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Leaf venation patterns in the genus *Saxifraga* (Saxifragaceae)

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Abstract

Details of leaf venation in 150 species of *Saxifraga* L. representing all 13 sections are reported. Three main patterns were observed: palinactinodromous, acrodromous and camptodromous. Species with lobed leaves have palinactinodromous patterns, whereas those with entire leaves are acrodromous or camptodromous. Thus species from sections *Heterisia, Irregulares*, *Cymbalaria*, *Cotylea* and *Mesogyne* are palinactinodromous; species from sections *Saxifraga*, *Ciliatae*, *Bronchiales* and *Trachyphyllum*, in which some have lobed and some have entire leaves, are either palinactinodromous or acrodromous, according to the leaf margin; species from sections *Ligulatae* and *Porphyrion*, whose hydathodes secrete calcium bicarbonate, have camptodromous venation. Intermediate states occur in section *Gymnopera* (between palinactinodromous and camptodromous) and in section *Porphyrion* subsection *Oppositifoliae* and section *Xanthizoon* (intermediate between acrodromous and camptodromous). The pattern of distribution across the genus and selected outgroups shows that the ancestral state is likely to be palinactinodromous.

Key words: leaf architecture; veins; hydathodes; taxonomy

Introduction

Leaf architecture plays an important role in ecology, plant systematics, paleobotany and conservation (Ellis *et al.* 2009). Venation patterns, in particular, have been demonstrated to be an important feature for identifying and classifying plants (Corner 1968, Walls 2011). Characters from leaf venation were once considered difficult to use for taxonomic purposes, owing to problems with their description. However, the work of Hickey (1973, 1979) has gone a long way to resolving these, notwithstanding some criticism by Pole (1991). The Hickey classification deconstructs leaf architecture into several elements, including shape, marginal configuration, venation, gland structure and gland position. It was further developed by Ellis *et al.* (2009) and has become the standard way to describe leaf architecture.

In this study we investigate the leaf venation patterns in *Saxifraga* Linnaeus (1753: 398), the largest genus (ca. 460 spp.) in the family Saxifragaceae s.str. (Stevens 2001>). It is widely distributed across the Northern Hemisphere, mainly in the Alps and the Sino-Himalayan area, but a few have a circum-polar distribution, with extensions southwards in the Americas down the Rocky Mountain–Andean cordillera (Webb & Gornall 1989, Pan 2001). The genus displays remarkable morphological variation, primarily in vegetative organs. Leaves vary in size from large (ca. 25cm^2) to very small (ca. 1mm^2), in shape from needle- or scale-like to cordate or reniform; the margin can be entire to toothed or lobed, and texture ranges from papery to leathery and stiff, or even stone-like when there is a secretion of calcium bicarbonate from specialized hydathodes called chalk-glands (Kurt 1930, Webb & Gornall 1989).

Given this variation, it is not surprising that leaf morphology has featured prominently among the suite of characters that have been used in the classification of the genus (e.g. Engler & Irmscher 1916/19). Nevertheless, very little attention has been paid to leaf venation, mainly because it is often invisible to the naked eye either in fresh or in pressed specimens. A few studies have described patterns in selected species, e.g. Galløe (1910) gave an account of patterns in ten Arctic species of *Saxifraga*; Watari (1939) presented details of the vascular anatomy of the leaves in the Saxifragaceae s.l., including eleven species of *Saxifraga*; and Fuller & Hickey (2005) included two species of *Saxifraga* among members of the Saxifragaceae s.str. used as outgroups in a study of leaf venation in the Gunneraceae. To date, however, there has not been an extensive genus-wide survey. In this study, species from all 13 sections have

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