INTRODUCING THE SPOTTED SAXIFRAGES: *SAXIFRAGA* SECT. *BRONCHIALES*, SECT. *NOV.* (SAXIFRAGACEAE)

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ABSTRACT. Recent molecular phylogenetic analyses have revealed that *Saxifraga* sect. *Trachyphyllum* as currently circumscribed is polyphyletic, with the designated type, *S. aspera*, falling outside of the more speciose clade. Several other lines of morphological, geographic, and ecological evidence also distinguish the two distantly related groups from one another. In combination, these data necessitate the circumscription of a new section, *S. sect. Bronchiales*, which is described herein. The section is hypothesized to have arisen in the southern Rocky Mountains of North America, followed by northwestward expansion across Beringia and diversification among refugia.


Plants of the genus *Saxifraga* L. (Saxifragaceae Juss.) are found primarily in the arctic, montane, and temperate environments of the northern hemisphere, but also in South America and northern Africa. The approximately 400 plus species of saxifrages are defined by a more or less consistent floral structure of five sepals, five petals, ten stamens in two whorls (outer opposite sepals and inner opposite petals), two carpels that are united at least in part, and an absence of a free hypanthium, though vegetative characters vary considerably (Brouillet and Elvander 2009; Gornall 1987; McGregor 2008; Webb and Gornall 1989). The taxonomic diversity within the genus has been subdivided into fifteen sections based primarily on variation in morphological characters (Gornall 1987; Webb and Gornall 1989), but further redefined by molecular phylogenetic analyses (Conti et al. 1999; Soltis et al. 1996; Vargas 2000; Zhang et al. 2008).

The taxonomy of *Saxifraga* sect. *Trachyphyllum* has been rewritten several times, with modern taxonomists agreeing that the section is in need of thorough revision (Brouillet and Elvander 2009; Elven et al. 2007; McGregor 2008; Webb and Gornall 1989; Zhmylev 1988). Gaudin (1828) described sect. *Trachyphyllum* as being low, alpine herbs with lanceolate, spinulose-ciliate leaves and
white flowers, and assigned *S. aspera* L. as the type for the section that also included *S. bryoides* L. Koch (1837) recircumscribed sect. *Trachyphyllum* to include *S. aspera*, *S. bryoides*, *S. tenella* Wulfen, and *S. aizoides* L., and provided a more detailed description. A few attempts were made to reclassify the members of sect. *Trachyphyllum* (among other *Saxifraga*) and place them in the genera *Ciliaria* Haworth or *Leptasea* Haworth, but those revisions were not followed (Don 1822; Haworth 1821; Small 1905; Weber 1982). The work of Engler and Irmscher (1919) broadened the description of sect. *Trachyphyllum* to also include taxa from Siberia and North America: *S. bronchialis* L. [including several infraspecific taxa that had been described at the rank of species (Don 1822; Small 1905)] and *S. tricuspidata* Rottb. (with three varieties). This account was followed by a number of regional assessments. For instance, Losina-Losinskaja (1939) and Siplivinsky (1971) added several Siberian taxa to the section. North American additions were provided by Calder and Savile (1959), who described the Haida Gwaii endemic *S. taylorii* Calder & Savile. Khokhryakov (1979) and then Zhmylev and Khokhryakov (1985) subdivided the section into subsections and series based on morphological characters. At that time, Zhmylev and Khokhryakov (1985) had suggested the possibility of dividing sect. *Trachyphyllum* into two sections—one section for subsect. *Fibrosophyllae* Zhmylev & A.P. Khokhr. (that included *S. aspera*, the type for sect. *Trachyphyllum*, and *S. bryoides*) and another section containing the remainder of the species. Later, Gornall (1987), followed by Webb and Gornall (1989) and McGregor (2008), provided a synthesis that included all known members of sect. *Trachyphyllum* to date.

Multiple lines of evidence support the division of sect. *Trachyphyllum* and the circumscription of a new section. First, subsect. *Fibrosophyllae* can be distinguished morphologically from the other taxa in sect. *Trachyphyllum* by leaves with fibrous margins (hence the name of the subsection) and forward-pointing cilia, conspicuous buds in the leaf axils at flowering, and a large yellow blotch at the base of their otherwise white petals. Second, both members of subsect. *Fibrosophyllae* are restricted geographically to the mountains of Europe (Alps, Appenines, Carpathians, and Pyrenees), whereas all the other species in sect. *Trachyphyllum* have a trans-Beringian distribution, ranging from the Rocky Mountains of North America across Beringia and westward to the mountains of Russia, Japan, and China (McGregor 2008; Webb and Gornall...
Third, subsect. *Fibrosophyllae* are distinct ecologically in their dependence upon silicaceous substrates. In addition to the aforementioned morphological, geographic, and ecological differences, recent molecular phylogenies clearly show that species traditionally associated with sect. *Trachyphyllum* are distributed across two distantly related clades. DeChaine et al. (2013) used chloroplast trnL-F and nuclear ITS (internal transcribed spacer, including the entire ITS1-5.8s-ITS2 region) genetic sequence data in both maximum likelihood and Bayesian analyses to reconstruct phylogenies for *Saxifraga*, focusing on 19 members (including all accepted species) of sect. *Trachyphyllum*. All genetic markers and phylogenetic analyses agreed that the section was polyphyletic. One of the inferred clades was restricted to subsect. *Fibrosophyllae* and included the type species for sect. *Trachyphyllum*, *S. aspera*, whereas the remaining taxa were nested within a separate, strongly supported monophyletic clade (referred to therein as “Clade T2”) positioned basally within the genus (DeChaine et al. 2013). The latter clade is the focus of this paper.

All members of the new section of *Saxifraga* described herein were previously included in sect. *Trachyphyllum* (Gaud.) Koch, the Rough-Leaved Saxifrages, because they usually exhibit stiff hairs along the margins and tips of their evergreen leaves that give them a rough appearance and feel. Now, morphology, geography, ecology, and phylogeny (DeChaine et al. 2013) all warrant the description and circumscription of sect. *Bronchiales* DeChaine, sect. nov.

**TAXONOMIC TREATMENT**

*Saxifraga* L. sect. *Bronchiales* DeChaine, sect. nov. Type: *Saxifraga bronchialis* L.

Members of sect. *Bronchiales*, the Spotted Saxifrages, are characterized (see Figure 1) as: Plants evergreen perennial herbs, loosely to densely mat-forming. Flowering stems leafy, terminal. Leaves in basal rosette and cauline, alternate; blades linear to lanceolate, usually stiff, entire or 3-toothed, apiculate or strongly mucronate apically, glabrous, sometimes glandular with multiserrate hairs; lime-secreting hydathodes absent. Inflorescence panicle or sometimes reduced to a solitary flower. Flowers regular; sepals 5, erect to ascending; petals 5, ± oblong, white to pale
Figure 1. Illustration of typical characters of *Saxifraga* sect. *Bronchiales*. A. Flower of *S. austromontana* (DeChaine 12-1250, wwb). B. Flower of *S. derbekii* (Zhmylev s.n., ALA). C. Whole plant of *S. funstonii* (DeChaine 11-37, wwb). D. Leafy rosette of *S. trachyphyllum* (DeChaine 12-176, wwb) showing 3-lobed leaves. E. Leafy rosette of *S. bronchialis* (Kharkevich 25, UBC). F. Leafy rosette of *S. omolojensis* (Roland 92-120, ALA). G. Leafy rosette of *S. funstonii* (DeChaine 11-921, wwb).
yellow, usually with yellow, orange, red, or pink-purple spots; stamens 10; ovary ± superior; styles 2; stigmas 2. Capsule ovoid to conical. Seeds oblong.

SIMILAR TAXA. Members of sect. Bronchiales are readily distinguished from sect. Trachyphyllum because the latter have leaves with fibrous margins and forward-pointing cilia, conspicuous buds in the leaf axils at the time of flowering, and a large yellow blotch at the base of their white petals.

KEY DISTINGUISHING SECT. BRONCHIALES AND SECT. TRACHYPHYLLUM

1a. Leaves usually with cartilaginous margins; buds not conspicuous at flowering; and petals with spotting or no coloring, but not a yellow blotch at base ........ sect. Bronchiales

1b. Leaves with fibrous margins and forward directed cilia; conspicuous buds in the leaf axils at the time of flowering; and a large yellow blotch at the base of their white petals .................. sect. Trachyphyllum

DISTRIBUTION AND HABITAT. Saxifraga sect. Bronchiales is a trans-Beringian section, occurring in the mountains of western North America (though not in the Sierra Nevada of California), from New Mexico to Alaska including Oregon and Washington and eastward from Alaska across boreal and arctic North America to Newfoundland and Labrador (Canada), and in Greenland. In Eurasia, populations are found across boreal and arctic Russia, from the Kuril Islands, Sakhalin, Kamchatka, and Chukotka, north to Wrangel Island and west to the Ural Mountains, in Heilongjiang and Nei Mongol China, and south to the alpine environs of Japan. Like other members of Saxifraga, plants primarily inhabit arctic, alpine, and sub-alpine environments, but also occur at lower elevations on islands around the North Pacific, such as Haida Gwaii (Canada). Plants generally grow on rocky cliffs, talus and scree slopes, and gravelly flats.

NOMENCLATURAL HISTORY

Many of the species of sect. Bronchiales are readily distinguishable, but questions regarding some taxonomic ranks and the
number of subspecies, varieties, and forms beg further scrutiny. Based on the genetic lineages inferred by DeChaine et al. (2013) and previous taxonomic assessments, the following species are included within sect. *Bronchiales*.


United States. Colorado: Ouray County, south of Ouray, junction of Engineer Mountain Jeep Road with Hwy 550, elev. 8200 ft, 24 Jun 1962, *Taylor* 4713 (UBC); Hinsdale County, Southern Gunnison Basin: San Juan Mountains: Alpine Gulch Trail from ca 1 trail mi S of trailhead to intersection of Alpine Gulch and Grassy Mountain trails, ca 3–4 air mi SW of Lake City, 37.9934′N, 107.3669′W, 29 Aug 1999, *Arnett* 7859 (RM); Gunnison County, Southern Gunnison Basin: San Juan Mountains: ca 2.3 air mi S of Powderhorn, ca 7.4 air mi ESE of Gateview, ca 10.5 air mi NNW of Cathedral, 38.2369′N, 107.1026′W, 20 Aug 1990, *Arnett* 7192 (RM); Hinsdale County, Southern Gunnison Basin: San Juan Mountains: along the Grizzly Gulch Trail from ca 0.5–0.6 mi from trailhead, ca 1.1–1.7 air mi E-ENE of Whitecross Mountain, 37.9356′N, 107.4584′W, 03 Aug 1999, *Arnett* 6232 (RM); Jackson County, North-central Colorado: Medicine Bow Mountains: ca 1/4 mi N of Montgomery Pass and to the W, ca 6 air mi ENE of Gould, ca 23 air mi SE of Walden, 40.5465′N,


Representative specimens examined: Russian Federation. Amur Oblast: Spurs of Yam-Alin’ mountain range, upper Selemdzha River, elev. 1700 m, 03 Aug 1983, Yakubov s.n. (UBC). Kamchatka Krai: Koryaksky Natsionalny Okrug, Olyutorsky Region, the upper Maly Kubaveyem river, 06 Jul 1976, Barkalov s.n.


**Representative specimens examined:** Canada. Yukon Territory: Ogilvie and Wernecke Mountains, 15 miles NNW of Mount Gibben, elev. 5300 ft, 64°55’N, 139°19’W, 12 Jul 1984, *Cody & Gims* s.n. (UBC).


UNITED STATES. Alaska: Philip Smith Mountains, Yukon River-Prudhoe Bay Haul Road, 68°09'N, 149°26'W, 04 Aug 1982, Murray 8538 (ALA); Solomon Quad, Seward Peninsula Mi 50 Kougarok Rd, 06 Jul 1993, Murray, Yurtsev & Kelso 11307 (ALA); Northeast Alaska, Okpilak Valley, 2 kilometers west of West Okpilak Lake, elev. 1902 ft., 69°N, 144°W, 05 Jul 1985, Grulke 1090 (WTU); North Slope County, Okpilak Valley, 1 km west of West Okpilak Lake, elev. 1902 ft., 69°N, 144°W, 16 Aug 1984, Grulke (WTU); Skagway-Hoonah-Angoon County: Point Hope, Northeast Alaska, 68°21’ 166°45’, 12 Jul 1977, Taylor 6066 (WWB); North Slope Borough, De Long Mountains, 07 Jul 2011, DeChaîne 11-37 (wwb); North Slope Borough, Pt. Lay, 07 Jul 2011, DeChaîne 11-921 (wwb).


**Representative specimens examined:** RUSSIAN FEDERATION. Kamchatka Krai: 20 Aug 1974, Kharkevich s.n. (ALA). Magadan Oblast: 130 km N of Magadan, upper part of Ola River (left bank) on the Olsokeje Plateau, 60°41’N, 15°18’E, 1554 m, 23 Jul 1988, Elias & Murray 11244 (ALA); 31 Aug 1973, Kharkevich s.n. (ALA).


**Representative specimen examined:** JAPAN. Hokkaido: Mt. Yubari, Gamaiwa, 06 Aug 1989, Brooks 89-38 (E).


district west, 13 Jun 1979, Kharkevich s.n. (ALA). Magadan Oblast: Kontakt Field Station at Kolymskaja Water Balance station near Kulu, 425 km NN of Magadan, logged floodplain on Itirkan River, 10 km SW of station, 24 Jul 1988, Elias 11254 (ALA); Tuva Tes-Khem district, 07 Aug 1979, Daniel s.n. (ALA).


   Representative specimens examined. Canada. British Columbia: Queen Charlotte Islands, 9 km west northwest of Queen Charlotte City, Mount Raymond, elev. 914 m, 53°16’N, 132°14’W, 09 Jul 1997, Douglas 13250 (UBC); Queen Charlotte Islands, Moresby Island, 3 km west of Apex Mountain, elev. 914 m, 52°42’N, 131°53’W, 19 Aug 1997, Lomer 97446 (UBC); Queen Charlotte Islands, Moresby Island, ridge above blue Heron Bay and Fairfax Inlet, on Gwaii Hansaas National Park boundary, elev. 600 m, 52°41’15”N, 131°58’17”W, 19 Aug 1998, Lomer 98-241 (UBC); Queen Charlotte Islands, 20 miles south of Moresby Camp, Moresby Island, elev. 2000 ft., 52°55’N, 132°3’W, 29 Jul 1957, Calder 23085 (WTU).


Northwest Territories: Banks Island, east of 1st camp, elev. 30 m, 30 Jul 1965, Krajina s.n. (UBC); Inuvik airfield, elev. 61 m, 68°16’N, 133°32’W, 01 Jul 1965, Krajina 65071936 (UBC); Frobisher Bay, 63°45’N, 67°15’W, 01 Jul 1964, D.E. Swales s.n. (UBC); Jacobsen McGill base camp, ca. 3.5 miles southwest base, Axel Heiberg Island, 79°23’N, 90°42’W, 20 Jul 1961, Parmelee 1172 (UBC); Ellesmere Island vicinity of Lake Hazen, 81°45’N–82°10’S, 68°30’W–72°45’W, 01 Aug 1959, Powell 678 (UBC). Nunavut: Baffin Island, Auyuittuq National Park, 14 Jun 12, DeChaine 12-176 (WWB).

**GREENLAND.** West Greenland, north Disko, Kugangup ivnarta, elev. 20 m, 70°17’N, 53°55’W, 24 Jul 1983, Byrge 742 (UBC).


**REPRESENTATIVE SPECIMENS EXAMINED.** **UNITED STATES.** Oregon: Saddle Mountain, 22 Mar 1978, Schofield s.n. (UBC); Clatsop County, Saddle Mountain, 05 Jun 1979, Bohm 1319 (UBC); Columbia Gorge, Horsetail Falls, 20 Jun 2012, DeChaine 12-725 (WWB).

**Biogeographic hypotheses.** The distribution of taxa and the molecular phylogeny of the section provide the foundation for a general hypothesis on the biogeographic history of sect. *Bronchiales*. The phylogenetic tree inferred for sect. *Bronchiales* [referred to as Clade T2 in DeChaine et al. (2013)] suggests that the section originated in the alpine environs of the southern Rocky Mountains of North America, and a subsequent north-westward expansion promoted genetic divergence across Beringia and into Asia. There is strong support for the North American arctic-alpine species, *Saxifraga austromontana* and *S. tricuspidata*, being positioned basally within sect. *Bronchiales*. Indeed, the basal-most lineages of
the section, individuals of *S. austromontana*, reside in the southern Rocky Mountains of New Mexico and Colorado, implying that this region set the stage for the origin and early evolution of the group. As populations of sect. *Bronchiales* expanded northwards and westwards across Beringia and into Asia, additional lineages arose. Multiple authors have noted the likely importance of isolation in refugia in promoting divergence among the members of this section (Calder and Savile 1959; Losina-Losinskaja 1939; Siplivinsky 1971), and their hypotheses were further supported by the biogeographic analyses of DeChaine et al. (2013). Indeed, geography underlies evolutionary relationships in this group: the North American arctic-alpine (*S. austromontana* and *S. tricuspidata*), coastal Cascadia of northwestern North America (*S. taylorii* and *S. vespertina*), Beringia (*S. codyana* and *S. funstonii*), the North Pacific (*S. cherlerioides*), the southeastern coast and islands of Asia (*S. caulescens*, *S. nishidai*, and *S. rebunshirensis*), the Okhotsk region (*S. derbekii* and *S. onoloi̇jensis*), and more central Asia (*S. bronchialis*, *S. kruhsiana*, and *S. spinulosa*). Several refugia around the Pacific Rim, including Beringia (Hultén 1937), those south of the ice in western North America [the southern Rocky Mountain Refugium, Klamath region, Haida Gwaii (Shafer et al. 2010; Soltis et al. 1997; Swenson and Howard 2005)] and eastern Asia [the mountains of Japan and neighboring islands (Ikeda et al. 2006; Ito 1981; Koidzumi 1919)], and west of Beringia in Central Asia (Hong 1993; Zhu and Rowe 1987) likely promoted divergence following the expansion of the section out of North America. This biogeographic framework sets the stage for further analyses into the role of dispersal and refugial isolation as a driver of genetic divergence and the rise of endemics in sect. *Bronchiales*.

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LITERATURE CITED

DeChaine—Saxifraga sect. Bronchiales, sect. nov.


