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Rhododendron smokianum, a New Species from the Great Smoky Mountains

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Abstract—Species delimitation in *Rhododendron* subsect. *Caroliniana* (Ericaceae) has been disputed in the past with one or three species accepted. Here we report a fourth species, ***R. smokianum***, a narrow endemic from the Great Smoky Mountains (Tennessee/North Carolina, USA). It is characterized by short-tubed corollas and small, compact growth. We support our conclusion by phylogenetic analyses of ITS and plastid *trnL-F* sequence data. The new species is a specialist of open mafic rock slopes and maintains morphological and phenological differences to the related species even in cultivation.

Keywords—Appalachian Mountains, endemic, ITS, *Rhododendron minus*, *trnL-F* region.

Rhododendron L. is one of the two largest genera of woody plants (Frodin 2004). Species numbers vary between 850 (Mabberley 1997) and 1025 (Chamberlain et al. 1996), and new species continue to be described. Accepting all 123 species published since 1996 (www.ipni.org), the genus would now include 1150 species. The cause for this diversity has amazed scientists and plant-lovers for centuries ever since Hooker (Hooker 1849) started a rhododendronmania in English gardens (Musgrave et al. 1998).

The majority of species are found in South-Central China (Sichuan, Yunnan) to southeastern Tibet with a secondary center of diversity in Malesia. Phylogenetic analyses in the past have helped to resolve relationships among the species and clades and helped to understand the causes for its diversification (Goetsch et al. 2005; Milne et al. 2010; Grimbs et al. 2017). Most recently, Shrestha et al. (2018) identified habitat heterogeneity and low seasonal variation in temperature as the main factors responsible for high species richness in *Rhododendron*. Thus, it is not unexpected that exploration of remote mountainous regions reveals more and more species in the genus. Furthermore, hybridization is a further factor increasing diversity in *Rhododendron* (Milne et al. 2010), with polyploidy a potential contributing factor (Jones et al. 2007; Nolzen and Albach unpubl.).

High species richness is also found in North America with 25 species recognized by Judd and Kron (2009). In contrast to earlier accounts, they excluded *R. camtschaticum* Pall. as genus *Therorhodion* (Maxim.) Small and included three species from the genus *Ledum* L. (Kron and Judd 1990). Subsequently, the genus *Menziesia* Sm. with two species also has been included (Craven 2011) and one species has been newly described (*R. colemanii* R.F.Miller; Zhou et al. 2008). This brings the number of currently accepted native species of *Rhododendron* in North America to 28. These species belong to different clades with more than half of them and the only one with more than three species being *R.* subg. *Pentanthera* (G.Don)Pojarkova.

Here we describe *R. smokianum* Ralf Bauer & Albach as a new species of *R.* subg. *Rhododendron* subsection *Caroliniana* (Hutchinson) Sleumer, which is distributed from Florida via Alabama, Georgia, South Carolina, and Tennessee to North Carolina (Judd and Kron 2009). Depending on the author, between one and three species were recognized in the past in this subsection, and species concepts either emphasized large variation in one species or subtle and sometimes overlapping variation in two or three species. To understand why we now recognize four taxa at the species level, it is important to consider the history of the subsection and the characters used to delimit taxa (Table 1).

The first species of the subsection was described by Michaux (in Lamarck 1792) as *R. minus* Michx. At about the same time, material of this new species from the more mountainous "back settlements of Carolina" arrived in England, where it was published and first depicted by Andrews et al. (1797) as *R. punctatum* Andrews. He was apparently unaware of Michaux´s description. In addition to the leaves and flowers, Andrews also noted that the flowers appear very late, at a time when new shoots are already almost fully developed. Further, for the description of *R. punctatum* a specimen with relatively short flower tubes compared with *R. minus* in general was used (Rehder 1912).

Unaware of the original description of *R. minus*, Small (1902) described *R. cuthbertii* Small from the vicinity of Augusta on the Savannah River (Georgia), differentiated from *R. punctatum* by its much longer flower tubes. Despite *R. cuthbertii* being synonymous with *R. minus*, the publication highlighted for the first time the distinction in lower-elevation long-tubed plants and "alleghenian" short-tubed mountain plants. Only by inspection of a large number of populations does it become obvious that *R. minus* has longer tubes in the south of its range and shorter tubes in the north towards and in the Appalachian region (Miller 2013). Rehder (1912) recognized that Small had overlooked the earlier publication of *R. minus* and described the short-tube plants from the high mountains of North Carolina with rather broad, wide-open corolla and shoots that only appear after flowering as a separate species, *R. carolinianum* Rehder. A more detailed account of the history of the subsection is given by Voss (2014).

The two species (*R. minus* and *R. carolinianum*) further differ in ecology, with *R. minus* preferring winter-mild and summer-hot lowlands. At higher altitudes, the plants occur in protected sites in forests. In contrast, *R. carolinianum* prefers winter-cold mountain areas, occurring in forests and even at exposed sites. At low elevations it grows in cool forested sites near water bodies or on north-facing slopes. Both species occur on well-drained soils and germinate in open areas (leafless humus or loamy forest soil, moss rock chinks) shaded by forest. With these ecological preferences, *R. carolinianum* blooms in early spring, its flowers being endangered by late frosts. Principally, it develops new shoots after flowering. Contrastingly, *R. minus* flowers four to six weeks later under the same conditions and

TABLE 1. Overview of synonyms and characters used to delimit taxa in *R.* subsect. *Caroliniana*.

	R. minus	*R. carolinianum*	*R. chapmanii*	*R. smokianum*
Synonyms	*R. punctatum* (short tubed) *R. cuthbertii* (long tubed)	*R. punctatum* var. *majus*		
Elevation	50–1500 m	200–1800 m	5–80 m	1200–2000 m
Flowering time relative to *Kalmia latifolia*	Synchronous	Earlier	Earlier	Synchronous to later
Growth height	(1–)2–3(–5) m	0.5–3 m	1–2 m	0.5–2(–2.5) m
Flower (tube and lobes) length	22–35 mm	ca. 25 mm	25–30 mm	20–25 mm
Length of narrowly tubular part of corolla	4–15(–24) mm	4–6 mm	10–15 mm	0–2 mm

in general after new shoots have developed (Bauer pers. obs.). Therefore, in the field flowering time is best compared with co-occurring species such as *Kalmia latifolia* L., which flowers long after *R. carolinianum* but together with *R. minus*.

Another variant deviating from the typical form was described by Wood (1870) from Florida, *R. punctatum* var. *chapmanii* Alph.Wood, which differs in its smaller, oval to inversely ovate non-pointed leaves and small sepals. In the following years, it was elevated to species rank by Gray (1876). Although *R. chapmanii* stays smaller than *R. minus* or *R. carolinianum*, with a height of only one to two meters, its shoots are much stiffer and more erect than those of the other two species, apparently an adaptation to be able to hold on between the saw palmettos to make its flowers visible to pollinators from afar. In contrast to their two relatives, the plants have smaller leaves with strongly downward curved edges and a very distinct venation. In strong shade, however, the leaves can be flat. The more or less white, pink, or magenta flowers appearing from February to the second half of April, before the new shoots are present or fully developed, are usually clearly red or yellow-orange spotted and have a tube that corresponds approximately to the tube length of the southern *R. minus* populations (Fig. 1D). The seedlings of the species seem to depend on bush fires, as only then are there enough open areas without competition for the small seedlings, which are practically unknown in the field. Most plants

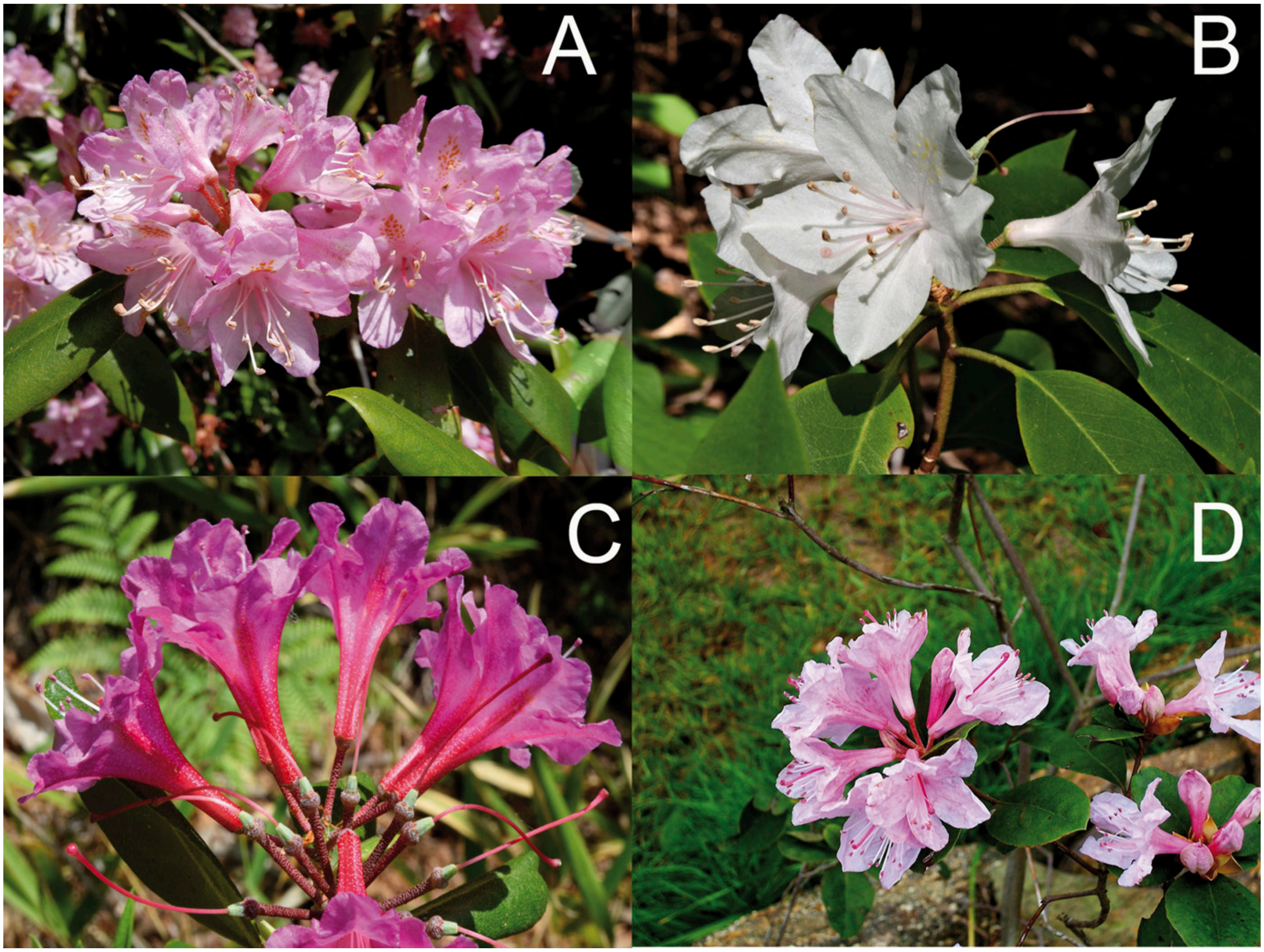

FIG. 1. Representatives of *R.* subsect. *Caroliniana*. A. Mountain-type *R. minus*, Toxaway Mt., Jackson Co., NC. B. *R. carolinianum*, Broad River, Cleveland Co., NC. C. Lowland-type *R. minus*, Gantt Lake, Covington Co., AL. D. *R. chapmanii*, Port St. Joe, Gulf Co., FL, cultivated in garden of Ron Miller. A–C by Ralf Bauer; D by Ron Miller.

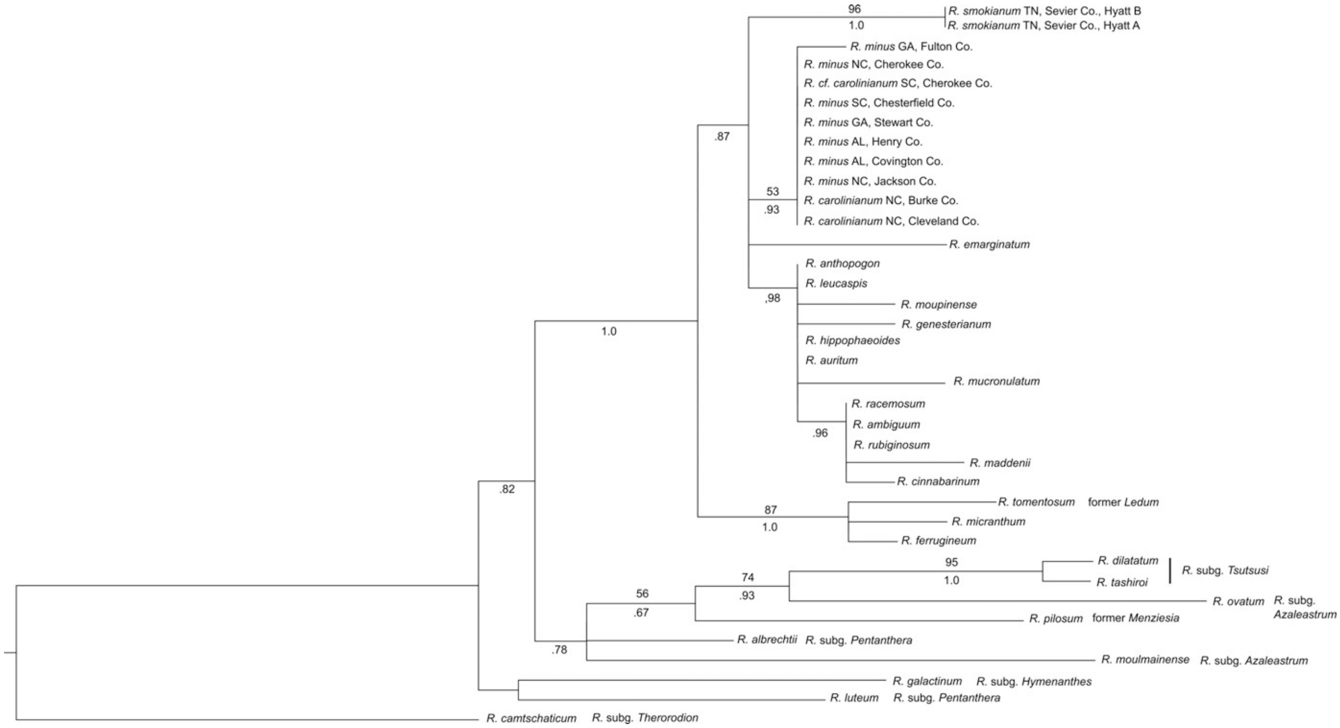

FIG. 2. Phylogenetic tree derived from analysis of ITS based on maximum likelihood. Values above the branches indicate maximum likelihood bootstrap support, those below posterior probabilities based on Bayesian analysis.

belong to monoclonal clusters (Miller pers. comm.). The sites of *R. chapmanii* are at least 100 km away from the nearest *R. minus* sites, and there are no populations with transitional forms.

Many authors today recognize only one species in the *R.* subsect. *Caroliniana*, namely *R. minus* with variation in flower tube length from short (*R. punctatum*-type) to long (*R. minus*-type, syn. *R. cuthbertii*) and consider *R. carolinianum* (syn. *R. punctatum* var. *majus*) as a synonym based on overlapping variation with short-tubed types. Only *R. minus* var. *chapmanii* (Alph.Wood) Gandhi & Zarucchi is still recognized (Duncan

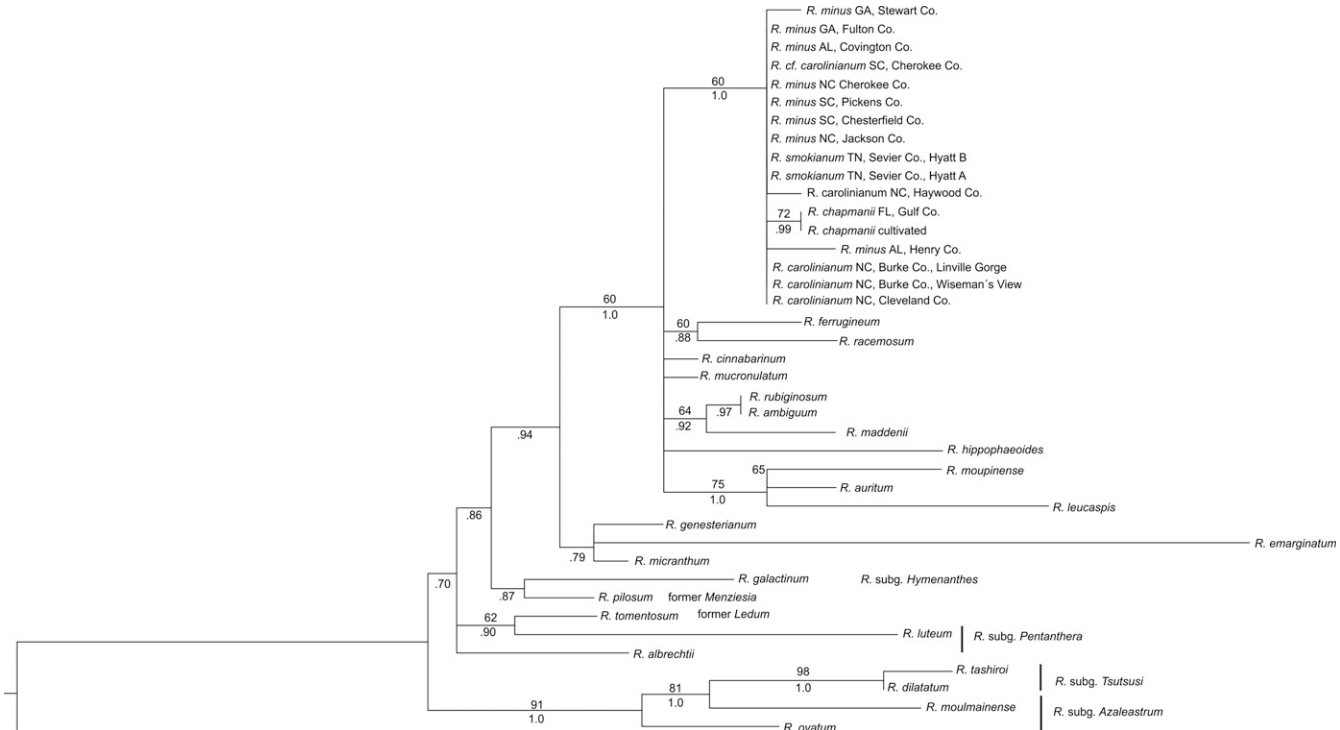

FIG. 3. Phylogenetic tree derived from analysis of plastid *trnL-F* region based on maximum likelihood. Values above the branches indicate maximum likelihood bootstrap support, those below posterior probabilities based on Bayesian analysis.

FIG. 4. *Rhododendron smokianum* at the type locality at the base of Anakeesta Ridge. The white flowering shrub is *Kalmia latifolia* L.

and Pullen 1962; Cox and Cox 1997; Gandhi and Zarucchi 2009; Judd and Kron 2009; see below).

However, we follow others (Davidian 1982; Miller 2013; Weakley 2015) in recognizing all three species at the species level. The three species differ in flower morphology, flowering time, and ecology (Table 1). *Rhododendron minus* has rather long-tubed populations in the south of its distribution area (southern Alabama and Georgia) (Fig. 1A), and these become shorter towards the north (Tennessee, South and North Carolina) and towards the mountains (Fig. 1C). *Rhododendron carolinianum* always has short tubes and also differs from long- and short-tubed *R. minus* in its flower being more explanate versus the more funnelform *R. minus* flower (see above, Fig. 1B). We consider it most likely that in northern and mountainous areas pollinators with short feeding tubes (e.g. bees) predominate, whereas plants further south rely rather on pollinators with long feeding tubes (e.g. butterflies). A taxonomic division of the *R. minus* populations into long and short tube populations, for example, does not seem possible to us, since the transitions seem indeed continuous (Bauer pers. obs.).

Here, we report on a fourth species in the group. This new taxon from the Great Smoky Mountains was highlighted for its different ecology and deviating morphology but only informally named "smokianum" by Miller (2013). The southern Appalachian Mountains are a biodiversity hotspot with several endemic species described from this region (Wiser 1994; Lendemer et al. 2013), most prominently *Abies fraseri* (Pursh) Poir., a late Pleistocene separation of the more widespread *A. balsaminea* (L.) Mill. (Clark et al. 2000). The region, especially the Anakeesta formation, is geologically unique in consisting of iron-sulfide-rich, rich bristle slate, shale, and sandstones of Precambrian origin (Hadley and Goldsmith 1963). Exposed rock oxidizes to brown color, and with water iron sulfate and sulfuric acid are formed. The rock is heavy metal-rich (Mathews et al. 1976) and acidic, which favors the occurrence of ericaceous species (e.g. *Rhododendron catawbiense* Hoffmanns., *Kalmia latifolia*). In addition, plants usually identified as *R. minus* grow on these rocks. Miller (2013) brought attention to these plants but refrained from a formal description. We, here, provide a morphological diagnosis combined with an analysis of nrDNA and plastid DNA markers and detailed report of their ecology. Finally, we provide the formal description of these plants as a species new to science.

MATERIALS AND METHODS

Plant Material—Plant material of all four species was studied in the wild by the second author between 2015 and 2019. Seeds from *R. smokianum* were distributed by the American Rhododendron Society in 2016 (collected in 2015) and grown in the second author's garden. Plants from these seeds were also distributed by the Rhododendron Species Foundation, Federal Way, WA. Leaves were taken from cultivated material and stored on silica gel until DNA was extracted. Voucher herbarium specimens are stored at OLD. Additional sequences generated by the first author for a previous study (Grimbs et al. 2017) were used to complement the dataset. Collection details, vouchers, and GenBank accession numbers are provided in Albach and Bauer (2021).

DNA-Based Phylogenetic Analyses—DNA was isolated from about 20 mg of tissue from either freshly collected or silica gel-dried material with the NucleoSpin Plant II (Macherey and Nagel, Düren, Germany) or the DNeasy plant minikit (Qiagen, Hilden Germany) following the provided protocol. The quality of the extracted DNA was checked on a 0.8% TBE-agarose-gel and the concentration measured spectrophotometrically with a GeneQuant RNA/DNA calculator (Pharmacia, Cambridge, UK).

The nuclear ribosomal ITS-region (hereafter ITS) and the plastid *trn*L intron, *trn*L 3′ exon and *trnL-F* spacer (hereafter *trnL-F* region) were amplified using primers ITS A (Blattner 1999) and ITS4 (White et al. 1990) for ITS, and the *trnL-F* region with primers c and f and sometimes including internal primers d and e (Taberlet et al. 1991). The PCR reactions included 2–2.5 mM $MgCl_2$, 8 mM bovine serum albumin, 0.4 μm primer, 0.2 mM dNTP, 1U/μl *Taq* polymerase (New England Biolabs, Ipswich, Massachusetts, USA), 1 × polymerase buffer and 1–5 μl DNA for a final volume of 25 μl. ITS sequences were amplified with a program consisting of 2 min at 95°C followed by 36 cycles of 1 min at 95°C, 1 min at 50–55°C, and 1.5–2 min at 72°C with a final extension of 5 min at 72°C on either a Mastercycler gradient (Eppendorf) or TProfessional Standard thermocycler (Biometra). The *trnL-F* region was amplified after 1 min denaturation at 95°C followed by 35 cycles with 30 sec at 95°C, 30 sec at 52°C and 1 min at

FIG. 5. Flowers of *R. smokianum* from the population at Mt. Kephart, The Jumpoff.

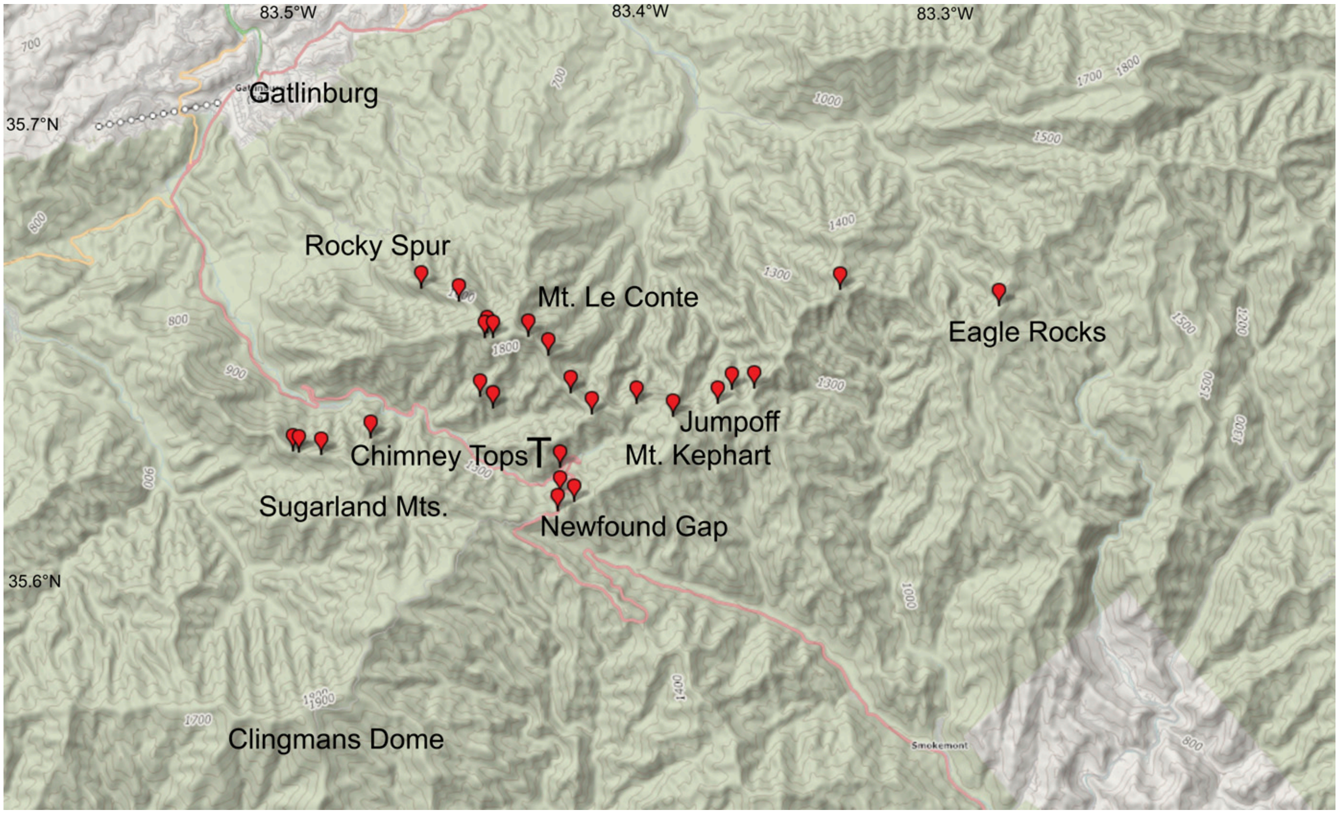

FIG. 6. Map of the known localities of *R. smokianum* based on personal observation of the second author. Elevations are given in meters. T = Type locality; map made with the TopoMap at gpsvisualizer.com.

72° with a final extension of 8 min at 72°C. The PCR products were cleaned using QIAquick PCR purification kits (Qiagen, Hilden, Germany) following the provided protocol. Sequencing reactions of 10 µl were carried out using 1 µl of the *Taq* dyeDeoxy terminator cycle sequencing mix (Applied Biosystems, Foster City, California, USA) and the same primers as for PCR. Sequences were generated by Sanger sequencing at commercial sequencing companies. All sequences are available from GenBank (Albach and Bauer 2021).

Sequences were manually aligned in Phyde v. 0.9971 (Müller et al. 2010) and evaluated for the best model of evolution in jModeltest2 (Darriba et al. 2012) with default options. No indel coding was conducted since indels were either autapomorphic or in mononucleotide repeats. Phylogenetic analyses were conducted in RAxML-NG (Kozlov et al. 2019) using the K80 + Γ for ITS and K81uf + Γ for *trnL-F* with four different rates and 200 bootstrap replicates. Posterior probabilities were estimated in MrBayes v. 3.2.6 (Ronquist et al. 2012) with the same models as for RAxML-NG. Two parallel runs were conducted with four chains each for one million generations sampled every 500 generations and the first 25% discarded as burn-in. Convergence was checked by inspecting the potential scale reduction factor, which was 1.000 for all parameters.

RESULTS

Data—The dataset for the nuclear ribosomal ITS region included 37 taxa and 617 characters, of which 31 are potentially parsimony informative. The dataset for the plastid *trnL-F* region included 41 taxa and 899 characters, of which 41 are potentially parsimony informative. All matrices and GenBank accessions used in this study are available from the Dryad Digital Repository (Albach and Bauer 2021).

Phylogenetic Analyses—Results of the analyses of ITS (Fig. 2) data revealed *R. smokianum* to be clearly distinct from other members of *R.* subsect. *Caroliniana* and all other members of *R.* subg. *Rhododendron*. Samples from both *R. minus* and *R. carolinianum* have mostly identical ITS-sequences and form a clade (53% bootstrap support (BS)/ .93 posterior probability (PP)), while DNA of *R. chapmanii* did not amplify for ITS despite several attempts. Results of the analyses of the *trnL-F* region (Fig. 3) revealed a monophyletic *R.* subsect. *Caroliniana* (60% BS/1.0 PP) with little differentiation within the subsection except for a separation of the two specimens of *R. chapmanii* (72% BS/.99 PP).

TAXONOMIC TREATMENT

Rhododendron smokianum Ralf Bauer & Albach, sp. nov. TYPE: USA. Tennessee; Sevier Co.; Route 441 from Gatlinburg to Cherokee, below Newfound Gap in rocks beside the road at base of Anakeesta Ridge, ca. N 35.6225 W 83.4225; Hyatt A, grown from seed collected in 2015, flowered in cultivation in 2019 in the second author's garden, accession number 1269 (holotype: OLD 6300; isotypes: NY, US).

Differs from *R. minus* in its much smaller and compact growth and in its smaller flowers having a very short or nonexistent tubular part of the corolla tube (0–2 mm long). Differs from *R. chapmanii* in its smaller flowers with a smaller opening and a very short or nonexistent tubular part of the corolla. Differs from *R. carolinianum* in its much later blooming time (end of June) and in its smaller flowers with a smaller opening and a very short or nonexistent tubular part of the corolla. The species differs from other species in two synapomorphic sites in the ITS sequence, but we refrain from calling them diagnostic in the absence of wider sampling of the species. Table 1.

Shrubs, upright, richly branched, compact, (0.2–) 0.5–2(–2.5) m tall, usually considerably wider, no runners and

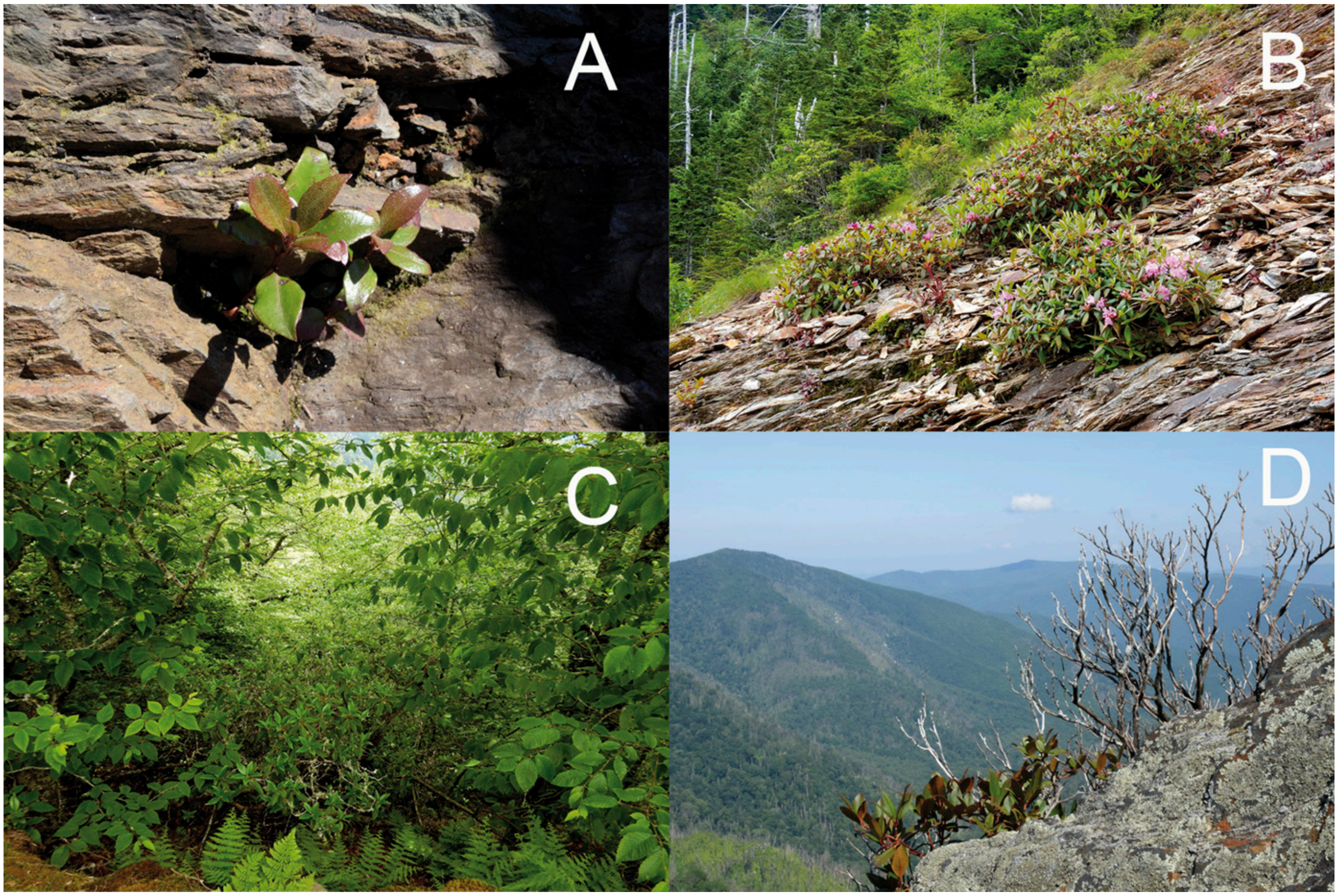

FIG. 7. Ecology of *R. smokianum*. A. Seedlings of *R. smokianum* on bare rock at Chimney Tops. B. *R. smokianum* on young landslide of pure Anakeesta rock at The Boulevard. C. Non-flowering *R. smokianum* under *Betula alleghaniensis* Britton. D. Burned *R. smokianum* regenerate quickly at Chimney Tops.

not spreading by layers. **Leaves** evergreen, leathery, petiolate for 4–8 mm, lamina oval, apex with distinct, slightly downward-curving tip, margins smooth, base attenuate, 40–80 mm long, 10–30 mm wide, green on top, brown below, covered on upper surface with 3, on lower surface with 12–15 peltate scales (ca. 150 μm in diameter) per mm^2. **Inflorescences** terminal on annual shoots that are usually 1–10 cm long, appearing before flowering and usually almost fully developed during the flowering period; buds 8–15 mm long in winter, green to brown-scaly; peduncle 8–20 mm, usually 4–8 flowers per inflorescences. **Flowers** fragrance-less, corolla usually magenta or bright pink, more rarely pale pink or lavender pink, 20–25 mm long and 20–35 mm wide, narrow part of tube scarcely noticeable (0–2 mm in length), rest of tube (10–12 mm) expanding in a trumpet-like manner before 5 perianth segments can be differentiated, each segment 8–15 mm long and just as wide with strongly rounded tips, inside the corolla in the area of the upper perianth segment often some orange-brown to red spots; stamens 9–10, 7–25 mm long, white; pistil 12–20 mm long, red to whitish. Figures 4, 5.

Distribution and Conservation—The main distribution area is in Sevier Co., Tennessee, with only a few plants in Swain Co., North Carolina, at the Tennessee border (Fig. 6). Closest populations of *R. minus* are ca. 37 km and those of *R. carolinianum* 42 km away. *Rhododendron smokianum* can be found in the whole area south of a line Mount Le Conte - The Boulevard - Mount Kephart from the highest peaks and ridges down to the valley of Walker Camp Prong between 1280 m and 2000 m above sea level. North from the Mount Le Conte summit it can be found along Rainbow Falls Trail on a ridge called Rocky Spur. Furthermore, there are few sites on Sugarland Mountain (Chimney Tops and along Sugarland Mountain Trail). The new species also grows along Route 441 going up from Walker Camp Prong to Newfound Gap. A single plant was observed along the Appalachian Trail between Newfound Gap and Mount Kephart, and an abundance of plants was encountered along the Appalachian Trail from Mount Kephart to Eagle Rocks. Despite its limited distribution area (19 km in east-west direction and 7 km at the widest point in north-south direction), the new species is not endangered by collecting, agriculture, or settlement. As long as there are steep, anakeesta rocks, which cause repeated landslides, the species will be able to occupy new settlement areas. All habitats are located in the Great Smoky Mountains National Park. With the exception of the artificially (by road construction) created site on the road from Gatlinburg to Cherokee, all sites can only be reached by long and/or steep hikes.

Etymology—The epithet is derived from the distribution range, the Great Smoky Mountains.

Key to the Species of Rhododendron sect. carolinianA in the Field

1. Narrow part of the corolla tube ca. 0–2 mm long; peak flowering simultaneous with peak flowering of *Kalmia latifolia*; only in the center of Great Smoky Mountains N.P. . . . . *R. smokianum*
1. Narrow part of the corolla tube > 4 mm long; main flowering before to simultaneous with *Kalmia latifolia*; Florida, Alabama, Georgia, Tennessee, South and North Carolina 2
    2. Leaves mostly 45–60 mm long, 17–24 mm wide, in the sun clearly revolute; typically occurring with *Serenoa repens*; Florida . . . . . *R. chapmanii*
    2. Leaves mostly 60–110 mm long, 20–40 mm wide, flat or only slightly revolute; Alabama, Georgia, Tennessee, South and North Carolina **3**
        3. Narrow part of the corolla tube 4–6 mm long; corolla explanate; main flowering in early spring, long before *Kalmia latifolia*; foliation starting with or after flowering; North and South Carolina . . . . *R. carolinianum*
        3. Narrow part of the corolla tube 4–15 mm long; corolla funnelform; main flowering in late spring, together with *Kalmia latifolia*; foliation before flowering (in southern parts of the range also after flowering); Alabama, Georgia, Tennessee, South and North Carolina . . . . *R. minus*

Discussion

We here propose *R. smokianum* as a species new to science. We follow the definition of a species as "separately evolving metapopulation lineage" (De Queiroz 2007), which can be differentiated from other species by morphological characters (Table 1), monophyly in phylogenetic analyses (Figs. 3, 4) and a distinct ecological niche (see below). Ideally, this lineage would also be reproductively isolated from other species but crossing studies have not been conducted and are not expected to indicate isolation given the wide cross-compatibility of *Rhododendron* species at least within subgenera typically used in horticulture.

Our phylogenetic analyses (Figs. 3, 4) show different but not incongruent results with respect to *R. smokianum*. Whereas our plastid marker provided support for the monophyly of *R.* subsect. *Caroliniana*, it was not able to distinguish the species from one another. One the other hand, ITS differentiated *R. smokianum* clearly but did not provide support for the monophyly of the section. The most likely explanation is that *R. smokianum* is an early diverging taxon within *R.* subsect. *Caroliniana* but a hybridization event between a member of *R.* subsect. *Caroliniana* and an unsampled species remains a possibility. Our analysis of ITS here is congruent with that from the wider sampling in *Rhododendron* (Khan, Nolzen, and Albach in prep.) and suggests that there is no extant species of *Rhododendron* related to *R. smokianum* based on ITS.

The flora of the southern Appalachians is unique in several ways. It harbors several endemics in the subalpine region and is the southernmost outpost for several alpine species otherwise only found much further north (Wiser 1994). These mountain areas tended to be forest-free down to 1500 m a. s. l. during the Pleistocene but are now almost completely forested (Wiser 1994). Therefore, previous species that lived in larger areas of alpine habitat are now restricted to open rock outcrops. However, given the heavy-metal rich rock of the Anakeesta formation, this habitat may be toxic to many species and lead to severe selection. Another endemic species known to be specialist to these rocks is *Calamagrostis cainii* Hitchc. (Wiser et al. 1996). *Rhododendron smokianum* may be another example, since the closest relatives occur in the surrounding lowland to mountainous areas.

In contrast to the other species in the subsection, which mainly inhabit forests and only in the case of *R. carolinianum* occur on exposed sites in mountains, *R. smokianum* thrives on vertically sloping rock of the Anakeesta Formation between Mount Le Conte and Sugarland Mountain, on the Appalachian Trail between Newfound Gap and Eagle Rocks, and along the Boulevard between Mount Kephart and Mount Le Conte and has not been sighted elsewhere despite extensive field work (Fig. 6). Juvenile and flowering plants have only been found on open rock from landslides (Fig. 7A, B), for which the Anakeesta slate is ideal due to its high brittleness. In addition, the acidic and heavy-metal-rich rock inhibits the development of many other potential competing plants and has led to the recognition of the vegetation as the *Calamagrostis cainii-Rhododendron carolinianum* outcrop community (Wiser et al. 1996). After decades, enough humus has accumulated around the evergrowing shrubs of *R. smokianum* that even small trees (e.g. *Sorbus americana* Marshall, *Betula alleghaniensis* Britton) have a chance to develop. As a specialist of open rock, *R. smokianum* may survive for some time under shade, elongating to 2.5 m, and may thin out but will not flower (Fig. 7C). This likely limits its lower distribution range to about 1200 m where the other species of the subsection are growing. However, after fire, it quickly regenerates and starts flowering again (Hooper 1969; Fig. 7D).

Acknowledgments

We thank Don Hyatt (McLean, VA) for company in the field, for showing the new species and for providing seed. We also thank Ron Miller (Pensacola, FL) for extremely fruitful botanical discussions, for pointing out that there might be a new taxon related to *R. minus* in the southern Appalachians, for help in collecting the closest relatives of *R. smokianum* and many valuable suggestions for this article. Thanks also to Charles Horn (Newberry, SC) for highly interesting joint excursions to various sites of *R. carolinianum*. We further thank Eike Mayland-Quellhorst (Univ. Oldenburg) for the work in the lab and Bernhard von Hagen and two anonymous reviewers for valuable comments on the manuscript. The research was not preregistered.

Author Contributions

RB provided the material and the initial idea to study the species. He also did extensive field work by hiking in order to determine the distribution area and ecology of the new species. DCA analyzed the sequence data and wrote the first draft based on information including the description of the new species by RB.

Literature Cited

Albach, D. C. and R. Bauer. 2021. Data from: *Rhododendron smokianum*, a new species from the Great Smoky Mountains. *Dryad Digital Repository.* http://dx.doi.org/10.5061/dryad.mgqnk98wv.

Andrews, H. C., T. Bensley, A. H. Haworth, J. Kennedy, and G. Jackson. 1797. *The Botanist's Repository, For New and Rare Plants*. London: printed by T. Bensley, and published by the author.

Blattner, F. R. 1999. Direct amplification of the entire ITS region from poorly preserved plant material using recombinant PCR. *BioTechniques* 27: 1180–1186.

Chamberlain, D., R. Hyam, G. Argent, G. Fairweather, and K. S. Walter. 1996. *The Genus Rhododendron: Its Classification and Synonymy*. Edinburgh: Royal Botanic Garden Edinburgh.

Clark, C. M., T. R. Wentworth, and D. M. O'Malley. 2000. Genetic discontinuity revealed by chloroplast microsatellites in eastern North American *Abies* (Pinaceae). *American Journal of Botany* 87: 774–782.

Cox, P. A. and K. N. Cox. 1997. *The Encyclopedia of Rhododendron Species*. Perth: Glendoick.

Craven, L. A. 2011. *Diplarche* and *Menziesia* transferred to *Rhododendron* (Ericaceae). *Blumea* 56: 33–35.

Darriba, D., G. L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9: 772.

Davidian, H. H. 1982. *The Rhododendron Species*, vol. 1, *The Lepidotes*. Portland, Oregon: Timber Press.

De Queiroz, K. 2007. Species concepts and species delimitation. *Systematic Biology* 56: 879–886.

Duncan, W. H. and T. M. Pullen. 1962. Lepidote Rhododendrons of the southeastern United States. *Brittonia* 290–298.

Frodin, D. G. 2004. History and concepts of big plant genera. *Taxon* 53: 753–776.

Gandhi, K. N. and J. L. Zarucchi. 2009. Validation of *Rhododendron minus* var. *chapmanii* (Ericaceae). *Harvard Papers in Botany* 14: 1.

Goetsch, L. A., A. J. Eckert, and B. D. Hall. 2005. The molecular systematics of *Rhododendron* (Ericaceae): A phylogeny based upon RPB2 gene sequences. *Systematic Botany* 30: 616–626.

Gray, A. 1876. Contributions to the botany of North America. *Proceedings of the American Academy of Arts and Sciences* 12: 51–84.

Grimbs, A., A. Shrestha, A. S. D. Rezk, S. Grimbs, I. H. Said, H. Schepker, M.-T. Hütt, D. C. Albach, K. Brix, N. Kuhnert, and M. S. Ullrich. 2017. Bioactivity in *Rhododendron*: A systemic analysis of antimicrobial and cytotoxic activities and their phylogenetic and phytochemical origins. *Frontiers in Plant Science* 8: 551.

Hadley, J. B. and R. Goldsmith. 1963. *Geology of the Eastern Great Smoky Mountains, North Carolina and Tennessee*. Washington, D.C.: US Government Printing Office.

Hooker, J. D. 1849. *The Rhododendrons of Sikkim-Himalaya*. Dehra Dun: Bishen Singh Mahendra Pal Singh.

Hooper, R. M. 1969. Prescribed burning for laurel and rhododendron control in the Southern Appalachians. *USDA Forest Service Research Note* 116.

Jones, J. R., T. G. Ranney, and N. P. Lynch. 2007. Ploidy levels and relative genome sizes of diverse species, hybrids, and cultivars of *Rhododendron*. *Journal - American Rhododendron Society* Fall 2007: 220–227.

Judd, W. S. and K. A. Kron. 2009. *Rhododendron*. Pp. 455–473 in *Flora of North America North of Mexico*, vol. 8, ed. FoNAE Committee. Oxford, UK: Oxford University Press.

Kozlov, A. M., D. Darriba, T. Fouri, B. Morel, and A. Stamatakis. 2019. RAxML-NG: A fast, scalable, and user-friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics* 35: 4453–4455.

Kron, K. A. and W. S. Judd. 1990. Phylogenetic relationships within the Rhodoreae (Ericaceae) with specific comments on the placement of *Ledum*. *Systematic Botany* 15: 57–68.

Lamarck, M. C. l. 1792. Notice de quelques Plantes rares ou nouvelles, observées dans l'Amerique Septentrionale, par M. A. Michaux. *Journal d'Histoire Naturelle* 1: 409–419.

Lendemer, J. C., R. C. Harris, and E. A. Tripp. 2013. *The Lichens and Allied Fungi of Great Smoky Mountains National Park: An Annotated Checklist with Comprehensive Keys*. New York: New York Botanical Garden Press.

Mabberley, D. J. 1997. *The Plant-Book: a Portable Dictionary of the Vascular Plants*. Cambridge, UK: Cambridge University Press.

Mathews R. C. Jr., J. D. Sinks, and E. L. Morgan. 1976. Acid drainage toxicity and assessment of sodium hydroxide neutralization in streams of the Great Smoky Mountains. *Proceedings of First Conference on Scientific Research in National Parks* 1: 559–564.

Miller, R. 2013. Stalking the wild Lepidote: *Rhododendron minus* reconsidered. *Journal - American Rhododendron Society* 67: 63–68, 78–83.

Milne, R. I., C. Davies, R. Prickett, L. Inns, and D. Chamberlain. 2010. Phylogeny of *Rhododendron* subgenus *Hymenanthes* based on chloroplast DNA markers: between-lineage hybridisation during adaptive radiation? *Plant Systematics and Evolution* 285: 233–244.

Müller, K. F., D. Quandt, and J. Müller. 2010. *Phyde*. Published by the authors.

Musgrave, T., C. Gardner, and W. Musgrave. 1998. *The Plant Hunters: Two Hundred Years of Adventure and Discovery Around the World*. London: Cassell Illustrated.

Rehder, A. 1912. *Rhododendron carolinianum*, a new *Rhododendron* from North Carolina. *Rhodora* 14: 97–102.

Ronquist, F., M. Teslenko, P. van der Mark, D. L. Ayres, A. Darling, S. Höhna, B. Larget, L. Liu, M. A. Suchard, and J. P. Huelsenbeck. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.

Shrestha, N., X. Su, X. Xu, and Z. Wang. 2018. The drivers of high *Rhododendron* diversity in south-west China: Does seasonality matter? *Journal of Biogeography* 45: 438–447.

Small, J. K. 1902. A Georgia *Rhododendron*. *Torreya* 2: 9–10.

Taberlet, P., L. Gielly, G. Pautou, and J. Bouvet. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.

Voss, D. 2014. A third botanical variety in *Rhododendron minus*. *Journal - American Rhododendron Society* 68: 85–89.

Weakley, A. S. 2015. *Flora of the Southern and Mid-Atlantic States*. Chapel Hill: University of North Carolina Herbarium, North Carolina Botanical Garden, University of North Carolina.

White, T. J., T. D. Bruns, S. Lee, and J. Taylor. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in *PCR Protocols: A Guide to Methods and Applications*, eds. M. Innis, D. Gelfand, J. Sninsky, and T. White. San Diego: Academic Press.

Wiser, S. K. 1994. High-elevation cliffs and outcrops of the Southern Appalachians: Vascular plants and biogeography. *Castanea* 85–116.

Wiser, S. K., R. K. Peet, and P. S. White. 1996. High-elevation rock outcrop vegetation of the southern Appalachian mountains. *Journal of Vegetation Science* 7: 703–722.

Wood, A. 1870. *The American Botanist and Florist: Including Lessons in the Structure, Life, and Growth of Plants; Together with a Simple Analytical Flora, Descriptive of the Native and Cultivated Plants Growing in the Atlantic Division of the American Union*. Chicago: A. S. Barnes.

Zhou, W., T. Gibbons, L. A. Goetsch, B. D. Hall, T. G. Ranney, and R. Miller. 2008. *Rhododendron colemanii*: A new species of deciduous azalea (*Rhododendron* section *Pentanthera*; Ericaceae) from the coastal plain of Alabama and Georgia. *Journal - American Rhododendron Society* 2008: 72–78.