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Morphological variation in eight taxa of *Anthyllis vulneraria s. lato* (Fabaceae)

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Depending on the literature source, the number of existing *Anthyllis* species differs almost three-fold. In addition to the well-defined species, there are many cryptic ones. Statistical analysis (general linear models, discriminant analysis) of the morphological variation of eight *Anthyllis* taxa (for simplification classified as species) resulted in three groups of species: *Vulneraria* (*A. vulneraria*, *A. maritima*, *A. arenaria* and *A.* × *baltica*), *Macrocephala* (*A. macrocephala*, *A.* × *colorata*, and *A.* × *polyphylloides*), and *Coccinea* (*A. coccinea*). Distinguishing features of these groups were calyx colour, corolla colour, hairiness of stems and petioles, and plant height.

Key words: *Anthyllis vulneraria*, morphology, suboptimal classification, taxonomy, variation

Introduction

The genus *Anthyllis* (Fabaceae) is one of eight genera in the tribe Loteae and is morphologically and molecularly closely related to the genus *Hymenocarpus* (Polhill 1994). This relationship has been confirmed in later studies (Allan & Porter 2000, Allan *et al*. 2003), which substantiate the sister group relationship between *Anthyllis* and *Hymenocarpus xerxinnatus*.

Anthyllis vulneraria s. lato occurs from the Volga River to England and from northern Europe to the Mediterranean (Hultén & Fries 1986a). It has also been introduced into North America and New Zealand (Hultén & Fries 1986b). The exact number of *Anthyllis* species is controversial and depends on interpretation of their morphological-geographical boundaries with respect to active speciation and hybridisation (Yakovlev *et al*. 1996). The species number has been given as 25 (Cullen 1986) up to 60 (Minjaev & Akulova 1987). Although some species in the genus are well defined and universally accepted, there are many cryptic forms that have been subject to different interpretations. The species are morphologically quite similar. Although the genus contains some shrubs and subshrubs, all European species are herbaceous (Cullen 1968). Cullen (1968) divided *A. vulneraria s. lato* into three groups: subsp. *vulneraria*, subsp. *maritima* and subsp. *polyphylla*.

There are two main schools of thought with respect to the taxonomy of the genus *Anthyllis*. The first, popular in the area of the former Soviet Union, distinguishes numerous species in *Anthyllis vulneraria s. lato* (Juzepczuk 1945, Minjaev & Akulova 1987). The other line of thought, prevalent in most of Europe, recognises

18 European species (Cullen 1968, Garcke 1972, Hegi 1975, Ulvinen & Lampinen 1998) with many species of the first school being recognised as subspecies or varieties.

Anthyllis vulneraria s. lato is a particularly polymorphic taxon (Krall 1983). Its intraspecific classification is complicated; subspecies and forms are closely similar and often have a hybrid origin. *Anthyllis vulneraria* consists of local forms in limited areas, which are almost morphologically indistinct (Jalas 1950, Talts 1959). On old arable lands in central and western Europe, hybrid complexes whose taxonomic status is difficult to determine have been found (Talts 1959). Estonian habitats are similar to those in central and southern Sweden, where several varieties of *Anthyllis* have been described and where populations of *Anthyllis* occur typically as hybrid complexes (Jalas 1950).

This article investigates eight taxa (*A. arenaria* (Rupr.) Juz., *A. coccinea* (L.) Beck, *A. macrocephala* Wend., *A. maritima* Schweigg. and *A. vulneraria* L., *s. stricto*, *A.* × *colorata* Juz., *A.* × *baltica* Juz., *A.* × *polyphylloides* Juz.), which are recognised as species in this study, as they are also in the Baltic States (Talts 1959, Krall 1983, Eglite & Krall 1996, Krall 1999, Kukk 1999). These species and their equivalents in other classifications are listed in Table 1.

Whereas these eight taxa are considered subspecies or varieties of *Anthyllis vulneraria s. lato* in Europe, their global distribution remains indeterminable. The most widespread taxa in the Baltic region, *A. vulneraria s. stricto*, *A. macrocephala*, *A. maritima* and *A. arenaria*, are distributed throughout the area, whereas *A. coccinea* occurs only in western Estonia and Latvia, and in southern Sweden (Tabaka 1982, Minjaev & Akulova 1987, Tabaka *et al*. 1988). *Anthyllis vulneraria* and *A. macrocephala* also occur in southern Finland (Ulvinen & Lampinen 1998). *Anthyllis* × *polyphylloides* has the same distribution as its probable parent species. *Anthyllis* × *baltica* is endemic to the Baltic region and *A.* × *colorata* is endemic to Estonia (Minjaev & Akulova 1987).

A few characteristics in different keys and floras distinguish these taxa (Table 2). Bicoloured rufous calyx teeth demarcate *A. vulneraria s. stricto*, *A. coccinea*, *A.* × *baltica* and *A.* × *colorata* from the other four species, which have concolorous, green calyces. Another readily detectable characteristic is hair disposition on the stem and petiole. *Anthyllis macrocephala*, *A.* × *polyphylla* and *A.* × *colorata* have patent hairs on the stems and petioles, whereas the other species have appressed hairs (Cullen 1968, Garcke 1972, Hegi 1975, Krall 1983, Eglite & Krall 1996, Krall 1999). *Anthyllis maritima* can be distinguished from the other species by concolorous calyces, by sericeous calyx pubescence and some inflorescences with few flowers (sometimes not fully developed) (Krall 1983, Eglite & Krall 1996, Roze 2004). Inflorescences of this species also feature long peduncles. *Anthyllis arenaria* has well-developed inflorescences that are sessile (Eglite & Krall 1996, Krall 1999). Branches of this species form an acute angle with the stem (Roze 2004). Of the species with bicoloured calyces, *A. coccinea* is most readily distinguished by its red corolla (Cullen 1968, Krall 1983, Eglite & Krall 1996, Krall 1999). *Anthyllis* × *baltica* has also some undeveloped inflorescences in axils, like *A. maritima* (Eglite & Krall 1996, Roze 2004). *Anthyllis vulneraria s. stricto* has unbranched stems and mainly apical inflorescences (Juzepczuk 1945, Eglite & Krall 1996, Krall 1999). According to the keys and floras these eight taxa can be readily distinguished, yet individual plants of genus *Anthyllis* in natural stands are difficult to identify.

There are also many infrequently used characteristics that can be found in other studies (Cullen 1968, Lukaszewska *et al*. 1983a, 1983b, Krall 1983, Tihomirov & Sokoloff 1996).

Becker (1912) distinguished two growth forms in *Anthyllis vulneraria s. lato*: *Vulgaris* and *Vulneraria*. They usually grow in similar conditions, but *Vulgaris* prefers moister habitats than *Vulneraria*. He also claimed that corollas are usually yellow in moister conditions, but principally red in dryer habitats. Becker's results contradict all traditionally used characteristics to distinguish *Anthyllis* species.

Lukaszewska *et al*. (1983a, 1983b, 1983c) analysed the morphological variability and Kalinowski (1983a, 1983b) the isoenzymatic variability of *A. vulneraria s. lato* populations from coastal areas of the Baltic Sea in Poland. Different methods of multivariate statistical analysis all confirm the differences between populations, both in vegetative and sexual characteristics. For most traits a correlation was found between the differentiation of

Table 1. Classification of species of the genus *Anthyllis* according to different taxonomic arrangements (– = taxon was not cited). *All infraspecific taxa are members of *A. vulneraria s. lato*.

Baltic countries	Former Soviet Union	Europe	Europe	Finland
Eglite & Krall 1996	Juzepczuk 1945	Gracke 1972	Hegi 1975	Ulvinen & Lampinen 1998
A. vulneraria L., *s. stricto*	*A. Linnaei* Sag.	ssp. *vulneraria* L.,* ssp. *vulgaris* (Koch) A. et G.	var. *vulneraria* (Kerner) Wohlf., var. *vulgaris* Koch.	ssp. *vulneraria,* ssp. *linnaei* Sag.
A. coccinea (L.) Beck	*A. coccinea* (L.) Beck	–	var. *coccinea* L.	–
A. arenaria (Rupr.) Juz.	*A. arenaria* (Rupr.) Juz.	–	–	–
A. maritima Schweigg.	*A. maritima* Schweigg.	ssp. *maritima* (Schweigg.) A. et G.	var. *maritima* (Schweiggrer) Koch.	–
A. macrocephala Wend.	*A. polyphylla* Kit.	ssp. *polyphylla* (Kit.) Arcang.	var. *polyphylla* (Kit.) Ser.	ssp. *polyphylla* (DC.) Nyman
A. × *colorata* Juz.	*A. colorata* (Meinsh.) Juz.	–	–	–
A. × *polyphylloides* Juz.	*A. polyphylloides* Juz.	–	–	–
A. × *baltica* Juz. *ex* Miniaev *et* Kloczkova	–	–	–	–

Table 2. Main characteristics of the Estonian *Anthyllis* species (Krall 1983, 1999, Eglite & Krall 1996).

Characteristics	*vulneraria, s. stricto*	*coccinea*	*arenaria*	*maritima*	*macrcocephala*	× *baltica*	× *colorata*	× *polyphylloides*
Plant height	15–30 cm	4–15 cm	20–50 cm	20–40 cm	16–40 cm	20–40 cm	20–50 cm	15–30 cm
Stem shape	ascending, erect	ascending, decumbent	erect	ascending	erect	ascending	ascending, erect	erect
Hair disposition on stem and petiole	appressed	appressed	appressed	appressed	patent	appressed	patent	patent
Number of stem leaves	2–3	1–2	2–4	3–4	3–5	2–3	2–3	3–5
Shape of the rosette leaves	pinnate	might be simple leaves	pinnate	might be simple leaves	pinnate	might be simple leaves	pinnate	pinnate
Length of bracts	as long as calyx	as long as calyx	as long as calyx	longer than calyx	as long as calyx	longer than calyx	as long as calyx	as long as calyx
Apexes of bracts	sharp or blunt-ended	blunt-ended	sharp or blunt-ended	sharp	sharp	sharp	sharp	sharp
Number of inflorescences	2–3	1–2	1–4	2–5	1–3	3–5	2–3	2–4
Colour of the calyx	bi-coloured with red teeth	bi-coloured with red teeth	concolorous, green	concolorous, green, hairy	concolorous, green	bi-coloured with red teeth, hairy	bi-coloured with red teeth	concolorous, green
Colour of corolla	yellow	red	yellow	yellow	yellow	yellow	yellow	yellow

populations and their geographic locations.

Chromosome numbers have been determined only for *A. maritima*, *A. vulneraria* and *A. macrocephala*, all of which have 2n = 12 chromosomes (Tshehov 1932, Jalas 1950, Bakšay 1959, Bolkohovskikh *et al*. 1969, Agapova *et al*. 1990), suggesting they are diploid.

As much as the determination of *Anthyllis* species and their hybrids remains problematic, the aims of this study were: (i) to determine the circumscription of the *Anthyllis* species, (ii) to analyse their variation patterns and, (iii) to determine which morphological characteristics distinguish these taxa reliably.

Material and methods

The analysis comprised herbarium material (198 individuals) from the Herbarium of the University of Tartu (TU), the Herbarium of the Institute of Zoology and Botany of the Estonian Agricultural University (TAA) and the Herbarium of the Estonian Natural Museum (TAL). In addition, the analysis included 300 specimens material collected from different localities in Estonia in July 2001 and June 2002. Eight *Anthyllis* species occurring in northern Europe and widespread in the Baltic region were analysed: *A. vulneraria* (86 individuals), *A. coccinea* (45), *A. arenaria* (81), *A. maritima* (95), *A. macrocephala* (25), *A.* × *baltica* (105), *A.* × *colorata* (39) and *A.* × *polyphylloides* (22).

Twenty-three diagnostic characteristics were selected for analysis (Table 3). These characteristics are those commonly used to identify species and those measurable in the herbarium material.

The length of the longest stem was designated as the height of the plant. The number of stem

Table 3. Characteristics used in analysis of *Anthyllis* species (degree of precision for metric interval characteristics 1 mm).

Abbreviation	Variable	Type	Scale
SR	habit	nominal	1 = erect, 2 = ascending
HLT	apexes of bracts	nominal	1 = sharp, 2 = blunt-headed
HP	hair of calyx	nominal	1 = oppressed, 2 = silky, patent hairs
SRL	shape of rosette leaves	nominal	1 = simple leaves, 2 = pinnate
HSP	hair of petiole	nominal	1 = no hairs, 2 = oppressed, 3 = patent
HST	hair of stem	nominal	1 = no hairs, 2 = oppressed, 3 = patent
CIF	colour of corolla	nominal	1 = yellow, 2 = orange, 3 = red
DIF	branching of inflorescence and without axes	nominal	1 = simple, 2 = ramiform without axes, 3 = ramiform with axes, 4 = ramiform with
HLB	hair on the upper side of leaf blade	ordinal	1 = no hairs, < 2 = few hairs (1–3 on 2.5 mm^2), > 3 = many hairs (3 on 2.5 mm^2)
CP	colour of calyx teeth	nominal	1 = concolorous, 2 = some red colour on teeth, 3 = clearly bi-coloured, with red
NS	number of stems	interval counted	
NIF	number of inflorescence	interval counted	
NSL	number of stem leaves	interval counted	
NRL	number of rosette leaves	interval counted	
L	height of the plant	interval metric (cm)	
LL	length of the leaf	interval metric (cm)	
WL	width of the leaf	interval metric (cm)	
LL/WL	ratio of the leaf length and width		
LP	length of calyx	interval metric (cm)	
WP	width of the calyx	interval metric (cm)	
LP/WP	ratio of the calyx length and width		
LF	length of the corolla	interval metric (cm)	
LHL	length of bract	interval metric (cm)	
WHL	width of bract	interval metric (cm)	
LHL/WHL	ratio of bract length and width		
LS	length of the petiole	interval metric (cm)	

Table 4. Characteristics distinguishing analysed species pairs ($p < 0.05$) according to GLM analysis. Characteristic abbreviations as in Table 3.

	A. vulneraria	*A. coccinea*	*A. arenaria*	*A. maritima*	*A. macrocephala*	*A.* × *baltica*	*A.* × *colorata*
A. coccinea	L, LL, WL, LF, LS, LNSL						
A. arenaria	L, LL, WL, LP, WP, LHL, WHL, LS, LNS, LNIF	L, LL, WL, LP, WP, LF, LHL, WHL, LF, LNS, LNIF, LNSL					
A. maritima	L, LL, WL, LP, LHL, LS, LNIF, LNSL	L, LL, WL, LP, LF, LHL, LS, LNS, LNIF, LNSL	No differences				
A. macrocephala	L, LL, WL, LP, LHL, WHL, LS, LNIF	L, LL, WL, LP, WP, LF, LHL, WHL, LS, LNIF, LNSL	No differences	No differences			
A. × *baltica*	L, LS, LNS, LNIF, LNSL, LNRL	L, LL, WL, LS, LNS, LNIF, LNSL	LL, WL, LP, WP, LNIF	LL, LNS, LNIF	L, LL, LP, LNS		
A. × *colorata*	L, LL, WL, LNS, LNIF	L, LL, WL, LS, LNS, LNIF, LNSL	No differences	LNSL	No differences	WL, LNSL	
A. × *polyphylloides*	L, LL, WL, LP, WP, LHL, WHL, LS, LNS, LNIF, LNSL	L, LL, WL, WP, LP, LHL, WHL, LS, LNS, LNIF, LNSL	L, LL, WL, LNIF	L, LL, WL, LP, WP, WHL, LNIF	L, LNIF	L, LL, WL, LP, WP, LHL, WHL, LNRL	L, LL, LP, WP, LNIF, LNSL, LNRL

leaves on the longest stem was also counted. The hairiness of the leaf blade was estimated from the biggest rosette leaf (if absent, from the biggest stem leaf). Hairs in the middle of the right part of the leaf blade were counted in an area of 2.5 mm^2 with a binocular microscope. The length and width of the same leaf were measured. The length and width of the corolla, calyx and bracts were measured on the same inflorescence. The degree of measurement precision was 1 mm. In addition, ratios of length and width were calculated for the leaves, bracts and calyces.

Data analysis

General linear model (GLM, StatSoft Inc. 2001) was used to analyse metric interval and counted interval characteristics and their differences among species. Counted interval characteristics were log-transformed. As the second step in GLM analysis, Tukey's HSD test was used to estimate which species differ statistically significantly in respect to the characteristics indicated by GLM results.

Nominal and ordinal characteristics were analysed with a nonparametric test (Kruskal-Wallis ANOVA).

Discriminant analysis (StatSoft Inc. 2001) was used to determine the subset of characteristics that reliably distinguish the species. Data were analysed by standard discriminant analysis methods including non-transformed data. A classification matrix was calculated to evaluate the results.

To achieve a suboptimal classification, iterative discriminant analysis (StatSoft Inc. 2001) was performed, in which the initial classification was iteratively corrected according to the posterior probabilities until all the specimens were 100% correctly reclassified according to the classification matrix. Next, canonical discriminant analysis was performed and classification similarity between groups of preliminary species classification and reclassified species were calculated in a frequency matrix. Canonical discriminant analysis (StatSoft Inc. 2001) was used for ordination of species-groups according to canonical roots.

Least squared means with confidence intervals of taxonomically important features were calculated by one-way ANOVA for reclassified species-groups.

Results

Results of the univariate GLM analysis of metric and counted interval characteristics showed that four species, *A. vulneraria*, *A. coccinea*, *A.* × *baltica* and *A.* × *polyphylloides*, were distinguishable from the other species (Table 4). However, some species remained indistinguishable with respect to the diagnostic characteristics. *Anthyllis arenaria* did not differ from *A. maritima*, *A. macrocephala* and *A.* × *colorata*, *A. maritima* did not differ from *A. macrocephala*, and *A. macrocephala* did not differ from *A.* × *colorata*. Characteristics that did not differ between any of the species pairs were ratio of leaf length and width, ratio of calyx length and width, and ratio of hypsophylls length and width. All other interval characteristics were suitable to distinguish at least one species pair.

Most of the nominal and ordinal characteristics were statistically significant (Table 5). The Kruskal-Wallis test showed that only the shape of rosette leaves failed to significantly distinguish species.

Standard discriminant analysis of all characteristics revealed that only 11 of them were statistically significant (Table 5), consisting of six nonparametric, three counted interval, and two metric interval characteristics. These significant characteristics consist of apices of bracts; hairiness of petiole, calyx, and stem; colour of corolla and calyx; number of inflorescences,

Table 5. Results of the characteristics analysed with different methods. Critical *p* value is 0.05. Characteristic abbreviations as in Table 3.

Characteristics used in analysis	*p* value of discriminant analysis	*p* value of Kruskal-Wallis test for nonparametric characteristics	*p* value of GLM test for interval characteristics	*p* value of discriminant analysis of iteratively reclassified species
SR	0.0876	0.0010		0.1876
HLT	< 0.0001	< 0.0001		< 0.0001
HSP	< 0.0001	< 0.0001		< 0.0001
SRL	0.3341	< 0.1147		0.5813
HP	< 0.0001	< 0.0001		< 0.0001
HST	< 0.0001	< 0.0001		< 0.0001
CIF	< 0.0001	< 0.0001		< 0.0001
DIF	0.4405	< 0.0001		0.0028
CP	< 0.0001	< 0.0001		< 0.0001
HLB	0.1501	0.0178		0.2809
NS	0.0002		< 0.0001	< 0.0001
NIF	< 0.0001		< 0.0001	< 0.0001
NSL	0.0632		< 0.0001	0.0056
NRL	0.0027		< 0.0001	0.1714
L	0.0090		< 0.0001	< 0.0001
LL	0.1967		< 0.0001	0.0469
WL	0.1784		< 0.0001	0.1382
LL/WL	0.1503		0.0603	0.1157
LP	0.5169		< 0.0001	0.0032
WP	0.2948		< 0.0001	0.0037
LP/WP	0.3238		0.5280	0.0018
LF	0.0002		0.0063	0.0046
LHL	0.7691		< 0.0001	0.0639
WHL	0.3083		< 0.0001	0.0135
LHL/WHL	0.2694		0.2307	0.1475
LS	0.2903		< 0.0001	0.7248

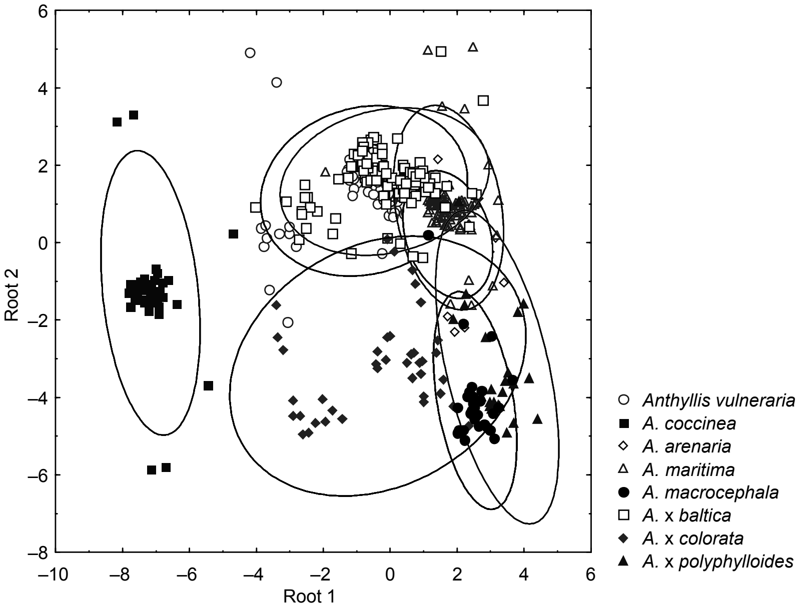

Fig. 1. Scatterplot of canonical discriminant analysis.

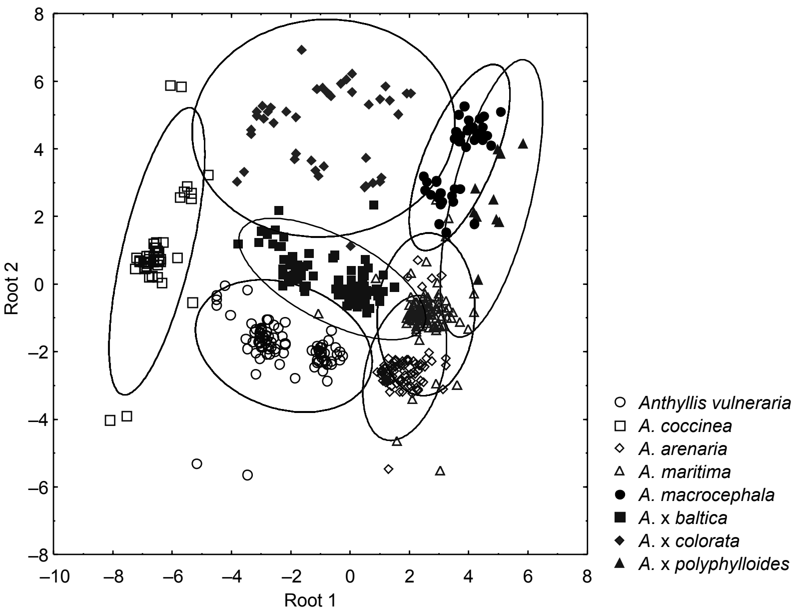

Fig. 2. Scatterplot of canonical discriminant analysis for reclassified species-clusters (by iterative discriminant analysis).

stems, and rosette leaves; height of plant; and length of corolla. Five metric interval characteristics were statistically significant according to GLM and discriminant analyses. These characteristics are number of stems, inflorescences and rosette leaves, height of plant, and length of corolla.

A scatterplot of canonical roots shows distinguishable mono-specific groups of *A. coccinea* and *A.* × colorata (Fig. 1) and three overlapping pairs of species: *A. vulneraria–A.* × *baltica*, *A. arenaria–A. maritima* and *A. macrocephala–A.* × *polyphylloides*.

After iterative canonical analysis with determination correction, the ordination of canonical roots yielded a scatterplot, in which seven of the eight species formed distinctive clusters (Fig. 2). Cluster edges overlap to some extent, but most of the overlap is caused by the variability of *A. maritima*.

A comparison of the initial and final classification cross-tabulation matrix revealed that *A. coccinea* was classified 100% correctly (Table 6). *Anthyllis arenaria*, *A. maritima*, *A. macrocephala* and *A.* × *colorata* were correctly classified > 90%, whereas 23.3% of *A. vulneraria* were classified as *A.* × *baltica* and 3.4% as *A.* × *colorata*. *Anthyllis* × *baltica* was classifed 21.9% as *A. vulneraria* and 6.7% as *A. maritima*. The most poorly classified species was *A.* × *polyphylloides*, of which only 31.8% were correctly classified. Half of these individuals were classified as *A. macrocephala*, 9.1% as *A. maritima* and 9.1% as *A. arenaria*.

Mean plant height, number of inflorescences, number of stems, and leaf length differentiated species most successfully (Table 7). For example, *A. coccinea* is the shortest species (mean height 10.7 ± 1.1 cm), whereas *A.* × *polyphylloides* is the tallest (mean height 41.2 ± 2.4 cm). Mean heights of other species ranged between 17.2 cm and 27.9 cm. The variation patterns of the other characteristics were similar.

Discussion

Several authors have suggested that *Anthyllis* taxa are distinguishable by plant height, shape of the hypsophyll apices, stem hairiness, and colour of corolla and calyx (Cullen 1968, Juzepczuk 1945, Eglite & Krall 1996, Krall 1999). These characteristics reliably distinguish the analysed species according to our statistical analysis (Table 5). The number of stems and inflorescences and hairiness of petiole and calyx, mentioned by Eglite and Krall (1996) and Krall (1999), also statistically distinguish the analysed species. Easily measured characteristics, such as number of rosette leaves and lengths of corolla and calyx also reliably distinguish these species, although they have not been mentioned in the literature.

GLM analysis indicates that *A.* × *colorata* does not differ from *A. macrocephala*. *Anthyllis* × *colorata* is probably a hybrid between *A. macrocephala* and *A. vulneraria* (Juzepczuk 1945, Eglite & Krall 1996), but five characteristics clearly distinguish the second probable parent species from *A.* × *colorata* (Table 4). *Anthyllis*

Table 6. Frequency matrix of analyzed species: the numbers are percentages of species reclassified after analysis of posterior probabilities.

Initial classification of species	Reclassified species							
	vulneraria	*coccinea*	*arenaria*	*maritima*	*macrocephala*	× *baltica*	× *colorata*	× *polyphylloides*
vulnereria	73.3	0	0	0	0	23.3	3.4	0
coccinea	0	100	0	0	0	0	0	0
arenaria	0	0	97.4	1.3	0	0	0	1.3
maritima	0	0	0	94.5	2.2	2.2	0	1.1
macrocephala	0	0	0	3.2	93.6	0	0	3.2
× *baltica*	21.9	0	1.0	6.7	0	69.4	1.0	0
× *colorata*	0	0	0	0	2.6	0	97.4	0
× *polyphylloides*	0	0	9.1	9.1	50.0	0	0	31.8

Table 7. Mean values of interval characteristics for analyzed species (mean ± standard error), characteristic abbreviations as in Table 3.

Characteristics	Species							
	A. vulneraria	*A. coccinea*	*A. arenaria*	*A. maritima*	*A. macrocephala*	*A.* × *baltica*	*A.* × *colorata*	*A.* × *polyphylloides*
NS	3.0 ± 0.3	2.0 ± 0.4	4.1 ± 0.3	3.8 ± 0.3	3.3 ± 0.4	4.3 ± 0.3	4.0 ± 0.4	6.0 ± 0.9
NIF	4.4 ± 0.5	2.3 ± 0.7	5.7 ± 0.6	5.5 ± 0.5	5.9 ± 0.8	6.2 ± 0.5	6.0 ± 0.8	16.6 ± 1.6
NSL	3.1 ± 0.1	3.0 ± 0.2	3.5 ± 0.1	3.8 ± 0.1	3.2 ± 0.2	3.5 ± 0.1	2.9 ± 0.2	4.8 ± 0.3
NRL	6.0 ± 0.6	5.2 ± 0.8	5.9 ± 0.6	6.5 ± 0.6	5.1 ± 0.9	7.6 ± 0.6	8.3 ± 0.9	3.6 ± 1.8
L	17.2 ± 0.8	10.7 ± 1.1	23.1 ± 0.9	22.5 ± 0.8	27.9 ± 1.2	19.6 ± 0.8	21.5 ± 1.2	41.2 ± 2.4
LL	2.4 ± 0.1	1.7 ± 0.1	3.3 ± 0.1	3.2 ± 0.1	3.5 ± 0.1	2.8 ± 0.1	3.1 ± 0.1	4.3 ± 0.3
WL	0.8 ± 0.0	0.6 ± 0.1	1.1 ± 0.0	1.1 ± 0.0	1.2 ± 0.1	1.0 ± 0.0	1.2 ± 0.1	1.7 ± 0.1
LL/WL	3.0 ± 0.1	2.7 ± 0.1	3.0 ± 0.1	3.0 ± 0.1	3.0 ± 0.1	2.9 ± 0.1	2.6 ± 0.1	2.6 ± 0.2
LP	0.8 ± 0.0	0.8 ± 0.0	0.9 ± 0.0	0.9 ± 0.0	0.9 ± 0.0	0.8 ± 0.0	0.9 ± 0.0	1.0 ± 0.0
WP	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.4 ± 0.0
LP/WP	2.9 ± 0.1	2.7 ± 0.1	2.8 ± 0.1	2.8 ± 0.1	2.7 ± 0.1	2.8 ± 0.1	2.8 ± 0.1	2.5 ± 0.2
LF	0.4 ± 0.0	0.4 ± 0.0	0.4 ± 0.1	0.4 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.4 ± 0.0
LHL	0.9 ± 0.0	0.8 ± 0.0	1.1 ± 0.0	1.0 ± 0.0	1.1 ± 0.0	1.0 ± 0.0	1.0 ± 0.0	1.4 ± 0.1
WHL	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0
LHL/WHL	5.2 ± 0.2	4.9 ± 0.0	5.1 ± 0.2	5.3 ± 0.2	4.3 ± 0.3	5.6 ± 0.2	4.7 ± 0.3	4.8 ± 0.7
LS	3.2 ± 0.1	2.1 ± 0.2	4.2 ± 0.2	4.0 ± 0.1	4.2 ± 0.2	3.7 ± 0.1	3.6 ± 0.2	5.0 ± 0.4

× *colorata* is also similar to *A. maritima* and *A. arenaria*, suggesting that these species might also be closely related. Interval characteristics clearly distinguish the other four species.

According to discriminant analysis, incorrectly classified individuals of *A. vulneraria* are mostly classified as *A.* × *baltica* (probably *A. vulneraria* × *A. maritima*; Minjaev & Akulova 1987), and vice versa (Table 6). Its other parent species, *A. maritima*, was not classified as *A.* × *baltica*, but their similarity is revealed by seven individuals of *A.* × *baltica* that were classified as *A. maritima*. According to this analysis, *A. maritima*, together with *A. arenaria* and *A. macrocephala*, are closely related to *A.* × *polyphylloides*. According to Krall (1999), *A.* × *polyphylloides* is the hybrid of *A. arenaria* and *A. macrocephala*, but Minjaev and Akulova (1987) suggested that three species — *A. arenaria* × *A. macrocephala* × *A. maritima* — contribute to the origin of this species.

In all analyses, only *A. coccinea* is distinctly different from the others (Fig. 1), which supports the distinction of a species or subspecies, *A. coccinea,* from *A. vulneraria s. lato*. Strongly expressed morphological similarity between all other species indicates the delimitation of a single species, *A. vulneraria s. lato* (Cullen 1968, Hegi 1975, Lukaszewska *et al.* 1983c). The formation of subgroups (*A. vulneraria–A.* × *baltica*, *A. arenaria–A. maritima*, *A. macrocephala–A.* × *colorata–A.* × *polyphylloides*) supports the idea of three subspecies (subsp. *vulneraria*, subsp. *maritima* and subsp. *polyphylla*) (Cullen 1968, Krall 1983).

This study incorporated an original method for iterative improvement of the classification structure. The suitability of this approach is indicated by improved cluster interpretation and correction of initial misclassification. Canonical discriminant analysis reveals that most of the reclassified *Anthyllis* taxa can be differentiated reliably using morphological features (Fig. 2), although all these species belong to the section *Anthyllis* (syn. *Vulneraria* DC.) (Juzepczuk 1945, Tabaka 1982), and are morphologically quite similar (Krall 1983). According to the statistical analysis, the similarity is expressed strongly for *A. arenaria*, *A. maritima*, and *A. macrocephala* and for their hybrids, or reflects a specific trait of *A. maritima*, a highly variable species. It is highly questionable whether separation of these three species is justified, and this in turn does not support differentiation of their hybrids.

Only molecular studies will clarify definitively the questions surrounding *Anthyllis* species taxonomy, and this work should be considered a framework for subsequent genetic analyses.

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