) in the southern Blue Ridge region, where the greatest diversity occurs, toward understanding growth habit and geographical patterns. Collections and/or observations were made in the following. Alabama: Jackson and Madison cos. Georgia: Habersham, Murray, Rabun, Stephens, Towns, Union, and White cos. North Carolina: Cherokee, Graham, Haywood, Jackson, Macon, Polk, and Swain cos. South Carolina: Oconee Co. Tennessee: Blount, Monroe, and Polk cos. Since it will be some time before my *Tiarella* collections are available via the internet, data are given here in Appendix 1. The first set will be deposited at NCU.

Tiarella and the Heuchera group

Tiarella (7 species) is a member of the "Heuchera group" of genera (Heuchereae Bartl.; Johnson & Soltis 1994; Tkach et al. 2015; Folk et al. 2021), which includes *Bensoniella* (1 species), *Conimitella* (1), *Elmera* (1), *Heuchera* (ca. 37), *Lithophragma* (10), *Mitella* (ca. 20, now represented by *Mitella* sensu stricto and 6 segregate genera), *Tellima* (1), and *Tolmiea* (2).

All species of Heuchereae with chromosome counts have a base number of $x = 7$ and individuals with $2n = 14$. Polyploids ($2n = 21, 28, 35$) occur in *Heuchera*, *Lithophragma*, *Mitella*, and *Tolmiea*.

In *Tiarella*, diploid counts are reported from four of the seven species: *T. polyphylla*, *T. trifoliata*, *T. stolonifera*, and *T. cordifolia*.

Soltis (1980 and Soltis & Bohm (1984) reported a chromosome number of $2n = 14$ for *T. cordifolia* sensu stricto (Wake Co., North Carolina) and *T. stolonifera* (Carter and Powell cos., Kentucky; Chittenden Co., Vermont) and observed that all karyotypes are similar. A count of $2n = 14$ for *T. stolonifera* also has been made from Sainte-Foy, Quebec (Plante 1995). Soltis & Bohm (1984) found similar flavonoid profiles in *T. stolonifera* (Hocking Co., Ohio) and *T. nautila* (Union Co., Georgia). All samples in these studies were identified as *T. cordifolia*; more precise identities are inferred here from localities (chromosome and flavonoid vouchers not found).

Among Heuchereae, leafy (or prominently bracteate) flowering stems occur in *Heuchera*, *Lithophragma*, *Tellima*, *Tiarella*, and *Tolmiea*. Leafy stems in *Heuchera* are characteristic of most species of the phylogenetically basal sect. *Heuchera* and the basal grade of *H. glabra* and *H. bracteata* (phylogeny fide Folk & Freudenstein 2014) — flowering stems in the rest of *Heuchera* are leafless/ebracteate, indicating that lack (loss) of stem leaves is a specialized condition. Among the eastern USA species of *Tiarella*, *T. nautila* and *T. austrina* produce leafy flowering stems, sometimes with axillary buds that produce lateral branches. *Tiarella polyphylla* (Asia) and *T. trifoliata* (western USA) invariably produce leafy stems and are similar in aspect to *T. nautila*. In the eastern USA, Lakela (1937) noted the constancy of ebracteate stems in northern plants (here identified as *T. stolonifera*) and a "fairly consistent," though variable, occurrence of bracts in southern plants — but she decided that bract occurrence is sporadic and without taxonomic significance.

Production of leafy stolons in *Tiarella* is a specialization. Among other genera of Heuchereae leafy stolons are present only in *Mitella* sensu lato — some of these species produce slender, leafy runners that may be slightly underground or above-ground (thus referred to as stolons). Species of the other genera are rhizomatous. Plants of *Tellima grandiflora* are said to arise from an "erect, scaly caudex" ... without rhizomes or stolons" (Wells & Elvander 2009), but the densely fibrous-rooted "caudex" almost certainly represents a foreshortened rhizome. All species of *Tiarella* are rhizomatous (*T. stolonifera* and *T. austrina* also produce stolons) and the rhizome sometimes may be thick and foreshortened, particularly in *Tiarella wherryi*, similar to that of *Tellima*.

In the non-stoloniferous forms of eastern USA *Tiarella*, basal offsets are produced (e.g., Fig. 42). These never are above-ground, rarely are more than 1-2 cm long, and may be lignescent with a tendency to thicken — plants remain caespitose, never with the tendency to form clonal, spreading colonies sometimes encountered in the stoloniferous forms (e.g., Fig. 33). Oliver & Oliver (2006) noted that basal offsets usually begin growth in summer and have formed offset crowns by early autumn. Short rhizomes or a branching caudex are sometimes formed (e.g., Fig. 15). *Tiarella* stolons root at the nodes and produce plantlets, but they apparently do not thicken and persist as rhizomes.

Tiarella in Asia and the western USA

Tiarella polyphylla D. Don occurs in Asia in the Himalayas (Bhutan, northern India, northern Myanmar, Nepal, Sikkim) through western and central China to Korea, Japan, and Taiwan (Pan & Soltis 2001). It is relatively constant in morphology and apparently without synonymy. Pan & Soltis noted that "The two North American species are more closely related to each other than to ... the Asian species" but the analysis by Folk et al. (2019, a phylogeny for Saxifragales inferred from a dataset of 301 genes and 627 species) shows *T. cordifolia* and *T. polyphylla* as sisters, coordinate with *T. trifoliata*.

Tiarella trifoliata L. occurs from coastal Alaska to California, neotypified by a collection from Sitka, Alaska (Reveal 1991). Three species (*T. trifoliata*, *T. unifoliata* Hook., *T. lacinata* Hook.) or three varieties have sometimes been recognized but infrapopulational variation often includes plants with 3-lobed and 3-foliolate leaves (Kern 1966) and relatively recent treatments recognize only a single

species (e.g., Jog 2009). Soltis et al. (1992) found no differentiation among the proposed taxa but instead found cpDNA evidence for a northern clade (Alaska to central Oregon) and southern clade (southern Oregon to California), with several disjunct outliers.



Figure 1. *Tiarella polyphylla*. Hokkaido, Japan, Murata et al. 38399 (L).



Figure 2. *Tiarella trifoliata* (var. *unifoliata*). Pierce Co., Washington, Kern 126 (TENN).

Taxonomy of eastern USA *Tiarella*

1. **TIARELLA CORDIFOLIA** L., Sp. Pl. 1: 405. 1753. **LECTOTYPE** (Reveal 1991, p. 480): **USA**. [Virginia.] *J. Clayton 554*, Herb. Clifford 175.9 (S, Fig. 8; isolectotypes: BM 000051654, Fig. 9; LINN 576.2, Fig. 10).

Clayton's 554 collection, apparently distributed variously by Gronovius some time before 1738, comprises only inflorescence branches and petiolate leaves. It was cited by Gronovius in *Flora Virginica* (1739, as "*Mitella scapo nudo*") and by Linnaeus (in 1738, as "*Mitella scapo nudo*"; in 1753, as "*Tiarella cordifolia*"). The collection presumably was made in northeastern Virginia, in the region of where Clayton lived, traveled, and collected plants before publication of the first edition of the *Flora*.

Clayton was appointed Clerk of Court of Gloucester County in 1720 (at the age of 26 or 27) and held this position for most of his life. He surely must have lived in the town of Gloucester, but he had property in the county on the Piankatank River (or creek) and the Poropotank River (or creek), whose headwaters are in close proximity. A map in the 1762 edition of *Flora Virginica* was drawn by Clayton (Fig. 11; drawn before 1743, fide Frye 1990) to show geographical features and travel routes of his area in Virginia. All of the area is within the range of 'non-stoloniferous' *Tiarella* (Fig. 4).

In late August into early September 1716, apparently with a group led by Alexander Spotswood (Campbell 1860), leaving from Williamsburg, Clayton crossed the Blue Ridge into the Shenandoah Valley in the region of the headwaters of the Rappahannock River, but it is unlikely even on this foray that he would have encountered stoloniferous plants, nor would *Tiarella* still have been in flower, nor is it clear that Clayton had begun collecting plants at this early age. His 1762 map also appears to show an approach to the Blue Ridge via Hanover County — current records do not show stoloniferous plants in that area (map in Fig. 4). Accounts of Clayton's life (Barton 1806; Berkeley & Berkeley 1963; Frye 1990) lack dates and other unambiguous information significant in understanding Clayton's travel and collecting.

Wherry (1940, p. 2) observed that "since the non-stoloniferous [variant] grows in the region where Clayton collected, the Gronovius plant cited by Linnaeus must have represented this. ... [but] ... Since the Linnaean species comprised two variants, the first post-Linnaean author to select a type is to be followed; and Miss Lakela designated as var. *typica* the northern stoloniferous plant." Lakela (1937), however, did not cite a type specimen for *Tiarella cordata* nor even discuss its typification — she merely adopted the Linnaean name for the stoloniferous variant. Surprisingly, Reveal's lectotypification (1991) did not catch this geographic association — he noted that "although it lacks roots and stolons, the lectotype appears to represent the stoloniferous northern expression," but he gave no basis for his judgement.

Because the base of *Clayton 554* is not present, an epitype provides an unambiguous identity for *Tiarella cordifolia* sensu stricto. The epitype locality is shown on Clayton's map (Fig. 11). Another representative collection from the same area of Virginia (Fairfax Co.) is shown in Figure 13.

EPITYPE (designated here): **Virginia**. Stafford Co.: Alluvial and deciduous forest at bridge over tributary of Rappahannock River and Rte 655, 21 May 1976, *T. Bradley 10346* (GMUF, Fig. 12).

Tiarella cordifolia var. *collina* Wherry, Notul. Nat. 42: 1. 1940. *Tiarella cordifolia* subsp. *collina* (Wherry) Wherry, Notul. Nat. 42: 4. 1940. **TYPE: Virginia**. [Henry Co.]: 1.5 mi SW of Spencer, wooded slope on the SW bank of the North Mayo River, 5 Jun 1939, *E.T. Wherry s.n.* (holotype: PH, Fig. 14). The label says "Patrick Co." but the locality is in Henry County, as noted by Wherry (1949).

In the protologue, Wherry first used varietal rank ("*Tiarella cordifolia collina* var. nov.," p. 3), but on page 4 he noted that since "there is an increasing tendency to classify such variants as

subspecies, it will simplify matters for future workers if the plants under consideration are here formally assigned to this status also."

- 2. TIARELLA NAUTILA** Nesom, **sp. nov.** **TYPE: Georgia.** Union Co.: ca. 10 mi S of Blairsville, between Wolfpen Gap and Slaughter Mt., moist rocky soil in oak woods, 3500 ft, 1 Jun 1947, A. Cronquist 4499 (holotype: GA, Fig. 44; isotype: IND, Fig. 45).

Distinct in its lack of herbaceous stolons, presence of leaves or bracts on the flowering stems, and relatively large basal leaves with an extended terminal lobe. The epithet alludes to the sail-like stem leaves.

- 3. TIARELLA WHERRYI** Lakela, Amer. J. Bot. 24: 349. 1937. **TYPE: Tennessee.** Polk Co.: 3 mi NW of Reliance, ravine on W side of Hiwasee River, near Hiwasee Beach, 12 Jun 1933, E.T. Wherry s.n. (holotype: MINN, Fig. 34; isotypes: NY image, PH!). The PH label says "1932" but it was annotated by Wherry as "COTYPE" — apparently 1932 was a mistake for 1933.

- 4. TIARELLA STOLONIFERA** Nesom, **sp. nov.** **TYPE: Pennsylvania.** Monroe Co.: Ca. 1/2 mi S of Clifton, rocky, acid woodland, 6 Jun 1978, F.B. Buser 11542 (holotype: GH, Fig. 19).

Tiarella cordifolia var. *bracteata* Farwell, Ann. Rep. Mich. Acad. Sci. 19: 248. 1917. **TYPE: Michigan.** Macomb Co.: Disco, 25 May 1916, O.A. Farwell s.n. (holotype: BLH, Fig. 20; isotype: MICH image).

Annotation on the MICH sheet by R.K. Rabeler & A.A. Reznicek, 1998: "Holotype at BLH consists of 2 flowering plants collected on 25 May. A fruiting plant collected on 4 June is "mounted with" the type. Presumably these plants were collected on 25 May and the 4 June label seen here was mistakenly placed with them by Farwell in the set he left at the Parke Davis & Co. Herbarium. See also McVaugh et al., Bull. Cranbrook Acad. Sci. 34: 73. 1953."

Distinct in its production of herbaceous stolons, lack of leaves or bracts on the flowering stems, and relatively small basal leaves without an extended terminal lobe.

- 5. TIARELLA AUSTRINA** (Lakela) Nesom, **comb. et stat. nov.** *Tiarella cordifolia* var. *austrina* Lakela, Amer. J. Bot. 24: 348. 1937. **TYPE: North Carolina.** Haywood Co.: Lower Mt. Pisgah, 16 Jun 1931, K.M. Wiegand s.n. (holotype: BH, Fig. 21).

Status of *Tiarella macrophylla* Small

Small typified *Tiarella macrophylla* by a collection from southwestern North Carolina, but the leaves of the specimen are from *Heuchera villosa* Michx., the leafy stem (peduncle) portion and the floral branches from *Tiarella austrina* (Lakela 1937 first pointed out that this is a mixed collection). The basal portion of the *Tiarella* is absent, but the leafy flowering branch is characteristic of *T. austrina*, the only species of the genus in Polk County.

Small's emphasis in the protologue and choice of epithet points out leaf morphology as the defining feature of his proposed new species. Following Turland et al. (2018, Article 9.14), the leaves are designated here as the lectotype, placing the name in synonym of *Heuchera villosa* — "When a type (herbarium sheet or equivalent preparation) contains parts belonging to more than one taxon (see Art. 9.11), the name must remain attached to the part (specimen as defined in Art. 8.2) that corresponds most nearly with the original description or diagnosis."

Tiarella macrophylla Small, Fl. Southeast. U.S., 502, 1331. 1903. **LECTOYPE** (designated here): **North Carolina.** [Polk Co.]: Tryon Mountain, Jun 1896, A.M. Huger s.n. (NY, the two leaves of *Heuchera villosa*, Fig. 3).

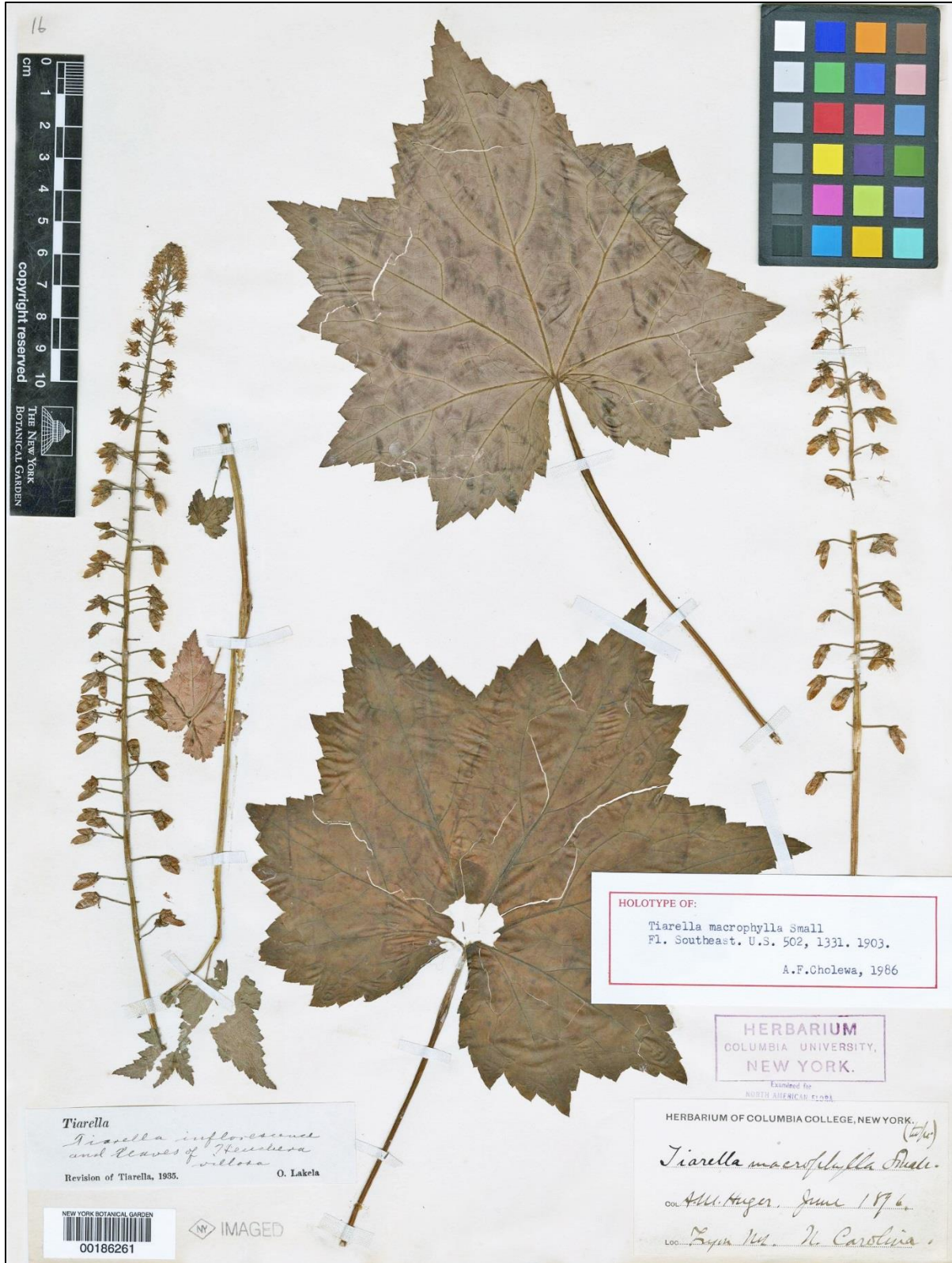


Figure 3. *Tiarella macrophylla*. Tryon Mt., Polk Co., North Carolina, A.M. Huger s.n. (NY). The name is lectotypified here by the two leaves from *Heuchera villosa*. The leafy branch and inflorescences are from *Tiarella austrina*.

Key to *Tiarella* species

1. Inflorescence a narrow panicle or thyrse (branches with 2–5 flowers), usually with a single axis; petals linear to subulate; styles 2–3 mm long; leaves simple to trifoliolate; western North America ***Tiarella trifoliata***
1. Inflorescence a raceme (branches usually with 1 flower), axis usually single but sometimes branched; petals absent or else present and oblanceolate to elliptic; styles 1 mm or less long; leaves simple; Asia and eastern USA and Canada.
 2. Petals absent; Asia ***Tiarella polyphylla***
 2. Petals present; eastern USA and Canada.
 3. Plants always with herbaceous, leafy stolons.
 4. Leaves usually with obtuse to rounded lobes, terminal lobe not prominently extended; flowering stem very rarely with a small bract; sepals 2.5–3.5 mm long . ***Tiarella stolonifera***
 4. Leaves usually with acute-acuminate lobes, terminal lobe prominently extended; flowering stem usually with 1–2 leaves or foliaceous bracts; sepals 1.5–2 mm long . ***Tiarella austrina***
 3. Plants without herbaceous, leafy stolons.
 5. Leaves usually about as long as wide, usually with obtuse to rounded lobes, terminal lobe not extended; sepals 2.5–3 mm long ***Tiarella cordifolia***
 5. Leaves usually longer than wide, usually with acute- acuminate lobes, terminal lobe prominently extended; sepals 1.5–2 mm long.
 6. Flowering stem usually with leaves or foliaceous bracts ***Tiarella nautila***
 6. Flowering stem without leaves or foliaceous bracts ***Tiarella wherryi***

Three morphological features are emphasized here in defining the eastern *Tiarella* species (Fig. 4) and inferring relationships (see Fig. 7). **Stolons:** the most unambiguous discontinuity is the presence or absence of herbaceous stolons (present in *T. austrina*, *T. stolonifera*). All plants in a *Tiarella* population either do or do not produce stolons. **Leaf shape:** plants from the southern Blue Ridge Mountains and southward have relatively large leaves with an extended terminal lobe, its apex sharp-pointed and often acuminate (*T. austrina*, *T. nautila*, *T. wherryi*). **Stem leaves/bracts:** leaves or foliaceous bracts consistently occur on the flowering stems of two of the southern Blue Ridge species (*T. nautila*, *T. austrina*); the other three species have ebracteate stems.

Differences in morphology sometimes noted as useful in distinguishing taxa (pedicel length, flower color, capsule length and shape, and absence of a stigma on the shorter fruit valve) are not consistent. All species (including *T. polyphylla* and *T. trifoliata*) produce a minute, glandular puberulence in the inflorescence (multicellular, gland-tipped hairs less than 0.1 mm long). Small differences in sepal length (noted in the key above) apparently are consistent, but other differences in floral morphology are not apparent.

***Tiarella nautila*.** This species is distinguished from *T. wherryi* by production of stem leaves (sometimes with axillary buds developing into branches, e.g., Fig. 49), but gene flow between the two perhaps occurs where they are contiguous in range. Even away from the parapatric margin, however, some individuals of *T. nautila* in otherwise typical populations may lack stem leaves or have bracts of reduced size. Typologically, such plants might be identified as *T. wherryi*, but the geographic boundary between the two entities appears to be relatively sharp (Figs. 5, 6) and the lack or reduction in size of bracts in such populations of *T. nautila* is interpreted here as within the range of typical variability. The holotype and isotype (Figs. 43 and 44) of *T. nautila* show populational variability in leaf/bract size and number.

Tiarella wherryi. Over its range, flowering stems are consistently leafless/ebracteate but in Polk Co., Tennessee, where *T. nautila* also occurs, some populations are variable in this feature (Fig. 35). This is interpreted here as a consequence of introgression. The type of *T. wherryi* is from the vicinity of such populational variability, and it probably was collected from an introgressed population. Southward (in Georgia), where the ranges of *T. nautila* and *T. wherryi* also are parapatric or slightly overlapping (Fig. 6), such variability is not evident in collections (but populational observations have not been made), perhaps because of more distantly separated populations.

Tiarella austrina. This species produces leafy flowering stems and is distinguished from *T. nautila* by the production of leafy stolons. Many collections of *T. austrina* have not included stolons and delimitation of its geography has been possible through field observations. The two species are sympatric only in a small area (Fig. 5), but where field work indicates that only *T. austrina* occurs, I have identified (without seeing the population) collections without stolons as *T. austrina*. As in *T. nautila*, populational variability in *T. austrina* sometimes includes plants with ebracteate stems; stems even on a single plant may show this variation. Variants from Jackson Co., North Carolina, are shown in Figs. 27, 28, and 29.

Two collections with deeply lobed leaves, distinct within the whole range of *Tiarella austrina*, have been made from the immediate vicinity of Tapoco (Graham Co.), North Carolina (Figs. 29, 30). Plants of typical morphology are abundant in the immediate area (Fig. 32; Nesom 2021-19 and 2021-20 — Appendix 1). I was not able to relocate the deeply lobed form but these plants are so distinctive that further attempt should be made to find them. Rare populational variants with similar leaf shape were encountered in *T. wherryi* from along the Hiwasee River in Polk Co., Tennessee.

Lakela (1937) recorded var. *austrina* in piedmont North Carolina, Tennessee (west of the Blue Ridge), southeastern Kentucky, and southern Alabama — areas where stoloniferous plants do not occur. Among her cited collections, Earle & Baker s.n. (US) from Lee Co., Alabama, has a short rhizome; Blomquist 926 (DUKE) from Orange Co., North Carolina has almost no basal parts — her rationale for identifying these and others as var. *austrina* is obscure.

Tiarella stolonifera. Field observations in northern Tennessee and adjacent Kentucky will be significant toward testing the observation (from herbarium collections only) that it is sympatric in that area with *T. wherryi*. The apparent parapatry of *T. stolonifera* and *T. austrina* also needs to be studied in the field. The two entities of stoloniferous plants are essentially continuous in geography and might be viewed conspecific, but the difference in leaf and stem morphology seems substantive and Lakela's formal recognition of var. *austrina* indicates that she viewed the two as distinct.

Tiarella cordifolia. This species is parapatric, without evidence of gene flow, with *T. stolonifera* along the Blue Ridge in Virginia and North Carolina and approaches the range of *T. austrina* in Rutherford Co., North Carolina, but it occurs in isolation at the northern and southern extremities of its range.

The morphological difference between *Tiarella cordifolia* and *T. wherryi* is subtle, mainly seen in leaf shape, especially considering populational variability over the range of each, but the qualitative difference in sepal length seems consistent. On the other hand, each has a distinctive geography, approaching each other only in Georgia, and it seems clear that two evolutionary entities are present.

In Swarthmore, Pennsylvania, Wherry (1949) grew plants from the type localities of var. *collina* (= *Tiarella cordifolia*) and *T. wherryi* and found (in the second year of cultivation) their leaves "strikingly dissimilar." Those of *T. wherryi* are "relatively narrow and deeply lobed, the major lobes acuminate, the lesser acute; they are, moreover, dull on the surface and brown-maculate. Those of *T. cordifolia collina* are relatively broad and shallow-lobed, the lobes acutish to obtusish; they are shining and non-maculate."

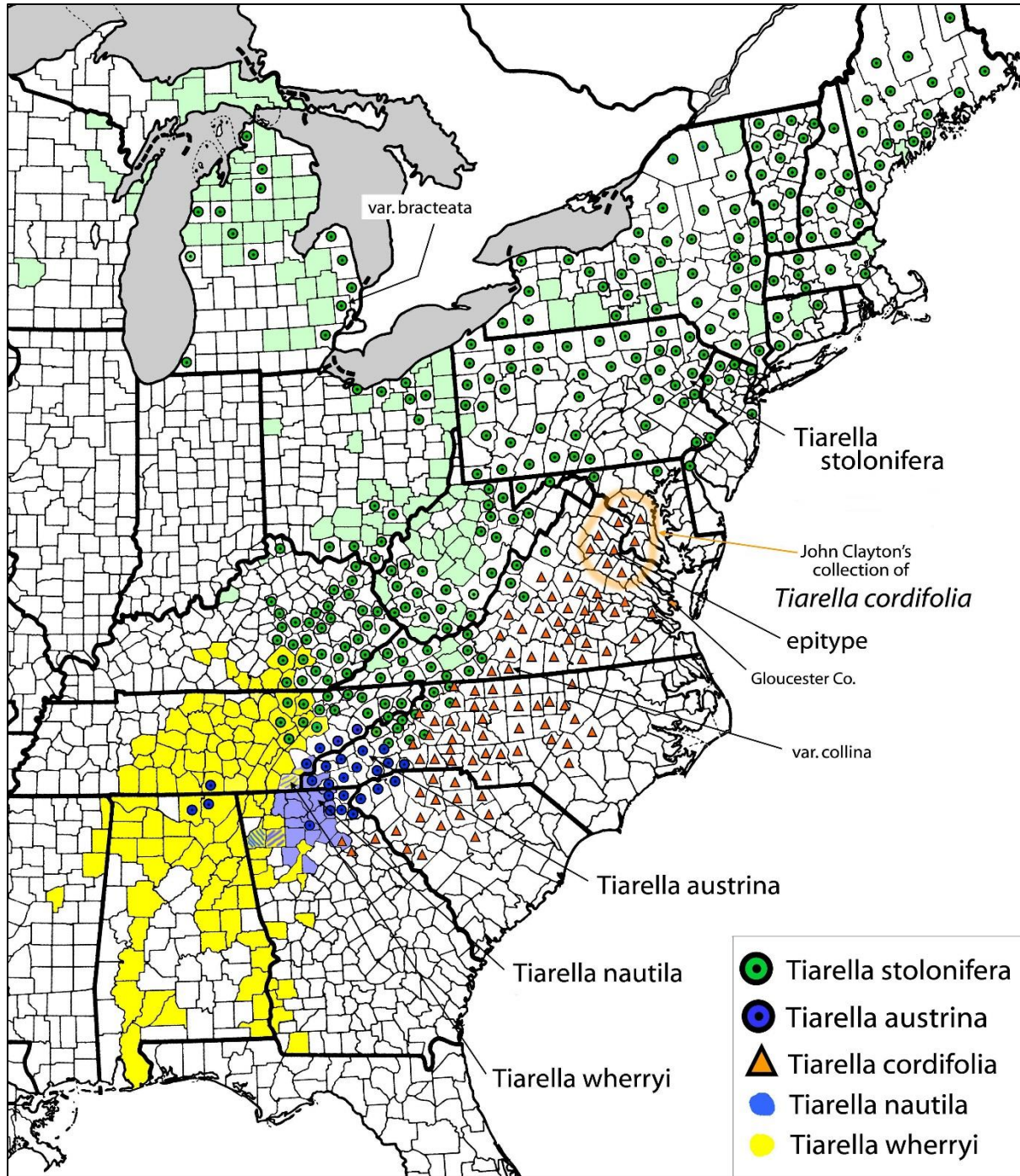


Figure 4. Distribution of *Tiarella* species in the eastern USA. Green-shaded counties are *T. stolonifera* records for which a voucher has not been seen. Arrows point to type localities. Clayton's type collection of *T. cordifolia* was made in the region within the orange circle (see text for discussion). "Var. bracteata" and "var. collina" are synonyms of *T. stolonifera*. Localities are not shown for *T. stolonifera* in Canada (Ontario, Quebec, New Brunswick, Nova Scotia).

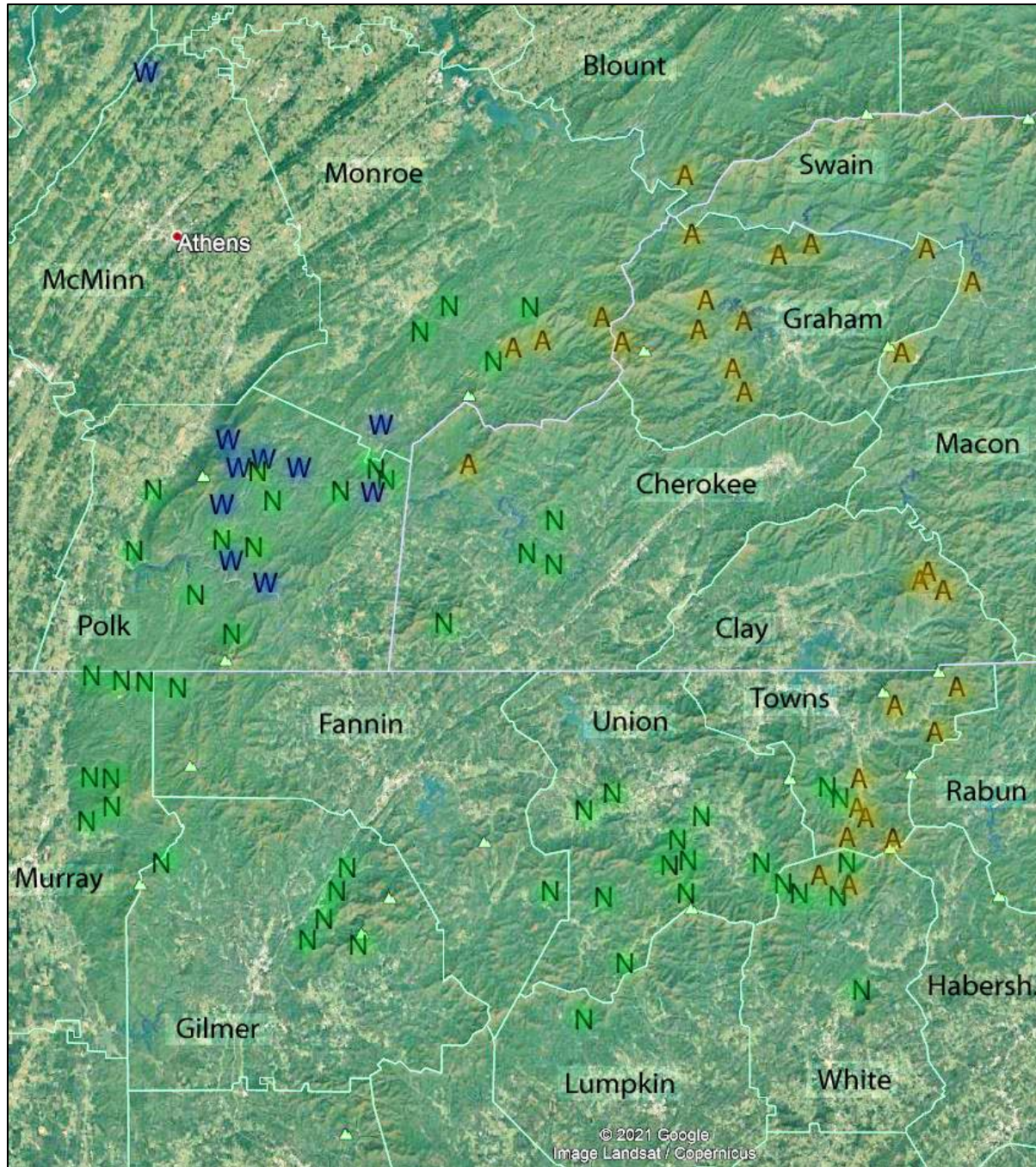


Figure 5. Distribution of *Tiarella nautila* (N), *T. wherryi* (W), and *T. austrina* (A) where their ranges are contiguous or slightly overlapping. Tennessee counties: Polk, McMinn, Monroe, and Blount. North Carolina counties: Cherokee, Graham, Polk, Swain, and Macon. Georgia counties: Murray, Gilmer, Fannin, Union, Lumpkin, Towns, White, Rabun, and Habersham. Distribution points are mostly from records summarized in SERNEC and from personal collections.

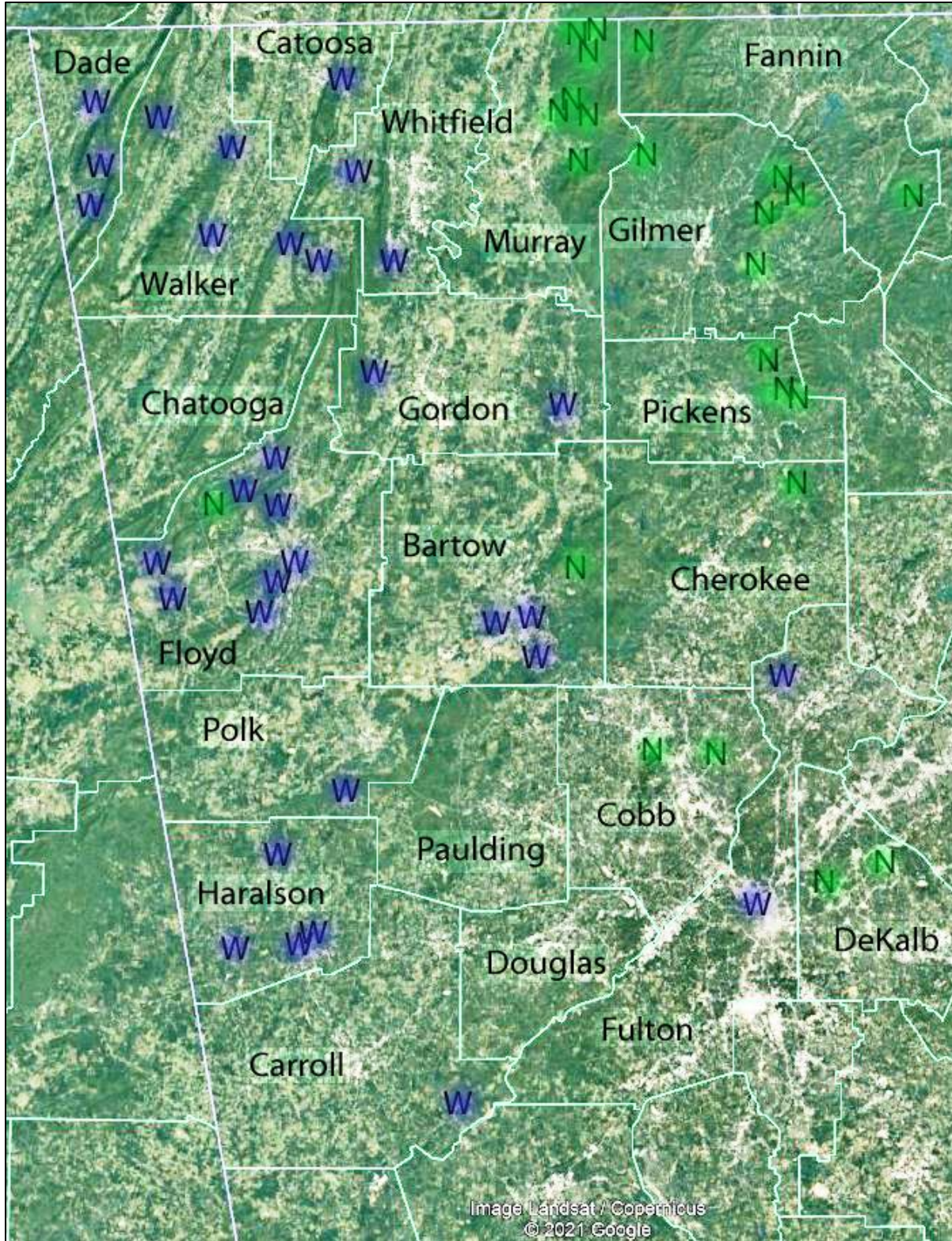


Figure 6. Distribution of *Tiarella wherryi* (W) and *T. nautila* (N) and where their ranges are contiguous or slightly overlapping. All labeled counties are in Georgia. Distribution points are mostly from records summarized in SERNEC and from personal collections.

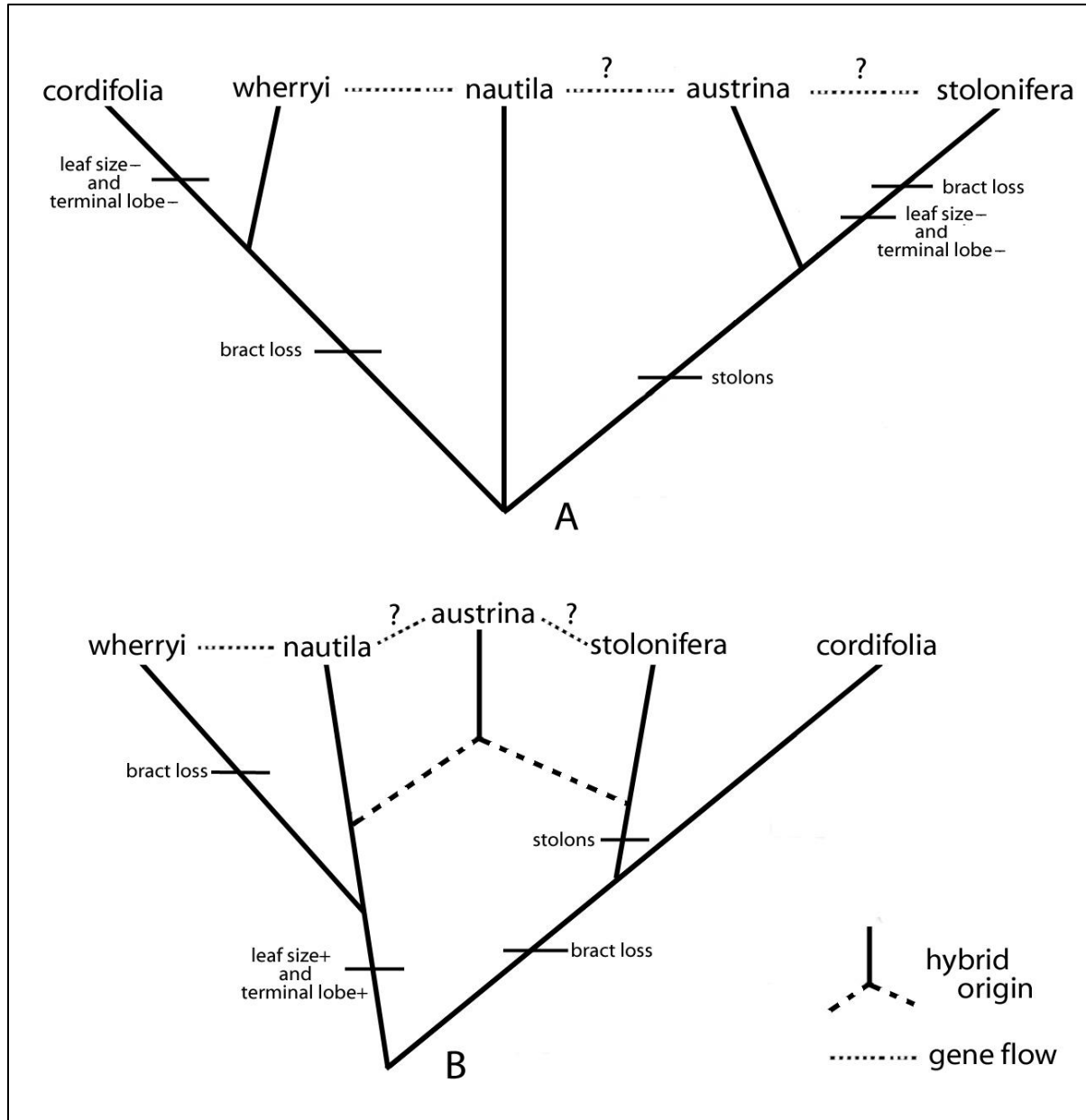


Figure 7. Alternative, hypothetical phylogenies of the eastern North American species of *Tiarella*, assuming that they are monophyletic. Both phylogenies assume that stolon production arose a single time and that presence of stem leaves is unspecialized. A. Assumption that the relatively small leaves of *T. cordifolia* and *T. stolonifera* are specialized and of independent origin. B. Assumption that the relatively small leaves of *T. cordifolia* and *T. stolonifera* are unspecialized; in this scenario, *T. austrina* is of hybrid origin and acquired stolons from *T. stolonifera*. Plausibility of phylogeny "A" is heightened by the observation that *T. nautila*, *T. wherryi*, and *T. austrina* are from the southern Blue Ridge region, where many evolutionary primitive species are endemic — *T. nautila* is the most primitive species, with lack of stolons, presence of stem bracts, and large leaves correlated as unspecialized features.



Figure 8. *Tiarella cordifolia* L. Lectotype: J. Clayton 554, Herb. Clifford 175.9 (S).



Figure 9. *Tiarella cordifolia* L. Isolectotype: J. Clayton 554 (BM 000051654).

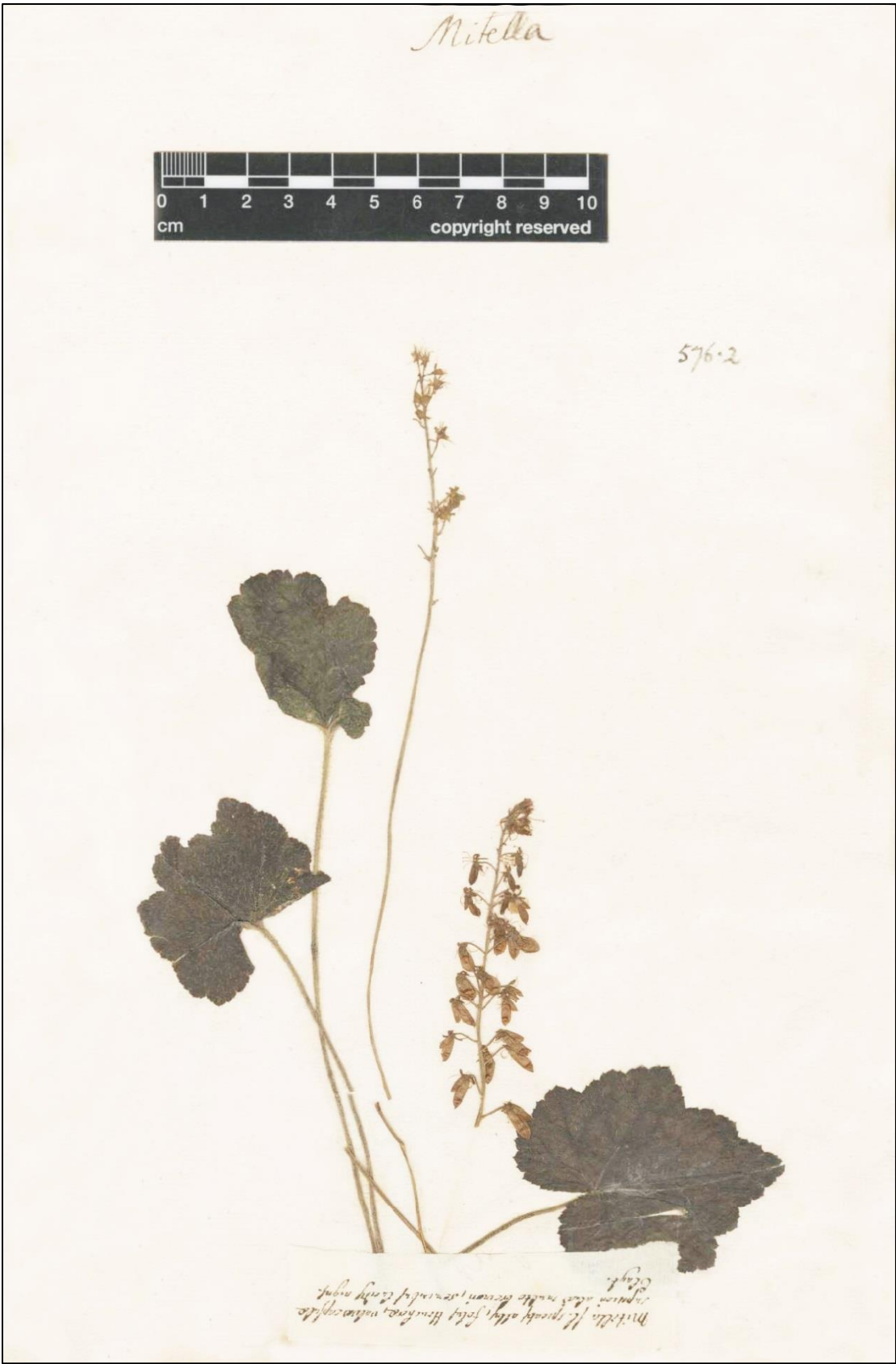


Figure 10. *Tiarella cordifolia* L. Isolectotype: J. Clayton 554 (LINN 576.2).

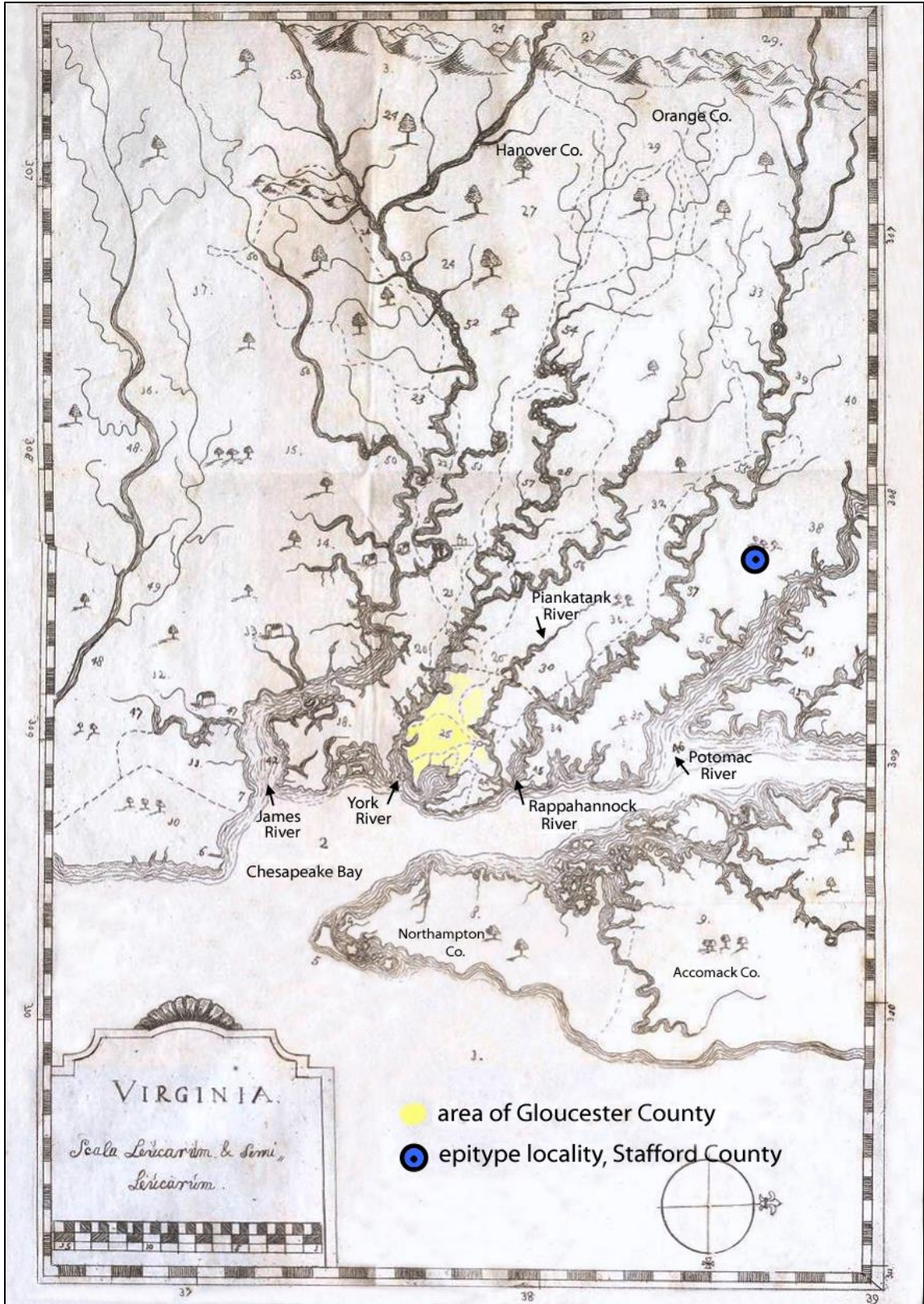


Figure 11. Map in the 1762 edition of *Flora Virginica* drawn by John Clayton showing his travel routes (dashed lines) in northeastern Virginia. The type collection (*Clayton 554*) presumably was made in this map region.



Figure 12. *Tiarella cordifolia* sensu stricto. Epitype: Stafford Co., Virginia, Bradley 10346 (GMUF).



Figure 13. *Tiarella cordifolia* sensu stricto. Representative morphology, Fairfax Co., Virginia, McMurchie 330 (GMUF).



Figure 14. *Tiarella cordifolia*. Holotype of *Tiarella cordifolia* var. *collina*. Henry Co., Virginia, E.T. Wherry s.n. (PH).



Figure 15. *Tiareella cordifolia*, sensu stricto — the elongate, rhizome-like caudex branches evidently developed from basal offsets. Abbeville Co., South Carolina, *Douglas 146* (CLEMS).



Figure 16. *Tiareella cordifolia* sensu stricto. Orange Co., North Carolina. Photo by Evan M. Raskin, 21 April 2018, iNaturalist.



Figure 17. *Tiareella cordifolia* sensu stricto. Near Kings Mountain, Cherokee Co., South Carolina. Photo by Sharon Watson, 16 April 2020, iNaturalist.



Figure 18. *Tiarella cordifolia* sensu stricto. Spotsylvania Co., Virginia. Photo by Penny Firth, 26 April 2020, iNaturalist.



Figure 19. *Tiareella stolonifera*. Holotype: Monroe Co., Pennsylvania, *Buser 11542* (GH).



Figure 20. *Tiarella stolonifera*. Holotype of *Tiarella cordifolia* var. *bracteata*, Macomb Co., Michigan, Farwell 4153 (BLH). Collected without stolons.



Figure 21. *Tiarella austrina*. Holotype of *Tiarella cordifolia* var. *austrina*. Haywood Co., North Carolina, K.M. Wiegand s.n. (Bailey Hortorium, Cornell University, BH, used with permission).



Figure 22. *Tiarella austrina*, representative morphology. Pickens Co., South Carolina, *Schwarzkopf 179* (FUGR).



Figure 23. *Tiarella austrina*, representative morphology. Transylvania Co., North Carolina, Powell s.n. (CONU).



Figure 24. *Tiarella austrina*, representative morphology. Macon Co., North Carolina, Whitten 5116 (FLAS).



Figure 25. *Tiarella austrina*, representative morphology (individual without stem leaves). Blount Co., Tennessee, Hudson s.n. (TENN).



Figure 26. *Tiarella austrina*, representative morphology. Rabun Co., Georgia, Kilpatrick s.n. (SALK).



Figure 27. *Tiareella austrina*, representative morphology. Jackson Co., North Carolina, Davis 110 (WCU). Stem leaves prominent.



Figure 28. *Tiarella austrina*, representative morphology. Jackson Co., North Carolina, Clodfelter 43 (WCUH). Stem leaves bracteate.



Figure 29. *Tiarella austrina*, representative morphology. Jackson Co., North Carolina, Craig 44 (WCUH). Stem leaves absent.



Figure 30. *Tiarella austrina* — form with deeply lobed leaves. Vicinity of Tapoco, Graham Co., North Carolina, Ahles 13290 (NCU). See also Ahles 38890 (Fig. 31) from nearly the same locality.



Figure 31. *Tiarella austrina* — form with deeply lobed leaves. Vicinity of Tapoco, Graham Co., North Carolina, Ahles 38890 (TENN). Compare Ahles 38891 (Fig. 32) from the same locality, which has typical leaf morphology.



Figure 33. *Tiareella austrina*, extensive clonal colony, plants spreading through stolons. Unicoi Gap at Towns/White county line, Georgia, at site of Nesom 2021-12. Photo by Nesom, 6 May 2021.



Figure 34. *Tiareella wherryi*. Holotype: Polk Co., Tennessee, E.T. Wherry s.n. (MINN).

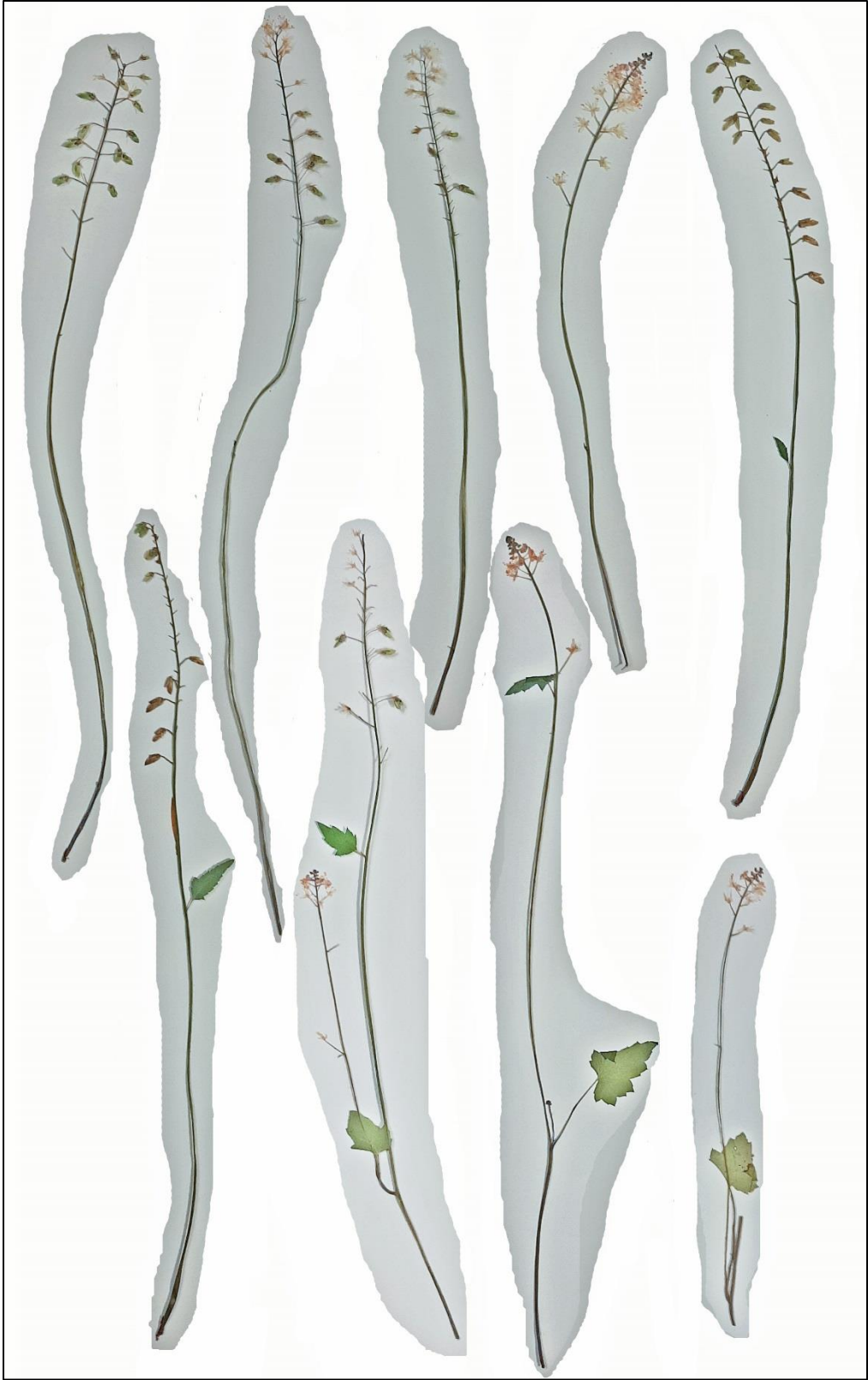


Figure 35. *Tiarella wherryi* in area with probable introgression from *T. nautila*. Polk Co., Tennessee, along the Hiwasee River, near the type locality of *T. wherryi*. From Nesom 2021-2. Most plants in the population have ebracteate flowering stems — variants like those in the bottom row occur sporadically.



Figure 36. *Tiarella wherryi*, representative morphology. Cumberland Co., Tennessee, Payne 97 (VDB).



Figure 37. *Tiarella wherryi*, representative morphology. Winston Co., Alabama, Jones 4822 (VDB).



Figure 38. *Tiareella wherryi*, representative morphology. Calhoun Co., Alabama, Kral 30697 (VDB).



Figure 39. *Tiarella wherryi*, representative morphology. Henry Co., Alabama, MacDonald 11185 (VDB).



Figure 40. *Tiarella wherryi*, representative morphology. Colbert Co., Alabama, Kirksey s.n. (VDB).



Figure 41. *Tiarella wherryi*, representative morphology. Lauderdale Co., Mississippi, Rogers 45321 (MMNS).



Figure 42. *Tiarella wherryi*, basal offset production. Polk Co., Tennessee, locality of Nesom 2021-3. Photo by Nesom, 5 May 2021.



Figure 43. *Tiareella wherryi*. South side of Hiwasee River, northwest of Reliance, Polk Co., Tennessee, vicinity of type locality. Photo by G. Nesom, 5 May 2021, locality of *Nesom 2021-3*.



Figure 44. *Tiarella nautila*. Holotype: Union Co., Georgia, A. Cronquist 4499 (GA).



Figure 45. *Tiarella nautila*. Isotype: Union Co., Georgia, A. Cronquist 4499 (IND).



•GA•
University
of Georgia
Herbarium
265032

Specimen Examined for
Georgia Atlas Project
31 July 2013

ex FSSR
Forest Service, USDA Herbarium
Atlanta, GA ~ [2009]



University of Georgia Herbarium (GA), Athens, Georgia, USA

PLANTS OF GEORGIA

<Saxifragaceae> -117
Tiarella cordifolia L.

UNION COUNTY Chattahoochee National Forest:
Sosebee Cove Scenic Area. Exposure: shady. Soil:
sandy loam. Site: wooded cove (NE slope). Vegetation
type: oak-tulip poplar. Associated plants: Solomon's seal,
may apple. Herb. Perennial. Height: 9". Abundance:
frequent. Flower color: white.

coll. Trisha Pepper # 32
Common name: foamflower
May 5, 1973

ex FSSR Herbarium, USDA, Atlanta, GA in 2009. Label retyped.

Figure 46. *Tiarella nautila*, representative morphology. Union Co., Georgia, *Peffer 32* (GA).



Figure 47. *Tiarella nautila*, representative morphology. Gilmer Co., Georgia, Williams 099 (GA).



Figure 48. *Tiarella nautila*, representative morphology. Lumpkin Co., Georgia, Kruse 01-47 (GA).



Figure 49. *Tiarella nautila*, representative morphology. Cherokee Co., North Carolina, Wherry s.n. (PH). Wherry identified this as *T. wherryi* but noted on the label that it was a "branchy form."



Figure 50. *Tiareella nautila*. West of Murphy, Cherokee Co., North Carolina. Photo by Nesom, 5 May 2021, locality of Nesom 2021-6.



Figure 51. *Tiareella nautila*. South of Vogel State Park, Union Co., Georgia. Photo by Kip Pelen, 25 April 2021, iNaturalist.



Figure 52. *Tiarella nautila*. Lake Conasauga, Murray Co., Georgia. Photo by Shannon Regina, 17 June 2020, iNaturalist. Branches from axillary buds on flowering stem.

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Appendix 1. Personal collections of *Tiarella*, May 2021.

Tennessee. Polk Co.: Nantahala Natl Forest, Hwy 30 along Hiwassee River, between Austral and Reliance, 0.2 mi W of Hiwassee Picnic Site, just ESE of Lowry Falls Trail, ca. 780 ft, rocky roadbank, loose cluster of about 6 plants, no stolons, mostly without peduncular bracts but some with bracts 5 May 2021, *G. Nesom 2021-1* **WHERRYI** (*T. nautila* introgression)

Tennessee. Polk Co.: Nantahala Natl Forest, Hwy 30 along Hiwassee River, between Austral and Reliance, 0.2 mi E Hiwassee Picnic Site, abundant on steep roadbank, ca. 780 ft, no stolons, mostly without peduncular bracts but some with bracts, 5 May 2021, *G. Nesom 2021-2* **WHERRYI** (*T. nautila* introgression)

Tennessee. Polk Co.: Nantahala Natl Forest, Hwy 30 along Hiwassee River, 1.2 mi NW of bridge at Reliance, abundant on steep roadcut, 800 ft, loose sandy loam, no stolons, mostly without peduncular bracts but some with bracts, 5 May 2021, *G. Nesom 2021-3* **WHERRYI** (*T. nautila* introgression)

Tennessee. Polk Co.: Nantahala Natl Forest, Hwy 30 along Hiwassee River, Reliance (bridge and junction), immediately across road from store, abundant on steep roadcut, 780 ft, no stolons, mostly without peduncular bracts (some peduncles with 2 small bracts), 5 May 2021, *G. Nesom 2021-4* **WHERRYI** (*T. nautila* introgression)

Tennessee. Polk Co.: Nantahala Natl Forest, ca. 2 mi SW of Reliance, Lost Creek Road to Lost Creek Campground, 0.5 mi SE of jct with Hwy 30, 950 ft, abundant on roadbank, no stolons, peduncular bracts sporadically present, 5 May 2021, *G. Nesom 2021-5* **WHERRYI** (*T. nautila* introgression)

North Carolina. Cherokee Co.: Nantahala Natl Forest, ca. 2 air mi NW of Murphy, Unicoi Turnpike, 0.2 mi N of jct with Hanging Dog Rd, 1730 ft, abundant on steep roadbank, no stolons, all with 1-2 large peduncular bracts, 5 May 2021, *G. Nesom 2021-6* **NAUTILA**

Georgia. Union Co.: Chattahoochee Natl Forest, ca. 7 air mi S of Blairsville, Wolf Creek Road (SR 107), 0.2 mi W of jct with Wolf Pen Gap Road (Hwy 180) at Burnett Gap, ca. 2800 ft, steep, loamy roadbank, abundant here but not common in the immediate area, no stolons, all with 1-2 large peduncular bracts, 5 May 2021, *G. Nesom 2021-8* **NAUTILA**

Georgia. Union Co.: Chattahoochee Natl Forest, ca. 6 air mi SE of Blairsville, Russell Scenic Hwy (Hwy 348) above Right Fork Notely River, 1 mi N of White County, 2950 ft, common along roadbank, no stolons, all with 1-2 large peduncular bracts, 5 May 2021, *G. Nesom 2021-9*

NAUTILA

Georgia. White Co.: Chattahoochee Natl Forest, ca. 0 mi N of Helen on Hwy 17, Andrews Cove Campground, population of ca. 15 plants on gentle slope under hardwoods close to campground entrance, 2400 ft, no stolons, all with 1-2 large peduncular bracts, 6 May 2021, *G. Nesom 2021-11*

NAUTILA

Georgia. Towns Co.: Chattahoochee Natl Forest, Unicoi Gap at Towns/White county line, huge, continuous population above Appalachian Trail on NW-facing slope under hardwoods, 3100 ft, stolons, all with 1-2 large peduncular bracts, 6 May 2021, *G. Nesom 2021-12* **AUSTRINA**

Georgia. Towns Co.: Chattahoochee Natl Forest, Hwy 180 ca. 3.5 mi WNW of jct with Hwy 17, 0.6 mi SSE of jct with Owl Creek Rd, along Soapstone Creek near its confluence with Flat Branch, terrace of creek immediately at creek bank, below (W side) of hwy, 2500 ft, population of ca. 10-15 plants, no stolons, all with 1-2 large peduncular bracts, 6 May 2021, *G. Nesom 2021-13* **NAUTILA**

Georgia. Towns Co.: Chattahoochee Natl Forest, Hwy 76 at Towns Gap (Towns/Rabun Co. line) and Appalachian Trail crossing, 2650 ft, abundant along banks and terrace of small creek below (SW side) of hwy, stolons, all with 1-2 large peduncular bracts, 6 May 2021, *G. Nesom 2021-14*

AUSTRINA

South Carolina. Oconee Co.: Along Chattooga River below Hwy 76 bridge (S side of bridge), locally abundant on steep banks, lip, and terrace of small creek feeding into the Chattooga River, 1180 ft, stolons, peduncular bracts sporadically present, 6 May 2021, *G. Nesom 2021-15*

AUSTRINA

Tennessee. Polk Co.: Nantahala Natl Forest, N of Farner on Hwy 68, abundant on steep roadbank below rhododendron along ca. 0.2 mi stretch along SW side of hwy immediately SW of bridge of Hiwassee River, 1300 ft, no stolons, peduncular bracts small and on few plants, 6 May 2021, *G. Nesom 2021-17* **WHERRYI** (*T. nautila* introgression)

Tennessee. Blount Co.: S of Maryville on Happy Valley Road, ca. 0.5 mi NE of turnoff to Montvale Springs, roadside in area of rhododendron and mixed hardwoods, N side of road just above small creek, ca. 1125 ft, small population with none in flower, 28 May 2021, *Nesom 2021-18* **AUSTRINA**

North Carolina. Graham Co.: Vicinity of Tapoco, ca. 0.3 mi WNW of Hwy 129 along Slickrock Trail, paralleling Little Tennessee River on its S side, abundant on slope above and below trail, ca. 1200 ft, 28 May 2021, *Nesom 2021-19* **AUSTRINA**

North Carolina. Graham Co.: Vicinity of Tapoco, trail crossing of Slickrock Creek (creek forming the Tennessee-North Carolina border), ca. 1.3 mi WNW of Hwy 129, ca. 1450 ft, scattered plants near the creek, 28 May 2021, *Nesom 2021-20* **AUSTRINA**

North Carolina. Graham Co.: Joyce Kilmer Memorial Forest, picnic/parking area and trailhead at loop of road, 2200 ft, extensive population of close-set and often interconnected plants, stoloniferous, few plants without peduncular bracts, 28 May 2021, *Nesom 2021-21* **AUSTRINA**

North Carolina. Graham Co.: Hwy 143 (Cherohala Skyway) W from jct with Santeetlah Rod, in high area where hwy follows Tenn/NC border and the Appalachian Trail, trailhead of Benton MacKaye Trail at Mud Gap (where all three meet), 4500 ft, common, leaves nearly round in outline, peduncular bracts absent or few, 28 May 2021, *Nesom 2021-22* **AUSTRINA**

Tennessee. Monroe Co.: Hwy 143/165 (Cherohala Skyway), 0.9 mi W of NC/Tenn state line, ca. 4300 ft, stolons, peduncular bracts absent or present in a few, abundant along roadbank, 28 May 2021, *Nesom 2021-23* **AUSTRINA**

Tennessee. Monroe Co.: Indian Boundary Road, ca. 0.1 mi from jct 345 to Indian Boundary Recreation Area, 0.2 mi NE of tip of hairpin turn in Hwy 165/143 (Cherohala Skyway), near small creek passing under road, 1990 ft, 28 May 2021, *Nesom 2021-24* **NAUTILA**

North Carolina. Macon Co.: Ca. 3.5 road mi W of Otto (unincorporated village on Hwy 23, 8 mi S of Franklin) on Co. Rd 1110, ca. 0.5 mi S of Coweeta Hydrologic Lab buildings along Ball Creek Road paralleling Ball Creek, 2300 ft, roadside beside rhododendron thicket, large population, stolons, some without peduncular bracts, 29 May 2021, *Nesom 2021-25* **AUSTRINA**

North Carolina. Macon Co.: Gold Mine Rd (Co. Rd 1679) 0.2 mi W of jct with Hwy 64/28, 0.1 mi W of jct with Gantes Gulch Rd, ca. 6.5 road mi NW of Highlands on Hwy 64/28, common on both sides of road, hardwoods and rhododendrons, 2830 ft, 29 May 2021, *Nesom 2021-26* **AUSTRINA**

North Carolina. Polk Co.: Holbert Cove Road (Co. Rd 1142) ca. 4 air mi NE of Saluda, near base of steep rhododendron slope along E side of Cove Creek where it crosses under road, at trail head/parking area to Little Bradley waterfall, S side of road, 1550 ft, few plants, 30 May 2021, *Nesom 2021-27* **AUSTRINA**