TAXONOMY, BIOGEOGRAPHY, AND PHYLOGEOGRAPHY OF THE GENUS *SHORTIA* (DIAPENSIACEAE)

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ABSTRACT

Shortia is a genus of evergreen perennials thought to have arisen in the Tertiary Flora of Laurasia. Its species are currently distributed in eastern and southeastern Asia and in southeastern North America. Herein, we report three new species (*S. amamiana*, *S. okinawensis*, and *S. pubinervis*), resurrect an historical species name (*S. exappendiculata*), and revise the status and distribution of *S. rotundifolia*, bringing the total number of species of the genus to 10. Finally, we contribute an intuitive phylogeographic tree of species relationships from RAD sequence DNA data.

INTRODUCTION

The genus *Shortia* (Diapensiaceae) was described in 1842 by John Torrey and Asa Gray based on a fruiting specimen collected in North Carolina by Andre Michaux. The generic name commemorates Charles Wilkins Short (1794-1863), a medical doctor and amateur botanist who had corresponded with Gray for many years. The epithet of the type species, "*galacifolia*," alludes to the resemblance of its foliage to that of the genus *Galax*, also of the Diapensiaceae. Early *Shortia* collections of *S. rotundifolia* and *S. uniflora* by Maximowicz (1888) were referred to the genus *Schizocodon* Siebold & Zucc. *Schizocodon,* which bears more than one flower on each scape, is now considered distinct from *Shortia*. Furthermore, *Schizocodon* flowers are brightly colored with fringed corollae (see Yamazaki 1968).

In the 2000s with the publication of *Flora of China* (Bartholomew, 2005) and *Flora of North America* (Nesom, 2009), and floras of Japan (Maximowicz, 1871; Honda, 1954), there were only four accepted species' names of *Shortia*: *S. galacifolia* (of North America), *S. sinensis*, *S. rotundifolia* (of China and Taiwan), and *S. uniflora* (of Japan). In 2017, Gaddy and Nuraliev (2017) described *S. rotata* from northern Vietnam, and Gaddy et al. (2019) erected *S. brevistyla,* formerly *S. galacifolia* var. *brevistyla,* to species level in 2019, bringing the total of known *Shortia* species to six. We herein present *S. amamiana, S. pubinervis, and S. okinawensis* as new species and conclude that *S. rotundifolia* is the *Shortia* of Iriomote Island and the discarded name *S. exappendiculata* is a valid taxon describing the species of *Shortia* on the island of Taiwan. After nearly a decade of herbarium reviews, field work in four countries, and DNA analyses, we recognize ten species of *Shortia*: two in the Carolinas of North America, two in Yunnan Province of China, one in Taiwan, one in Vietnam, and four in Japan, three of which are found on separate islands in the Ryukyu Archipelago of southern Japan. These species, their taxonomic histories, biogeography, ecology, microhabitat preferences, and phylogeny are discussed below.

METHODOLOGIES

Herbarium/Literature Review

From 2017 into 2022, we reviewed herbarium sheets of *Shortia* from international and regional herbaria—primarily, Komarov Botanical Institute of St. Petersburg (LE), Paris (P), Beijing (PE), Kunming (KUN) in Yunnan, China and Kagima (KAG) in southern Japan. From this review, we discovered two new species' names that were proposed on herbarium sheets—*S. amamiana* and *S. pubinervis,* but never published elsewhere. We also learned that *Shortia rotundifolia* originally found on Iriomote Island in the Ryukyu Archipelago (by Maximowicz in 1888 and described as *Schizocodon rotundifolium*) flowering in October is obviously different from *Shortia exappendiculata* (described from Taiwan in 1913 by Hayata), which blooms in spring on the island of Taiwan.

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Field Work/Authors

The senior author has carried out field work in *Shortia* populations in the Carolinas since 1980. Field and DNA studies on a North Carolina disjunct distribution of *Shortia galacifolia*, thought to be a variety (var. *brevistyla*), revealed that it was a species (Gaddy et al., 2019).

The senior author conducted field work along the Vietnam-Chinese border in 2017 and 2018. *Shortia rotata* (Gaddy and Nuraliev, 2017) was discovered in northern Vietnam in 2017. Numerous historic sites for *Shortia* "sp." in Vietnam were searched in 2018; *Shortia* plants were found, but no flowers were present and positive identification was impossible.

In October of 2022, the senior and junior authors traveled to Iriomote Island in the Ryukyu Archipelago of Japan in order to search for the type locality of *Shortia rotundifolia*, which was found there in 1888 by Maximowicz and was reputed to flower in October. The plant was found there in flower in mid-October.

Field Work/Proxy

L L Gaddy III, son of the senior author, explored Lao Jun Shan (in China), searching for *Shortia pubinervis* in 2019. The plant could not be found. Atsuhito Ikegami and Shuichi Morita contributed unpublished field data on the distribution and abundance of *Shortia amamiana*. Atsushi Abe contributed unpublished data on the distribution and abundance of *S. okinawensis* and *S. rotundifolia*.

DNA Analysis

The junior author is preparing a DNA analysis of the phylogeny of the genus *Shortia* with emphasis on the genetic distance between species (Sakaguchi, in manuscript). He has collected and analyzed leaf samples of the all the species discussed herein. For preliminary data, he has used RADSeq DNA sequencing, a relatively new methodology that can identify and score thousands of genetic markers across the target genome (Davey and Blaxter, 2010), as well as be used to analyze species with limited available sequence data. From preliminary data, he has kindly constructed Figure 1, a RADSeq phylogenetic tree of the genus *Shortia*, based primarily on genetic distance, for this paper.

RESULTS: THE SPECIES

SHORTIA Torrey & A. Gray, Amer. J. Sci. Arts 42: 48. 1842. **TYPE: USA.** "Hautes Montagnes de Carolinae," 1839, *A. Michaux s.n.* (holotype: P).

Schizocodon Siebold & Zuccarini, Abh. Akad. Muench. 3: 723. T. 2. 1843.
Sherwoodia House, Torreya 7: 235. 1907.
Shortiopsis Hayata, Icon. Pl. Formsan. 3: 147. 1913.

Plants short (usually less than 25 cm tall), often creeping and/or clonal, evergreen perennial herbs. Leaves round to elliptic-ovate, margins in most species with serrate mucronate tips. Flowers solitary and borne on a scape with several persistent bud scales at the base and a few small bracts near the top. Calyx lobes 5. Corolla white, pink, or lavender, funnel-shaped with 5 more or less spreading or rotate, toothed lobes. Stamens 5, attached near the mouth of the corolla tube. Capsule globose, 3-valved, dehiscent, style persistent in fruit. Seeds numerous, small, oblong or ovoid.

In temperate forests, flowering March to May. In subtropical cloud forests in China and Vietnam, flowering December through February. In the Ryukyu Islands, flowering July to October.

1. *SHORTIA AMAMIANA* (Owhi) ex Gaddy & Sakaguchi, **sp. nov**. Figures 4 and 6.
TYPE: JAPAN. AMAMI-OSHIMA. 25 August 1955, Hatusima & Shimabukuro 20126 (holotype: KAG 150820).

Shortia rotundifolia (Makino) Maximowicz var. *amamiana* Ohwi. Unpublished, from type sheet.

Differs from *Shortia rotundifolia* with leaves with triangular serrations as deep as 3 mm with long mucronate tips. Label on the type sheet reads "*A typo diversa: foliorum dentibus triangulatis, acutis vel subacutis incurvatomicronatis*."

Flowers white, late summer. Shaded rocky areas in mountains on the island of Amami. Ryukyu Islands, Japan.

2. *SHORTIA BREVISTYLA* (P.A. Davies) Gaddy. Figure 3.
Gaddy et al., Phytologia 101: 113-119. 2019.

Shortia galacifolia Torrey & A. Gray var. *brevistyla* P. A. Davies. *Rhod.* 54: 151. 1952.

Flowers white, March-April. Mesic ravines, headwaters of Catawba River in North Carolina, USA.

3. *SHORTIA EXAPPENDICULATA* Hayata. Figures 4 and 8.
Hayata, Icon. Plantarum Formosan. 3:143-147. 1913.

Shortia rotundifolius Maximowicz, Bull. Acad. Imp. Science St. Petersb. 32:397. 1888.
Shortia rotundifolia (Maximowicz) Makino, Bot. Mag. (Tokyo) 9: 327. 1895.
Shortia subcordata Hayata, Icon. Plant. Formosan. 3: 147. 1913.
Shortia transalpina Hayata, Icon. Plant. Formosan. 3: 147. 1913.
Shortia ritoensis Hayata, Icon. Plant. Formosan. 4: 17. 1914.
Shortia rotundifolia var. *ritoensis* (Hayata) T. C. Huang & A. Hsiao, Fl. Taiwan IV: 1. 1984.
Shortia rotundifolia var. *subcordata* (Hayata) T. C. Huang & A. Hsiao Hayata), Fl. Taiwan IV: 1. 1984.
Shortia rotundifolia var. *transalpina* (Hayata) Yamazaki, Fl. Taiwan IV: 1. 1984.

In the *Flora of China* (Bartholomew 2005) and in other recent floras of Taiwan, *Shortia exappendiculata* has been listed as a synonym of *Shortia rotundifolia,* which was originally found on Iriomote Island in the southern Ryukyus northeast of Taiwan. We have resurrected *exappendiculata* to include all *Shortia* on the island of Taiwan. *Shortia rotundifolia* (Maximowicz) Makino), which flowers in October, occurs only on Iriomote Island in the Ryukyus (see below).

Flowers white. March-May. Rocky evergreen forests and alpine regions; Taiwan.

4. *SHORTIA GALACIFOLIA* Torrey & A. Gray. Figures 3 and 10.
Gray, Am. J. Sci. & Arts 4:48. 1842.

Flowers white, rarely pink. March-April. Mesic ravines and humid gorges on headwaters of Keowee-Toxaway drainage of the Savannah River in North and South Carolina.

5. *SHORTIA OKINAWENSIS* Gaddy & Sakaguchi, **sp. nov.** Figure 4 and 7.
TYPE: JAPAN. Okinawa. Mt. Yonaha, November 02, 1955, Amano 7503 (holotype: KAG 150813).

Differs from *Shortia rotundifolia* and *Shortia amamiana* in that shallow serrations on leaves are to 2 mm with short mucronate tips. Intermediate between *Shortia rotundifolia* and *Shortia amamiana*. DNA evidence indicates significant genetic distance among these three closely-related species.

Flowers white. Late summer. Rocky evergreen forests, Okinawa, Ryukyu Islands, Japan.

6. *SHORTIA PUBINERVIS* (C.Y. Wu) Y.M. Shui ex Gaddy & Sakaguchi, **sp. nov.** Figure 2.
TYPE: CHINA. Yunnan. Ching-Kou, Lao Chun Shan: in mixed woods, fruit green, common, December 07, 1947, K.M. Feng 13690 (holotype: KUN 0235234). Label on type reads: "*Shortia pubinervis* (C.Y. Wu) Y.M. Shui, *nov. stat*." (inedit.).

Shortia sinensis Hemsley var. *pubinervis* C.Y. Wu. Unpublished, on type label.

Differs from *Shortia sinensis* in having short (1-2 mm) white hairs on veins of underside of leaves. One known locality; may be extirpated.

Several expeditions to Lao Jun Shan — including one by the senior author and one by his son, L L Gaddy III — in the last few decades have failed to find this plant. Our determination of this taxon as a new species is based on Y.M. Shui's analysis of the type specimen and the junior author's genetic analysis of a leaf from the type specimen.

Flowers white? December-January?

7. *SHORTIA ROTATA* Gaddy & Nuraliev. Figure 2.
Gaddy & Nuraliev, Wulfenia 24: 53-60. 2017.
Shortia sinensis auct. non. Hemsley. Nuraliev, Wulfenia 17: 25. 2010.

Flowers pink to lavender. November-January. Gorges and shaded deep ravines, northern Vietnam.

8. *SHORTIA ROTUNDIFOLIA* (Maximowicz) Makino. Figures 4 and 9.
Makino, Botanical Magazine (Tokyo) 9: 327. 1895.

Schizocodon rotundifolium Maximowicz, Bull. Acad. Imp. Science St. Petersb. 32:397. 1888.
Sherwoodia rotundifolia (Maximowicz) House, Torreya 7: 235. 1907.
Shortiopsis exappendiculata (Hayata) Hayata, Icon. Pl. Formosan. 3: 134. 1913.
Shortia rotundifolia var. *subcordata* (Hayata) T. C. Hoang & A. Hsiao, Fl. Taiwan VI: 1. 1984.
Shortia rotundifolia var. *transalpina* (Hayata) Yamazaki, Fl. Taiwan VI: 1. 1984.

Flowers white to pinkish white. October. Uncommon on forested mossy cliffs along rivers in mountains of Iriomote Island, Ryukyu (Yaeyama) Islands, Japan.

9. *SHORTIA SINENSIS* Hemsley. Figures 2 and 8.
Hooker, Icon. Plant. 27(1): t. 2624. 1899.

Shortia sinensis var. *pubinervis* C.Y. Wu. Unpublished, on type label of *Shortia pubinervis.*

Flowers white. December-February. Wet, rocky cliffs usually facing north or northeast at 1000-2000 m in forests. Southeastern Yunnan Province, China.

10. *SHORTIA UNIFLORA* (Maximowicz) Maximowicz. Figure 3.
Maximowicz, Bull. Acad. Imp. Science St. Petersb. 16: 225. 1871.

Schizocodon unifolius Maximowicz, Bull. Acad. Imp. Science St. Petersb. 12: 71. 1868.
Shortia uniflora var. uniflora Honda, J. Jap. Bot. 29:1-3. 1954.
Shortia uniflora var. *kantoensis* Yamazaki, J. Jap. Bot. 29: 162. 1954.
Shortia uniflora var. *orbiculatis* Honda, J. Jap. Bot. 29: 1-3. 1954.

Flowers pink, rarely white. April-May. Woods and low mountains, Honshu, Japan.

KEY TO SPECIES OF *SHORTIA*

Leaves round
- Flowers white
  - Plant of North America
    - Style 12-18 mm in length, plant of Carolinas……..…….**Shortia galacifolia**
    - Style 6-12 mm in length, plant of Catawba drainage, NC……...**Shortia brevistyla**
  - Plant of Japan or Taiwan
    - Teeth on leaves absent or less than 2 mm in length
      - Plant flowering in October……..……..**Shortia rotundifolia**
      - Plant flowering in spring……..……..**Shortia exappendiculata**
    - Teeth on leaves present to 2-4 mm in length
      - Plant of Okinawa, flowering in August-September……..…**Shortia okinawensis**
      - Plant of Amami Island, flowering in July-August……..…….**Shortia amamiana**
- Flowers pink…….**Shortia uniflora**

Leaves elliptical
- Leaves with sparse white hairs 1-3 mm long on underside…….**Shortia pubinervis**
- Leaves without white hairs on underside
  - Flowers white…….……..**Shortia sinensis**
  - Flowers pink to lavender……**Shortia rotata**

DISCUSSION

Shortia species are well-separated by "island" biogeography and phenology. Its species are found on small islands in the Ryukyus, high elevations in Taiwan, and on cloud forest-covered island "peaks" in China. In North America and Vietnam, it occurs in deep gorges and their narrow ravines. Most species of *Shortia* are rare or of conservation concern; only *S. galacifolia, S. uniflora, S. exappendiculata*, and *S. sinensis* could be considered common or locally common within their respective ranges. In delimiting species of *Shortia*, phenological and leaf morphology data has been proven more useful than floral data, especially in the four island species. *Shortia exappendiculata* of Taiwan flowers March-May; the closely-related *S. rotundifolia* on Iriomote Island blooms in October; the few known flowering specimens of *Shortia okinawensis* appear to also have flowered in September, while *S. amamiana* flowers from July to August. As to leaf morphology, *Shortia amamiana* has deep serrations, with long mucronate tips on its leaves; *S. okinawensis* has shallower serrations and mucronate tips on its leaves; *S. rotundifolia* leaves are more rounded with very shallow serrations on which the short mucronate tips are hardly visible. Preliminary DNA data indicate little gene flow from population to population, much less island to island in the Ryukyus (Dan et al. 2013; Gaddy et al. 2019).

Shortia appears to be part of the original Laurasian Arcto-Tertiary Flora of Asia and North America. Cain (1943), Chaney (1947), and Braun (1950) were early supporters of the idea that much of the flora of the deciduous forests of North America and Asia is relictual. In their review of the Diapensiaceae, Scott & Day (1983) noted that it is an ancient plant family and suggested that *Shortia* and *Galax* were probably "relicts of the Arcto-Tertiary forest of circumboreal distribution." In the late 1900s, Tiffney (1985) and others expanded the concept of the Tertiary Relictual flora. Based on fossil evidence, they concluded that from the Tertiary to the present, the northern temperate deciduous forest was built by species migrations from continent to continent across the Bering land bridge or a North Atlantic land bridge. Each continental constituent of the northern temperate deciduous forest evolved independently, though from the same source species, they concluded.

Recent molecular studies of Higashi et al. (2015) and Gaynor et al. (2020) estimated divergence times of the Diapensiaceae plant groups. Higashi et al. (2015) sequenced multiple nuclear genes to construct a phylogenetic tree by assuming a strict clock model with a substitution rate of 6.0×10^{-9} substitutions/site year. The divergence time between *Galax* and the rest of the family was estimated by Higashi et al. (2015) as at ~9.5 Mya in the late Miocene. Gaynor et al. (2020) dated this divergence as much older as ca. 65 Mya, by constraining the age of the Diapensiaceae crown group based on fossil calibration points. The age of the clade containing *Diapensia*, *Schizocodon*, *Shortia*, and *Berneuxia* was estimated to be between 45–54 Mya. The divergence between *Shortia galacifolia* from eastern North America and the remaining species of *Shortia* from eastern Asia has occurred approximately 24 Mya, the transitional period from Oligocene to Miocene. The distributional and genetic data indicate that origin of the genus probably predates the breakup (some 60 million years ago) of Laurasia. These data are further supported by Wen (1999), who has proposed that much of the speciation in the Tertiary flora took place in the Miocene Epoch.

We see this as an organizational, transitional paper and not an end-all on the subject of the taxonomy and biogeography of *Shortia*. Further study is needed on the varieties of *uniflora* in Japan and those of *exappendiculata* in Taiwan and on the relationship between *Shortia* and *Schizocodon*. Results from Sakaguchi's forthcoming study of genetic distance in the genus may clarify some issues, but will also raise more questions (Sakaguchi, in manuscript). More field work is called for in the Ryukyu Islands of Japan, in northern Vietnam, southeastern China and, possibly, in the higher elevations of Laos, Thailand, and Burma, where the genus may also be found.

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Table 1. Summary of species of *Shortia* (Diapensiaceae) recognized in this study.

Species	Geographic Range	Flowering Phenology	Flowering Color	Known Population Occurences[1]	Year Described
amamiana	Japan, N. Ryukyus. Amami-oshima	July-August	White	10-50	2023
brevistyla	USA, North Carolina	March-Apr	White	Less than 25	2019
exappendiculata	Taiwan	March-May	White	100s	1913
galacifolia	USA, Carolinas	March-Apr	White, rarely Pinkish	100s	1842
okinawensis	Japan, Ryukyus, Okinawa	August-September	White?	10-50	2023
pubinervis	China, SE Yunnan	Winter?	White?	Less than 10	2023
rotata	Northern Vietnam	December-January	Pink to Lavender	Less than 10	2017
rotundifolia	Japan, S. Ryukyus, Iriomote	October	White	Less than 10	1886
sinensis	China, SE Yunnan	December-February	White, rarely Pinkish	100s	1899
uniflora	Japan, Honshu	April-May	Pink, rarely White	100s	1871

[1]Note the low number of known population occurrences of most species.

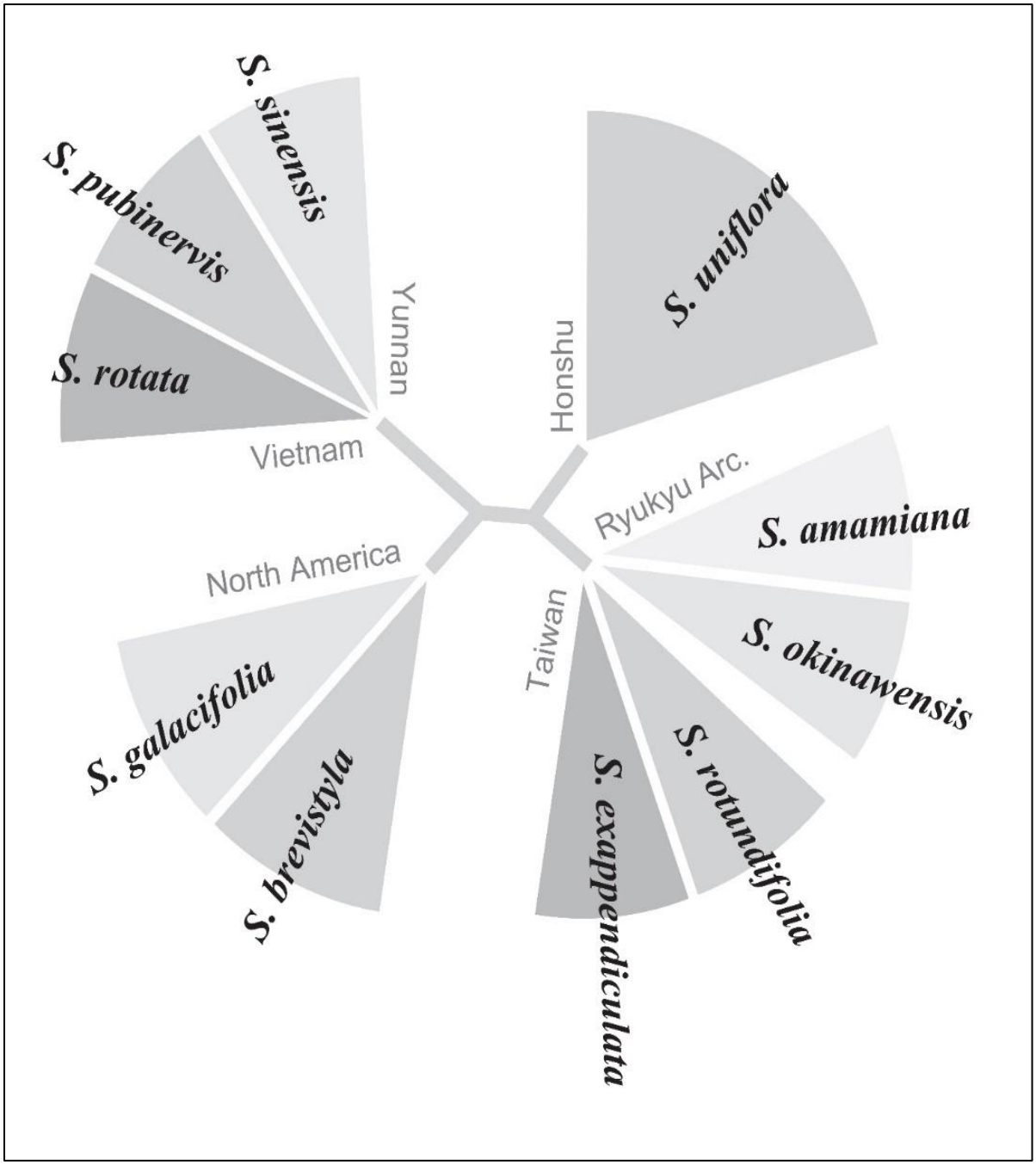

Figure 1. Genetic relationship between *Shortia* species, based on RADSeq phylogenetic tree (from Sakaguchi, in manuscript).

Figure 2. Distributions of *Shortia sinensis* and *S. pubinervis* in China and of *S. rotata* in Vietnam.

Figure 3. Distribution of *Shortia uniflora* in Japan.

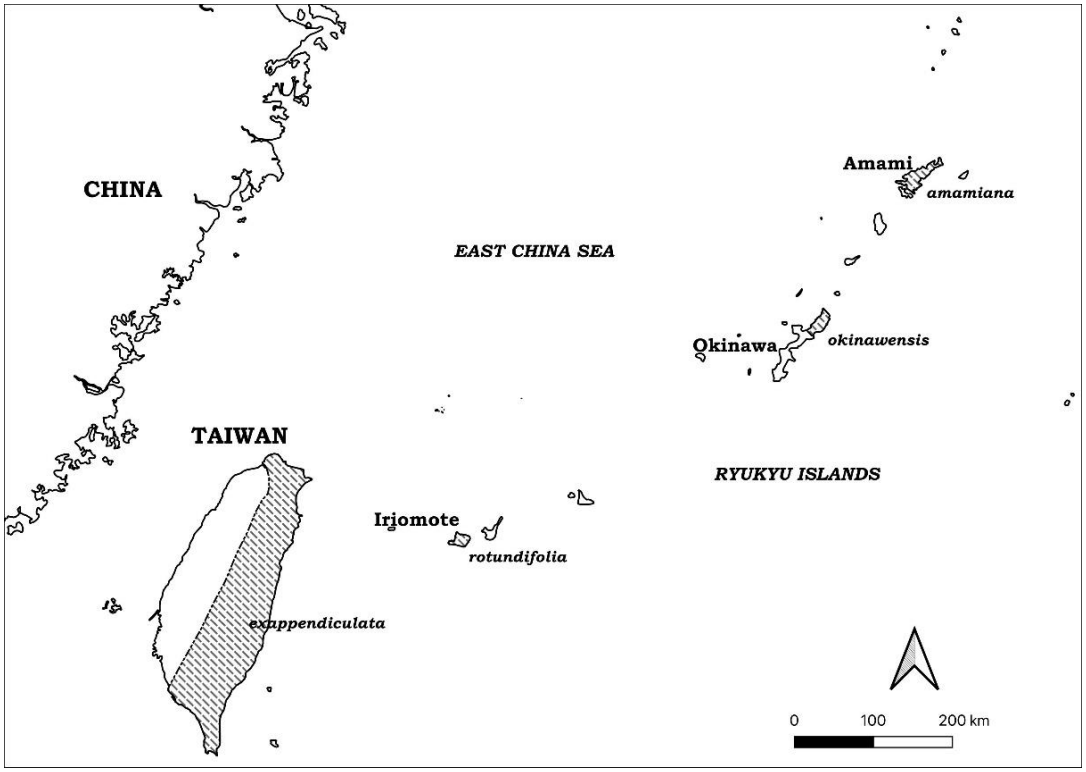

Figure 4. Distributions of *S. amamiana*, *S. okinawensis*, *S. rotundifolia*, and *S. exappendiculata*.

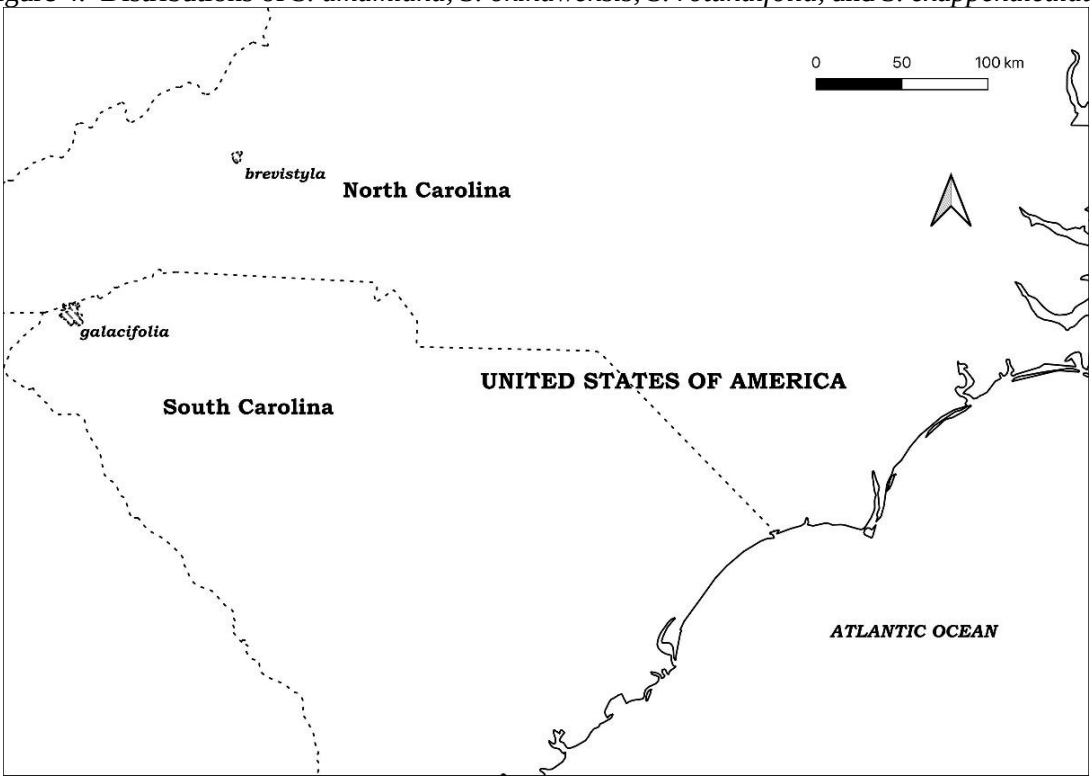

Figure 5. Distributions of *Shortia galacifolia* and *S. brevistyla* in North Carolina and South Carolina, USA.

Figure 6. From type specimen of *Shortia amamiana* from Amami Island, northern Ryukyus, Japan. Note deep serrations and long mucronate leaf tips (KAG).

Figure 7. *Shortia okinawensis* from Mt. Yonaha, Okinawa: note depth of serrations.

Figure 8. *Shortia sinensis* and *Shortia exappendiculata* from the Flora Popularis Reipublicae Sinicae (1990).

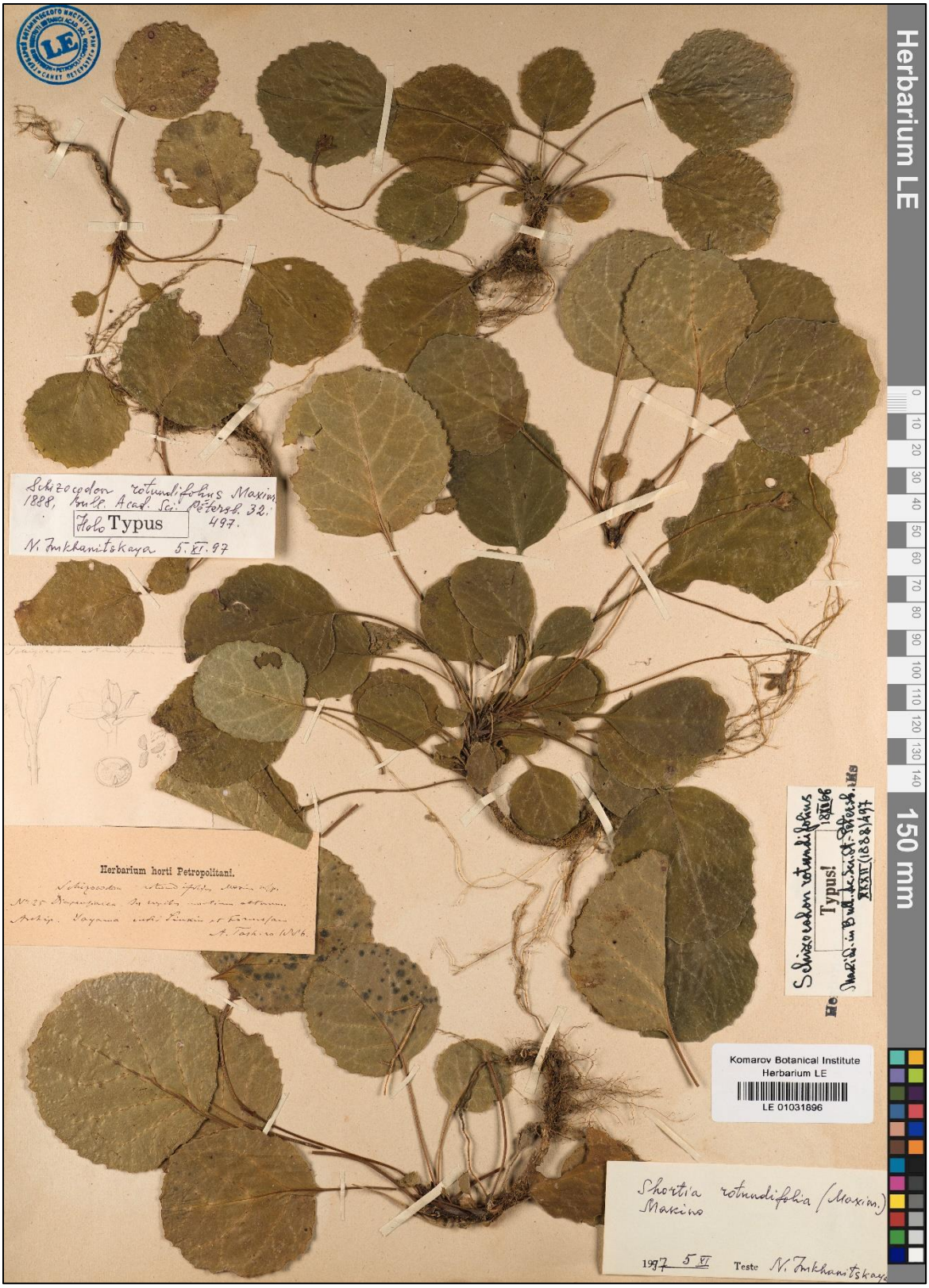

Figure 9. Holotype of *Shortia rotundifolia* (LE). Note the rounded leaves with shallow teeth and short to non-existent mucronate tips.

Figure 10. *Shortia galacifolia* in South Carolina, USA.