A new invasive hawkweed, *Hieracium glomeratum* (Lactuceae, Asteraceae), in the Pacific Northwest

Linda M. Wilson, Judith Fehrer, Siegfried Bräutigam, and Gitta Grosskopf

Abstract: During the summer of 2001, a newly recorded species of exotic hawkweed (*Hieracium glomeratum* Froel.) for North America was identified from specimens collected in southeastern British Columbia, Canada, and eastern Washington state, United States. The specimens had previously been identified as the closely related *Hieracium caespitosum* Dumort. DNA fingerprints of plants from different localities proved to be identical. Their clonality, along with a spot-like distribution, indicates that this apomictic species probably originated from a single introduction from Europe, which subsequently spread. This species adds to the complex of 14 other exotic *Hieracium* species belonging to the Eurasian subgenus *Pilosella* that are adventive in the United States and Canada. A distribution map of the native and adventive range of *H. glomeratum*, and a key to distinguish it from related species in subgenus *Pilosella* that occur in North America are provided. The evolutionary and invasive potential of *H. glomeratum* is also discussed.

Key words: Hieracium, *Pilosella*, hawkweed, invasive plants, neophytes, DNA fingerprinting.

Résumé : Pendant l'été 2001, une nouvelle espèce d'épervière exotique (*Hieracium glomeratum* Froel.) d'origine européenne a été identifiée en Amérique du Nord à partir de deux échantillons récoltés dans le Sud-Est de la Colombie-Britannique, Canada, et dans la partie orientale de l'état de Washington, États-Unis. Les plantes ont d'abord été identifiées comme *Hieracium caespitosum* Dumort., une espèce très proche de *H. glomeratum*. Les empreintes génétiques des spécimens récoltés sur les deux sites sont identiques. La clonalité et la distribution restreinte de cette espèce apomictique indiquent qu'elle a été probablement introduite une seule fois d'Europe et s'est répandue rapidement. Cette espèce s'ajoute à un complexe de 14 autres *Hieracium* exotiques appartenant au sous-genus *Pilosella* et qui sont naturalisées au Canada et aux États-Unis. Dans cette publication est présentée la distribution de *H. glomeratum* dans son lieu d'origine (Europe) natale et en Amérique du Nord. Une clef pour distinguer *H. glomeratum* des autres épervières du sous-genus *Pilosella* naturalisées en Amérique du Nord est fournie. Les potentiels invasifs et évolutifs de *H. glomeratum* sont discutés.

Mots clés : Hieracium, *Pilosella*, épervière, plantes adventices, neophytes, empreintes génétiques.

[Traduit par la Rédaction]

Introduction

Hawkweeds (*Hieracium* L. spp.) are herbaceous perennial herbs belonging to tribe Lactuceae (Asteraceae), with all ligulate flowers and a milky latex in stems and leaves. The distribution of the genus is Holarctic (with a centre of diversity in Europe), but extending to the mountainous regions of Central and South America (Bräutigam 1992). The genus is divided into three subgenera, that is, *Pilosella* (Hill) S. F. Gray, *Hieracium*, and *Chionoracium* Dumort. (syn. *Stenotheca* (Monn.) Torr. et Gray). A fourth described subgenus, *Mandonia* (Schultz-Bip.) Arv.-Touv., restricted to the Andes Mountains of South America, is a synonym of subgenus *Chionoracium* (Sleumer 1956). Within North America, native *Hieracium* species are classified into two subgenera, *Chionoracium* and *Hieracium*. Subgenus *Hieracium* is Holarctic and includes both New and Old World polyploid taxa that reproduce asexually by apomixis of the diplosporous type, that is, the embryo is formed from the unreduced megaspore mother cell (Guppy 1978; Chinnappa and Chmielewski 1987; and see Chrtek et al. 2004 and references therein). Subgenus *Chionoracium* is an entirely New World subgenus comprising sexual, diploid taxa (Guppy 1978; Beaman 1990). The approximately 25 North American native species are diverse and distributed across Canada and the United States. In contrast, subgenus *Pilosella* is wholly Palearctic, and is characterized by a mixture of sexual and facultatively apomictic taxa (apomixis of the aposporous type, that is, the embryo is formed from a somatic nucellar cell instead of the megaspore mother cell; for reviews see Koltunow et al. 1995; Krahulcová et al. 2000). Facultatively apomictic plants typically produce viable pollen and can therefore regularly take part in hybridization and backcrossing (Gadella 1991). Additionally, most

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taxa within subgenus *Pilosella* are allopolyploids (Gadella 1991) and stoloniferous (Schuhwerk and Lippert 1997).

Hawkweeds are distinguishable from each other largely using a few key morphological characters, including the type and amount of leaf, stem, and phyllary pubescence. Within subgenus *Pilosella*, a high degree of morphological variation results from facultative apomixis, occasional outcrossing, and polyploidy, with a correspondingly heavily reticulate taxonomic structure. This makes species delineation difficult and has lead to the description of hundreds of species, subspecies, and types worldwide (Fernald 1950).

Approximately 21 *Hieracium* species of Eurasian origin belonging to two subgenera have been introduced into Canada and the United States (Table 1). Six species belong to subgenus *Hieracium*, and 15 species to subgenus *Pilosella*, seven of which occur in the Pacific Northwest (Table 1): *Hieracium aurantiacum* L., *Hieracium bauhini* Schult., *Hieracium caespitosum* Dumort., *Hieracium flagellare* Willd., *Hieracium floribundum* Wimm. & Grab., *Hieracium pilosella* L., and *Hieracium piloselloides* Vill. In their native Eurasia, species in subgenus *Pilosella* are generally weak competitors, growing on poor soils, and preferring open, disturbed habitats. Elsewhere, they have proven to be highly invasive, not only in North America (Voss and Böhlke 1978; Wilson et al. 1997), but also in New Zealand (Hunter 1991; Jenkins 1992 and references therein), Australia (Burton and Dellow 2005), and Chile (Domínguez 2004).

In August 2001, S. Bräutigam examined herbarium specimens and live plants in culture (provided by G. Grosskopf) from eastern Washington and southeastern British Columbia as *H. glomeratum* Froel. (Fig. 1). The specimens had been erroneously identified as the closely related *H. caespitosum*. *H. glomeratum* also belongs to subgenus *Pilosella*. It is regarded as a fixed hybrid between *H. caespitosum* and *Hieracium cymosum* L., combining morphological characters of both species (Nägeli and Peter 1885; Fehrer et al. 2005). According to the Central European taxonomic concept for *Hieracium* represented by Zahn (1921–1923) and followed here, the parental species are "basic species", that is, they possess unique morphological characters. The majority of species in subgenus *Pilosella*, including *H. glomeratum*, are categorized as "intermediate species". Most of these are exclusively polyploid and they show a combination of morphological characters of two or more "basic species". They are considered to be of hybrid origin and can consist of recent hybrids, young "hybridogenous" taxa, or old (several hundred years), fixed taxa that are widespread and form stable populations (Krahulec et al. 2004).

Like most *Pilosella* species, *H. glomeratum* is polymorphic. This species in its entire morphological complexity is marked by the following characters:

Stolons either above ground, below ground, or absent. Soboles (stems arising from roots) sometimes present. Rosette-leaves mostly 3–8, 1–18 cm long, oblong-spatulate to lanceolate, obtuse to acute, entire or subdenticulate, yellow-, grass- or grayish-green, sometimes subglaucous, on both surfaces with ± numerous 0.5–1(–1.5) mm long simple hairs and stellate hairs, sometimes with few glandular hairs. Stems 30–70 cm, occasionally with lateral stems at the base; simple hairs at the base numerous, otherwise few to moderate; stellate hairs and glandular hairs ± numerous, especially in the upper part. Cauline leaves 1–4, colour and indumentum like the rosette-leaves, glandular hairs usually present. Synflorescence corymbose, often umbellate above, dense to lax, usually with 10–25 capitula. Peduncles usually with few to moderate simple hairs, and moderate to numerous glandular hairs. Involucres 7–8(–9) mm long, their bracts black or dark-green, partly with pale margins; simple hairs absent to numerous; stellate and glandular hairs moderate to numerous. Ligules yellow. Styles yellow. The native range of *H. glomeratum* is the temperate and boreal zone of North, Central, and East Europe and temperate West Siberia (Fig. 2).

The discovery of *H. glomeratum* in the Pacific Northwest prompted us to examine further its current distribution and to conduct preliminary genetic screening using DNA fingerprinting to assess the clonal structure of *H. glomeratum* and to address the question of single versus multiple introductions of this new, potentially invasive species. Following molecular analysis and morphological comparisons, a diagnostic key was developed to distinguish *H. glomeratum* from other adventive species in *Hieracium* subgenus *Pilosella* that occur in the Pacific Northwest.

Materials and methods

Distribution survey

Surveys of the literature and of 21 herbaria across Canada and the United States were conducted during 2002 and 2003 to determine if *H. glomeratum* had been previously reported in North America. During the summers of 2002 and 2004, field surveys to map the distribution of *H. glomeratum* in the Pacific Northwest were conducted in coastal, southern and northern interior of British Columbia, southwestern Alberta, northwestern Montana, northern and southern Idaho, and coastal, central and northeastern Washington. A total of 58 sites were examined. Several specimens from each site were collected for further examination and voucher specimens were deposited in the herbarium at the Lambert C. Erickson Weed Diagnostic Laboratory at the University of Idaho, Moscow, Idaho.

Molecular analysis

To conduct a preliminary analysis of the clonal structure of the newly detected *H. glomeratum* and to address the question of single versus multiple introductions, samples from two populations in Washington and British Columbia (about 80 km apart) were subjected to DNA fingerprinting and compared with European representatives of the taxon. While additional clones from North America would be useful, examining two populations provides sufficient information to derive initial inferences as to the clonal structure of the species. In addition, the clonal structure of the closely related and supposedly parental species, *H. caespitosum*, collected from Santa, Idaho, and from several Central European populations, was compared with *H. glomeratum*.

Southern hybridization with mini- and micro-satellite probes was used to make inferences about clonality. Minisatellite sequences were used because they usually give individual-specific patterns (Bruford and Saccheri 1998). Human minisatellites have been used to distinguish between

Table 1. List of non-native *Hieracium* species in North America and their distribution.

Species names	Distribution
Subgenus *Pilosella*	
H. arvicola Nägeli et Peter	NB*
H. aurantiacum L.	AB, BC, MB, NB, NL, NS, ON, PE, QC, SK; AK, AR, CA, CO, CT, FL, ID, IL, IN, IO, MA, MD, ME, MI, MN, MT, NC, NH, NJ, NY, OH, OR, PA, RI, SD, VA, VT, WA, WV, WI, WY
H. bauhini Schult. [*H. praealtum* auct. p.p.*]	BC; CT, ID, MA, MN, NH, NY, VT, WA
H. brachiatum Bertol. ex DC.	QC; NY
H. caespitosum Dumort. [syn. *H. pratense* Tausch]	AB, BC, NB, NL, NS, ON, PE, QC; CT, DE, GA, ID, IL, IN, KY, MA, MD, ME, MI, MN, MT, NC, NH, NJ, NY, OH, OR, PA, RI, SC, TN, VT, VA, WA, WV, WI
H. derubellum Gottschl. et Schuhw. [*H. atramentarium* auct.]	QC, MI, NY, WI
H. flagellare Willd. [incl. *H. macrostolonum* G. Schneid.]	BC, NB, NS, PE, QC; CT, IN, MA, ME, MI, NH, NY, PA, VA, VT
H. floribundum Wimm. & Grab.	BC, NB, NL, NS, ON, PE, QC; CT, ID, MA, MD, ME, MN, MT, NH, NJ, NY, OH, OR, RI, VA, VT, WA, WV
H. fuscoatrum Nägeli & Peter	CT, NY, RI
H. glomeratum Froel. [syn.: *H. ambiguum* Ehrh.]	BC; ID, WA
H. lactucella Wallr.	NS
H. pilosella L.	BC, NB, NL, NS, ON, PE, QC; CT, DE, GA, MA, MD, ME, MI, MN, NC, NH, NJ, NY, OH, OR, PA, RI, TN, VA, VT, WA, WV; Saint Pierre and Miquelon
H. piloselliflorum Nägeli et Peter [incl. *H. apatelium* Nägeli et Peter]	NB, NL, NS, ON, PE, QC
H. piloselloides Vill. [incl. *H. praealtum* Vill. ex Gochnat†]	BC, NB, NL, NS, ON, PE, QC; CT, DE, GA, IL, IN, IA, MA, ME, MI, MN, MT, NC, NH, NY, OH, PA, RI, SC, VA, VT, WI, WV
H stoloniflorum Waldst. et Kit.	QC
Subgenus *Hieracium*	
H. atratum Fries.	WA
H. lachenalii C. C. Gmel.	BC, NB, NL, NS, ON, PE, QC; CT, DE, MA, ME, MI, MN, NH, NJ, NY, OR, PA, RI, VT, WA, WI
H. laevigatum Willd. [excl. *H. canadense* Michx.]	BC, NB, NS*, ON, QC; WA, NE USA (precise distribution unknown)
H . maculatum Schrank	BC, NB*, NS*, QC; AK, MI, WA
H. murorum L.	BC, NB, NL, NS, ON, QC; AK, CT, IL, MA, ME, MI, NH, NJ, NY, PA, VT
H. sabaudum L	BC, NS, QC; CT, MA, NJ, NY, PA, WA

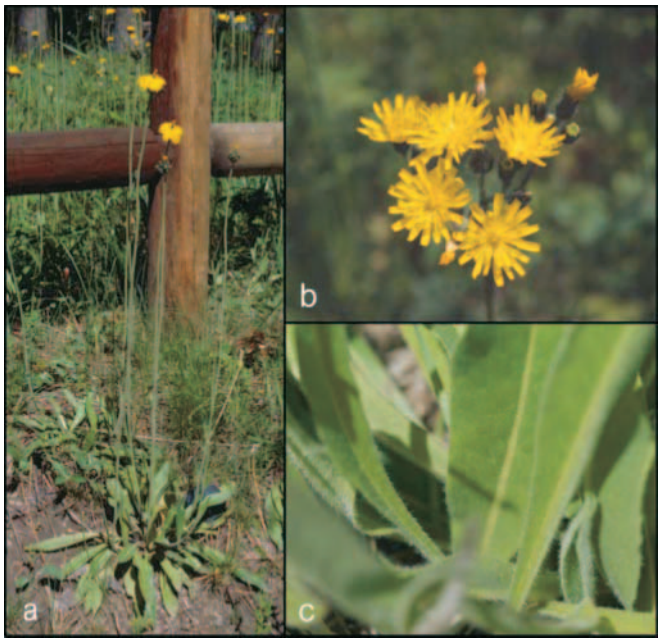
Note: Canadian provinces and US states (listed in that order) follow standard abbreviations. This species list was compiled from Bräutigam and Schuhwerk (2002); Lepage (1971); Scoggan (1979); USDA-NRCS 2004; and *H. glomeratum* (this study). The list includes some intermediate species ("*species intermediae*" sensu Nägeli and Peter 1885; and Zahn 1921–1923) of putative hybrid origin. Nomenclature in the classical monographs as well as in recent Central European studies usually does not treat them as hybrids. Some of these species are fixed taxa with unique characteristic distribution areas (as in Fig. 2). Moreover, their hybrid origin is sometimes merely assumed from their morphology. In North America, *H. floribundum* and *H. glomeratum* are examples of such taxa. *Hieracium flagellare* occurs as either a fixed taxon or as a recent hybrid.

*Unpublished records, leg. H. Harries (Sackville, New Brunswick), det. S. Bräutigam.

†Current taxonomic treatment of the closely related species *H. bauhini* and *H. piloselloides* varies among authors, both in European and American publications. As usual in most European countries, we follow the classical monographs (see note) rather than Sell and West (1976).

apomictic clones in *Rubus* (Nybom and Kraft 1995) and *Hieracium* (Fehrer et al. 2005). In the latter, the combination of *Taq* I restriction with the human minisatellite probe 33.15 (Jeffreys et al. 1990) produced very complex and highly polymorphic patterns for *H. glomeratum* and *H. caespitosum* in their European native range. The markedly different patterns allowed straightforward qualitative identification of clonal lineages. A previous survey of sexual and apomictic types of *Hieracium* subgenus *Pilosella* species had shown that a recombination event consistently produced a distinct fingerprint pattern, proving useful for the distinction of apomictic lineages in this group (Fehrer et al. 2005). DNA isolations, restriction digests of genomic DNA, Southern blotting, and minisatellite fingerprinting were performed as described previously (Fehrer et al. 2005). Additionally, microsatellite fingerprinting was performed. The sequence motive $(GATA)_n$ is widespread in plants (Weising et al. 1989) and also occurs in Asteraceae, where it can be used to identify uniclonal and multiclonal apomictic microspecies in *Taraxacum* (van Heusden et al. 1991). In *Hieracium* apomicts, $(GATA)_5$ showed somewhat higher resolution compared with the minisatellite probe (Fehrer, unpublished data), that is, it detected variation within genotypes (once established by a recombination/hybridization event) that can be attributed to subsequent somatic mutations and related to different age of the clones. The probe was 5′-end-labeled with digoxigenin ($(GATA)_5$-dig, MWG Biotech, Ebersberg, Germany) and applied according to the

Fig. 1. *Hieracium glomeratum* whole plant (*a*), synflorescence (*b*), and leaf pubescence (*c*).



DIG Application Manual (Roche, Mannheim, Germany) with the following specifications: 50 pmol/mL of dig-labeled probe were used and hybridized overnight at 36 °C. The comparatively low temperature is due to the high A/T-content of the probe. Detection was performed with anti-digoxigenin-antibody conjugated to alkaline phosphatase (DIG Nucleic Acid Detection Kit, Roche) and the chemiluminescent reagent CDP-Star™ (NICE oligo kit, Cellmark Diagnostics/Tepnel Lifesciences Plc., Abington/Maryland, UK/USA) according to the manufacturer instructions. Digoxigenin-labeled DNA Molecular Weight Marker II (Roche) was used as a size standard.

Fingerprint phenotypes were only compared qualitatively, as minisatellite patterns were complex and microsatellite patterns usually too different between individual clones to make quantitative comparisons (i.e., having too few or no bands at all in common (Fehrer, unpublished data)). The obvious similarities detected with the $(GATA)_5$ marker between North American *H. glomeratum* and *H. caespitosum* in this study (see below) are notable exceptions.

Voucher specimens of the plants used for DNA fingerprinting were deposited in the herbarium GLM at the State Museum of Natural History, Görlitz, Germany. They are the following: *H. glomeratum*: Nelson, British Columbia (GLM 156768); Pend Oreille Country, Ione Airport, east Washington (GLM 156771); *H. caespitosum*: Santa, Idaho (GLM 156769); Jakuszyce/Sudetes, Poland (GLM 44511); Zweibach/Erzgebirge, Germany (GLM 155674). Samples and vouchers from 13 European populations of *H. glomeratum* and additional 11 European populations of *H. caespitosum* are specified in Fehrer et al. (2005).

Results

Distribution survey

Surveys of the literature and herbaria revealed that *H. glomeratum* had not been previously reported elsewhere in North America. The results of field surveys indicate that the current distribution of *H. glomeratum* in North America is restricted to southeastern British Columbia, northeastern Washington, and northern Idaho. Populations extend from the Canadian border north to Trail, Nelson, and Castelgar, B.C. In the United States, it is located in Stevens and Pend Oreille Counties in northeastern Washington, and in Boundary County in northern Idaho (Fig. 3). This area encompasses roughly 48 500 km^2. *Hieracium glomeratum* was found associated with diverse habitats. However, all sites examined were open, modified sites in forest zones having coarse, well-drained soils. Populations ranged in size from small (0.01 ha) roadside patches to large, contiguous infestations of 150 ha or more in large openings, on abandoned farmland, and in pastures and meadows. At many locations, *H. glomeratum* completely dominated the site. Sites ranged from openings in Douglas fir (*Pseudotsuga menziessii* (Mirb.) Franco) and lodgepole pine (*Pinus contorta* Dougl.) forest zones in Washington at elevations ranging from 700 to 1200 m, to the Interior Cedar–Hemlock Biogeoclimatic Zone in southeastern British Columbia at elevations ranging from 650 to 1020 m. These habitats are generally similar to those found in its native range.

In contrast to the high phenotypic plasticity described above for *H. glomeratum*, the North American populations are morphologically uniform, although a few characters (colour and density of stellate hairs on the leaves) vary somewhat depending on environmental conditions. They are distinguished by the following characters: Stolons always absent. Rosette-leaves elliptic-lanceolate, length/width 3.5–6, dark grass-green, with very short (ca. 0.5 mm) simple hairs on both surfaces, and with glandular hairs on the lower surface and margins. Stems (with the exception of the basal part) with very few simple hairs, but with many glandular hairs along the entire length. Peduncles and most involucral bracts without simple hairs, but always with numerous glandular hairs.

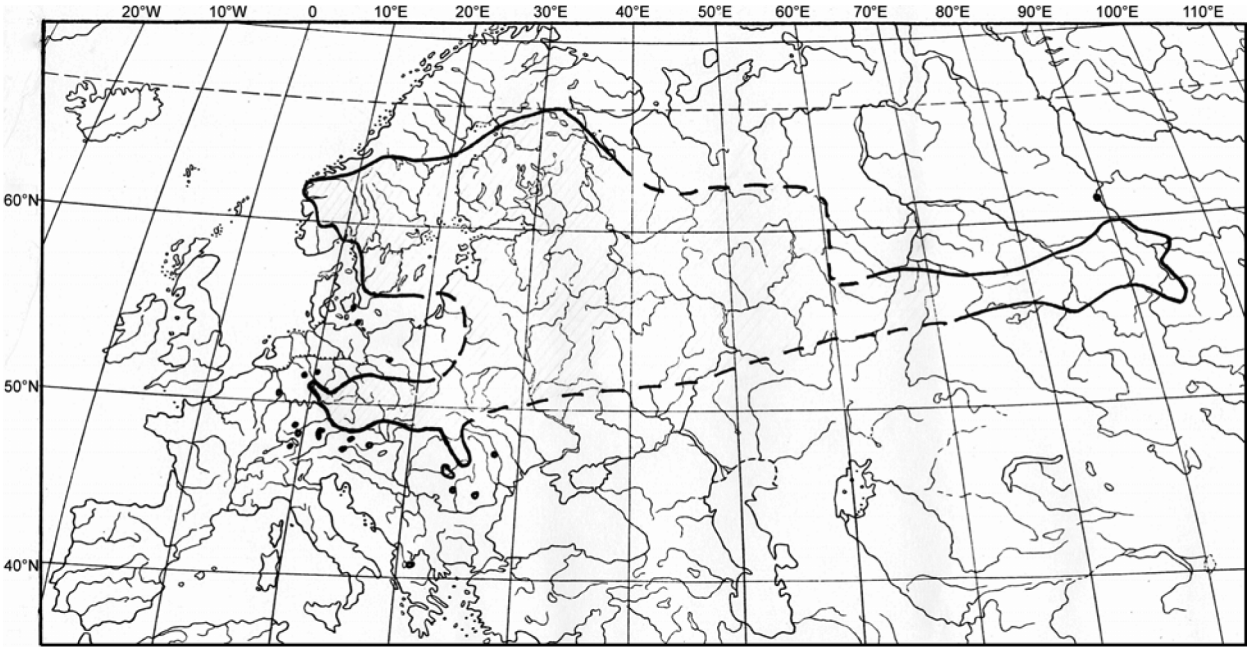
The following provides a diagnostic key to distinguish *H. glomeratum* from other species in subgenus *Pilosella* that occur in the Pacific Northwest. The common name, yellowdevil hawkweed, is suggested for *H. glomeratum*. Synonyms, author names, details and references for taxonomic treatment are given with the species list in Table 1.

Key to the species of *Hieracium* subgenus *Pilosella* in the Pacific Northwest of North America

1 Ligules red or orange. Capitula usually 5–15 . . . . . (Orange Hawkweed) *H. aurantiacum*
1′ Ligules yellow, sometimes with red stripes on outer face. 2

2 Stems unbranched, leafless, with a solitary capitulum. Abaxial surface of rosette leaves white to gray tomentose owing to numerous stellate hairs. Plants always stoloniferous . . . . . (Mouse-ear Hawkweed) *H. pilosella*

Fig. 2. Map of the distribution of *Hieracium glomeratum* in its native range in Eurasia. The broken line indicates where the exact limit of distribution is unclear.



2′ Stems branched, with 1–4 cauline leaves, capitula 2– many. Abaxial surface of rosette leaves green or gray-green, without or with stellate hairs, but not tomentose. 3

3 Synflorescence ± deeply furcate, capitula 2–6. Involucre 9–11 mm long. Plants stoloniferous . . . . (Whiplash Hawkweed) *H. flagellare*

3′ Synflorescence paniculate, corymbose or umbellate-paniculate, capitula (5–)10– many, involucre 5–8 mm long 4

4 Leaves yellow- to dark-green, rarely subglaucous, both surfaces with ± numerous simple hairs. Abaxial surface with numerous stellate hairs. 5

4′ Leaves glaucous, glabrous or with simple hairs on both surfaces and along the margin. Abaxial surface of leaves with simple hairs along the midrib and with or without a few stellate hairs. 6

5 Leaves and lower part of stem with 2–6 mm long simple hairs. Adaxial surface of leaves without or with very few stellate hairs. Styles dark. Synflorescence not umbellate. Plants stoloniferous . . . . . (Meadow Hawkweed) *H. caespitosum*

5′ Leaves and lower part of stem with 0.5–1.5 mm long simple hairs. Adaxial surface of leaves with numerous stellate hairs. Styles yellow. Synflorescence in the upper part often umbellate. Plants (of the North American populations) without stolons . . . . . (Yellowdevil Hawkweed) *H. glomeratum*

6 Rosette leaves lanceolate-spatulate, obtuse. Stolons usually present, their leaves increasing. Abaxial surface of leaves usually with few stellate hairs. Involucre ca. 8 mm long. Plants 15–50 cm . . . . . (Queendevil Hawkweed) *H. floribundum*

6′ Rosette leaves lanceolate, acute. Stolon leaves decreasing or stolons absent. Abaxial surface of leaves without or with few stellate hairs on the midrib. Involucre 5–8 mm long. Plants 20–80 cm 7

7 Plants stoloniferous . . . . . (Kingdevil Hawkweed) *H. bauhini*

7′ Plants always without stolons . . . . . (Tall Hawkweed) *H. piloselloides*

Molecular analysis

DNA fingerprints of the *H. glomeratum* samples from eastern Washington and British Columbia were identical with both markers (Figs. 4 and 5). This North American genotype differed markedly in mini- as well as microsatellite patterns from 13 Central European populations examined previously (Fehrer et al. 2005). The latter comprise three clones across a distance of a mere few hundred kilometers, only one of which was tetraploid. The North American *H. glomeratum* was tetraploid as well (A. Krahulcová, unpublished data). These results together with the spot-like distribution and morphological uniformity of all plants examined to date suggests that *H. glomeratum* is derived from a single introduction from Europe, but from a different area than the investigated populations, and that this genotype subsequently spread as a single clonal lineage by apomixis (reproduction mode ascertained by J. Chrtek, unpublished data).

In contrast, the Idaho plants of *H. caespitosum* proved to belong to the same clone as the widespread European genotype *H. caespitosum* ssp. *caespitosum* (Figs. 4 and 5) repre-

Fig. 3. Map of the distribution of *Hieracium glomeratum* in the Pacific Northwest.

senting a single clonal lineage across different European mountain ranges (Fehrer et al. 2005). Despite the high degree of similarity among fingerprint patterns of this genotype, slight variability between Idaho and European populations can be detected (Fig. 4), corresponding in extent to very small differences that exist between different European populations (Fig. 5). These variations are attributed to somatic mutations and to the relatively older age of this clone in comparison to *H. glomeratum*. Thus, the Idaho plants belong to the widespread European lineage, which is maintained there as an obviously successful genotype, although the species frequently introgresses other taxa by taking part in hybridizations in Europe (Krahulec et al. 2004), either as a pollen donor or even as a seed parent (Fehrer et al. 2005) — in the latter case exhibiting residual sexuality of the facultative apomict.

The microsatellite banding patterns between North American *H. glomeratum* and *H. caespitosum* were remarkably similar (Fig. 5). The pattern of shared bands between these particular clones is suggestive of a direct contribution of this *H. caespitosum* genotype to the origin of North American *H. glomeratum*. In contrast, patterns of the four apomictic lineages of *H. glomeratum* — three European and one North American — hardly shared any bands at all (not shown). It is somewhat surprising that the only sampled *H. glomeratum* to retain evidence of *H. caespitosum* parentage is one that migrated to North America. However, the lack of similarity between European *H. glomeratum* microsatellite patterns and *H. caespitosum* need not rule out the possibility of a parental relationship, as the genomic distribution and segregation of the $(GATA)_5$ microsatellite regions are as yet unknown.

Discussion

The results of this study indicate that *H. glomeratum* occurs as a single genotype, maintained as a clone through apomixis and distributed across a relatively small region in the inland Pacific Northwest. If *H. glomeratum* is a fixed hybrid between *H. caespitosum* and *H. cymosum*, as seems

Fig. 4. Fingerprinting with the human minisatellite probe 33.15. The European *Hieracium caespitosum* samples (1–3) from a population in the Iser Mts. (Sudetes) show an almost identical pattern to two samples from a population in Idaho (4–5). Complete identity is seen in the *Hieracium glomeratum* samples (6–9) for two plants each from eastern Washington (EW) and southeastern British Columbia (BC).

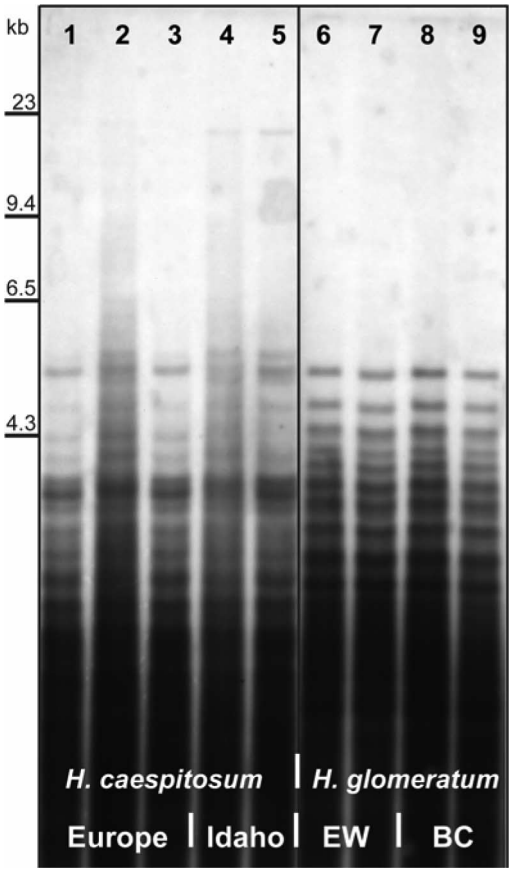
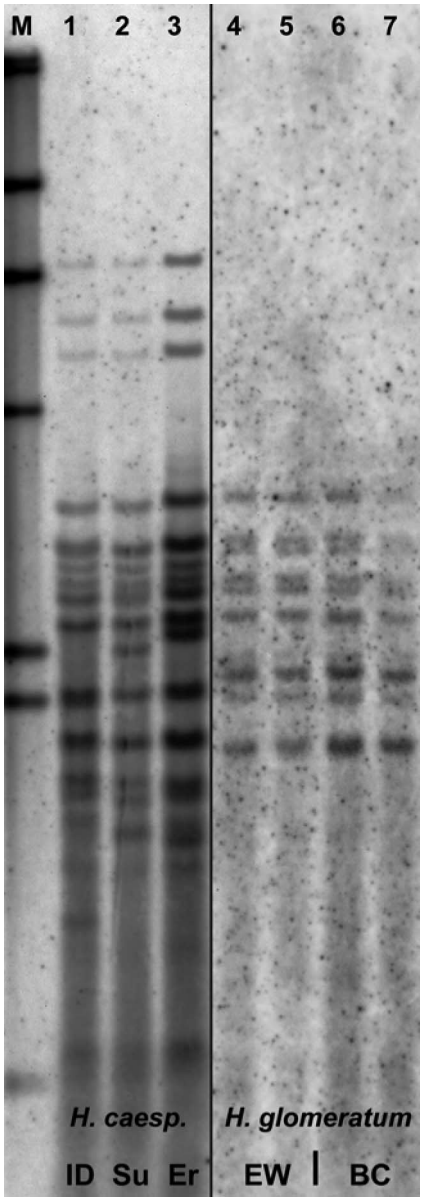


Fig. 5. Fingerprinting with the microsatellite probe $(GATA)_5$. Between *Hieracium caespitosum* samples from Idaho (ID, 1) and two plants from different Central European mountain ranges, Iser Mts./Sudetes (Su, 2) and Erzgebirge (Er, 3), small differences are detected, which can be attributed to somatic mutations (see results). The Central European populations (ca. 300 km apart from each other) differ as much from each other as from the American sample. In contrast, all four *Hieracium glomeratum* plants (4–7, same as in Fig. 4) are identical even with this extremely variable marker, indicating a single very recent origin. Above 2.3 kb, *H. glomeratum* shows a subset of *H. caespitosum* parental bands, indicating that this particular clone might be one of the actual parental genotypes involved in the formation of the Pacific *H. glomeratum*; patterns below that line differ between the two species and have to be contributed by the second parent, probably *H. cymosum* (see text).



likely based on morphology, then its origin by de novo hybridization in North America ought to be excluded because the second parental taxon, *H. cymosum*, is apparently lacking in North America. Therefore, the occurrence of *H. glomeratum* in North America most likely resulted from a single introduction from Europe, which later spread by apomictic seed production.

Precise details on the origin of *H. glomeratum* in North America are unknown. However, its current distribution and recent discovery (this study and independently discovered herbarium specimens from 2000 and 2001, G. Gottschlich (personal communication, 2004)) suggests that it may be a recent introduction. Other invasive hawkweeds have been reported in the region since the 1940*s* and 1950*s* (Wilson et al. 1997), thus *H. glomeratum* may have been established since that time. Large, continuous infestations along roadways increase the opportunity for *H. glomeratum* to spread into susceptible areas of the Pacific Northwest.

Hieracium glomeratum likely failed to be identified because of its similarity to *H. caespitosum*, a common species found throughout Canada and the United States (Wilson 1999). *Hieracium glomeratum* can be distinguished from *H. caespitosum* by very short simple hairs, which give the leaves and the lower part of stems a soft-lanuginose appearance, relatively numerous stellate hairs on the upper surface of leaves, its ± umbellate synflorescence and the light colour of the styles (see taxonomic key). Moreover, the North

American plants do not produce stolons, in contrast to *H. caespitosum.*

Hybridization between *Pilosella* species is common and leads to both sexually or apomictically reproducing plants (Krahulcová and Krahulec 2000, Houliston and Chapman 2001, Morgan-Richards et al. 2004). Both *H. caespitosum* and *H. glomeratum* are known to frequently hybridize with other species in subgenus *Pilosella*, continuously creating novel genotypes, most of which reproduce by apomixis (Lepage 1967; Krahulcová and Krahulec 2000; Krahulcová et al. 2000; Krahulcová et al. 2004; Morgan-Richards et al. 2004). Hybridization increases the probability for novel, successful genotypes to arise de novo, some of which may become invasive. In New Zealand, hybridization has contributed to the success of highly invasive *Pilosella* biotypes (Chapman et al. 2000, 2003; Houliston and Chapman 2004).

Examination of populations from several locations in Europe revealed that *H. glomeratum* there consists of local clones of relatively recent origin as well as older, fixed clones that form stable populations and which occupy ranges of a few hundred square kilometres or more (Fehrer et al. 2005; Gottschlich 2006). *Hieracium glomeratum* in the Pacific Northwest appears to represent such a stable taxon, although the populations are probably much younger.

The success of a facultative apomictic reproductive strategy has been widely attributed to the invasive success of non-native plants. For example, the invasion success of related *Chondrilla juncea* (Williamson 1996) and *Taraxacum officinale* (Asker and Jerling 1992) have been attributed, in part, to apomixis. The apomictic mode of reproduction combines with other characteristics frequently observed in invasive plant species: vegetative reproduction by stolons, the perennial habit, (allo)polyploidy, fixed heterozygosity, and extensive hybridization (reviewed by Stebbins 1985; Ellstrand and Schierenbeck 2000; and Soltis and Soltis 2000). The lag time usually observed before an introduced species becomes invasive might not apply to apomictic polyploids such as *H. glomeratum*, because of their autonomous reproduction mode. A single introduction of a suitable genotype may result in a successful invasion, in contrast to the multiple introductions that may be required of sexual species. It has been suggested that the presence of facultative sexuality in predominantly apomictic individuals has been important in facilitating a more rapid invasion, with both intra- and interspecific hybridization playing a role in this (Houliston and Chapman 2004; Trewick et al. 2004). Although the North American populations of *H. glomeratum* at present appear to have little or no sexual interactions with other taxa, their presence in a new environment and fertile congeners may enable a more rapid increase in range than has been observed until now. Additional surveys will be conducted from 2005 to 2008 to determine how rapidly the range of *H. glomeratum* is expanding in the Pacific Northwest.

To accurately identify the origin of this particular *H. glomeratum* clone from the Old World would require a complete screening of its entire native range in Eurasia. This was not considered promising within the scope of this study, as the species is known for its recurrent origin by hybridization. In contrast to *H. caespitosum*, the fingerprint patterns observed for *H. glomeratum* did not correspond to any of the *H. glomeratum* clones examined from Central Europe, but that study area was relatively small compared with its native distribution range. We strongly suspect that it did not originate in Central Europe, as it lacks stolons and these are typical for *H. glomeratum* in that area.

Further surveys may reveal that *H. glomeratum* occurs in other regions of Canada and the United States, or that its range is expanding in the Pacific Northwest. Moreover, other European species of *Hieracium* subgenus *Pilosella* may have been introduced into North America, but remain unreported or misidentified, as has been reported in New Zealand (G. Houliston, personal communication, 2005). Once its North American distribution is better known, genetic analyses from a larger number of populations can be conducted, and likewise the European source population may be traceable through a broad screening of populations across its native distribution area. Ongoing molecular and morphological studies may also elucidate species relationships among non-native hawkweeds, which are needed before a coherent and acceptable taxonomic treatment of the complex of invasive *Hieracium* species in North America can be developed.

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