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Hybridisation in *Saxifraga* Subsection *Kabschia* (*Saxifragaceae*) from the Central Himalaya

By

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With 6 Figures

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Summary

BÜRCEL J. 2007. Hybridisation in *Saxifraga* subsection *Kabschia* (*Saxifragaceae*) from the Central Himalaya. – *Phyton* (Horn, Austria) 47 (1–2): 191–204, with 6 figures. – English with German summary.

Field studies of populations of *S. andersonii* in the Dhaulagiri-Annapurna region (C. Himalaya) revealed recognition of *S. alpigena* as a hybrid with *S. quadrifaria*, and the discovery of *S. × hetenbeliana* (nothosp. nova) as a hybrid with *S. pulvinaria*. The most important characteristics of these hybrids and their parents are presented.

Zusammenfassung

BÜRCEL J. 2007. Hybridisierung in *Saxifraga* subsectio *Kabschia* (*Saxifragaceae*) im Zentral-Himalaya. – *Phyton* (Horn, Austria) 47 (1–2): 191–204, mit 6 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Geländestudien von Populationen von *Saxifraga* subsectio *Kabschia* in der Dhaulagiri-Annapurna Region des Zentral-Himalaya führten zur Deutung von *S. alpigena* als Hybride mit *S. quadrifaria* und zur Entdeckung von *S. × hetenbeliana* (nothosp. nova), einer Hybride mit *S. pulvinaria*. Die wichtigsten Merkmale dieser Hybriden und ihrer Eltern sind dargestellt.

1. Introduction

The Himalayas are the largest and most diverse region as far as saxifrages of the subsection *Kabschia* (ENGLER) ROUY & E. G. CAMUS are con-

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cerned. More than fifty species have been described from the Sino-Himalayan region, thirty-five of these by Harry SMITH (SMITH 1958). Individual species usually were described from herbarium collections without any field study. Though without detailed field observation it was not possible to fully understand the phenomenon of hybridisation. SMITH was well aware that hybridisation events might have occurred in the Himalayan Kabschias. For instance, SMITH 1958: 87 noted in some taxa: "The arrangement of the leaves in both species [*S. vacillans* and *S. subternata*] is unstable and changing. In *S. vacillans* they are essentially decussate, but alternate in vigorous or prolonged parts of the caudicles. This variation may be due to hybridisation between a decussate-leaved species, for instance *S. georgei*, and some Kabschias with alternate leaves. The plant looks like a somewhat enlarged *S. georgei*" ... "As puzzling is *S. subternata*, which is unique among saxifrages in having its leaves in whorls, at least partly. Yet the arrangement is not perfect. The majority of the leaves are opposite, but, especially in crowded parts of the caudicles, they are ternate or, rather, subternate. The leaves of the whorls are not completely connate at the base." ... "This arrangement is peculiar and hard to explain. Some disturbance must have influenced the organization of the plant. Again, one might guess that some remote hybridisation was the original cause of the instability."

The present author has undertaken field expeditions to study saxifrages in the western part of the Central Himalaya and eastern part of the Western Himalaya in 1997, 2000 and 2001. Especially the region of the Annapurna, Dhaulagiri and Manaslu Himal peaks appears to be rich in *Kabschia* saxifrages where nine species and four hybrids have been found.

2. Material and Methods

The present study relates to the following species (or hybrids) of *Saxifraga* subsect. *Kabschia*. The first ones (1–4) are treated in detail in chapter 3, the others (5–10) are mentioned for comparison in the text.

1. *Saxifraga andersonii* ENGLER in Bot. Jahrb. Syst. 48: 609. 1913.

Type: ANDERSON 596, Sikkim, 4000–4300 m [CAL, fide ENGLER & IRMSCHER; not seen].

This species is known to be extremely variable. It forms large cushions and has a branched inflorescence with up to 5 white flowers. It occurs in the mountains of Nepal, Bhutan and Tibet above 3500 m (WEBB & GORNALL 1989).

2. *Saxifraga quadrifaria* ENGLER & IRMSCHER in ENGLER, Pflanzenr. IV.117(69): 575. 1919.

Type: Kings collector, Beerom um 3000 m [CAL, fide ENGLER & IRMSCHER; not seen].

This species belongs to a group with decussate leaves that includes species with tetramerous flowers (like *S. octandra* HARRY SM., *S. decussata* J. ANTHONY, *S. monantha* HARRY SM.; *S. nana* ENGLER) as well as with pentamerous ones (*S. georgei* J. ANTHONY, *S. quadrifaria*, *S. alpigena* HARRY SM., *S. roylei* HARRY SM., *S. vacillans*

Harry SM.). An unsolved problem relates to the coalescence of the decussate leaves in *S. quadrifaria* as highlighted by WEBB & GORNALL 1989: 270: "whether the margins of the leaf pairs meet at an acute angle and have a fringe of hairs or teeth at the base, or whether the margins are confluent and entire".

3. *Saxifraga alpigena* Harry SM. in Bull. Brit. Mus. (Nat. Hist.) Bot., 2: 97. 1958. Holotype: LOWNDES 935, Marsiandi, 3450, 5 June 1950 [BM].

Originally described as a species from material collected at Marsiandi Valley and Sabche Khola, 4200 and 3900 m during a British Museum expedition.

4. *Saxifraga pulvinaria* Harry SM. in Bull. Brit. Mus. (Nat. Hist.) Bot., 2: 105. 1958 = *S. imbricata* ROYLE, Ill. Bot. Himal. Mts. 1: 226. 1835, non LAMARCK 1779, nec BERTOLONI 1830.

SMITH 1958: 106 used, as substitute for the type not available to him, the following collection: LUDLOW & SHERRIFF 8444 Kashmir, Mashoo Nullah, 4500 m, 24 June 1941 [BM].

This species forms attractive dense cushions with pillar-like stolons (columnar leafy shoots). It is a typical Himalayan saxifrage preferring rock crevices and cracks, found in high mountain regions (HORNY & al. 1986). It grows on slopes from Kashmir to Nepal, at an altitude of 4000–6000 m (WEBB & GORNALL 1989).

5. *Saxifraga cinerea* Harry SM. in Bull. Brit. Mus. (Nat. Hist.) Bot., 2: 128. 1958. Holotype: LOWNDES 916, Marsiandi, 2700 m, 29 May 1950 [BM].

6. *Saxifraga hypostoma* Harry SM. in Bull. Brit. Mus. (Nat. Hist.) Bot., 2: 103. 1958.

Holotype: LOWNDES 1108, Jargeng Khola, 4800 m, 3 July 1950 [BM].

This species is distinguished from *S. pulvinaria* easily by the membranous margins of the leaf tips fringed with hairs. This is a Nepalese endemic, occurring high up in the mountains on rock ledges and screes at an elevation of 4300–5250 m (WEBB & GORNALL 1989).

7. *Saxifraga lowndesii* Harry SM. in Bull. Brit. Mus. (Nat. Hist.) Bot., 2: 106. 1958.

Holotype: LOWNDES 958, Sabze Khola, 4050 m, 3 June 1950 [BM].

A species forming mats among wet rocks on steep hillsides; flowers brilliant rose-lilac (SMITH 1958).

8. *Saxifraga poluniniana* Harry SM. in Bull. Brit. Mus. (Nat. Hist.) Bot., 2: 114. 1958.

Holotype: POLUNIN, SYKES & WILLIAMS 4070, between Padmara and Bumra, Padmara Lagna, 3450 m, 13 May 1952 [BM].

9. *Saxifraga stoltzkae* DUTHIE ex ENGLER & IRMSCHER in ENGLER, Pflanzenr. IV.117(69): 569. 1919.

Type: [Syntypes at WU; not seen].

This species grows on wet cliffs at elevation above 3000 m in the mountains from Kumaun to Bhutan where it forms loose cushions (WEBB & GORNALL, 1989).

10. *Saxifraga ×tukuchensis* BÜRGELE in Saxifrage Mag. 10: 34. 2002 pro hybr.: *S. andersonii* × *S. hypostoma*.

Holotype: BÜRGELE 11488, Nepal, west part of Central Himalaya, Hidden Valley, 5100 m, 23 July 1997 [PR].

This hybrid shows intermediate characteristics (BÜRGELE 2002).

Plant populations were studied in natural habitats at Kaligandaki Valley, Hidden Valley and Marsiandi (Marsyangdi or Marsyandi) Valley and other sites with oc-

currence of *Saxifraga alpigena*, *S. andersonii*, *S. cinerea*, *S. hypostoma*, *S. lowndesii*, *S. poluniniana*, *S. pulvinaria* and *S. quadrifaria*. Of these species, *S. alpigena* and *S. quadrifaria* are widely distributed, growing at altitudes from 2200 to 5000 m.

My personal herbarium contains more than 160 specimens of species of *Saxifraga* subsect. *Kabschia*, including duplicates. There is also a collection of 20 different seed samples, mainly from identified plants of *S. andersonii* and its hybrids, harvested from 1997 to 2001. The herbarium samples will be preserved at the herbarium of the National Museum at Prague [PR] once my studies have been completed and published. Additionally, also live material was collected. Only small samples (one to three rosettes) were taken, bearing in mind plant conservation. These samples, mostly one rosette, were cultivated by several plants-persons in different personal gardens, both in the Czech Republic and England. The same collection numbers are used for both live and herbarium samples: DEBU 20/ = Dhaulagiri Expedition BUrgel 2000, MEBU 01/ = Marsiandi Expedition BUrgel 2001. Herbarium specimens were mostly taken from natural populations but were supplemented with material in cultivation.

In addition to fieldwork and observation on cultivated material more than four hundred herbarium sheets of *Saxifraga* subsection *Kabschia* from the Himalayas have been studied at the British Museum (Natural History). These include the type specimen of *S. alpigena* as well as other materials determined by H. SMITH in 1958.

3. Observations

In most of the localities where saxifrages were studied, two or three *Kabschia* species occurred sympatrically. During this study, attention was mainly focused on species variation within populations and recognition of natural hybridisation between species in such mixed populations. Different leaf arrangement (alternate versus opposite) is an important character in the species treated in the present paper, and its variation was carefully analysed keeping in mind the conjectures of Harry SMITH already addressed to in the introduction.

3.1. *Saxifraga andersonii*

Though otherwise known as a species with "wide range of variability" (SMITH 1958: 126), leaf arrangement in *S. andersonii* is invariably alternate (Fig. 1). It is unchanging even under different habitat conditions (altitude, exposition), and is not liable to change in cultivation. Thousands of individual plants of this species were studied at Kaligandaki Valley, Hidden Valley, Hetenbeli Khola, Lungpa Khola, Marsiandi Valley, Sabche Khola and the ravine of the Jargeng River. In other respects, however, many plants were observed showing introgression from other species; traces of such inter-specific introgression is documented in my herbarium collections. [See also under 4.2.]

In Hidden Valley, *S. andersonii* is an abundant species. It varies in flower size and the number of flowers per inflorescence, colour of stem (from green to purple) and of corollas (usually white, but rosy in some

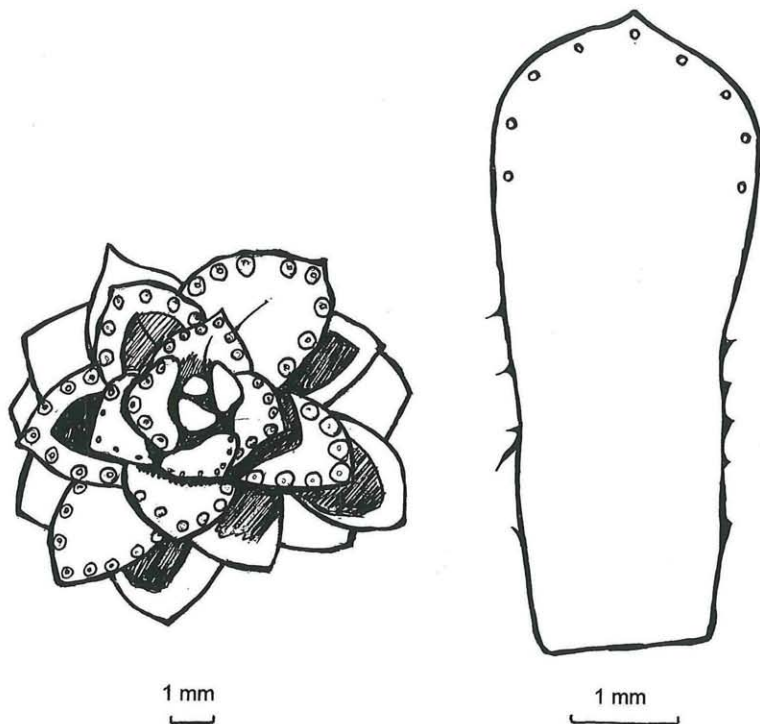


Fig. 1. *Saxifraga andersonii*, MEBU 01/9/2, Yak Kharka, 4200 m, rosette diameter 11,5 mm, leaves dimension 2.4 × 7.2 mm.

plants). A truly pink flower was found only once, in Sabche Khola, where a still higher degree of variation can be observed. Here unusually many-flowered plants were noted, some having 9–12 flowers (instead of less than 6) per inflorescence. On the contrary, only 3-flowered inflorescences were found in populations of Kone Khola and Lungpa Khola valleys.

Sixty-one herbarium sheets (52 from Nepal, 9 from Bhutan) determined as *S. andersonii* were studied at BM. Some of these specimens show morphological characteristics such as leaf shape, number and position of pores, number of flowers per stem and other features, which match the characteristics of *S. stoltzkae*.

As presently defined, *S. andersonii* includes plants with a wide range of variation probably caused by interspecific hybridisation.

3.2. *Saxifraga quadrifaria*

The rosette leaves of *S. quadrifaria* are always decussate (Fig. 2), with amplexicaul leaf-pairs connected basally. This opposite leaf arrangement is similarly stable in cultivation as the alternate one in *S. andersonii*.

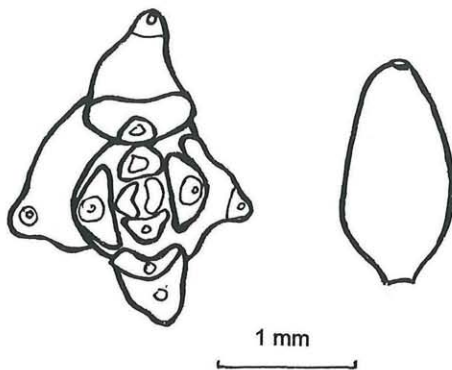


Fig. 2. *Saxifraga quadrifaria*, DELE 6/98, Dhaulagiri moraine 3700 m, rosette diameter 2,3 mm, leaves dimension 0.8–1.5 × 1.6–2.5 mm.

meter, they grew on large rocks and a disintegrating rock cliff. The population in the river-bed of Panga Khola, not far from Taglung village, alt. 3000 m, is probably of secondary occurrence due to seed floating, as also in the Larjung River, alt. 2500 m.

All plants from these localities had smooth leaves (excepting those from Jargeng Khola – see below) with only one hydrotode apically; in living state the margins of the leaf-pairs were confluent and entire, forming a shallow arch where they meet. There is a divergence on leaf shape in the descriptions of *S. quadrifaria* (see above under 2.2!). ENGLER and IRMSCHER 1919: 575 described the leaves glabrous (“foliis omnino glabris”) and figured it (loc. cit. 574 Fig. 121) with leaf-pairs joining at an acute angle; so they appear in SMITH’S 1958: 89 key but with margins denticulate-ciliate, while WEBB & GORNALL 1989: 270 observed the leaf-pairs to be confluent and entire in most cultivated plants. Tests were arranged whereby one sample was studied live and then dry. While in living plants the decussate leaf-pairs were entirely confluent with margins curved as described above, in dried material, however, the leaf connection is often at an acute angle or the curve is more or less retained. Such changes may be observed on one and the same specimen. Thus the supposed differences observed on the coalescent leaf margins in herbarium specimens can be regarded as artefacts.

At the locality of the Jargeng River ravine plants of *S. quadrifaria* show leaves marginally with several hairs looking rather like outgrowths or fringed leaf margins; one pair of the connected leaf-pairs had no hairs, others of the same shoot have several hairs. As the species is growing sympatrically with *S. andersonii* (and *S. alpigena*) here, it can be assumed that the occurrence of these marginal hairs is the result of introgression from the latter species.

This species was studied at a number of localities. On a mountain ridge south of Marci Bugli (a glacial circle between Dhaulagiri and Annapurna), alt. 4000 m, several plants of *S. quadrifaria* grew in horizontal cracks of stone tumulus, the largest plant being about 40 cm in diameter. In a spring terrain at Hetenbeli Khola, alt. 5000 m, about 50 small plants were found, 10 cm in diameter. In the ravine Jargeng or Kone River, alt. 4520 m, about 200 plants were seen, 10 cm in dia-

3.3. *Saxifraga alpigena*

Populations of *S. alpigena* have been studied in Marsiandi Valley, in Bhratang, alt. 2800 m, and Sabche Khola, alt. 3865–3900 m. Herbarium collections preserved at BM had been made in the same localities. We investigated further populations at the following localities: ravine of the Jargeng River, alt. 4520 m, opposite Thorung Phedi, alt. 4525 m, above Thorung Phedi, 4960 m, Thorung High Camp, alt. 4930 m, and upper Yamkim Khola (see below). In all these sites *S. alpigena* occurred sympatrically with *S. andersonii* except in the Bhratang population, where *S. andersonii* was replaced by *S. quadrifaria*. In the ravine of Jargeng River all three taxa, *S. alpigena*, *S. quadrifaria* and *S. andersonii* co-occurred.

In 1997 and 2000, a population was studied in Kali Gandaki Valley, at upper Yamkim Khola, 83°35'N, 28°47'E, alt. 4500 m (3 km SW of Dampus Pass). It was composed of plants on the whole smaller than *S. andersonii* and showed rosettes with partly alternate, partly decussate leaf arrangement in different proportions. A series of specimens (DEBU 20/6/100 to 20/6/111) was collected. They differ in some characters: they have lower stems (5–10 mm long as compared to 30–50 mm in *S. andersonii*), with 1–3 convex cauline leaves and only 1–3 flowers. The rosettes are open, measure 4–7 mm in diameter; the rosette leaves are straight, ovate to obovate to spatulate-cuneate, 3,5–5 × 1,5–2,4 mm long and wide, mostly with a single pore (but in some leaves with 2 or 3 pores), and with a few usually widely spaced short cilia in the lower part. *S. quadrifaria* was not found in this place either in 1997 or 2000. (The nearest occurrence of *S. quadrifaria* was 4 km SW, on a ridge above Alubari and Yak Kharka, 3000 m, above Kalopani 3000 m, 10 km from here in Hetenbeli Khola at 5000 m and in a moraine near French Pass, 3700 m.) Though *S. quadrifaria* was missing from that locality, it was assumed that the studied plants were hybrids between *S. andersonii* and *S. quadrifaria*, i.e. species with different arrangements of leaves (alternate and decussate).

Another journey was undertaken in 2001, revealing a new sympatric occurrence of *S. alpigena* with *S. andersonii* and *S. quadrifaria* in the ravine of Jargeng River. Their co-occurrence in nature corroborated the recognition of hybridisation. There were about 200 plants of *S. quadrifaria*, 20 plants of *S. alpigena*, 20 plants of *S. andersonii*. Both presumed parents, *S. andersonii* and *S. quadrifaria* did not match fully the characteristics of their typical expressions. Such differences may be due to introgression, e. g., the occurrence of some cilia on the leaf-pairs of *S. quadrifaria*.

The presumed hybrid origin of *S. alpigena* (with both, alternate and decussate, leaves) from *S. andersonii* (leaf arrangement alternate) and *S. quadrifaria* (leaf arrangement opposite) is suggested by the frequent sympatric occurrence of the parent species and is supported by the variation in leaf arrangement and structure (ciliation, hydathodes) and in other

often intermediate characters (Fig. 4, 5; see also Tab. 1). The majority of plants studied in the field has decussate leaves like in the type specimens. The rather uniform appearance of characters in some populations is probably due to multiple hybridisation and eventual stabilisation.

3.4. *Saxifraga pulvinaria*

Plants of this species were found only once, in the ravine Hetenbeli Khola, alt. 5000 m. *S. pulvinaria* grew in a fissure at the foot of a north facing cliff. The plants of this population were morphologically rather uniform; the only difference from the standard specimen cited by SMITH 1958 were slightly more widely spaced cilia of the leaves (Fig. 3).

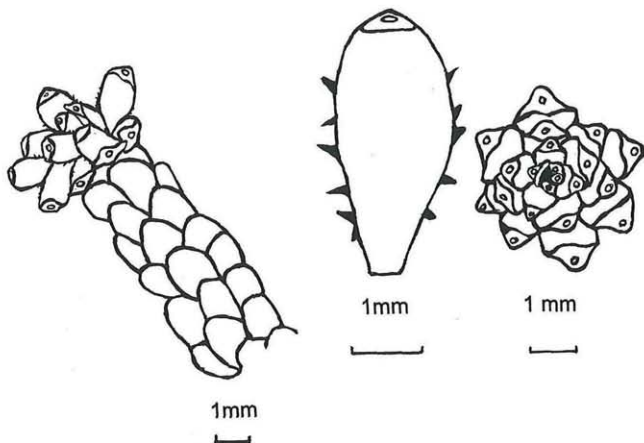


Fig. 3. *Saxifraga pulvinaria*, DEBU 20/9/1, rosette with caudicle, DEBU 20/9/1 leaf and rosette, gap Hidden valley to Hetenbeli Khola 5000 m, leaf dimension 3.7×1.1 mm, rosette diameter 3.9 mm.

3.5. A Hybrid Swarm with *Saxifraga andersonii* and *S. pulvinaria*

In 2000 a flowering population of *S. andersonii* was studied in Hidden Valley. We slowly proceeded through northern part of the Hidden Valley to Hetenbeli Khola Valley. Ecological conditions in the ravine Hetenbeli Khola changed as a result of vertical rock cliffs and proximity of a river. A population with plants deviating from typical *S. andersonii* was found, which differed in having smaller leaf-rosette diameters, leaves with fewer pores and flower-stems up to 2,5 cm long bearing only 1–3 flowers. Having discovered and studied *S. pulvinaria* on a vertical rock cliff (see 3.4), it was obvious that the sympatric occurrence has lead to hybridisation events. The population of *S. andersonii* at this location is affected by the introgression from *S. pulvinaria*. The hybrid swarm of *S. andersonii* \times *S. pulvinaria* grows on a horizontal surface of the rock cliffs. The hybrids

approach *S. andersonii*, but also plants of typical *S. andersonii* grow alongside the hybrids, giving opportunity to back-crossing between the hybrid population and *S. andersonii*. The distance between the plants of pure *S. pulvinaria* and of *S. andersonii* with their hybrids is only 10 m (!). In line with the above facts and knowledge we propose to treat the hybrid population as a new natural hybrid species.

4. Taxonomic Conclusions

4.1. *Saxifraga* × *alpigena* Recognised as a Hybrid Species

For the reasons explained in chapter 3.3 *S. alpigena* is accepted here as a hybrid species with the parentage of *S. andersonii* and *S. quadrifaria*:

Saxifraga* × *alpigena Harry SM. (pro sp.) = *S. andersonii* × *S. quadrifaria*: differs from its parents by the leaf arrangement showing both, decussate and alternate leaves, it differs from *S. andersonii* by smaller leaf rosettes and shorter stems (up to 1 cm) with fewer flowers (up to 3 per flowering shoot), and from *S. quadrifaria* by leaves with up to 5 hydathodes and flowering stems with often more than 1 flower.

In all localities studied (see under 3.3), except in upper Yamkin Khola, *S. × alpigena* is occurring as more or less uniform (stabilised) hybrid. The populations of Yamkin Khola show a higher variability with characteristics of a hybrid swarm, displaying unstable features in direction of one or the other parent.

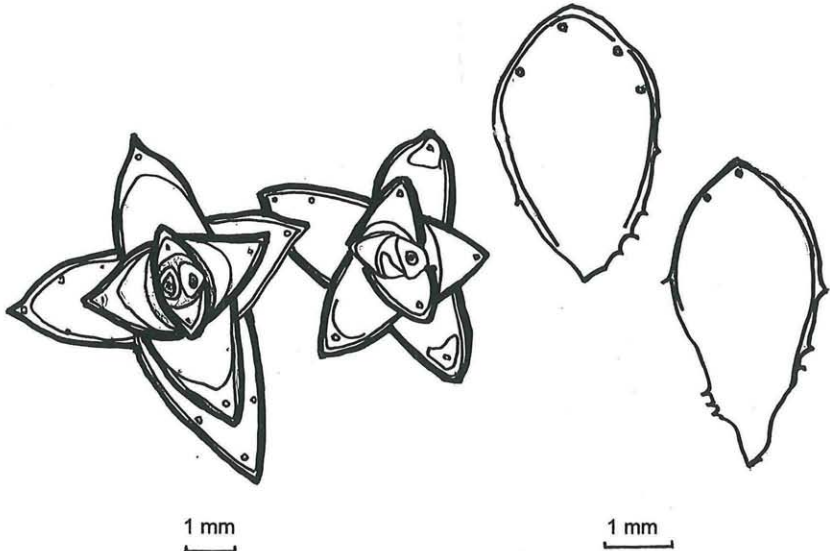


Fig. 4. *Saxifraga* × *alpigena*, MEBU 01/2/61, Bhratang 2807 m, rosette diameter 7 mm, leaves dimension 2.6 – 2.8 × 4.3 mm.

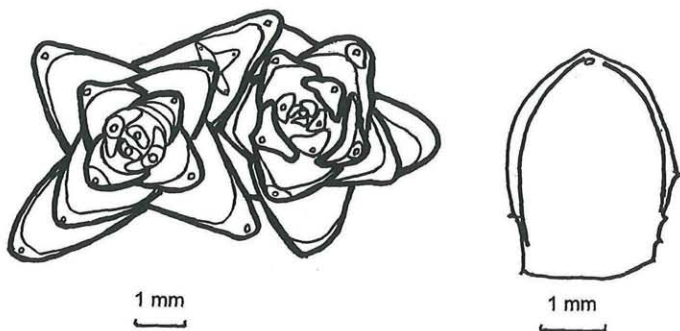


Fig. 5. *Saxifraga x alpigena*, MEBU 01/2/103, Bhratang 2807 m, rosette diameter 7 mm, leaves dimension 2.8 x 3.9 mm.

Studying our seed samples, undeveloped sterile seeds were often found. In Sabche valley for instance from 20% to 100% of *S. x alpigena* plants failed to develop seed.

Table 1. Comparison of main diagnostic characteristics of *S. andersonii*, *S. x alpigena* and *S. quadrifaria*

Characters	<i>Saxifraga andersonii</i>	<i>Saxifraga x alpigena</i>	<i>Saxifraga quadrifaria</i>
Cushion	(A) slightly domed, up to 20 cm Ø (B) small, domed (C) deep cushions or mats	(A) small, up to 20 cm Ø (B) small and loose; dense and flat in exposed position (C) little loose turfs, deep cushions	(A) dense, small turfs or cushions up to 20 cm Ø (B) dense, pulvinate, flat or slightly domed (E) very densely caespitose
Caudicles (cm)	(A) 1-3 (B) short to slightly elongated (E) 2-5	(A) 0.5-1.5 (B) short (D) 2	(A) up to 1 (E) 2-3
Rosette diameter (mm)	(A) 6-12 (B) 7-16	(A) 3-8 (11) (B) 4 or 2-4 (D) 4	(A) 2.3-5 (B) 3-4 or 2-4,5 (E) 3-4
Rosette leaves shape	(A) cuneate, linear-spathulate to spathulate, apex mucronate or obtuse (B) spathulate-oblong, linear-spathulate to cuneate- or obovate-linear (D) broadly cuneate-linear, obtuse (E) spathulate-lingulate or oblong-lingulate, moderately obtuse	(A) ovate to obovate (B) ovate to obovate (D) ovate to obovate, very obtuse at the apex	(A) obovate with truncate apex (B) ovate, thickened in apical part with slightly truncate apex (E) ovate
Position (and coalescence) of caudicle leaves	(A) alternate	(A) opposite or opposite and alternate or alternate (B) opposite (D) opposite, with bases joining in an unbroken line	(A) opposite, in live leaf-pairs with coalescent bases forming a shallow arch, but in dry state may meet at an acute angle or arch (B) opposite (E) opposite

Characters	<i>Saxifraga andersonii</i>	<i>Saxifraga × alpigena</i>	<i>Saxifraga quadrifaria</i>
Leaf dimension (mm)	(A) 4.5-8 × 2.4-3.5 (B) 5-10 × 1.5-4 (C) 5-10 (length) (D) 5-7(8.5) × 1.5-2(4) (E) 5-6 × 1.5-1.8	(A) 3.4-6 × 1.5-2.6 (B) 1.5-2.5 × 1-2 (D) 1.5-2.5 × 1-2	(A) 1.6-2.5 × 0.8-1.5 (B) 2-2.5 × 1.2-1.5 (E) 2-2.5 × 1.2-1.5
Position of marginal leaf cilia	(A) ciliate in the basal half of leaf (B) ciliate on lower margins (E) glabrous, ciliate only at base	(A) glabrous or sparsely ciliate, with a few cilia at base and some more in the basal half of leaf (B) non-ciliate (D) without cilia	(A) glabrous (exceptionally a few cilia in case of introgression) (B) non-ciliate (E) without cilia
Number of leaf pores	(A) 3-7(9) (B) 3-7 (D) 3-7 (E) 3	(A) 1-3(5) (B) 1 (D) 1	(A) 1 (B) 1 (E) 1
Number of flowers per inflorescence	(A) 3-5 (12) (B) 1-5 (C) up to 5 (E) 3-5	(A) 1-3 (B) 1 (D) 1	(A) 1 (B) 1 (E) 1
Length of flower stem (mm), stem leaves	(A) 30-50 (B) 25-35 (E) 25-30, densely leafy	(A) up to 10, with 2-3 leaves (B) 5-7, with 2 leaves (D) 5-7, with 2 leaves	(A) 0-5, with 0 to 5 leaves (B) 5-6, with 0-1 leaf (E) 5-6, with 0-1 leaf

Tables 1 and 2 are a compilation of plant features derived from personal observation plus additional details from published items (as listed below). Some morphological features such as petal shape and nerve numbers have been omitted because of excessive variation.

(A) – Own measurement and characteristics based on from herbarium material of BM, own herbarium specimens and live material.

(B) – Characters reported by HORNY & al. 1986, mostly taken from SMITH 1958 and/or ENGLER & IRMSCHER 1919, but sometimes complemented by data from collections of cultivated plants (*S. quadrifaria* and *S. alpigena*).

(C) – Data in WEBB & GORNALL 1989.

(D) – Data in SMITH 1958.

(E) – Data in ENGLER & IRMSCHER 1919.

4.2. *Saxifraga × hetenbeliana*, a new hybrid species

Saxifraga × hetenbeliana BÜRCEL, nothosp. nova (Fig. 6) = *S. andersonii* × *S. pulvinaria*.

Holotypus: Nepal, west part of Central Himalayas, Hetenbeli Khola, 29°50'N, 83°15'E, alt. 5000 m, leg. J. BÜRCEL, DEBU 20/10/1 [PR].

Hybrida e subsect. *Kabschia*, inter *Saxifraga andersonii* et *S. pulvinaria* media, differt a *S. andersonii* caulibus floriferis brevioribus (ad 22 mm longis), ad maximum 3floris, a *S. pulvinaria* foliorum rosulis majoribus (plus quam 6 mm diametro) et caulibus saepe 2-3floris.

The name of the hybrid *S. × hetenbeliana* is derived from the valley Hetenbeli Khola, where it was found.

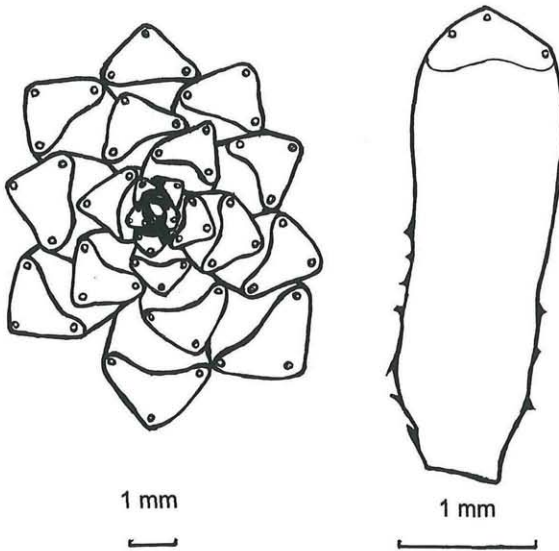


Fig. 6. *Saxifraga × hetenbeliana* DEBU 20/10/1, Hetenbeli Khola, spring, 5000 m, rosette diameter 9 mm, leaf dimension 3.4 × 1.1 mm.

Characteristics: The hybrid plants are smaller than *S. andersonii*, forming cushions up to 10 cm in diameter, with leaf rosettes open, 7–10 mm in diameter; rosette leaves straight, obovate to obovate-linear, 2.5–6.6 × 1.0–1.6 mm, with 1 to 7 pores, sparsely ciliate below; flowering stems up to 22 mm long, with 1–7 obliquely spreading cauline leaves, 1–3-flowered; flowers 10 mm in diameter, with white petals.

The hybrid *S. × hetenbeliana* shows characteristics of a hybrid swarm (partly approaching the one parent or the other parent). For instance, specimen DEBU 20/9/10 approaches *S. andersonii*, whereas DEBU 20/9/80 approaches *S. pulvinaria*, the latter characterised by 1 (2–3) pores per leaf. Three hundred leaves of hybrid specimens have been examined of which 297 had one pore, two had three pores and one leaf had two pores.

Table 2. Comparison of main characters of *S. andersonii*, *S. × hetenbeliana* and *S. pulvinaria*.

Characters	<i>Saxifraga andersonii</i>	<i>Saxifraga × hetenbeliana</i>	<i>Saxifraga pulvinaria</i>
Cushion	(A) slightly domed, up to 20 cm Ø (B) small, domed (C) deep cushions or mats	(A) small, up to 10 cm Ø	(A) dense, compact, cushions of column caudicles, up to 40 cm Ø (B) hummocks, pulvinate, dense, low and flat (C) dense cushion with columnar leafy shoots
Caudicles (cm)	(A) 1-3 (B) short to slightly elongated (E) 2-5	(A) up to 1.5	(A) columns very short: 0.5 to 1 (B) short
Rosette diameter (mm)	(A) 6-12 (B) 7-16	(A) 7-10	(A) 2-5 (B) 3-6
Rosette leaves shape (and colour)	(A) cuneate, linear-spathulate to spathulate, apex mucronate or obtuse (B) spathulate-oblong, linear-spathulate to cuneate- or obovate-linear (D) broadly cuneate-linear, obtuse (E) spathulate-lingulate or oblong-lingulate, moderately obtuse	(A) obovate, obovate-linear (green to pale green)	(A) oblong to obovate, or ovate with truncate apex (B) oblong to oblong-linear, straight, obtuse, thick, green
Leaf dimension (mm)	(A) 4.5-8 × 2.4-3.5 (B) 5-10 × 1.5-4 (C) 5-10 (length) (D) 5-7(8.5) × 1.5-2(4) (E) 5-6 × 1.5-1.8	(A) 2.6-6.6 × 1-1.6	(A) 3-3.7 × 1.3-2 (B) 2-4 × 0.8-1.5 (C) 2-4 (length)
Position of marginal leaf cilia	(A) ciliate in the basal half of leaf (B) ciliate on lower margins (E) caudicle leaves glabrous, ciliate only at base	(A) sparsely ciliate in lower part	(A) ciliate except in the apical fifth (cilia 0.2-0.35 long) (B) sparsely glandular-hairy on lower half of margins
Number of leaf pores	(A) 3-7(9) (B) 3-7 (D) 3-7 (E) 3	(A) 1-7	(A) 1 on the truncate apex (B) 1 on the truncate area
Number of flowers per inflorescence	(A) 3-5 (12) (B) 1-5 (C) up to 5 (E) 3-5	(A) 1 to 3	(A) 1 (B) 1
Length of flower stem (mm), stem leavers	(A) 30-50 (B) 25-35 (E) 25-30, densely leafy	(A) up to 22, with (1) 2-7 leaves	(A) stemless (B) stemless

For symbols see the table 1.

In Hidden Valley only *S. andersonii* occurs profusely. Its characteristics correspond usually to typical *S. andersonii*, but tiny individuals occur sparsely with characteristics approaching the hybrid *S. × hetenbeliana* or *S. pulvinaria*. They are plants with rosette diameter only 10 mm, some

stemless or with stems up to 10 mm and 1–2-flowered inflorescence. A possible explanation for these aberrations is introgression from the latter species, since hybridisation with *S. hypostoma* or with *S. × tukuchensis* can be excluded, the plants having no stiff hairs on the apical leaf margin.

4.3. Concluding Note

Based on the study of *Saxifraga* subsect. *Kabschia* populations in the Dhaulagiri-Annapurna region it can be stated that sympatric occurrence of species leads to hybridisation and introgression which are not rare, but common events. *Saxifraga andersonii* hybridises with three species, *S. hypostoma* (BÜRCEL 2002), *S. quadrifaria* and *S. pulvinaria* (this study) in this region.

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