Phylogenetic Relationships of *Geum* (Rosaceae) and Relatives Inferred from the nrITS and *trnL-trnF* Regions

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ABSTRACT. This is a molecular phylogenetic study of the group formerly known as Dryadeae, based on DNA sequences from the internal transcribed spacers, ITS, of nuclear ribosomal DNA and the *trnL* intron and the *trnL-trnF* intergenic spacer of the chloroplast. A total of 1.9 kb, for 26 ingroup species, were analyzed using parsimony and model-based Bayesian inference. Some clades are well supported by both data sets: the ingroup, with *Fallugia* as the sister to the rest of the clade; *Sieversia* in a strict sense; a clade consisting of all the herbaceous perennials, and some clades within this last group. Other clades, within the group of herbaceous perennials, differ between the analyses. The data sets in the present study do not support any previous circumscriptions of *Geum* nor any of the suggested segregate genera, except for the southern hemisphere *Oncostylus*. Morphological characters, notably fruit characters, mapped onto the combined tree show patterns of widespread parallel evolution and reversals—or possibly the effects of reticulations. Allopolyploidy has been suggested by previous workers and there are some indications of this in our results. *Geum andicola* appears in different well supported groups in the two separate analyses. This may be caused by inheritance of chloroplast DNA from one parental species and homogenization of ribosomal DNA from the other. Also, the intricate fruit type present in, for example, the type species of *Geum*, *G. urbanum*, appears to have evolved twice from progenitors with plumose styles. We propose the name Colurieae for this entire clade and the name Geinae for the group of herbaceous perennials.

The delimitation of *Geum* has varied greatly over the last century and several segregate genera have been described. *Geum* belongs in the Rosoideae, in the group formerly known as Dryadeae. *Dryas* L., however, is no longer considered to be closely related to *Geum*, despite similarity in fruits and embryology, but actually belongs outside the Rosoideae (Wallaart 1980; Morgan et al. 1994; Eriksson et al. 1998). The remainder of Dryadeae, about 75 species in *Fallugia*, *Sieversia*, *Geum* (including segregates), *Coluria*, *Waldsteinia*, and *Taihangia*, is the focus of this paper. This group of plants occur in temperate and Arctic regions all over the world, often at high elevations, and are most frequent in the northern hemisphere, with a few representatives occurring in South America, New Zealand, Australia, and Tasmania. Most of the species are herbaceous perennials with a rosette of imparipinnate leaves and a thick caudex, but a few species are small shrubs. The petals are yellow, white, orange, red, or purplish and the fruits are achenes. In some species the style persists on the fruit and is either hooked at the apex (Fig. 1G) or straight (Fig. 1A, D), often becoming elongate and plumose (Fig. 1A). It may also be wholly or partly deciduous (Fig. 1B, C, E, F). The length of the segment remaining on the fruit varies and it is sometimes equipped with various means of adhesion, such as bristles (Fig. 1C) or a hook at the apex. Some species (e.g., the type species of *Geum*, *G. urbanum*) have a jointed style where the terminal segment is deciduous, leaving a hooked lower segment that attaches to animals, thereby dispersing the fruit (Fig. 1E). This has been called the fish-hook fruit type

(Iltis 1913). So far no morphological synapomorphies have been identified for the remainder of Dryadeae.

Several species are popular garden ornamentals, such as *G. coccineum* Sibth. & Sm., *G. triflorum* Pursh, *G. rhodophaeum* Stoj. & Stefanov, and *Waldsteinia ternata* Fritsch. Some species have been used in folk medicine to treat various diseases. Pliny (77) wrote in his Natural History: ''*Geum* has little roots, slender, blackish and with a pleasant smell. It not only is a cure for pains in the chest or side, but also dispels indigestion, having besides a pleasant taste''. Recent studies have shown that the underground stems contain compounds which are effective against inflammatory diseases (Tunon et al. 1995), herpes virus infection (Kurokawa et al. 1995) and fungal diseases (McCutcheon et al. 1994).

The phylogeny of this group has been suggested to be strongly influenced by reticulate evolution. Based on cytogenetic studies and interspecific crossings Gajewski (1957, 1958) put forward the hypothesis that the hexaploid species of subgenus *Geum* (all but one of the species with the fish-hook fruit type) are allopolyploids which have been formed through hybridization between an ancestor of the tetraploid *G. montanum* and a diploid ancestor of *Waldsteinia* or *Coluria*. He concluded that the two genomes of *G. montanum* were homologous to two of the genomes of subgenus *Geum*. The structure of the epidermal cells of the persistent basal part of the style of the fish-hook fruits (Fig. 1E) is similar to that of the long plumose style of *G. montanum* (Fig. 1A), while the outer deciduous part is similar to that of *Waldsteinia* (Fig. 1F), which has a style
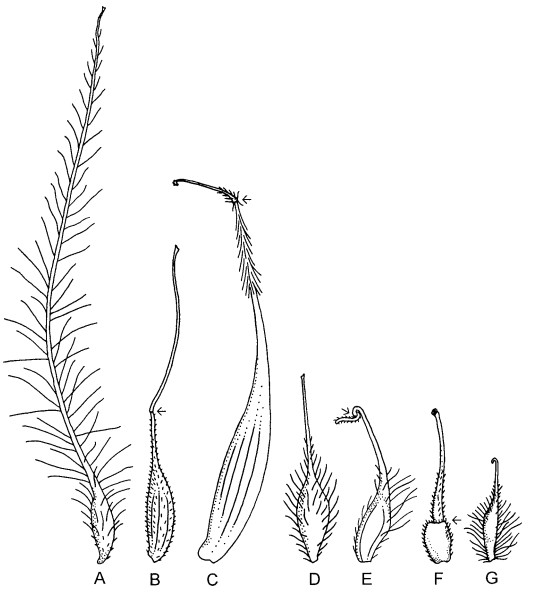
FIG. 1. Fruit types. Achenes, some of them with a joint (region of thin walled cells) on the style where it is partly or entirely abscised at maturity. The position of the joint is indicated by an arrow. A. *Geum montanum*, plumose style; elongating in fruit, covered with soft, long hairs, persistent in its entirety. B. *Geum speciosum*, style jointed below middle, terminal segment glabrous, deciduous. C. *Geum heterocarpum*, harpoon fruit type; style jointed above middle, terminal segment deciduous, lower segment with stiff deflexed bristles at apex. D. *Acomastylis rossii*, stiff, glabrous style, persistent in its entirety. E. *Geum urbanum*, fish-hook fruit type; style jointed, terminal segment deciduous, lower segment hooked at apex. F. *Waldsteinia geoides*, style jointed at base, deciduous in fruit. G. *Oncostylus cockaynei*, style stiff with hooked apex, persistent in its entirety. Scale bar = 1 cm.

that is deciduous in its entirety (Iltis 1913). Gajewski (1957) considered this to support his hypothesis and also proposed that the wind dispersed species of *Geum* subgenera *Erythrocoma* and *Acomastylis* had been formed by hybridization and allopolyploidy between several possibly extinct species. If the hypothesis of widespread allopolyploidy within *Geum* is correct, one would expect morphological variation to be hard to interpret. Indeed, taxonomic history in *Geum* is almost chaotic, with widely varying classifications reflecting the lumping and splitting of *Geum* and several segregate genera.

Taxonomic History of **Geum.** The name *Geum* first appeared in the literature in 77 AD (Plinius Secundus 77). Hence, Linnaeus (1753) selected *Geum* and rejected *Caryophyllata* (Bauhin 1623), which was in use at the time. Linnaeus included five species in *Geum*.

Scheutz (1870) monographed *Geum* and included 43 species, which were divided into eight sections. He included all species with non-deciduous styles in section *Sieversia*. This name had been used previously (Willdenow 1811) at the generic level for a single species, *S.*

anemonoides, including what had earlier been described as two species, *Dryas pentapetala* L. and *Anemone pusilla* Gaertn. Today these two species are classified either in *Sieversia* (Yuzepchuk 1941) or in *Geum* (Hultén 1968). The species with the fish-hook fruit type were divided by Scheutz into several sections, one of which was sect. *Stylipus. Stylipus* had been described earlier as a genus including the single species *S. vernus* from North America (Rafinesque 1833). This species has the fish-hook fruit type and very small petals but lacks an epicalyx.

Focke (1894) divided *Geum* into two subgenera *Geum* and *Sieversia*. The former was characterized by partly deciduous styles and the latter by non-deciduous styles.

Greene (1899) accepted the broad circumscription of *Sieversia* of previous authors but ranked it as a genus. Later, however, (1906) he stated that the North American species were not congeneric with *Sieversia pentapetala* (= *S. anemonoides* in part) and described two new genera: *Acomastylis* for the species with yellow flowers and straight non-plumose persistent styles (Fig. 1D) and *Erythrocoma* for species with a reddish calyx and plumose accrescent styles.

Rydberg (1913) went back to a broader circumscription of *Sieversia*, but kept *Acomastylis* for species with non-elongating styles. *Geum*, on the other hand, was circumscribed narrowly, comprising only the species with fish-hook fruit type.

Hultén (1929) lumped all species, including *Sieversia*, in *Geum* and thus followed Scheutz's (1870) concept of *Geum*.

In a second monograph, Bolle (1933) divided *Geum* into several genera, two of them new: *Novosieversia* for a single circumboreal Arctic species, *N. glacialis* with solitary yellow flowers and plumose styles, and *Oncostylus* comprising a number of southern hemisphere species characterized by persistent styles with an apical hook (Fig. 1G). Bolle (1933) included in *Geum* not only the fish-hook species, but also two species with harpoon type fruits (Iltis 1913), characterized by an apical deciduous portion of the style, and a straight basal segment with deflexed bristles toward the apex (Fig. 1C). He also included some species with plumose styles in *Geum*, treated *Sieversia* narrowly like Willdenow (1811) and recognised *Acomastylis* and *Erythrocoma*. Bolle's (1933) work is the most comprehensive recent treatment of the group.

After Bolle (1933), authors have continued splitting or realigning the species into new constellations emphasising various characteristics. Hara (1935) described *Parageum*, including *Geum montanum* and four species previously placed in *Acomastylis*. Of the latter is the type species of the new genus, *P. calthifolium*, included in the present study. Yuzepchuk (1941) went further in splitting by describing two additional gen-

era: *Woronowia* (only a single species, *W. speciosa*) with straight, glabrous, articulate styles (Fig. 1B) and *Orthurus* (including *O. heterocarpus* and *O. kokanicus*) for the harpoon fruit type species.

Gajewski (1957, 1968) classified *Geum* based upon a major cytogenetic study including extensive interspecific crossing experiments. In short, he lumped everything into *Geum*, transferring all of Bolle's (1933) segregate genera to subgeneric rank, adding most later segregates as well as his own *Andicola* as subgenera. In the latter he placed *G. andicola*, which is included in this study. Gajewski (1957, 1958) concluded from his work that allopolyploidy has been an important mode of speciation within *Geum* and that the subgenus *Geum* originated through allopolyploidy, probably between ancestors of *G. montanum* and *Waldsteinia*.

The work and classification of Gajewski (1957, 1958, 1968) has been very influential. Most later authors have given *Geum* a rather broad circumscription recognizing a varying selection of subgenera and segregate genera (Huber 1961; Schulze-Menz 1964; Hutchinson 1967; Robertson 1974; Kalkman 1988).

The considerable disagreement among botanists of what to include in and what to separate from *Geum* is notable. The few points of agreement are that the species with the fish-hook fruit type belong in *Geum*, perhaps with the exception of *G. vernum*, which has sometimes been split off (Rafinesque 1833), and that *Waldsteinia* and *Coluria* are separate from *Geum*.

Relationships Among Genera Within the Former Dryadeae. In the first generally accepted classification of the Rosaceae, Focke (1894) placed *Geum* in the subtribe Dryadinae along with *Coluria*, *Cowania* D.Don, *Dryas*, *Fallugia*, and *Waldsteinia*. He was later followed in principle by several authors, (Schulze-Menz 1964; Hutchinson 1967; Robertson 1974; Kalkman 1988), but these ranked Focke's (1894) subtribe as the tribe Dryadeae and in some cases included *Chamaebatia* Benth., *Cowania*, and *Purshia* DC.

Rydberg (1913) kept all the genera with styles that at least in part remain on the fruit in Dryadeae, while he placed *Coluria* and *Waldsteinia*, both characterized by wholly deciduous styles, in Colurieae. This is the only classification where *Coluria* and *Waldsteinia* are placed in a suprageneric group that does not include *Geum*.

The second widely accepted classification was introduced by Juel (1918) in his classification of the Rosaceae. He divided Dryadoideae, characterized by straight ovules, into two tribes based on the shape of the stigma. In the first one, Geeae, he placed *Coluria*, *Geum*, and *Waldsteinia* and in the second one, Cercocarpeae, he placed *Cercocarpus* Humb., *Chamaebatia*, *Cowania*, *Dryas*, *Fallugia*, and *Purshia*. In general, his scheme was adopted by several authors (Bolle 1933; Gajewski 1957; Huber 1961).

Recent classification places *Dryas* and *Fallugia* in Dryadeae, while *Chamaebatia*, *Cowania*, and *Purshia* are placed in Purshieae and *Cercocarpus* in Cercocarpeae. *Coluria*, *Geum*, *Novosieversia*, *Orthurus*, *Sieversia*, *Taihangia*, and *Waldsteinia* are all placed in Geeae (Takhtajan 1997).

Wallaart (1980) considered Dryadeae to be heterogeneous based on karyological and chemical evidence. His studies showed that the species with the basic chromosome number $x = 9$ (*Cercocarpus*, *Dryas*, and *Purshia*) contain sorbitol, while those with $x = 7$ (*Coluria*, *Geum*, and *Waldsteinia*) lack sorbitol. He suggested that the species with $x = 9$ belong outside the Rosoideae. This theory was further supported by a pollen morphological study of the Rosaceae (Hebda and Chinnappa 1994), which showed that *Coluria*, *Fallugia*, *Geum*, *Orthurus*, and *Waldsteinia* all have striate microperforate pollen while *Cercocarpus*, *Cowania*, and *Purshia* on the other hand have tuberculate perforate pollen.

A phylogenetic study of the Rosaceae based on *rbcL* (Morgan et al. 1994) showed that the species with $x = 9$ do not belong in the Rosoideae. According to their results *Fallugia*, *Geum*, and *Waldsteinia*, with $x = 7$, form a well supported lineage within the Rosoideae, while *Purshia* and *Cercocarpus* on the other hand belong outside the Rosoideae. Morgan et al. (1994) noted that several lines of evidence, in addition to chromosome base numbers, were congruent with their result, such as the presence of nitrogen-fixing bacterial root nodules (Rodriguez-Barrueco 1969), distribution of chemical compounds (Hegnauer 1973; Challice 1974; Wallaart 1980), as well as the distribution of rust fungi. Later, Eriksson et al. (1998) confirmed that *Dryas*, which has a base chromosome number of nine, also belongs outside the group consisting of *Fallugia*, *Geum*, and *Waldsteinia*.

Here we present a phylogenetic study of *Geum* and related genera aiming to test the monophyly of *Geum* under the various circumscriptions. We also investigate whether the phylogenetic information from a maternally inherited chloroplast marker in combination with a biparentally inherited ribosomal DNA marker can confirm or reject earlier hypotheses of allopolyploid speciation. Further we aim to gain an understanding of the evolution of fruit types, to determine whether the Chinese species *Taihangia rupestris* is related to *Geum*, as has been suggested, and to create a phylogenetic taxonomy for the group, applying the principles of phylogenetic nomenclature (de Queiroz and Gauthier 1990).

MATERIALS AND METHODS

We have chosen to follow the classification of Bolle (1933) regarding names of species in this paper because his monograph is the most comprehensive taxonomic work available for this group.

TABLE 1. List of included taxa. Genera, subgenera, and species according to the classification of Bolle (1933) with information about chromosome number, geographical origin, voucher specimen and EMBL accession numbers (trnL-trnF above and ITS below). Bolle included the genera Fallugia and Sieversia in the tribe Dryadeae, while the rest of the genera were placed in Geeae. Species not treated by Bolle are presented in the lower part of the table.

Genus	Subgenus	Specific epithet/species	2n=	Origin	Voucher	EMBL accession
Fallugia Endl.		paradoxa (D. Don) Endl.	28 (Goldblatt 1988)	USA (Colorado)	T. Eriksson No. 796 (SBT)	AJ297331 AJ302345
Sieversia Willd.		pentapetala (L.) Greene	14 (Goldblatt and Johnson 1996)	Unknown	T. Eriksson No. 749 (SBT); cult. Göteborg Botanic Garden	AJ297345 AJ302359
		pusilla (Gaertn.) Hultén	14 (Ornduff 1969)	Kamtchatka	R. Malaise No. 155 (S)	AJ297346 AJ302360
Novosieversia F. Bolle		glacialis (Adams) F. Bolle	28 (Goldblatt 1984)	USA (Alaska)	C. Parker 115 (S)	AJ297342 AJ302356
Erythrocoma Greene		triflora (Pursh) Greene	42 (Goldblatt 1985)	Unknown	T. Eriksson No. 756 (SBT); cult. Göteborg Botanic Garden	AJ297330 AJ302344
Oncostylus (Schltdl.)	Neoncostylus F. Bolle	cockaynei F. Bolle	70 (Dawson 1995)	New Zealand	U. Swenson No. 518 (S)	AJ297343 AJ302357
		leiospermus Petrie	70 (Dawson 1995)	New Zealand	Chase; cult. Royal Botanic Gardens Kew, Acc. no. 1996–1076	AJ297344 AJ302358
Geum L.	Oregeum (Ser.) F. Bolle	andicola Reiche	Unknown	Chile	M. F. Gardner NO. 3449 (K)	AJ297332 AJ302346
		reptans L.	42 (Goldblatt and Johnson 1994)	Unknown	T. Eriksson No. 766 (SBT); cult. Göteborg Botanic Garden	AJ297337 AJ302351
		montanum L.	28 (Moore 1973), 42 (Goldblatt 1985)	Unknown	T. Eriksson 722 (SBT); cult. Bergius Botanic Garden	AJ297336 AJ302350
		bulgaricum Pancic	70 (Gajewski 1957)	Bulgaria	M. Kropf, private collection	AJ297333 AJ302347
	Orthostylus (Fisch. & Mey.) F. Bolle	speciosum Albov	70 (Gajewski 1957)	Caucasus	No voucher	AJ297340 AJ302354
		heterocarpum Boiss.	28 (Goldblatt and Johnson 1994)	Albania	A.H.G. Alston No. 1663 (S)	AJ297335 AJ302349
	Eugeum Focke	rivale L.	42 (Goldblatt and Johnson 1985)	Sweden	T. Eriksson No. 743 (S)	AJ297338 AJ302352
		geniculatum Michx.	Unknown	USA	No voucher	AJ297334 AJ302348
		urbanum L.	42 (Goldblatt 1984)	Sweden	J. Smedmark No. 3 (S0	AJ297323 AJ302337
	Stylipus (Raf.) Torr. & Gray	vernum (Raf.) Torr. & Gray	42 (Moore 1973)	USA (Miss.)	G.N. Jones No. 35322 (S)	AJ297341 AJ302355
Acomastylis Greene	Megacomastylis F. Bolle	calthifolia (Sm.) F. Bolle	42 (Goldblatt and Johnson 1996)	Japan	A. Anderberg & R. Lundin No. 32 (S)	AJ297324 AJ302338
		sikkimensis (Prain) F. Bolle	Unknown	Nepal	F. Miyamoto et al. No. 9430080 (A)	AJ297327 AJ302341
		elata (G. C. Wall.) F. Bolle	42 (Goldblatt and Johnson 1996)	Unknown	T. Eriksson No. 765 (SBT); cult. Göteborg Botanic Garden	AJ297325 AJ302339

TABLE 1. Continued.

Genus	Subgenus	Specific epithet/species	2n=	Origin	Voucher	EMBL accession
	Micracomastylis F. Bolle	rossii (R. Br.) Greene	56 (Goldblatt and Johnson 1990), 70 (Goldblatt 1984), 112 (Scoggan 1978)	Unknown	T. Eriksson No. 754 (SBT); cult. Göteborg Botanic Garden	AJ297326 AJ302340
Coluria R. Br.		elegans Cardot	14 (Ying et al. 1993)	China	Smith No. 3739 (S)	AJ297328 AJ302342
		geoides (Pall.) Ldb.	14 (Goldblatt 1985)	Unknown	J. Smedmark No. 2 (SBT); cult. Bergius Botanic Garden	AJ297329 AJ702343
Waldsteinia Willd.		geoides Willd.	14 (Goldblatt and Johnson 1996)	Unknown	J. Smedmark No. 4 (SBT); cult. Stockholm University	AJ297348 AJ302362
N/A		Filipendula vulgaris Moench.	14 (Goldblatt 1988)	Sweden	(Eriksson et al., in mss)	AJ297339 AJ302353
N/A		Geum schofieldii Calder & Taylor	112 (Calder and Taylor 1968b)	Canada	J.A. Calder & R. L. Taylor No. 36114 (S)	
N/A		Rosa persica J.F. Gmel.	14 (Goldblatt and Johnson 1991)	Unknown	(Eriksson et al., in mss)	U90803
N/A		Rubus chamaemorus L.	56 (Moore 1973)	Sweden; Sweden	(Eriksson et al., in mss); (Eriksson et al. 1998)	AJ297347 AJ302361
N/A		Taihangia rupestris Yü & Li	14 (Ying et al. 1993)	China	Yü & Li No. 1044 (PE)	
N/A		Sanguisorba officinalis L.	28, 56 (Moore 1973)	Sweden; Unknown	(Eriksson et al., in mss); (Helfgott et al. 2000)	AF183533 AF183556

Selection of Taxa. Twenty-six ingroup taxa, corresponding to 35% of the total number of species in the group, were chosen to represent the different genera and subgenera that have been described by earlier workers as well as possible, and to cover the morphological variation, mainly of fruit characters. Species suggested to have been involved in hybridizations resulting in speciation through allopolyploidy were also included in the study. The four outgroup species, *Filipendula vulgaris*, *Rosa persica*, *Rubus chamaemorus*, and *Sanguisorba officinalis*, were chosen from within the Rosoideae based on the ITS analysis of Eriksson et al. (1998). All species included in the study are listed in Table 1, with information on ploidy level, origin, voucher, and EMBL accession number.

Molecular Methods. Extractions were carried out using a slightly modified version of the CTAB extraction method described by Doyle and Doyle (1990). In some cases the extracted DNA was cleaned using GENECLEAN Spin Kit from Bio101, Inc. The plant material was either fresh or in most cases dried. PCR amplification was performed using a Techne Genius thermal cycler, and a kit from Boehringer Mannheim. The ITS region was amplified using the primers "ITS4" (White et al. 1990) and "ITSI" (Urbatsch et al. 2000), and the amplification program described by Eriksson et al. (1998). The *trnL* intron and *trnL-trnF* intergenic spacer were amplified using the primers "c" and "f" of Taberlet et al. (1991). Their amplification settings were also used.

Sequencing reactions were performed using ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction Kit. Both DNA regions were sequenced in both directions. For all species the *trnL-trnF* region was sequenced using four primers. New external primers were constructed, one starting five base pairs in the 3′ direction of "c" and the other seven base pairs in the 5′ direction of "f". Both of these were 20 base pairs long. The other two were the "d" and "e" primers of Taberlet et al. (1991). The ITS region was sequenced using the amplification primers. For some species, for which only old or poor herbarium material was available, two additional primers located in the 5.8S region were needed to get complete sequences of both strands, ITS2 (White et al. 1990) and ITS3B (Baum et al. 1994). The sequencing was performed by KISeq at the Center for genomics research, Karolinska Institute, Stockholm, Sweden, using Applied Biosystems 373A and 377 automated sequencers.

Alignment. Sequence editing and assembly used the Staden package (Staden 1996) under Linux. Sequences were aligned by eye using the sequence alignment editor Se-Al (Rambaut 1996). The *trnL-trnF* matrix included 1.3% aligned positions scored as missing data and the ITS matrix 0.8%. All aligned positions were included in the analyses. For the ITS region, the same analyses that were performed on the entire data set were also run on a reduced matrix, where a variable, ambiguously aligned region (positions 95–159) had been excluded. Fifteen indels in the ITS (positions 39, 40, 53, 66, 70, 76–77, 166, 174, 175–177, 231, 486–487, 633, 643, 646, 668), and 16 in the *trnL-trnF* data set (positions 155–164, 205–208, 255–262, 391–392, 396, 443–448, 730–732+734, 806–813, 824–827, 880–885, 952–957, 997, 1013–1021, 1064–1069, 1092, 1177–1186) were scored for absence (0) or presence (1) and added at the end of the matrix. These correspond to informative gaps of equal length in unambiguously aligned regions.

Phylogenetic Analyses. Parsimony analyses were conducted using PAUP* 4.0b8 (Swofford 1999). All characters were weighted equally and unordered. Indels were treated as missing data, except for a number of informative gaps, see above. Heuristic searches with MULTREES and TBR branch swapping were conducted on the ITS and combined data sets. Starting trees were constructed using 1000 replicates of random addition sequence. A branch-and-bound search was performed for the *trnL-trnF* region.

For the model-based Bayesian inference analyses (Lewis 2001; Huelsenbeck and Ronquist 2001), the data sets were pruned to contain only non-coding regions. Likelihood models were selected by the Akaike Information Criterion (AIC) in Modeltest Version 3.06 (Posada and Crandall 1998). For the *trnL-trnF* intron and intergenic spacer, the transversional (TVM) model was used, with gamma distribution (shape=1.0499) of substitution rate variation among sites. For ITS1 and ITS2, the general time-reversible (GTR) model was selected with gamma distribution (shape=0.6292). A combined Bayesian inference analysis of the non-coding regions was also performed. For this analysis we used the general time-reversible (GTR) model with gamma distribution (shape=0.4687). Bayesian inference analyses were performed using MrBayes 2.01 (Huelsenbeck and Ronquist 2001). A random starting tree was used and the Markov Chain Monte Carlo analyses were run for 500,000 generations, saving one tree every ten generations. The trees sampled after the likelihoods of the trees had converged on a stable value were used to construct a majority-rule consensus tree and to calculate the posterior probabilities of clades, see below.

To test whether the two data sets could be regarded as two samples of the same underlying data set, a partition-homogeneity test was carried out (ILD test, Farris et al. 1994). PAUP* was set up to perform 1000 replicates with heuristic search, each time constructing 10 starting trees using random addition sequence. These were rearranged with TBR branch swapping, not keeping more than 25 trees each time.

Support for individual nodes was assessed with bootstrap values (Felsenstein 1985), decay indices (Bremer 1988; Donoghue et al. 1992) and Bayesian inference. For the bootstrap analyses PAUP* was set to run 100,000 replicates with one random addition start tree and TBR branch swapping, saving a single tree each time. Decay values were obtained using AutoDecay 4.0 (Eriksson 1999). In the reverse constraint runs for the decay analyses PAUP* was set to run 100 replicates of random addition sequence with TBR branch swapping, saving a single tree in each replicate. MrBayes-values represent the fraction of the time that each clade occurs among the sampled trees (48,500 for *trnL-trnF,* 48,637 for ITS and 44,607 for the combined analysis), that is the probability of a clade existing (Huelsenbeck and Ronquist 2001).

All trees were rooted on the branch to *Filipendula vulgaris* based on previous analyses by Morgan et al. (1994) and Eriksson et al. (1998). Data sets and trees have been submitted to TreeBase (www.herbaria.harvard.edu/treebase/).

RESULTS

trnL-trnF *Region.* There were a total of 1252 aligned nucleotide positions of which 633 positions constituted the *trnL* intron and 529 the *trnL-trnF* intergenic spacer, and an additional 16 binary coded indels. Of these, a total of 156 characters were parsimony informative and 979 were constant. The *trnL* intron included 9.8% and the *trnL-trnF* intergenic spacer 17.6% informative characters. Twenty-six shortest trees with a length of 388 steps were found. One of these, selected at random, is shown in Fig. 2. The bootstrap 50% majority-rule consensus tree (Fig. 4, left) is well resolved and has good support, i.e. bootstrap values (B) >70%, decay values (D) of several steps and posterior clade probabilities (P) of 1.00, for many of the nodes. The strict consensus of the 26 most parsimonious trees is identical to the bootstrap consensus, except it includes one additional group, a clade consisting of *Novosieversia glacialis* and *Acomastylis calthifolia*.

The majority-rule consensus tree from the Bayesian inference analysis is congruent with the parsimony bootstrap consensus tree, but includes two additional clades. One consists of *Novosieversia glacialis* and *Acomastylis calthifolia* (P=0.99), and another of *Geum andicola* and *Geum schofieldii* (P=0.65). The posterior probabilities of nodes also supported by parsimony
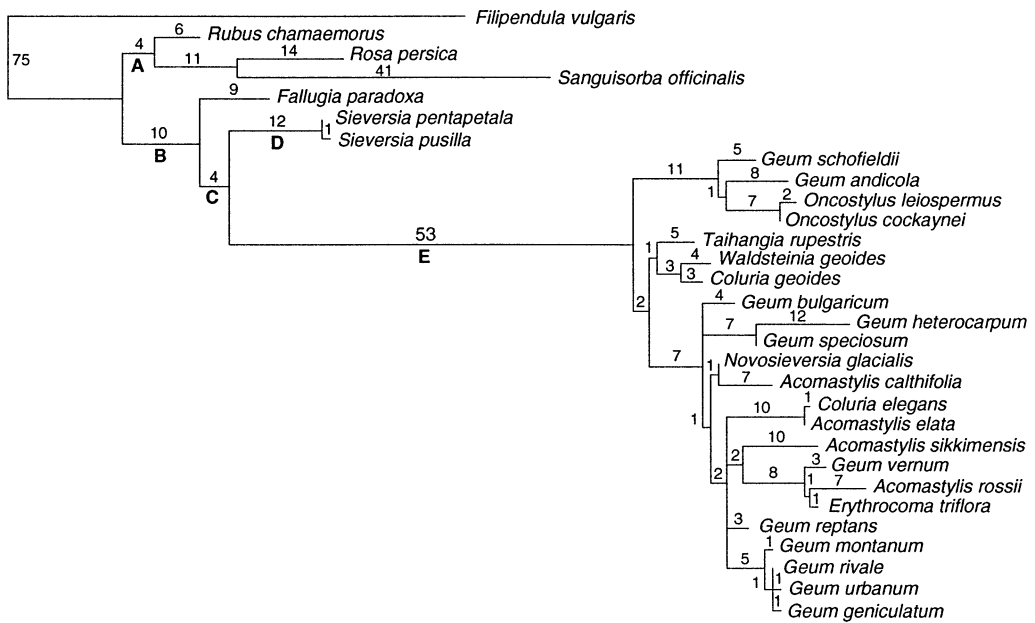
FIG. 2. Phylogram from the parsimony analysis of the *trnL-trnF* region. One of the 26 most parsimonious trees with a tree length of 388 steps. Branch lengths, using acctran optimisation in PAUP*, are marked above the branches. CI = 0.76 excluding uninformative characters and RI = 0.90. Nodes discussed in the text are indicated by capital letters.

are marked on the bootstrap consensus tree (Fig. 4, left).

ITS. Of the 678 aligned ITS region nucleotide positions and 15 coded indels, 194 characters were parsimony informative and 395 were constant. The search-

es found ten shortest trees of 632 steps in two different islands. Another island, two steps longer, consisting of 61 trees was also found. One of the most parsimonious trees, chosen at random, is shown in Fig. 3. The bootstrap majority-rule consensus tree (Fig. 4, right) is
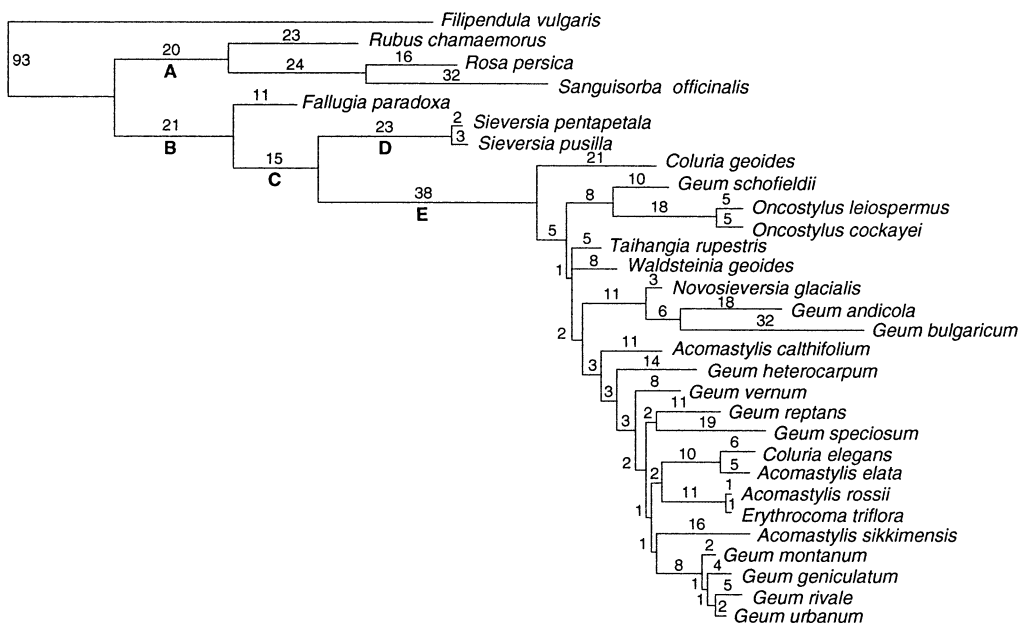

FIG. 3. Phylogram from the parsimony analysis of the ITS region. One of the ten shortest trees with a tree length of 632 steps. Branch lengths, using acctran optimisation in PAUP*, are marked above the branches. CI = 0.54 excluding uninformative characters and RI = 0.67. Nodes discussed in the text are indicated by capital letters.
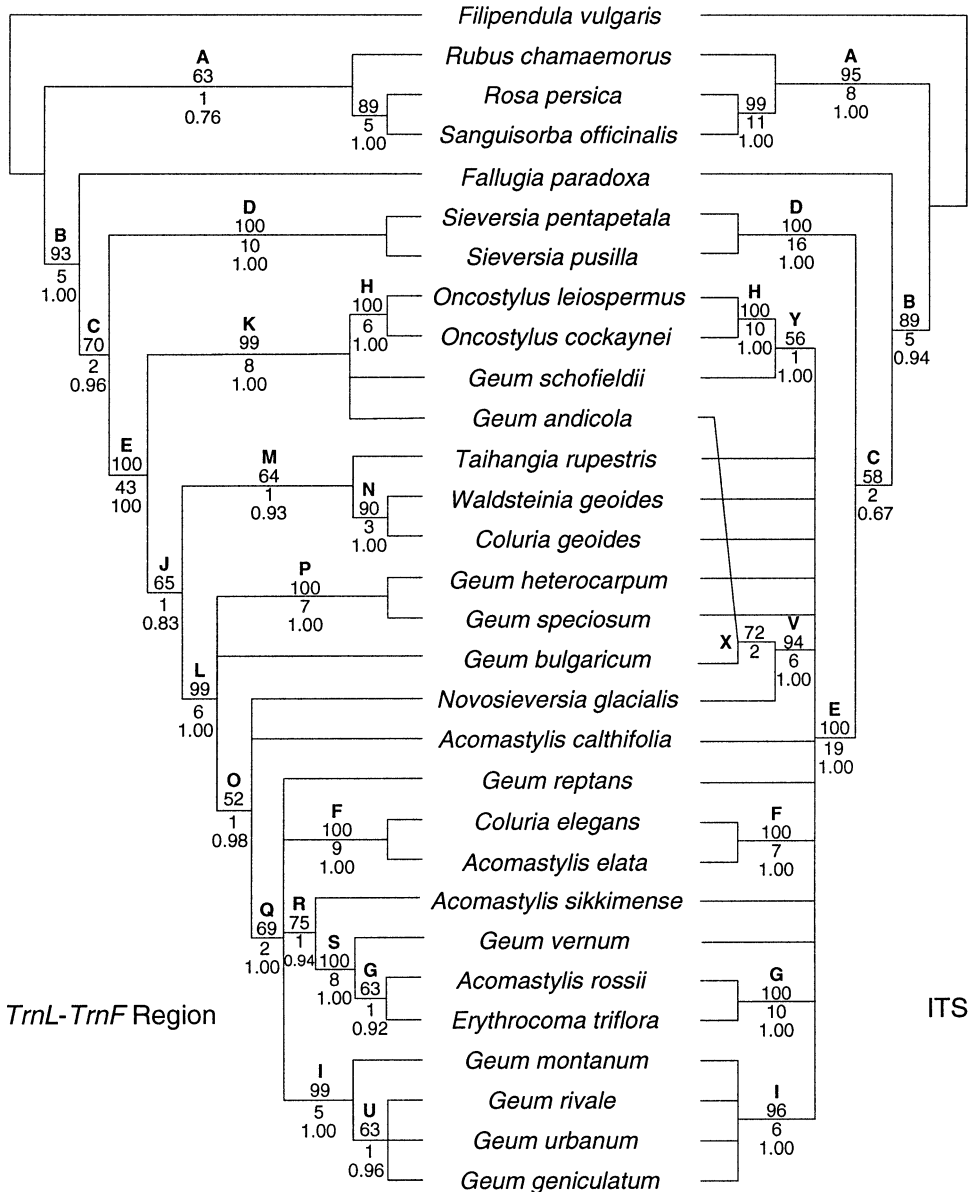
FIG. 4. Parsimony bootstrap 50% majority-rule consensus trees; *trnL-trnF* region to the left and ITS region to the right. Bootstrap values are marked above branches and decay indices and posterior clade probabilities below branches. Nodes discussed in the text are indicated by capital letters.

poorly resolved and many of the nodes are weakly supported. There are, however, a few well supported clades. When a highly variable region (positions 95–159) was excluded from the ITS data set, the analyses resulted in a similar topology containing the same well supported groups. A strict consensus of the ten shortest trees includes nine groups that are not present in the bootstrap consensus. Only one of these is present in the *trnL-trnF* bootstrap consensus (Fig. 4, right, node U).

The majority-rule consensus tree from the Bayesian inference analysis includes one node that is incongruent with the topology supported by parsimony. Within clade V (Fig. 4, right), *G. andicola* is the sister of *N. glacialis* (P=0.52), instead of being the sister of *G. bulgaricum* (B=72). Bayesian inference also supports four nodes that are congruent with, but not present in, the parsimony bootstrap consensus tree.

Comparison Between ITS and trnL-trnF Trees. The ITS and *trnL-trnF* data sets both support the same topology in the lower part of the trees (Figs. 2–4, nodes A–E). For these nodes the support values increase when
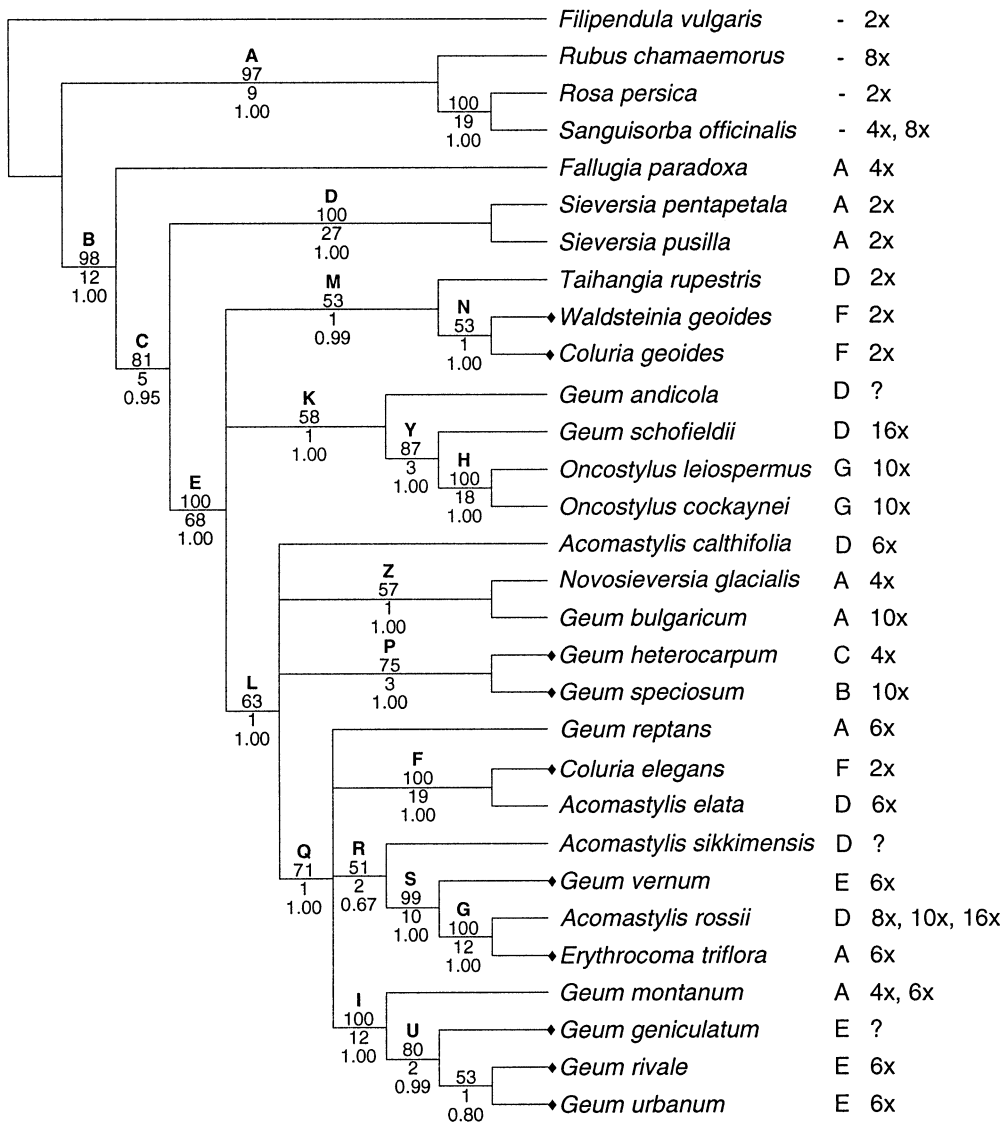
FIG. 5.   Parsimony bootstrap 50% majority-rule consensus of the ITS and *trnL-trnF* data sets combined. Bootstrap values are marked above branches and decay indices and posterior clade probabilities below branches. Nodes discussed in the text are indicated by capital letters. Fruit type is stated to the right of the species name with capital letters referring to illustrations in Fig. 1. Note that the illustrations represent single species and that there is variation within each fruit type ''class''. A=Plumose style. B=Straight style, jointed below middle. C=Harpoon fruit type. D=Entirely persistent style, not elongating. E=Fishhook fruit type. F=Style jointed at base. G=Style hooked at apex. The second column shows ploidy levels. Species with jointed styles are indicated by diamonds (♦).

the data are combined (Fig. 5), which suggests that there is no strong conflict in the data concerning this part of the phylogeny. The same is true for four well supported clades (F, G, H, I) within clade E. The most parsimonious trees (Figs. 2, 3) have relatively long branches in the lower parts of the trees, especially the branch leading to the clade consisting of the herbaceous perennials (node E). Within this group, however, many of the branches are relatively short.

There is only one aspect of the ITS bootstrap con-

sensus tree where it clearly, and with high support values, is incongruent with the *trnL-trnF* phylogeny. The clade formed by *Novosieversia glacialis, Geum andicola,* and *G. bulgaricum* (Fig. 4, right, node V, B94/D6/P1.00) does not exist in the *trnL-trnF* bootstrap consensus. *Geum andicola* is instead found in a well supported clade (Fig. 4, left, node K, B99/D8/P1.00) outside the strongly supported clade containing *G. bulgaricum* and *N. glacialis* (node L, B99/D8/P1.00).

Combined Analysis. The partition homogeneity

test yielded a p-value of 0.001, which rejects the null hypothesis of homogeneity between the data sets. Several authors suggest that rejection of homogeneity by the partition homogeneity test does not preclude data set combination (see Yoder et al. 2001 and references therein). We combined the two data sets to investigate how a combined analysis compares to the topologies of two separate data sets, and where they agree and disagree. In particular, clades that get lower support in the combined analysis might indicate data conflict.

The parsimony analysis resulted in 11 shortest trees with a length of 1048 steps, which is 28 steps longer than the sum of the shortest trees from the separate analyses—an indication that there is conflict between the two data sets. The shortest trees had a consistency index of 0.57 excluding uninformative characters and 0.69 including them and a retention index of 0.77. The topology of the bootstrap majority-rule consensus tree (Fig. 5) is similar to that of the *trnL-trnF* tree (Fg. 4, left), but has higher support values for many of the nodes, and a larger proportion of well supported nodes. The Bayesian inference analysis of the combined data set resulted in a majority-rule consensus tree which is congruent with the parsimony bootstrap tree, but includes two additional nodes.

DISCUSSION

The monophyly of the ingroup, consisting of *Fallugia*, *Sieversia* in a strict sense, and large clade of herbaceous perennials, is well supported in all three analyses. This result agrees with those of earlier studies (Morgan et al. 1994; Eriksson et al. 1998), which have shown that *Fallugia*, *Waldsteinia*, and *Geum* constitute a well supported monophyletic group.

Regarding the position of *Rubus* L., it is notable that both the *trnL-trnF* and the ITS analyses place it as the sister of *Rosa* L. and *Sanguisorba* L. (Figs. 2–5, node A). This relationship has been suggested before, based on *rbcL* (Morgan et al. 1994), but a study of Rosoideae phylogeny based on ITS (Eriksson et al. 1998) indicated that *Rubus* is the sister group of *Geum*, *Waldsteinia*, and *Fallugia*. Here there is greater support for the node joining *Rubus* with *Rosa* and *Sanguisorba* (Fig. 4, node A) with nrITS data than with chloroplast data.

The white flowered shrub *Fallugia paradoxa*, which occurs in south-western North America, is sister to the rest of the ingroup (Figs. 4, 5, nodes B and C). The two species of *Sieversia* s. str., which also are woody and white flowered, form a strongly supported monophyletic group (node D), diverging early in the history of the group.

The herbaceous perennials, Geeae sensu Juel (1918), form a clade that has a very long branch in the shortest trees from both the ITS and the *trnL-trnF* analyses (Figs. 2, 3, node E). This group gets very high support in all three analyses (Figs. 4, 5, node E). Although we have not yet studied thoroughly the morphology of these species, there seem to be several clades within this group of herbaceous perennials that are unexpected from a morphological point of view. For example, there are several well supported clades containing both species with lyrate leaves and species with equally pinnate basal leaves (Fig. 5, nodes K, R, Y, Z), as well as clades including species with plumose styles and those with shorter, jointed styles (Fig. 5, nodes I, M, S). When the character ''jointed, partly or entirely deciduous style'', is mapped onto the consensus tree from the combined analysis (Fig. 5), it appears either to have evolved at least five times independently or there have been several reversals to plumose and other types of non-jointed styles.

Geum in a wide sense, sensu Scheutz (1870) or Gajewski (1957), appears to be paraphyletic, including *Waldsteinia*, *Coluria* and *Taihangia* (Figs. 2–5, node C). In the *trnL-trnF* and combined analyses *Taihangia rupestris* has a rather weakly supported sister group relation (Figs. 4, left & 5, node M) with a clade containing *Waldsteinia geoides* and *Coluria geoides* (node N), while ITS (Fig. 4, right) does not resolve their position. The inclusion of *Waldsteinia* and *Coluria* in *Geum* has never been suggested, although they have almost always been considered to be closely related. It should be noted however, that the node (J) that makes the clade consisting of *Waldsteinia*, *Coluria*, and *Taihangia* an ingroup in the group of herbaceous perennials (node E) in the *trnL-trnF* tree (Fig. 4, left) does not have strong support (B65/D1/P0.83), and it gets less than 50% bootstrap in the combined analysis (Fig. 5). When a branch and bound analysis is performed on the *trnL-trnF* data with a constraint forcing these three species to form a sister group to the rest of the herbaceous perennials, the resulting trees are two steps longer than those of the unconstrained analyses.

Sieversia in the strict sense of Willdenow (1811) is monophyletic (Figs. 2–5, node D) and constitutes the sister group to the rest of *Geum* s.l. in all three analyses. *Sieversia* in a wide sense, on the other hand, comprising all the species with plumose styles (Rydberg 1913; Huber 1961), is not monophyletic according to any of the three analyses (Figs. 2–5, node C). This result is hardly surprising, since *Sieversia* s.l. is based on the presence of a persistent, plumose style, which is probably a plesiomorphy in the group as a whole, occurring also in *Fallugia*.

Geum in the sense of Bolle (1933) is polyphyletic according to these analyses, as is *Acomastylis*. The only one of Bolle's segregate genera which is monophyletic in our analyses is the southern hemisphere *Oncostylus* (node H). It appears to be a morphologically distinct group. The styles persist on the fruits and have characteristically hooked stigmas (Fig. 1G), often resembling the ''fish-hook fruit'' (Iltis 1913) of *G. urbanum*

once the distal part has fallen off. The two species included in this study are from New Zealand. The majority of the *Oncostylus* species occur in Australasia but there are also two species that are restricted to southern South America. *Geum andicola*, which appears in the same clade in the *trnL-trnF* and combined analyses (Figs. 4, left & 5, node K), is from Chile. This result may be an indication that *Oncostylus* originated within a South American clade. The biogeographical pattern is somewhat disturbed by *G. schofieldii*, an endemic of the Queen Charlotte Islands, off the western coast of Canada, which also is a part of this group (node K). Calder and Taylor (1968a) classified it in the subgenus *Acomastylis*, but that is contradicted by our results. It has also been suggested to be an allopolyploid between *A. calthifolium* and *A. rossii* (Hultén 1968; Scoggan 1978), which is not supported by our data either, because *G. schofieldii* forms a clade with the two *Oncostylus* species (Figs. 4, 5, nodes K, Y).

Not even in the stricter sense, employed by Rydberg (1913), where *Geum* comprises only the species with fish-hook fruits, is it monophyletic according to our results. The problematical species is *G. vernum*, which does not form a group with the other three species in this study possessing this type of fruit. This result is particularly well supported in the *trnL-trnF* analysis (Fig. 4, left). Here, the clade consisting of the fish-hook fruited *G. urbanum*, *G. rivale*, *G. geniculatum* (node U) are the sister of *G. montanum*, which has a plumose style (node I, B99/D5/P1.00), while *Geum vernum* on the other hand, is the sister of *A. rossii* and *E. triflora* (node S, B100/D8/P1.00). ITS resolves the first of these two clades (I) and the clade with only *A. rossii* and *E. triflora* (Fig. 4, right, node G), while the position of *G. vernum* is unresolved.

Geum vernum has been suggested to belong to its own genus *Stylipus* (Rafinesque 1833) because it lacks an epicalyx and has exceptionally small petals. Several authors have classified *Stylipus* as a subgenus in *Geum* (Bolle 1933; Gajewski 1957; Robertson 1974). From the artificial crossing experiments by Gajewski (1957) it appears as if there is some chromosomal difference between *G. vernum* and the species of subgenus *Geum*, represented in this study by *G. urbanum*, *G. rivale* and *G. geniculatum*. Gajewski (1957, 1958) easily produced hybrids between different species of subgenus *Geum*. When crossing two species the offspring generally showed full conjugation of the chromosomes during meiosis. On the other hand, when crossing one of these species with *G. vernum* only a few bivalents were formed during meiosis in the offspring. The only species included in Gajewski's (1957, 1958) crossing experiments that forms a group with *G. vernum* according to our results, is *E. triflora* (Fig. 4, left & 5, node S). Gajewski (1957, 1958) concluded that each of these two species has two 7-chromosome genomes in common with the subgenus *Geum* species, but only one with *G. montanum*. Unfortunately he either did not cross these two species with each other or tried and failed.

The other three species with the fish-hook fruit type included in this study make up a clade with *G. montanum* in all three bootstrap trees (Figs. 4, 5, node I). All four species have the typical lyrate *Geum* leaves, but *G. montanum* differs in having plumose styles. Gajewski (1957, 1958) easily obtained hybrids between the tetraploid *G. montanum* and most of the species of subgenus *Geum* that he tried to cross. His cytogenetic studies showed that 14 bivalents and seven univalents were formed during meiosis in the hybrids. He concluded that the two 7-chromosome genomes of *G. montanum* were homologous with subgenus *Geum* chromosomes.

Iltis (1913) noted that the epidermal cells of the rostrum, the basal part of the style which remains on the fruit, are different from the cells in the epidermis of the deciduous stigmatic part in subgenus *Geum*. In the rostrum there are few stomata and no chlorophyll, while these are abundant in the stigmatic part. He also noted that the structure of the rostrum is very similar to the plumose style of *G. montanum*. The deciduous stigmatic part on the other hand resembles the styles of *Waldsteinia* and *Coluria*, which are shed at the base, where stomata are numerous and chlorophyll abundant. As mentioned above, Gajewski (1957, 1958) assumed that subgenus *Geum* had been formed through allopolyploidy between ancestors of *G. montanum* and *Waldsteinia* or *Coluria*. He thought that the fish-hook fruit type was formed as a result of this hybridization. Our results do not support this hypothesis (see below).

Coluria appears to be polyphyletic. There is strong support in both the *trnL-trnF* (Fig. 4, left, node F, B100/D9/P1.00) and ITS (Fig. 4, right, node F, B100/D7/P1.00) analyses for the Chinese *C. elegans* being the sister to the Himalayan species *Acomastylis elata*, which it resembles morphologically. On the other hand, *C. geoides*, which is the type species of *Coluria*, forms a clade with *Waldsteinia geoides* according to *trnL-trnF* (Fig. 4, left, node N, B90/D3/P1.00). This relationship is not contradicted by ITS (Fig. 4, right), but there appears to be some conflicting signal in the data since the parsimony support values for this node decrease when ITS data are added to the analysis (Fig. 5, node N, B53/D1).

Geum heterocarpum and *G. speciosum* form a well supported group according to the *trnL-trnF* analysis (Fig. 4, left, node P, B100/D9/P1.00). ITS data do not resolve the positions of these two species (Fig. 4, right), but there seems to be phylogenetic signal conflicting with the *trnL-trnF* data, since the parsimony support values for this clade decrease when the two data sets are combined (Fig. 5, node P, B75/D3). These two spe-

cies comprise subgenus *Orthostylus* sensu Bolle. They are both characterized by lyrate leaves with a large terminal segment, a tubular hypanthium, a gynophore with at least one of the fruits inserted at its base, and articulate styles with a straight basal segment. Gajewski (1957) found that the tetraploid *G. heterocarpum* has one partly homologous genome with subgenus *Geum*.

Based on ITS data, *G. andicola* from Chile forms a well supported group with *Novosieversia glacialis* of Arctic Siberia and Alaska and *G. bulgaricum* of the Balkans (Fig. 4, right, node V, B94/D6/P1.00). This position is contradicted by *trnL-trnF*, which instead joins *G. andicola* with *G. schofieldii* and the two *Oncostylus* species with good support (Fig. 4, left, node K, B99/D8/P1.00, cf. also above). In the combined consensus tree, *N. glacialis* and *G. bulgaricum* still form a group (Fig. 5, node Z, B57/D1/P1.00), while *G. andicola* is in the position as in the *trnL-trnF* tree (node K, B58/D1/P1.00). A bootstrap analysis of the combined data set omitting *G. andicola* yields higher support for clade Z consisting of *N. glacialis* and *G. bulgaricum* (an increase from B57 to B89) and clade Y consisting of *G. schofieldii* and the two *Oncostylus* species (from B87 to B99). Apparently there is strong conflict regarding the position of *G. andicola* in the two separate data sets. However, *G. andicola* is not the only source of discordance between the two data sets. A partition homogeneity test omitting *G. andicola* yields a higher p-value, 0.002 compared to 0.001, but the null hypothesis of homogeneity between the data sets is still rejected.

There are some morphological characters supporting the relationship between *N. glacialis* and *G. bulgaricum*. Both species lack a nectar disk and both have hypanthia that are shortly pubescent on the inside. *Geum andicola* on the other hand has a disk and the whole plant is glabrous. The general morphology of *G. andicola* resembles *G. schofieldii* but it shares a 19 base pair insertion in ITS1 with *G. bulgaricum* and *N. glacialis*.

Ancient Allopolyploidy.   Most current methods of phylogeny reconstruction presuppose divergent evolution and are unable to resolve the reticulate patterns of hybridization. In several studies, the different modes of inheritance of cpDNA compared to nrDNA have been used to gain understanding about reticulate events in phylogenies (see e.g. Soltis et al. 1992). In a tree based on chloroplast data, a hybrid is expected to be the sister of its cytoplasmic donor. Ribosomal DNA usually undergoes concerted evolution, homogenization of repeats via unequal crossing over and gene conversion. Divergent parental ITS repeats in an allopolyploid generally are homogenized over a number of generations, resulting in a new lineage with ITS repeats identical to those of either of the parent species (Wendel et al. 1995). This means that in some cases,

when the nrDNA repeats of the pollen parent have been homogenized, a reticulation in the phylogeny of a group will be evident as contradicting positions of a species in cpDNA and rDNA trees respectively. Sometimes concerted evolution is not complete or does not occur. Polymorphic and/or chimeric ITS repeats have been found in hybrids or species of hybrid origin (Campbell et al. 1997; Alice et al. 2001). This may be due to recent derivation or may have persisted in a lineage through vegetative propagation, polyploidy or agamospermy. A case where concerted evolution has not occurred in allopolyploid species approximately one million years of age, is known (Sang et al. 1995).

A possible explanation for the contradicting positions of *Geum andicola* in the separate phylogenies of the two genes (Fig. 4) is that this species is of hybrid origin. In that case an ancestor of *G. bulgaricum* may have been the pollen parent and an ancestor of *G. schofieldii* and *Oncostylus* may have been the ovulate parent.

Although our results give no clear support for Gajewski's (1957, 1958) hypotheses about allopolyploidy within *Geum*, it is still possible that the fish-hook fruited species of subgenus *Geum* are of allopolyploid origin. A hybridization between *G. montanum* and *Waldsteinia* may have occurred, where *G. montanum* was the ovulate parent. If the ribosomal DNA of the hybrid was subsequently homogenised through concerted evolution in the direction of the maternal genome, the information about the other parent would be lost and gene trees like the ones presented here would be the result.

Classification.   The *trnL-trnF* region provided good information about the relationships within the group, but some of the relationships cannot be corroborated either by ITS data or by morphology. Other types of data supporting the results presented here would therefore be desirable before giving these results any far reaching consequences for the naming of clades. In particular it seems premature at this point to decide which node should be assigned the name *Geum*. One possibility would be to include the entire clade of herbaceous perennials (Figs. 4, 5, node E), thus making *Waldsteinia*, *Coluria*, and *Taihangia* part of *Geum*. Another alternative would be to restrict the name to comprise only subgenus *Geum* sensu Gajewski, in which case the genus would include all the species with the fish-hook fruit type (Figs. 4, 5, node U) except *G. vernum*. Additional data may show that *Taihangia*, *Waldsteinia*, and part of *Coluria* are in fact the sister group of the rest of the herbaceous perennials, which would make *Geum* and its segregate genera a monophyletic group. If this was the case, that clade might perhaps best be chosen for the name *Geum*.

A group that currently lacks a name is the entire ingroup of this study, the remains of the former Dry-

adeae, which has unambiguous support in our analyses (Figs. 4, 5, node B) as well as in previous ones (Morgan et al. 1994; Eriksson et al. 1998). The legitimate name at the tribal level according to the rules of the International Code of Botanical Nomenclature (Greuter 2000) is Colurieae. It was described by Rydberg (1913) and at that point only included the two genera *Coluria* and *Waldsteinia*. We here propose to enlarge the tribe Colurieae to also include *Fallugia*, *Sieversia*, *Taihangia*, *Geum*, and its segregates. Colurieae Rydberg has priority over Geeae Juel (1918). To give a phylogenetic definition (de Queiroz and Gauthier 1990) of this clade (node B), we choose a stem based definition. This helps to accommodate for the possible discovery of species that have diverged on the branch leading to this clade.

Phylogenetic definition: Colurieae is the clade consisting of *Fallugia paradoxa* and all organisms that share a more recent common ancestor with *Fallugia paradoxa* than with *Rubus caesius* L., *Filipendula vulgaris* or *Rosa centifolia* L. These specifiers are the type species of the respective genera (Farr et al. 1979). The fact that the phylogenetic position of *Rubus* is not yet certain will not make any difference for the attachment of this name to this clade. *Rubus* is either the sister of Colurieae or the sister of a clade containing *Rosa*, Sanguisorbeae, and Potentilleae.

We also propose a phylogenetic definition of the well supported group of herbaceous perennials (Figs. 4, 5, node E): Geinae is the clade consisting of *Geum urbanum* and all organisms that share a more recent common ancestor with *Geum urbanum* than with *Sieversia pentapetala*, *S. pusilla* or *Fallugia paradoxa*. Geinae was described and ranked as a subtribe (Schulze-Menz 1964) consisting of *Geum*, including *Sieversia* and other segregates, *Waldsteinia*, and *Coluria*. The use of this name under the International Code of Botanical Nomenclature at the rank of a subtribe might make the placement of the rest of the tribe as well in subtribes desirable. One of these would include the single species *Fallugia paradoxa* and the other the two species of *Sieversia* s.str. However, describing these two additional subtribes does not add any information about phylogenetic relationships as one would be identical to *Fallugia* and the other to *Sieversia*, and therefore we refrain from adding these subtribes.

In summary, Colurieae receives good support from ITS and *trnL-trnF* data, analyzed separately as well as in combination. It includes *Fallugia*, a monophyletic *Sieversia* s. str. and Geinae, a large and very well supported clade of herbaceous perennials. The relationships within this last group are not unambiguously resolved. However, it is clear that none of the previously suggested circumscriptions of *Geum* are monophyletic according to our data. Neither are *Acomastylis*, *Coluria* or *Sieversia* s. l. While *Waldsteinia*, *Coluria*, and

Taihangia are nested within a group of species that previously have been included in *Geum*, the data give poor resolution regarding these relationships. The interpretation of the evolution of fruit characters is complex based on the phylogenies presented in this study. Either the jointed style evolved five times independently or there have been several reversals to plumose and other types of non-jointed styles. The results do not unequivocally indicate whether allopolyploid speciation has taken place in the evolutionary history of Colurieae. However, the fact that *G. andicola* appears in two different well supported groups in the cpDNA tree and in the ITS tree may be an indication of reticulate evolution. Gajewski's hypothesis (1957, 1958) that the group of fish-hook fruited species that he calls subgenus *Geum* have been formed through allopolyploidy can not be confirmed, nor can it be rejected.

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