The flower of *Koenigia islandica* L. (Polygonaceae): an interpretation

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ABSTRACT

It is suggested that the structure of the flower of *Koenigia islandica* L. can be linked with that of *Polygonum* sensu lato through a number of intermediate species that have been included under *Koenigia*. The flower is derived from a structure with five tepals, eight stamens and a trimerous gynoecium, by the fusion of two pairs of tepals and the consequent loss of two stamens. The two inner stamens are lost through lack of space in the small flowers during development; the remaining stamens belong to the outer whorl.

INTRODUCTION

Koenigia (Polygonaceae) was for a long time known only by a sole representative, *Koenigia islandica* L. The isolation of this species was reduced by Hedberg (1946), who removed a number of species from *Polygonum* to *Koenigia* on the basis of pollen similarity. Several authors before him had tried to link the anomalous flower of *K. islandica* with that of other Polygonaceae (e.g. Gross 1913; Jaretzky 1928; Edman 1929; Laubengayer 1937). The normal polygonaceous flower has a generalized pattern of five tepals, eight stamens in two whorls and a trimerous gynoecium (Ronse Decreane & Akeroyd 1988; Gross 1913; Galle 1977). The flower of *K. islandica*, however, consists of three tepals, alternating with three stamens and a trimerous or dimerous ovary (Fig. 1, 2D), and is generally thought to be strongly reduced. This reflects the habit of the plants, i.e. low-growing annuals with tiny flowers. The tepal vasculature is reduced to a minimum, consisting of one main vein flanked by two laterals (Vautier 1949), or a single small vein only (Laubengayer 1937; Ronse Decraene & Akeroyd 1988). The species is mostly described as having three outer tepals and three alternating stamens, which are regarded as belonging to an inner whorl (Laubengayer 1937). This interpretation is strengthened by the occasional occurrence of tetramerous flowers (Gross 1913; Bauer 1922; Laubengayer 1937). Juel (1886; see Edman 1929) compared the three tepals of *K. islandica* with the outer perianth whorl of *Rumex*. Bauer (1922) compared the trimerous perianth of *Koenigia* with strongly reduced flowers of *Polygonum* sensu lato. Occasionally a trimerous flower is produced in nutrient-low culture. Gross (1913) linked the species with *Persicaria* (*Polygonum* sect. *Persicaria*) because of the loss of two outer tepals and associated stamens. Vautier (1949) described the unequal splitting of vascular bundles in two of the three tepals and considered that they were bivalent through the fusion of four tepals, the third inner remaining unaltered. She concluded from the stamen insertion that they belong to an outer whorl: "Leur filet est court et soudé assez haut dans le receptacle, elles sont le plus souvent exsertes et ne s'appuient jamais contre les parois de l'ovaire comme le font les internes." Vautier (1949) linked *K. islandica* with the hexamerous Eriogoneae. In her view, the three alternating stamens have not undergone doubling up ("dédoublement") as in other Polygonaceae, for example *Rumex*, *Rheum*, *Polygonum* sensu lato, *Fagopyrum*, *Fallopia* (Jaretzky 1928; Galle 1977; Ronse Decraene & Akeroyd 1988).

I have had the opportunity to study the six species included in *Koenigia* on the basis of pollen similarity by Hedberg (1946). Other characters have been found and described that stress the distinctness of the enlarged genus (Ronse Decraene & Akeroyd 1988). In the present paper I have

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FIGURE 1. *Koenigia islandica* L., stamen with tepal. Note filament adnate to tepal and short vein.

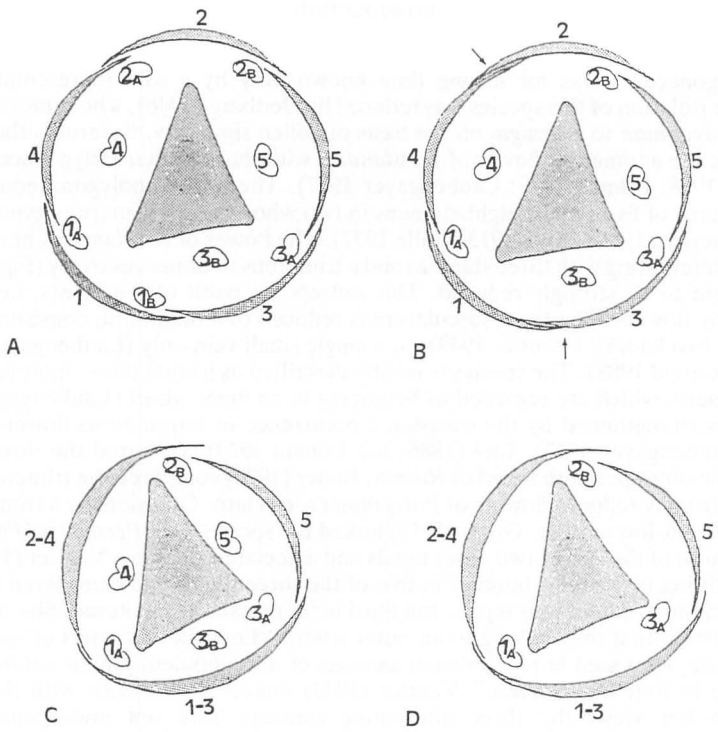

FIGURE 2. Diagrammatic representation of a putative reductive trend in the genus *Koenigia*. Numbers are according to position and appearance in ontogeny (Galle 1977).
A, Regular polygonaceous flower, such as *Koenigia forrestii* (Diels) Hedb., with floral formula P5A8G3.
B, Fusion of tepals 2–4 and 1–3 (arrows) and consecutive loss of stamens opposite to point of fusion, e.g. *Koenigia pilosa* Maxim.
C, Complete fusion of Tepals 1–3 and 2–4 but inner stamens still present.
D, The situation in *Koenigia islandica* L. The inner stamens are lost due to lack of space or nutrients for their development.

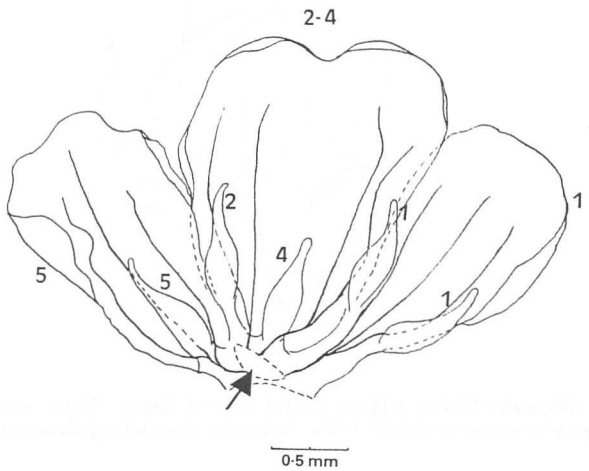

FIGURE 3. *Koenigia pilosa* Maxim., view of opened flower. Numbers according to position and appearance of tepals in ontogeny (Galle 1977). Note fusion of tepals 2 and 4 and their irregular venation. Arrow pointing to position of gynoecium. The third tepal and stamens are lost.

tried to link the unusual, strongly reduced, trimerous flower of *K. islandica* with these other species and with *Polygonum* in general.

METHODS

The floral morphology of the following species was studied (see Ronse Decraene & Akeroyd 1988 for provenance): *Koenigia islandica* L., *K. delicatula* (Meissn.) Hara f. *brevistyla* (Meissn.) Hedb., *K. pilosa* Maxim., *K. nummularifolia* (Meissn.) Mesicek & Soják, *K. forrestii* (Diels) Hedb. and *K. filicaulis* (Wall. ex Meissn.) Hedb. Flowers were soaked in boiling water, cleared in a diluted solution of sodium hydroxide and stained in saffranin before observation under a dissecting or light microscope.

RESULTS AND DISCUSSION

All species of *Koenigia* share the same habit, being low growing alpines or annual weeds of arctic or montane regions. *K. forrestii* always shows a constant number of floral parts, arranged as in the generalized polygonaceous flower (floral formula, P5A8G3). Other species have a more variable floral diagram, as reductions affect the tepals and stamens in relation to dimery in the gynoecium (*K. pilosa*, *K. nummularifolia*, *K. filicaulis*; Fig. 3). In *K. nummularifolia* no inner stamens are present except for one occasional transitional. In the case of *K. pilosa* and *K. delicatula*, the tepal number is often four, and two outer stamens are always present. I have been able to confirm Vautier's interpretation that the stamens of *K. islandica* belong to an outer whorl, as reductions seem to affect especially the inner stamens of related members of the genus. In *K. pilosa* one flower was found with a trimerous perianth, one tepal being much larger with two apices and an irregular venation, which is clearly the result of fusion. The position in the flower reveals that these tepals are '2' and '4'. One of the outer stamens is lost in the process (Fig. 3). Similar fusions occur in other families, e.g. Cruciferae and Capparidaceae (Merxmüller & Leins 1967; Leins & Metzenauer 1979), and are probably the basis of many tetramerous flowers.

Further evidence is provided by the zones of trichomes occurring in relation to the nectaries. Tutin (1964) described them as three gland-like staminodes, Vautier (1949) as nectaries ("écailles nectarifères"). The other genera show a continuous central disc around the inner stamens with

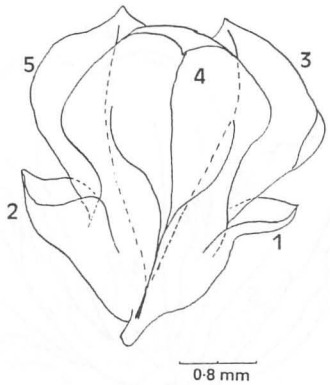

FIGURE 4. *Koenigia delicatula* (Meissn.) Hara, lateral view of flower. Tepals numbered according to their position and appearance in ontogeny (Galle 1977). Note smaller outer tepals without veins.

trichomes spreading on the receptacle behind (Ronse Decraene & Akeroyd 1988). The outer stamens are inserted clearly higher, alternating with these zones. The nectaries, which occur as receptacular protuberances or 'mamillae', are not fused with the filament bases. This would be the case in *K. islandica* if the existing stamen whorl were the inner one. The fact that the anthers are introrse is further evidence for their origin as outer stamens, as the inner stamens are mostly extrorse (Fig. 2).

However, it is difficult to accept the assumption of Vautier (1949) that the three stamens of *K. islandica* are primitively single structures and are not part of a stamen pair, one of which has been lost. Their position would be opposite to the tepals and not lateral, as is the case (Fig. 1). Interpretation by Gross (1913) of a loss of outer tepals seems valid (compared with its occurrence in some related species), but he is incorrect in stating that the associated stamens are also lost. The remaining stamens would be in the centre of a tepal if that were the case.

I was also able to confirm Vautier's interpretation of the fusion of four outer tepals in pairs by examples which have an outer tepal fused with an inner (*K. nummularifolia*, *K. pilosa*: Fig. 3). However, other cases point to a reduction of the outer tepals (Fig. 4). *K. delicatula* and *K. pilosa* sometimes have much smaller outer tepals without venation. In one flower an outer tepal was missing, together with the associated stamens.

A model can be conceived for *K. islandica* based on a comparison with the other species with a pentamerous perianth, and the acceptance of fusion of tepals and consequent loss of stamens. The fusion of two tepal pairs (1–3 and 2–4) is linked with the loss of a stamen on each side of the point of fusion between two tepals (Figs. 2B, 3). The innermost stamens (3b, 4 and 5) have been lost in the reductive process by lack of space for their development (Fig. 2D; similar cases occur in *K. pilosa* and *K. nummularifolia*). The remaining stamens are 1a, 2b and 3a. In the case of *K. pilosa* and *K. delicatula* the tepal number is often four, and two outer stamens are always present.

Another reason for reduction in stamen number is found in the transgression of the gynoecium from trimery (trigonous nut) to dimery (lenticular nut). In the process the transitional stamens and tepal are often lost. Other evidence might suggest the progressive loss of two outer tepals, which are reduced and may be lost altogether. Crowding may be the cause of the loss of more parts, the inner stamens by the pressure of the gynoecium against the tepal surface, the outer by a lack of space for their inception. This last interpretation is less plausible as it is difficult to explain which stamen of the pair is to disappear, unless one postulates an absence of dédoublement. This is inconsistent in comparison with the generalized occurrence of stamen pairs in the Polygonaceae and would contradict other evidence of a close relationship between *K. islandica* and species of *Polygonum* sensu lato.

It is therefore postulated that *K. islandica* has been derived from an ancestor like *K. nummularifolia* or *K. pilosa* by the fusion of two outer tepal pairs and the consequent loss of five stamens.

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