



Flower symmetry in *Saxifraga* revisited

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Abstract

Monosymmetry in flowers has evolved many times from ancestors with polysymmetrical flowers. Flower symmetry characteristics often lack intraspecific variability. The genus *Saxifraga* represents an exception with high variations of floral symmetry between and within species and even within individual plants. Lab-based studies could show that this variation is to some extent caused by the flowers' response to gravity and thus varies regularly between horizontally and vertically oriented flowers. Here, we investigate inter- and intra-individual variation in flower size, flower colouration, and floral symmetry in three species, *Saxifraga stellaris*, *S. rotundifolia*, and *S. paniculata*. In all three species, the stamen that initiates the sequential stamen movement is mostly downward pointing. In *S. stellaris* and *S. paniculata*, the terminal flowers are larger than the other flowers. In *S. stellaris* and *S. rotundifolia*, the size of floral guides is larger and the colour is stronger on the upward pointing 3 petals of diagonally and vertically oriented flowers, whereas the other two petals have paler or smaller floral guides. The septum between the two carpels is mostly oriented horizontally. We discuss the evolution of flower monosymmetry in regard to the morphological symmetry referring to symmetry defined by the mirror plane between carpels, petals and moving stamens, and visual symmetry defined by the pollinators view on the floral colour pattern and visible morphological features.

Keywords Flower symmetry · Gravity · Monosymmetry · Polysymmetry · *Saxifraga*

Introduction

The symmetry of flowers is a key feature of pollination ecology. The shape, number and arrangement of floral organs are considered to be a species-specific feature and to have an important influence on the overall visual appearance of flowers (Endress 1999, 2001). The arrangement of floral organs and thereby the flower symmetry is assumed to be a constant character of flowers in a given species. The genus *Saxifraga* represents an exception with high variations of floral symmetry between and within species and even within individual plants. Observations of this phenomenon arouse our interest to investigate the factors that lead to a polysymmetrical or monosymmetrical arrangement of floral organs. In general, polysymmetrical flowers represent an ancestral, whereas monosymmetrical flowers represent a derived

status. In many families of flowering plants, the evolution of monosymmetrical flowers from ancestors with polysymmetrical flowers has been documented (Citerne et al. 2010; Reyes et al. 2016), whereas reversions from monosymmetry to radial symmetry are rare (Spencer and Kim 2018). Primarily radially symmetrical flowers are generalist flowers, visited by a number of unrelated pollinator taxa. Many derived monosymmetrical flowers are specialized and visited by limited number of pollinators (Neal et al. 1998).

Flower symmetry is often correlated with flower orientation. Most of the radially symmetrical flowers (also termed actinomorphic or regular) are presented horizontally. These flowers thus look similar to flower visitors from all approach directions. By contrast, monosymmetrical flowers (also termed zygomorphic, dorsiventral, or irregular) are mostly presented vertically and have only a single approach direction displaying a unique bilateral symmetrical shape (Wilmer 2011). It has been argued that the evolution of monosymmetry could have originated in flowers on racemes, spikes, or thyrses that were vertically oriented and that the transition from polysymmetry to monosymmetry was promoted in these structures as a gravitropic physiological response that was further selected by insect-pollination (Endress 1999;

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Robertson 1888). The inflorescence structure in the genus *Saxifraga* is a monotelic thyrsum and thus the orientation of flowers on the main axis and on subaxes varies and could be relevant for the development of floral symmetry (a; Fig. 1).

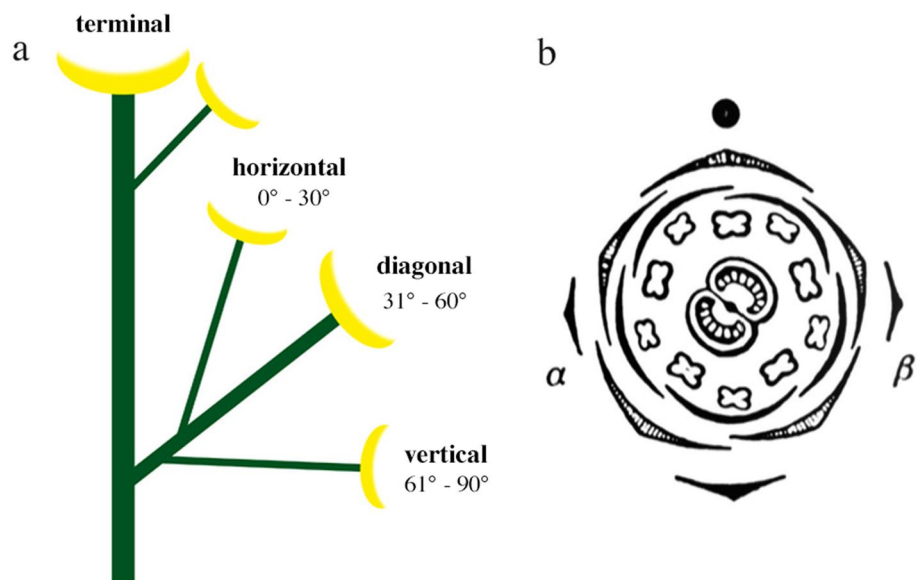
The categorization of flowers as being radially symmetrical or monosymmetrical is often not done in a very strict manner and the taxonomic descriptions often do not cover intraspecific variation. For instance, the flowers of many species in the genus *Saxifraga* share some common features, which are the alternating whorls of 5 sepals, 5 petals, 5 outer and 5 inner stamens, as well as 2 carpels. They are categorized as radially symmetrical flowers (Soltis 2003), although the position of the sole septum between the two carpels does not fit to polysymmetry of the other flower organs. Theoretically, it is possible that flowers with these properties possess one definite mirror plane; nevertheless, not all *Saxifraga* flowers do meet this criterion. The 10 possible mirror planes defined by the sepals, petals and stamens are not identical with the four possible mirror planes defined by the two carpels (b; Fig. 1). Thus, in the narrow sense the flower symmetry has often to be categorized as asymmetrical. Flower symmetry is commonly defined from an “en face” view at anthesis, presupposing a planar projection of the flower and reflecting a generalized ground plan of floral patterns. The gynoecium is often disregarded when characterizing floral symmetry because of its inconsiderable morphology and the frequent aberrance of carpel number compared to other floral organs (Citerne et al. 2010). Neal et al. (1998) claimed that symmetry designations should be applied to the patterns of the flower as a whole to adhere to a thorough perception of symmetry.

Many studies on visual pattern recognition of flower visitors show evidence for a pollinator preference for symmetrical shapes and especially monosymmetrical shapes

with a perpendicular symmetry plane over all other patterns (Lehrer et al. 1995; Gómez et al. 2006; Ushimaru et al. 2009). Endress (2001) argued that the frequent evolution of floral monosymmetry from ancestors with polysymmetrical flowers affects numerous aspects of the interaction between flowers and pollinators such as visual signalling, pollen transfer, and morphological fit, and this has potential for efficient precision mechanisms in pollination biology. He further differentiated between various degrees of floral symmetry for example in the Lamiales including highly monosymmetrical lip flowers with odd staminode mostly lacking, floral monosymmetry expressed to various degrees with odd staminode present or lacking, and floral monosymmetry relatively weakly expressed with odd staminode present (Endress 2001). The importance of floral orientation for monosymmetrical flowers becomes apparent by the fact that they reorientate after mechanical bending for restoring their original orientation to achieve pollination accuracy (Armbruster and Muchhala 2020). Monosymmetry provide benefits through an extended possibility to optimally display visual patterns (Davenport and Kohanzadeh 1982). Morphological differentiation of flower patterns and visual cues can improve precision in pollen placement and thereby increase cross-fertilization by restriction and control of pollinators' access and movements within flowers (Citerne et al. 2010). Additionally, some flowers actively move the stamens to improve pollen placement (Ren 2010), including species of the genus *Saxifraga*. This mechanism ensures that—given a uniform behaviour of the flower visitor—the anthers deposit the pollen onto those areas of the pollinators' body that contact the stigma in the pistillate flowering phase.

Accuracy of pollen placement is improving pollination success (Armbruster et al. 2009). The placement of pollinators on flowers is very important in Saxifragaceae and

Fig. 1 **a** Illustration of the inclination of flowers in a thyrsum inflorescence and four categories of flower orientation that can be derived. **b** Floral diagram of *Saxifraga granulata* with bracteoles (α , β) (after Eichler 1875–78)



related families with similar stamen-bending mechanism, since the flowers are dichogamic and benefit from similar placement of pollinators in the staminate and pistillate flowering phase. The stamens bend to the centre of the flower one after the other during male flowering phase and open when positioned above the stigma (Armbruster et al. 2013). Thus, the presentation of pollen and the delivery of pollen grains onto the stigma occurs in a similar position and is thus optimal if similar movements of flower visitors occur in the male and female flowering phase. This is furthermore achieved through the colour pattern of monosymmetrical flowers that underlines their symmetry. Floral colour patterns affect the orientation of flower visitors at close range and thus the landing position (Lunau et al. 2009). Even the movements of flower visitors that have already landed on a flower are guided by visual floral guides (Dinkel and Lunau 2001). The combination of a stamen-bending mechanism and floral colour guides in the genus *Saxifraga* might provide a form of functional heteranthery, that divides the anthers into pollinating anthers on the lower half, ensuring pollen placement (Koch et al. 2017; Tong and Huang 2018), and rewarding anthers that serve in combination with floral colour guides, as flower visitor attracting cues on the upper half of the flower. The importance of the inconspicuousness of pollination stamens in heterantherous flowers for pollination has been demonstrated in Melastomataceae (de Brito et al. 2021) and *Commelina* (Ushimaru et al. 2009).

Previous studies have documented a large diversity of floral symmetry within the genus *Saxifraga* including species with polysymmetrical flowers, species with monosymmetrical flowers and species with intraspecific and even intra-individual diversity of flower symmetry. Using a vertical clinostat as a gravity compensator and a horizontal clinostat as a light incidence compensator, it was shown that environmental factors like the angle of incident light has no apparent impact on flower symmetry, whereas gravity affects the angular position of petals in *S. cuneifolia* and *S. umbrosa* and the petal colouration in *S. rotundifolia* (Koethe et al. 2017). In *S. cuneifolia* and *S. umbrosa*, the absence of directional gravity resulted in the development of actinomorphic flowers, whereas the corresponding control flowers were zygomorphic. The development of flowers in *S. rotundifolia* was not altered by this treatment. The length of the two elongated petals in *S. stolonifera* and *S. imparilis* was not affected by gravity, but rather was determined by the position of the flowers within the inflorescence and resulted in asymmetrical flowers with the larger petal being positioned closer to the main axis (Koethe et al. 2017).

In this study we document the prevalence of flower monosymmetry in three *Saxifraga* species in the field, which are mostly categorized as radially symmetrical. We study the impact of the flowers' orientation and position in the inflorescence on floral symmetry. We asked the following

questions: Does the orientation of flowers in regard to the perpendicular axis affect length of petals, pigmentation of petals, and angle between petals? Do the visual symmetry axis, the initial stamen movement, and the orientation of the two carpels correspond to the perpendicular? Therefore, we investigated three abundant species—*Saxifraga stellaris*, *S. rotundifolia*, and *S. paniculata*—under natural conditions in the line with field surveys in Graubünden, Switzerland. The aim of this study was to compare the apparent flower symmetry of these species and to analyse the impact of environmental factors, especially gravity through its flower orientation on flower symmetry by measurements of flowers orientation towards the perpendicular axis and the position of the flowers within the inflorescence. In order to differentiate between intrinsic and external factors on flower symmetry and colouration we compared flower symmetry and colouration of terminal flowers, and of flowers with horizontal, diagonal, and vertical orientation. Furthermore, we discuss potential consequences for pollination.

Material and methods

Plant material and study site

The three investigated species—*Saxifraga stellaris*, *S. rotundifolia*, and *S. paniculata*—were studied by M.W. under natural conditions in the Beverin Nature Park near Mathon (Switzerland). All species were investigated at several places in that area, occupying approximately 50–100 m² each. The field work was carried out mainly in July of 2016 and all three species flowered abundantly in the study area. *Saxifraga stellaris* subspecies *robusta* was studied at three different study sites (1. 46°37'53.3"N 9°21'58.1"E; 2. 46°38'03.2"N 9°21'43.7"E; 3. 46°38'11.3"N 9°21'51.3"E) on the eastward mountain slope of Piz Beverin. The study populations were in wet spring hallways of subalpine and alpine habitats. *S. rotundifolia* was found in moist areas with bushes around the treeline of montane and subalpine habitats. *S. rotundifolia* was studied at two study sites (1. 46°37'44.7"N 9°22'43.5"E; 2. 46°38'51.6"N 9°25'03.9"E). *S. paniculata* was studied in rocky places above treeline of montane and subalpine habitats at two study sites (1. 46°38'02.6"N 9°22'18.8"E; 2. 46°38'35.8"N 9°24'13.9"E). The study sites did not differ considerably for each species.

The three species belong to different sections within the genus *Saxifraga* (Deng et al. 2015). All three species are characterized by 5 petals, two whorls of 5 stamens each and a bicarpellate gynoeceum:

- White Mountain Saxifrage, *Saxifraga paniculata* Mill. sect. *Ligulatae* Haw; Round-Leaved Saxifrage

- *Saxifraga rotundifolia* L. sect. *Cotylea* Tausch; and Starry Saxifrage
- *Saxifraga stellaris* L. sect. *Micranthes* (Haw.) D. Don. Tkach et al. (2015) put *S. stellaris* in the genus *Micranthes*

For the identification of species, Parolly and Rohwer (2016) and Lauber et al. (2012) were used. Voucher specimens were not collected.

Data collection and processing

All species have proterandric flowers; only those flowers that allowed for clear evidence of the initial stamen movement, were investigated. The following floral features were included to estimate flower symmetry: petal length, angle between petals, petal colouration, carpel' septum alignment and orientation of the initial stamen for stamen movement, which are known to contribute to flower monosymmetry of saxifrages in experimental settings (Koethe et al. 2017). The following data were collected for each flower in the field: cardinal direction to which the flower is facing, angle of the flower towards the perpendicular direction and towards the mountain slope using a clinometer that was attached to a sounding lead, position of initial stamen movement and position of the separating line between the two carpels in relation to the perpendicular axis, and length of the petals with an accuracy of 0.5 mm. The measurement of the petal length was done with a piece of graph paper because of its flexibility to adjust it to the petals' bending.

A colour photograph was taken of each flower from an "en face" view with a horizontally aligned camera position. Flowers were photographed with a Canon EOS 60D and a EF-S24mm f/2.8 STM lens. The interior electronical spirit level was used to ensure a horizontal alignment of the camera. The photographs were used to collect the following data: angle between the petals and the angle between visual symmetry axis and the perpendicular axis. The flower petals were consecutively named beginning with the lower left one P1 in a clockwise manner to P5 (c; Fig. 2). The pigmentation of the floral guides of the white petals in *Saxifraga stellaris* and *S. rotundifolia* was categorized to 4 categories which were strong, medium, weak, and absent (h-o; Fig. 3). The alignment of the septum between the two carpels was categorized by the measured angle to 4 different positional variants named horizontal, left-diagonal, vertical, right-diagonal (a; Fig. 2). The initial stamen movement was categorized to 8 categories each encompassing an angle of 45°, named bottom, bottom-left, left, top-left, top, top-right, right, bottom-right (b; Fig. 2).

Four flower categories were distinguished, which are terminal flowers, horizontal flowers (perpendicular angle

0°–30°), diagonal flowers (perpendicular angle 31°–60°), and vertical flowers (perpendicular angle 61°–90°). Terminal flowers were treated separately irrespective of their perpendicular angle (mean perpendicular angle in *S. stellaris* is $27.8^\circ \pm 17.1^\circ$ ($n=29$), in *S. paniculata* is $41.5^\circ \pm 12.3^\circ$ ($n=10$)).

We distinguish between three kinds of flower symmetry axes. (1) The morphological symmetry axis is defined by the orientation of the septum between the two carpels and by the position of initial stamen movement (a, b; Fig. 2). (2) The visual signalling symmetry axis was defined by the colouration of the petals' floral guides that differed in size, shape and intensity. To evaluate the orientation of the visual symmetry axis to the perpendicular axis a petal designation was necessary, which reflects the distinct angle of each petal to the perpendicular axis. Therefore, the petal with the smallest angle to the perpendicular axis was measured and labelled P11, the following petals were subsequently labelled P12 to P15 with an increasing angle (d; Fig. 2). The signalling apparatus is defined by the pollinators view on the floral colour pattern and the arrangement of the perianth, as the main visible morphological features. (3) The symmetry axis of the perianth is determined by the angle between the petals as the bisecting line of the flower with the smallest difference of inter-petal angles between the two halves of the flower according to a formula (see below). For this purpose, the angles between all petals (P1–P5) were measured and labelled a–e (c; Fig. 2), using the free computer program Image J (see supplement; Schneider et al. 2012). The deviation from the ideal angle of 72°, that mathematically results from an equal distribution of the 5 petals, between each two petals was calculated. The petals were renamed afterwards starting with the petal intersected by the symmetry axis, which was labelled Ps1. The petals following clockwise were labelled Ps2 to Ps5 (e; Fig. 2). The purpose of renaming the petals was to allow a comparison of the flowers from a uniform view point, where all symmetry axes are oriented in the same way.

$$a+b + \frac{c}{2} = \frac{c}{2} + d + e; \quad b + c + \frac{d}{2} = \frac{d}{2} + e + a; \dots e + a + \frac{b}{2} = \frac{b}{2} + c + d$$

Formula 1 Calculation of the symmetry axis of the signalling apparatus. Formulas for the determination of the bisecting line of the angles a–e with the smallest difference between the two halves of the flower.

Statistical analysis

All statistical analyses were performed using the statistical software *R* (R Development Core Team 2010). For

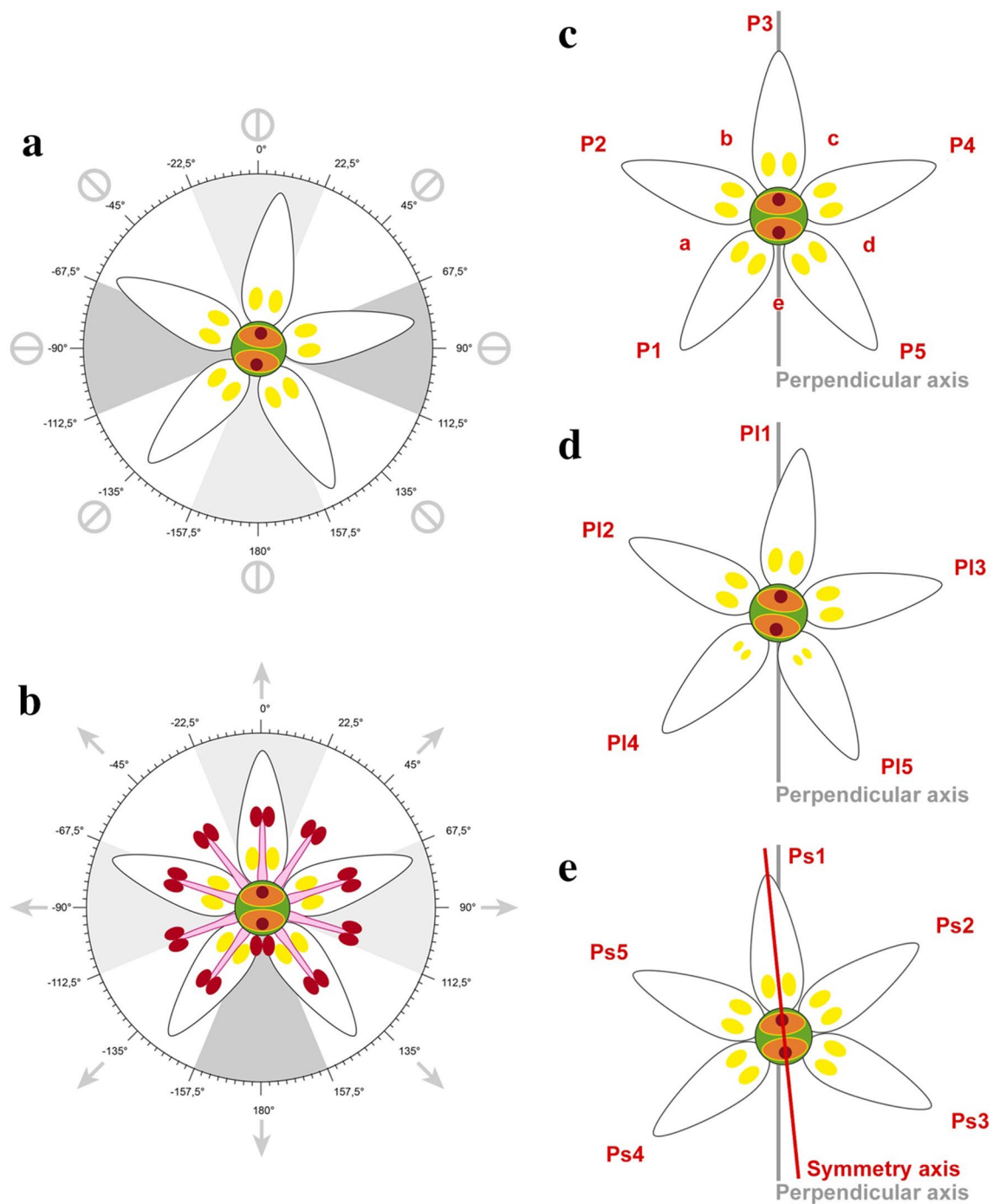


Fig. 2 Terminology of petals. **a** Sectors and icons indicating the position of the septum between the two carpels. **b** Sectors and arrows indicating eight categories for initial stamen movement. **c** Designation of petals for data collection as P1 to P5 and inter-petal angles

a–e. d Designation of petals according to the perpendicular axis as P11 to P15; P11 has the smallest angle to the perpendicular axis, P15 the largest. **e** Designation of the petals according to the symmetry of the perianth as Ps1 to Ps5; Ps1 is in line with the symmetry axis

comparison of data with multiple groups, like comparison of petal angles and petal colouration, we used one-way ANOVA for normally distributed data and Kruskal–Wallis test for non-normally distributed data. We applied

post hoc tests to make further differentiation among groups (e.g. between single petals). For comparison of differences in the petal length of individual flowers we used Friedman test. Pairwise comparisons of flower

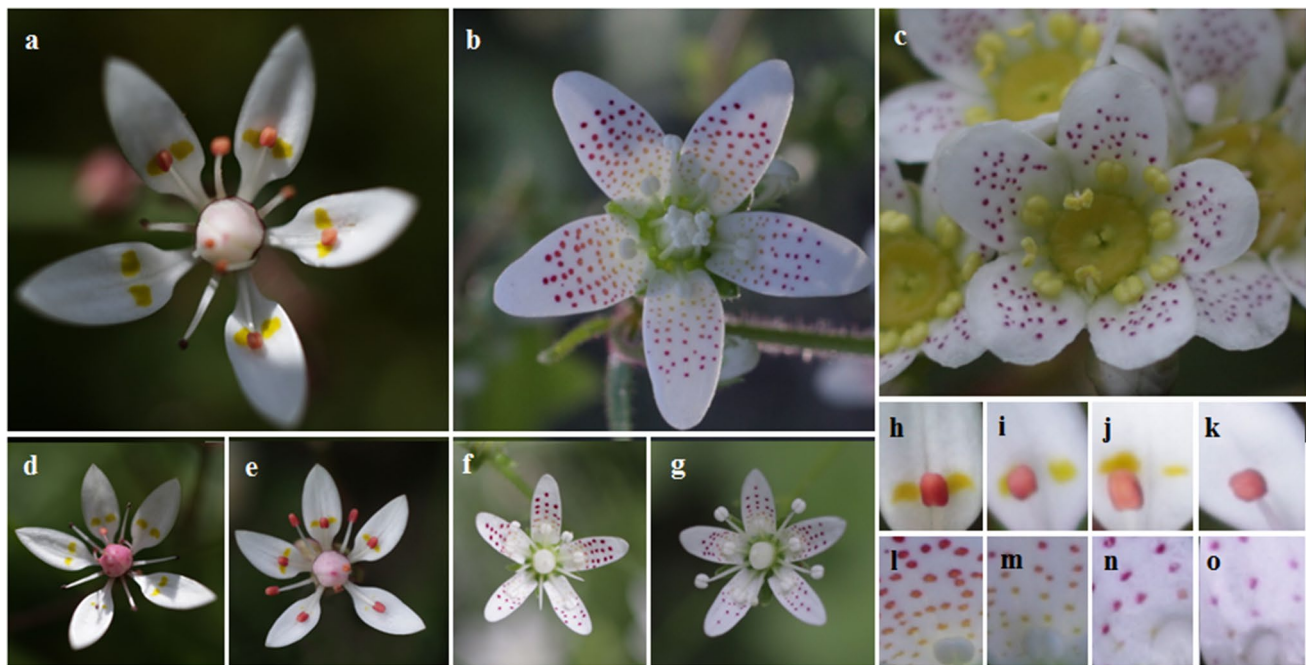


Fig. 3 Visual appearance of flowers of *Saxifraga stellaris*, *S. rotundifolia* and *S. paniculata*. **a** single flower of *S. stellaris*; **b** single flower of *S. rotundifolia*; **c** single flower of *S. paniculata*; **d**, **e** variation in dot guide colouration in *S. stellaris*; **f**, **g** variation in dot guide col-

ouration in *S. rotundifolia*; **h–k** categories of dot guide colouration in *S. stellaris*: very strong (3), strong (2), weak (1), very weak or absent (0); **l–o** categories of dot guide colouration in *S. rotundifolia*: strong (3), middle (2), weak (1), very weak or absent (0)

orientations were performed using Mann–Whitney U test. The analyses of the frequencies of initial stamen orientations and carpel septum alignments were performed with Chi²-Test.

Results

The intraspecific variability of flowers in the genus *Saxifraga* has several aspects. One aspect is that in some species the position within the inflorescence determines flower size, mostly dependent on petal length. In combination with the distribution of the five petals, the petal length influences the symmetry of the signalling apparatus. In *S. stellaris* terminal flowers' petals with 5.70 ± 0.58 mm length ($n = 29$) surpassed horizontal flowers' petals with 5.40 ± 0.63 mm length ($n = 35$, $p = 2.664 \times 10^{-6}$), and the latter surpassed diagonal flowers' petals with 5.03 ± 0.58 mm length ($n = 26$, $p = 1.527 \times 10^{-6}$); vertically oriented flowers were not found. In *S. rotundifolia* the petal length varied from 6.62 ± 0.77 mm ($n = 17$) in horizontal flowers over 6.16 ± 0.51 mm in diagonal flowers ($n = 30$, $p = 1.917 \times 10^{-6}$) to 6.08 ± 0.65 mm in vertical flowers ($n = 4$, no statistics). In *S. paniculata* the petal length in horizontal flowers (5.28 ± 0.64 mm; $n = 26$) was not significantly larger than in diagonal flowers (5.18 ± 0.67 mm; $n = 29$), and these not significantly larger in vertical flowers (5.01 ± 0.76 mm;

$n = 14$) ($p > 0.05$); terminal flowers again are significantly larger with an average petal length of 5.5 ± 0.41 mm ($n = 10$, $p = 3.051 \times 10^{-5}$) than the other flowers within an inflorescence. In both categories of *S. rotundifolia* ($p_H = 8.987 \times 10^{-7}$, $p_D = 3.645 \times 10^{-6}$) and in diagonally oriented flowers of *S. stellaris* ($p_D = 6.871 \times 10^{-5}$) the petals of individual flowers did significantly differ in length reflecting a monosymmetrical symmetry of the perianth (Fig. 4). In all other categories and species, the petals of individual flowers did not differ in length ($p > 0.05$) reflecting a polysymmetrical symmetry (Fig. 4).

All three *Saxifraga* species possess floral dot guides on their petals. The intensity of pigmentation was investigated to define the visual symmetry axis (d; Fig. 2). *Saxifraga stellaris* has two yellow spots on each petal that vary in size, shape and intensity (Fig. 3). Flowers of the horizontal category as well as flowers of the diagonal category exhibit stronger pigmentation on the upper three petals, whereas the lower two petals are significantly less pigmented (Fig. 5). Variations between those two categories were not observed. Terminal flowers' petals in contrast do not vary in strength of pigmentation and are established in a radial symmetrical manner. *S. rotundifolia* has many small spots on each petal, which are reddish at the distal and yellow at the proximal end, and vary in colour intensity and density (Fig. 3). Similar results could be found in *S. rotundifolia* as were found in *S. stellaris*. *S. paniculata* has many small red dots on each

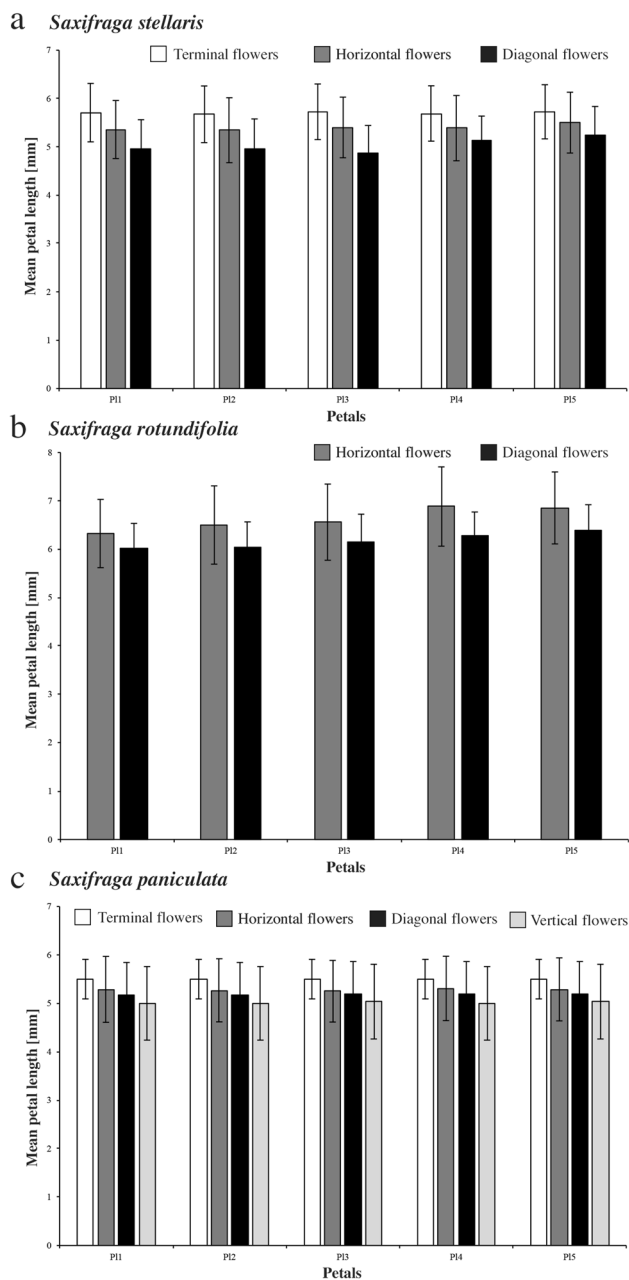


Fig. 4 Petal length of flowers in *Saxifraga stellaris* (a), *S. rotundifolia* (b) and *S. paniculata* (c) dependent of the position and orientation of flowers in the inflorescence. Results of statistical analyses are provided in the supplements

petal and no obvious variation of dot size, shape or intensity within a given flower (c; Fig. 3).

The arrangement of the petals represents another parameter to determine floral symmetry of the visual apparatus (e; Fig. 2). The ideal angle between each of the five petals is 72° if the petals are evenly distributed around the floral disc. In some *Saxifraga* species there are regular deviations from this ideal distribution of petals depending on flower orientation. Only in diagonally oriented flowers of *S. stellaris* a

significant deviation from this ideal angle was found (Fig. 6). In 20 out of 26 cases the angle between the two downward-facing petals is above, the angles between the three upward-facing petals are below the ideal angle.

The first stamen that bends over the still closed stigma is always belonging to the outward whorl of stamens and mostly oriented downwards, with 75% in *S. stellaris*, 29% in *S. rotundifolia* and *S. paniculata* (Fig. 7). Considering the three out of eight categories with the most downward oriented stamens, in *S. stellaris* 97%, in *S. rotundifolia* 88%, and in *S. paniculata* 74% of the cases fall into these categories, in which the expectancy by chance amounts to 37.5%. This effect was not found in the more horizontally oriented terminal flowers of *S. stellaris* ($n=29$, $\chi^2=7.69$, $df=7$, $p=0.361$) and *S. paniculata* ($n=10$, $\chi^2=4.4$, $df=7$, $p=0.733$).

The alignment of the morphological symmetry axis was analysed in regard to the perpendicular axis. In all three species the septum between the two carpels is mostly horizontally and rarely vertically oriented; however most clearly in *S. stellaris* (Fig. 8). In contrast to that, the alignment in terminal flowers seems to be established randomly in *S. stellaris* ($n=29$, $\chi^2=4.241$, $df=3$, $p=0.237$) and *S. paniculata* ($n=10$, $\chi^2=0.4$, $df=3$, $p=0.940$).

Discussion

Flower symmetry in saxifrages

In the flowers of all three species, *S. stellaris*, *S. rotundifolia*, and *S. paniculata*, deviations from radial symmetry were found. The size, shape and/or colour of the floral guides are more conspicuous in the three petals facing upwards in *S. stellaris* and *S. rotundifolia* as compared to the two petals facing downwards. Moreover, the angular arrangement of the petals in diagonally oriented flowers deviates from a regular distribution in *S. stellaris*. The petals of individual flowers in *S. rotundifolia* and in diagonally oriented flowers of *S. stellaris* are elongated on the lower flower half. The stamen movement is initiated by a stamen from the outer whorl that is facing downwards. The septum between the two carpels has the tendency to show a horizontal orientation.

Intra-individual variation also includes features that do not contribute to floral monosymmetry. In *S. stellaris* and *S. rotundifolia*, horizontally oriented flowers possess longer petals compared to diagonally oriented flowers. In *S. paniculata*, the petal length is similar in all petals of a given flower.

Gravity and the position within the inflorescence have decisive effects on flower symmetry. Koethe et al. (2017) have shown that flower symmetry in the genus *Saxifraga* could be influenced by gravity. Especially in *S. stellaris* the

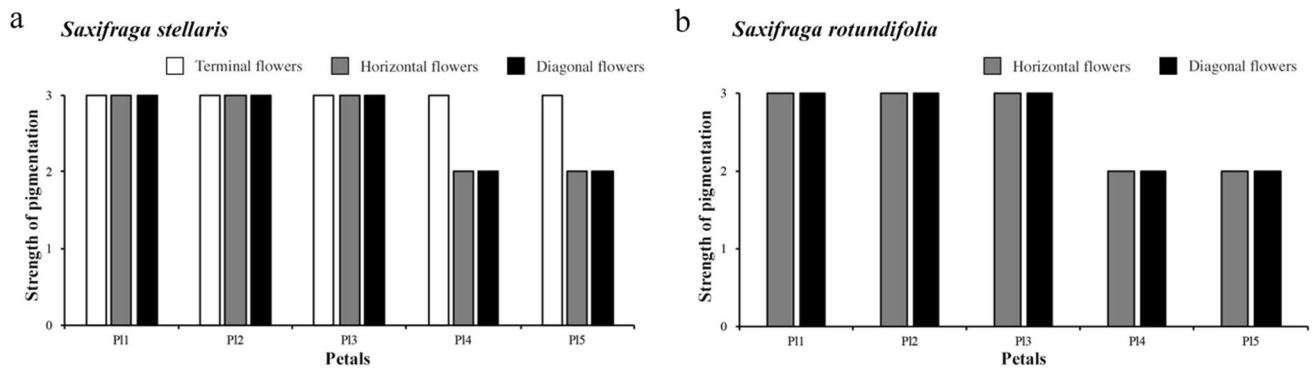


Fig. 5 Pigmentation of petals in *Saxifraga stellaris* (a) and *S. rotundifolia* (b) dependent of the perpendicular orientation of petals. The strength of pigmentation of the floral guides is given in 4 categories (0, 1, 2, 3). Statistical analysis for *S. stellaris*: terminal flowers: $n=29$, $p_T=0.996$; horizontal flowers: $n=35$, $p_H<2.2\times 10^{-16}$; diagonal flowers: $n=26$, $p_D<2.2\times 10^{-16}$. Between terminal and

lateral flowers $p_{T+L}<0.001$. Between horizontal and diagonal flowers $p_{H+D}=0.989$. Statistical analysis of *S. rotundifolia*: horizontal flowers: $n=13$, $p_H=1,739\times 10^{-6}$; diagonal flowers: $n=29$, $p_D=7.347\times 10^{-13}$. Between horizontal and diagonal flowers: $p_{H+D}=0.487$. Results of post hoc tests are provided in the supplements

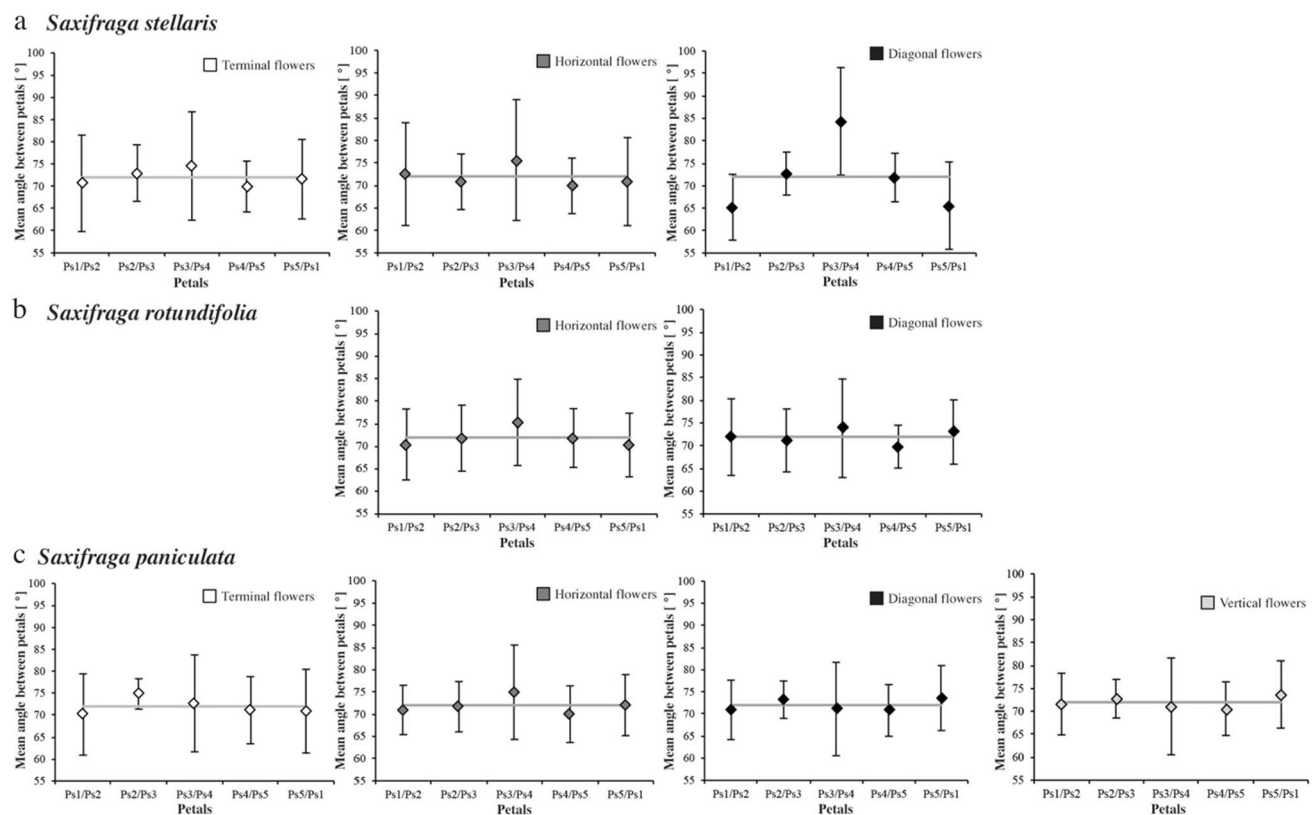


Fig. 6 Angle between adjacent petals in horizontal, diagonal, vertical, and terminal flowers in *Saxifraga stellaris* (a), *S. rotundifolia* (b), and *S. paniculata* (c). Statistical analysis for *S. stellaris*: terminal flowers $n=29$, $p_T=0.322$; horizontal flowers $n=35$, $p_H=0.367$; diagonal flowers $n=26$, $p_D=1.243\times 10^{-9}$; *S. rotundifolia*: horizon-

tal flowers $n=17$, $p_H=0.324$; diagonal flowers: $n=30$, $p_D=0.304$; *S. paniculata*: terminal flowers $n=10$, $p_T=0.757$; horizontal flowers $n=26$, $p_H=0.307$; diagonal flowers $n=29$, $p_D=0.396$; vertical flowers $n=14$, $p_V=0.659$

flower symmetry seems to be not fixed. *S. stellaris* flowers show monosymmetry by arranging the pigmentation along the perpendicular axis and mostly horizontally aligned

carpels, but exhibits polysymmetry in length of petals and in the arrangement of petals in horizontal and terminal, but not in diagonal flowers.

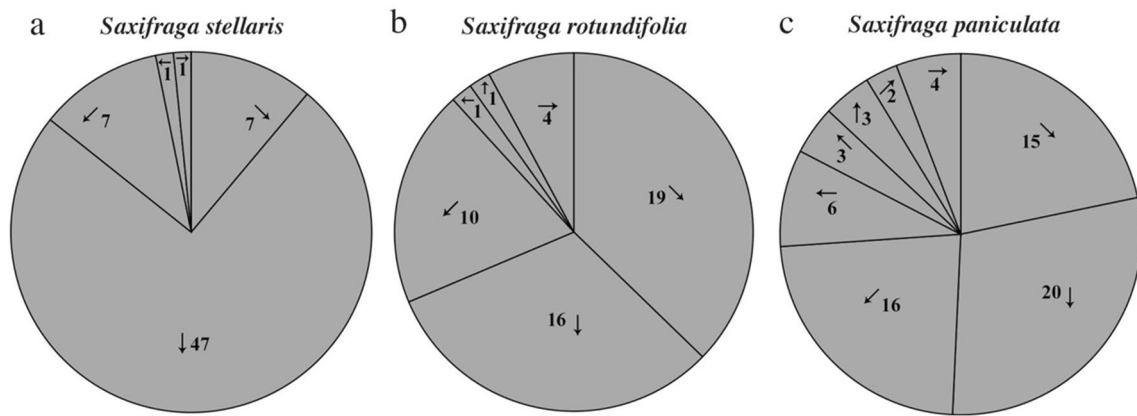


Fig. 7 Orientation of the initial stamen for stamen movement in flowers (except terminal flowers) of *Saxifraga stellaris* (a), *S. rotundifolia* (b) and *S. paniculata* (c). The orientation towards the perpendicular axis is categorized in 8 equal directions indicated by the direction of the arrow. Statistical analysis for *S. stellaris*: $n=63$,

$\chi^2=120.25$, $df=7$, $p < 2.2 \times 10^{-16}$; *S. rotundifolia* $n=51$, $\chi^2=64.294$, $df=7$, $p=2.084 \times 10^{-11}$; *S. paniculata*: $n=69$, $\chi^2=41.725$, $df=7$, $p=5.875 \times 10^{-7}$. Results of post hoc tests are provided in the supplements

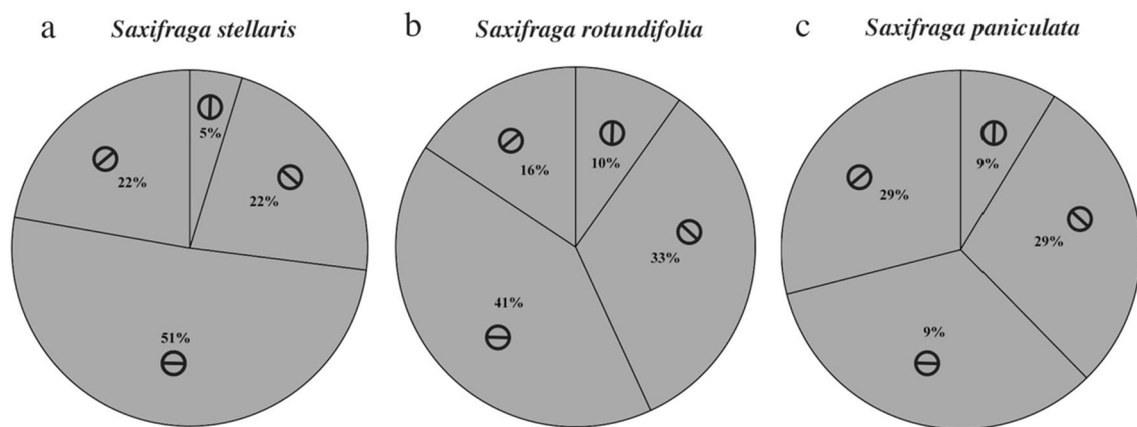


Fig. 8 Orientation of the septum between the two carpels in flowers (except terminal flowers) of *Saxifraga stellaris* (a), *S. rotundifolia* (b), and *S. paniculata* (c) categorized in 4 types (horizontal, left-diagonal, right-diagonal, vertical) given as percentage dependent of the perpen-

dicular axis. Statistical analysis for *S. stellaris*: $n=63$, $\chi^2=27.476$, $df=3$, $p=4.678 \times 10^{-6}$; *S. rotundifolia*: $n=51$, $\chi^2=13.235$, $df=3$, $p=0.004$; *S. paniculata*: $n=69$, $\chi^2=10.13$, $df=3$, $p=0.017$. Results of post hoc tests are provided in the supplements

S. rotundifolia flowers have a predominantly polysymmetrical arrangement of petals in combination with a monosymmetrical shape through the elongation of downward-facing petals, only the carpels are not consistently arranged. Furthermore, the pigmentation of the petals shows monosymmetry.

Although *S. paniculata* exhibits a variable alignment of the carpels, it can be categorised as radially symmetrical, due to homogeneous arrangement in all other floral organs.

Flower orientation and inflorescence structure

The field study shows that the mean angles between the petals of *S. stellaris* differ in regard to the orientation of

the flower to the perpendicular axis. Flowers oriented horizontally establish radial symmetrical flowers and flowers oriented diagonally show monosymmetry. Generally, these differences in the arrangements and size of petals can be caused physiologically by the distribution of phytohormones which regulate the development of primordia in flower buds (Okada et al. 1991; Reinhardt et al. 2000; Heisler et al. 2005). The asymmetrical distribution of auxin along the gravitational axis, for instance, can have direct impact on the arrangement of petal primordia and thus the symmetry of the flower (Hudson 2000). By contrast, *S. paniculata* flowers develop polysymmetry without being affected by the orientation of the flowers to the perpendicular axis. It has been shown that the *CYCLOIDEA*

gene and its homologues have been implicated in many transitions from radial to bilateral flower symmetry (Hileman 2014). Interestingly, the mean petal length of the flowers decreases with an increasing angle to the perpendicular axis. It is known that the terminal flowers in monotelic thyrse are larger than the other flowers and open first (Leins and Erbar 2010). Followed by the terminal flowers of the partial inflorescences, the flowering sequence successively continues from the main axis to the lateral axes and from terminal to basal. The size of the flowers and petal length are thus the result of the position in the inflorescence and thereby a matter of increasing intra-individual competition for resources between developing flowers along the stem (Harder and Prusinkiewicz 2012). The visual symmetry axis of *S. stellaris* and *S. rotundifolia* is congruently aligned to the perpendicular axis, so that the three upper petals are more pigmented than the two lower ones. A difference in the orientation of the flowers to the perpendicular axis has no impact on the pigmentation, except for terminal flowers; the visual axis seems to be established genetically.

Flower visitors' view

Flower symmetry has not only been used by botanists to characterize flower morphology (Eichler 1875–1878; Ijiri et al. 2005), but also has been used by pollination ecologists to study flower preferences and visual orientation in flower visitors (Giurfa et al. 1996, 1999; Rodríguez et al. 2004). It seems useful to discriminate between a morphological flower symmetry defined by the arrangement of sepals, petals and reproductive organs, and its orientation to the perpendicular axis, and a visual flower symmetry defined by the orientation of the visual colour pattern to the perpendicular axis, but ignoring the morphology behind it. The visual flower symmetry is likely most important for visual orientation at the flower and while landing, thus it will match the dorso-ventral body axis of approaching flower visitors. From the flower visitors' view radially symmetrical flowers, which are presented horizontally, look monosymmetrical for approaching pollinators from most directions, as they are mostly approached from the side rather than above. Consequently, the visual symmetry axis is additionally reinforcing the perception of symmetry for approaching pollinators here, which may be beneficial for the pollinators' flower approach and correct landing. It is therefore conceivable that a development towards the vertical presentation of flowers, which provides many advantages, such as protection of pollen and nectar from rain, may necessarily be accompanied by the development of a monosymmetrical symmetry axis. The presentation of a vertical symmetry axis that matches the

dorso-ventral body axis of flower visitors may be further advantageous to effectuate correct landings by pollinators. Ushimaru and Hyodo (2005) were able to show, that the number of legitimate landings on monosymmetrical flowers is higher when they are presented vertically. Furthermore, plants benefit from monosymmetrical flowers because pollen transfer is enhanced. None of the studied species showed any alteration in the initiation of anther dehiscence.

Evolution of floral monosymmetry in saxifrages

The floral features in saxifrages known to be affected by the flowers' orientation include the angle between petals, the length of petals, the pigmentation of petals, the initiation and the sequence of stamen movement (Koethe et al. 2017). The stamen movement starts with the lower stamens of the outer whorl. It is remarkable that the septum between the two carpels is variable among flowers, but mostly oriented horizontally rather than vertically. Only those *Saxifraga* species with clearly monosymmetrical flowers belonging to the section *Irregulares* as for example *Saxifraga stolonifera*, *S. nipponica*, *S. fortunei*, and *S. imparilis* possess a vertically oriented septum between the two carpels. Two aspects seemingly determine the orientation of monosymmetrical flowers, which are the induction of the angle between petals, length and pigmentation of petals, and initiation of the stamen movement by gravitational input, as well as the alignment of the visual axis with the septum of the two carpels. Architectural constraints limit the number and arrangement of organs in a whorl. Due to the restricted space especially in the centre of the flowers, carpels are often reduced to three or two organs (Endress 1999; Ronse De Craene 2015). In the related *Saxifraga bryoides* carpels emerge as ring-shaped structure that divides into two carpels; thus abortion of carpels has not been observed (Ladinig and Wagner (2009). Since an anisomerous arrangement makes it harder to develop regular patterns, variability in the alignment of the bicarpellate gynoecium can be explained. The terminal flower of *S. stellaris*, and *S. paniculata* illustrate, by a consistent polysymmetrical development in all tested floral characters, that the position of the flowers within the inflorescence is an important factor determining flower symmetry.

Heteranthery?

Does stamen movement lead to a kind of functional heteranthery? Heteranthery, the presence of different kinds of stamens in the same flower, in most cases results in a division of labour between conspicuous feeding anthers and camouflaged pollinating anthers depositing the pollen grains on the pollinators' body. The sequential ripening, elongation and movement of the stamens in *Saxifraga*

species leads to the concurrent presence of stamens in different developmental stages. The anthers might thus serve attraction and rewarding for pollinators at different stages. The filaments possess the same colour as the petals in all three studied species. In *S. stellaris* the anthers and pollen are reddish and thus not attractive to bees and flies (Lunau et al. 2017; An et al. 2018); in *S. rotundifolia* the anthers and pollen are white and thus camouflaged against the petals; in *S. paniculata* the anthers and pollen are yellowish and contrasting against the petals' colour and thus might be attractive to pollinating insects. Sequential stamen movements have been observed in several families, including Loasaceae, Rutaceae, Celastraceae/Parnassiaceae and Tropaeolaceae (Ren 2010; Henning and Weigend 2012; Ren and Tang 2012), but its association to monosymmetry of flowers is unique for *Saxifraga*. Does stamen movement increase the accuracy of pollen placement on the pollinators' body? The stamen movement is regarded as a solution for the herkogamy dilemma (Armbruster et al. 2013). Avoiding self-pollination benefits from large distances between pollen presenting anthers and stigma; however, pollination success is improved if the pollen-loaded body parts of the pollinators come into contact with the stigma. Assuming similar pollinator movements on the conspecific flowers, stamen movement is leading to pollen deposition on those sites of the pollinators body which in the pistillate flowering phase will touch the stigma, and thus enhancing pollination success. Vertically oriented and monosymmetrical flowers might further increase accuracy of pollen placement due to the limitation of possible movements (Claßen-Bockhoff et al. 2003; Westerkamp and Claßen-Bockhoff 2007; Culbert and Forrest 2016). Since most pollinators land head upwards on flowers pollen placement is likely to take place from the beginning of the anthesis if the downward-facing stamens move and open first. In *Commelina communis* a stamen-polymorphism is known, where shorter anthers with yellow pollen attracts pollinators, while longer anthers with inconspicuous brownish pollen function as pollinating units (Ushimaru and Hyodo 2005) and thus may have similar signalling functions as the floral guides in *S. stellaris* and *S. rotundifolia*. The orientation of the flowers in *C. communis* influences the pollination by hoverflies (Ushimaru et al. 2009). In this context it is interesting that the signalling by means of coloured anthers and pollen (Lunau 2000) varies among the three species studied. *S. paniculata* has conspicuous yellow anthers and pollen contrasting against the petals. The floral guides are red and thus less attractive than the yellow anthers and pollen to bees and flies that are insensitive to red light (Lunau and Maier 1995). *S. stellaris* has reddish anthers and pollen providing colour contrast against the petals that are more attractive to flower-visiting bees and flies which are insensitive to red light (Lunau and

Maier 1995). *S. rotundifolia* displays white anthers pollen that does offer little colour contrast against the petals combined with floral guides that are red in the peripheral and yellow in the central part of petals and thus guide the flowers visitors towards the flower centre (Dinkel and Lunau 2001).

Conclusion

The high inter- and intra-individual variations in flower symmetry of the tested species and in comparison to other *Saxifraga* species studied before (Koethe et al. 2017), show that the genus *Saxifraga* is in an intermediate state of evolution between polysymmetry and monosymmetry and that environmental factors like gravity, as well as intrinsic factors have an influence on flower symmetry. It seems that several features in *Saxifraga* flowers, i.e. vertical orientation and monosymmetry of flowers, start of stamen movement with downward-facing stamens, and more conspicuous floral guides on petals at the upper half of the flower reinforce each other. Future research will show how floral orientation, conspicuousness of floral guides and initiation of stamen movement might contribute to increase pollination success. Although the incipient monosymmetry in some flowers of the inflorescences in some *Saxifraga* species might provide benefits in terms of pollination success, the evolution of monosymmetry in all flowers of the genus *Saxifraga* seems to be hampered by the orientation of the two carpels in the pentameric flowers and other constraints resulting in an evolutionary and developmental lability of floral symmetry (Naghiloo 2020).

Information on Electronic Supplementary Material

Online Resource 1. Illustration of the data processing of a photograph taken in the field of *Saxifraga stellaris*.

Online Resource 2. Field data and processed data of *Saxifraga stellaris*.

Online Resource 3. Field data and processed data of *Saxifraga rotundifolia*.

Online Resource 4. Field data and processed data of *Saxifraga paniculata*.

Online Resource 5. Results of statistical tests and post-hoc tests.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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