

## Trichomes in the tribe Lactuceae (Asteraceae) – taxonomic implications

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**Abstract:** Although the infratribal classification of the Lactuceae has been the focus of several studies, relationships between the genera are not yet fully resolved. While trichome characters have been shown to be an important tool in taxa delimitation in many plant families, a detailed study on trichomes within the Lactuceae was still lacking. We assess here how trichome types can contribute to the clarification of generic relationships in this tribe. Trichome diversity was investigated on stems and leaves of 135 representatives of 53 genera by light and scanning electron microscopy. According to their morphology and anatomy, trichomes were classified into eight types and several subtypes. Phenetic analysis based on the presence or absence of particular trichome types was performed. The previously supposed monophyly of exclusively American genera and affinities between several closely related genera were confirmed. A new circumscription of the subtribe Hieraciinae is proposed, in accordance with recent molecular data. According to the present study, this subtribe is characterized by a unique combination of two trichome types and comprises the following genera: *Andryala*, *Hieracium*, *Hispidella*, *Pilosella*, *Stenotheca*. The previously included genera *Arnoseris*, *Hololeion* and *Tolpis* do not belong to this assemblage and their removal from the Hieraciinae should be reconsidered.

**Key words:** Compositae; light microscopy; micromorphological characters; SEM; systematics

### Introduction

The tribe Lactuceae Cass. comprises 98 genera and more than 1550 species (Bremer 1994). The milky latex and the floral structure make the tribe easily distinguishable from all other Asteraceae. This evident distinction was the reason of raising the Lactuceae to subfamilial or familiar rank by some authors (e.g. Cronquist 1977). Currently, the Lactuceae are considered a tribe within the Asteraceae (Bremer 1994). Phylogenetic studies in Asteraceae based on both morphological (Karis et al. 1992) and molecular (Jansen et al. 1991; Kim et al. 1992) data have indicated that the Lactuceae are monophyletic. The Liabeae (Cass.) Rydb. and Veroniae Cass. are considered their closest relatives.

The Lactuceae are mostly herbs, only a few are shrubby plants. Leaves are generally alternate or arranged in rosettes. The florets are exclusively ligulate and zygomorphic with five lobes of the corolla fused or nearly fused to the tips (Bremer 1994). The most common pollen type is echinolphate, though echinate grains have been found in most subtribes (Tomb 1975; Blackmore 1984). Basic chromosome num-

ber varies from  $x = 3-10$  with 9 being the most common (Stebbins 1953; Whitton et al. 1995). The Lactuceae are mostly confined to the Northern Hemisphere, with three main centres of diversity: the Mediterranean area, Central Asia and southwestern North America. A few genera and generic groups are also distributed in the Southern Hemisphere, for example *Hypochaeris* L. in South America. The subtribe Sonchinae K. Bremer has scattered, almost cosmopolitan distribution. Many Lactuceae are widespread weeds, including species of *Sonchus* L. and *Taraxacum* Weber (Bremer 1994).

Although the circumscription of the Lactuceae has not changed since its recognition by De Jussieu in the 18th century, the subtribal classification is problematic and remains unstable. The early attempts of subdividing the Lactuceae were based on only a few characters and in view of modern taxonomy they are considered to be artificial (Stebbins 1953; Bremer 1994; Whitton et al. 1995).

A major improvement of the classification within the tribe was carried out by Stebbins (1953). Instead of placing the genera into a few major subdivisions based on one or two key characters, he considered each genus

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separately and placed it next to the most similar genera with respect to the largest number of shared characters (morphological, palynological and karyological). Accordingly, he subdivided the Lactuceae to eight subtribes, within which he recognized several lines. Jeffrey (1966) slightly enlarged this character set and informally subdivided the Lactuceae into five groups, eight subgroups and 18 series. His groups and subgroups correspond to Stebbins' subtribes, while Stebbins' lines and Jeffrey's series are roughly equivalent.

In a most recent classification of the Lactuceae (Bremer 1994) cladistic approach was used. Selected characters (morphological, palynological and karyological) were scored on 23 genera that were selected to represent presumably monophyletic groups within the Lactuceae, or had been considered as isolated or important for the tribe's phylogeny. This approach resulted in 11 subtribes (three of them were newly circumscribed); the genera *Cichorium* L. and *Scolymus* L. were not assigned to any of the subtribes in order to avoid monogeneric subtribes.

To evaluate the support for each of the previous classifications, restriction site variation of the chloroplast DNA was examined (Whitton et al. 1995). The monophyly of several lineages, as suggested by previous authors, was confirmed. But none of Stebbins' (1953) or Bremer's (1994) North American subtribes were confirmed as monophyletic, however, all studied North American genera form a well supported monophyletic group.

Trichomes are defined as uni- or multicellular surface structures possessing both, cell wall and lumen. They originate from epidermal cells and develop on the outer surface of various plant organs (Werker 2000). Their direct contact with the surrounding environment determines their role for protection from adverse biological, chemical and physical conditions, their absorbing and secretory activities and influence pollination and seed dispersal (Uphof 1962; Werker 2000). Because of their enormously high morphological diversity, different origin, location and surface microstructure, capability and mode of secretion, their classification is not easy (Werker et al. 1985). The basal classification of trichomes distinguish between glandular and eglandular types (Werker 2000). With respect to morphology, trichomes may differ in cell number (uni/multicellular), arrangement (uni-, bi- or multiseriate), shape (e.g., branched, unbranched, symmetrical, asymmetrical) and length (Werker 2000). More than 300 forms of plant trichomes have been described (Spring 2000). Despite this obvious morphological heterogeneity, often a similarity in the nature of indumentum was observed among genera that resemble each other also in other characters (Stebbins 1953). Trichome types are therefore considered as important accessory characters, especially at lower taxonomic levels (e.g. Stebbins 1953; Faust & Jones 1973; Napp-Zinn & Eble 1980; Sahu 1982, 1984; Hoot 1991; Al-Shamary & Gornall 1994; Koryuk 1997).

While the main studies aiming at the classifica-

tion within the Lactuceae (Stebbins 1953; Jeffrey 1966; Bremer 1994) touched on trichomes to various extents, none of them were primarily interested in this aspect. Sporadically, some trichome figures of several representatives of the Lactuceae have been published (e.g. Zahn 1921–1923; Chambers 1955; Pittoni 1974; Lack 1977), but studies specializing on trichome morphology of particular genera or groups of taxa are extremely rare.

The present study is the first attempt to elaborate a detailed survey of these structures in the Lactuceae. Our main aims are: (i) to describe the morphology and anatomy of trichomes on vegetative organs in a representative set of genera; (ii) to prepare a classification of trichome types based on their anatomy and morphology; (iii) to investigate affinities among the analysed genera based on the distribution of trichome types; and (iv) to discuss these results with respect to taxonomic arrangements based on other (morphological, karyological, palynological and molecular) data.

## Material and methods

### *Plant material*

Our selection of genera was such as to represent Bremer's subtribal classification. As far as material was available, the size of the genera was reflected by the number of investigated taxa. Most of the plant material was obtained from herbarium specimens deposited in the following institutions (BRA, BP, BEO, PR, M, MAF, SAV, TNS; acronyms according to Holmgren et al. 1990) and from the herbarium collection of P. Mráz (deposited at the Institute of Biology & Ecology, P. J. Šafárik University in Košice). The rest of the material originated from living plants collected in the field or from plants cultivated in the Botanical Garden of P. J. Šafárik University. Voucher specimens of the latter are deposited in the herb. Mráz. A list of all studied taxa and their origin is given in Appendix 2. Our generic taxonomic concept generally follows Flora Europea (Tutin et al. 1976). The genera *Hieracium* L., *Pilosella* (Hill) S.F. Gray and *Stenothecca* (Monn.) Torr. & A. Gray are treated separately. Splitting the genus *Scorzonera* L. s. l. into *Scorzonera* L. s. str. and *Podospermum* DC. is supported by their respective monophyly according to ITS data (Mavrodiev et al. 2004). The nomenclature of non-European taxa is based on particular monographs (e.g., Jeffrey 1966; Vuilleumier 1973; Jarvis 1980) or on Bremer (1994). In many cases, the online version of Index Kewensis (The International Plant Names Index 2004) was consulted for nomenclature.

### *Light and scanning electron microscopy*

Trichome structures were studied on vegetative parts only (stems and leaves). Samples were prepared from hand cut or peeled epidermis. Trichomes structures change their shape, due to the loss of water during the drying, therefore small pieces of stems and leaves from herbarium specimens were boiled in distilled water for a short time before the preparation of samples. In some cases, the sections were stained with safranin to sharpen the cell walls of the observed structures. In case of glandular trichomes with very dense secretory material deposited in glandular heads, samples were made transparent using the technique of Dizeo de Strittmatter (described in Stenglein et al. 2003). Light microscope figures were drawn with help of Abbe's apparatus. Light microscope photographs were taken from samples mounted

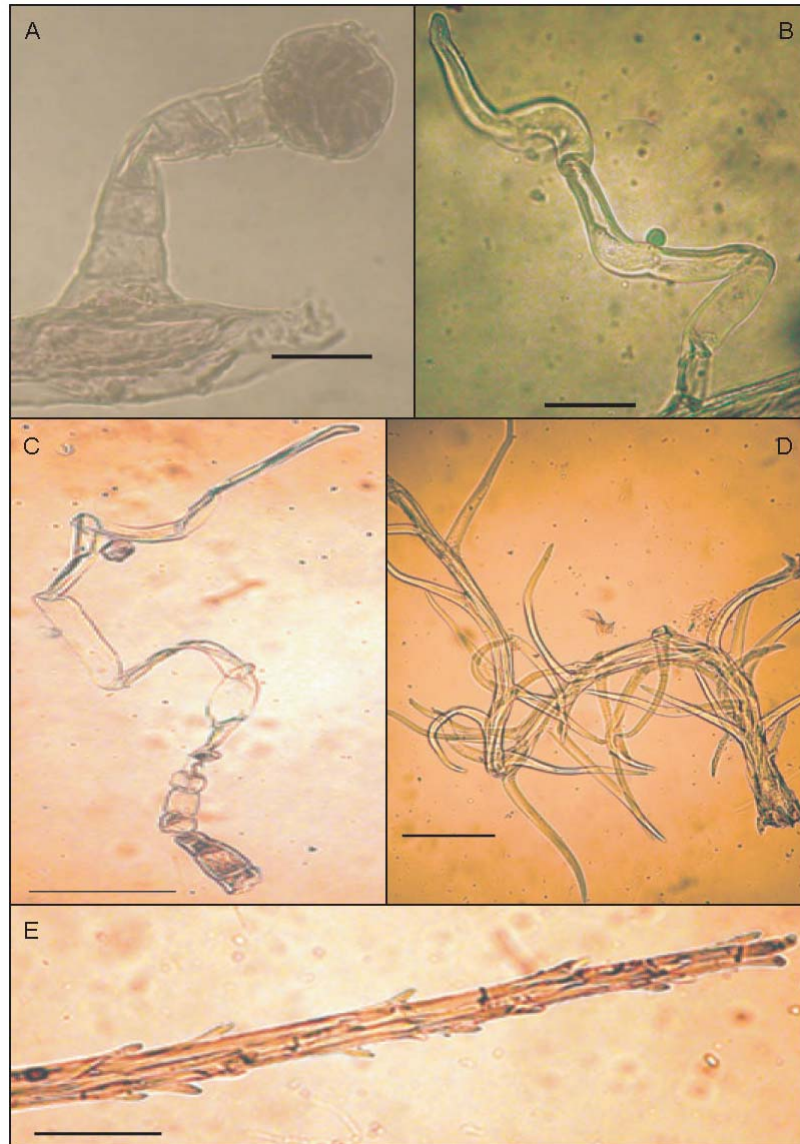


Fig. 1. A – Uniseriate glandular trichome with multicellular head; *Stephanomeria exigua* subsp. *daneii* (scale bar 10  $\mu\text{m}$ ). B – Uniseriate filiform unbranched trichome; *Crepis jacquini* (scale bar 10  $\mu\text{m}$ ). C – Uniseriate filiform trichome with elongated apical cells; *Hypochaeris uniflora* (scale bar 20  $\mu\text{m}$ ). D, E – Multiseriate eglandular trichomes with projecting cell apices; *Hieracium lanatum* (D), *Hispidella hispanica* (E), (scale bars 20  $\mu\text{m}$ ).

in glycerol jelly with acetocarmine with an Olympus digital camera.

For SEM, small pieces of herbarium specimens were coated with 20 nm golden layers. The samples were examined in a Tesla BS-340 scanning electron microscope in the Laboratory of Electron Microscopy and Microanalyses at the Institute of Material Research of the Slovak Academy of Science in Košice.

Samples from fresh material (*Hieracium*) were prepared according to the protocol of Mráz & Polónyi (1988). After this procedure the samples were coated with 20 nm thick golden layers, observed and photographed with a JEOL JXA-840A scanning electron microscope at the Central Laboratory of Electro-optic Methods, Faculty of Sciences of the Comenius University in Bratislava.

#### Trichome classification

The two major, well-established groups, glandular and eglandular trichomes were accepted and further subdivided

into several trichome types according to morphological and anatomical criteria. For glandular trichomes, these were number of rows of basal and stalk cells, number of the neck and head cells. A further categorisation of the eglandular trichomes was done according to the number of cells they were composed of and the arrangement and shape of these cells (see Results).

#### Data analysis

The data obtained from the analyzed taxa (species, subspecies) were generalized at the generic level. If both, glabrous and hairy taxa were found in a particular genus, trichome types observed in the hairy one(s) were considered characteristic for the whole genus. The particular trichome types were scored by 0 (absence) and 1 (presence) in all accessions. If trichome types were subdivided into several subtypes, the main type and the subtype were scored separately. To get an overall view on the phenetic relationships among

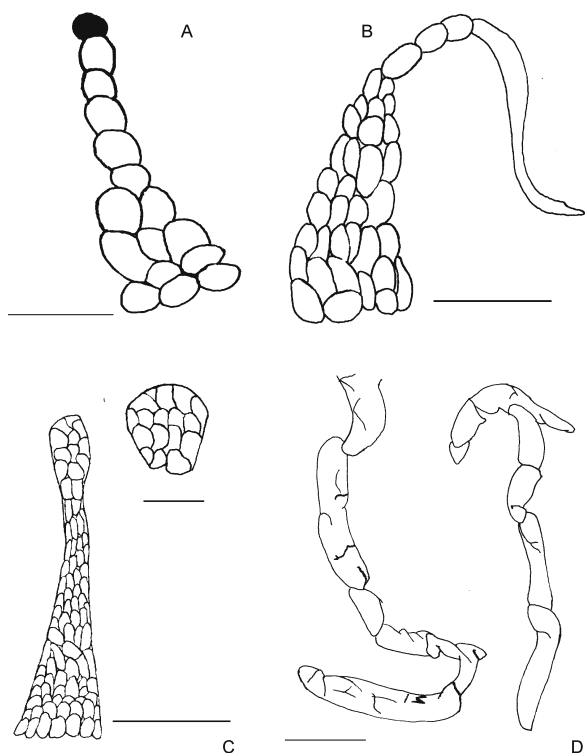


Fig. 2. A – Uniseriate glandular trichome with multiseriate base and unicellular head; *Prenanthes barbata* (scale bar 100  $\mu\text{m}$ ). B – Uniseriate eglandular trichomes with multiseriate base; *Prenanthes barbata* (scale bar 100  $\mu\text{m}$ ). C – Multiseriate glandular trichome; *Dubyaea hispida* (scale bar 200  $\mu\text{m}$ , detail 50  $\mu\text{m}$ ). D – Uniseriate filiform branched trichome; *Chondrilla juncea* (scale bar 100  $\mu\text{m}$ ).

genera, cluster analysis based on genera as operational taxonomic units (OTUs) was performed. The average linkage method (UPGMA) using Jaccard coefficient was chosen as clustering algorithm. The primary data matrix was analyzed with the Freetree software (Pavliček et al. 1999). The final layout of the dendrogram was constructed with Treeview (Page 1996).

## Results

### Trichome classification

Based on the studied material we are describing a number of trichome types and subtypes for the tribe Lactuceae. Trichomes with glandular cell(s) filled with secrete material that form uni- or multicellular heads comprise types A–C, eglandular trichomes are classified as types D–H. In the latter group we can macroscopically distinguish trichomes that give plant hairy and hirsute character (types D–G) and those that form a fine cobweb-like and often dense coating on plant organs (type H).

#### A. Uniseriate glandular trichomes with multicellular head

Composed of a unicellular base, multicellular stalk and a multicellular head with a number of stalk cells arranged in one row varying from five to ten, with seven being the most common number observed (Fig. 1A).

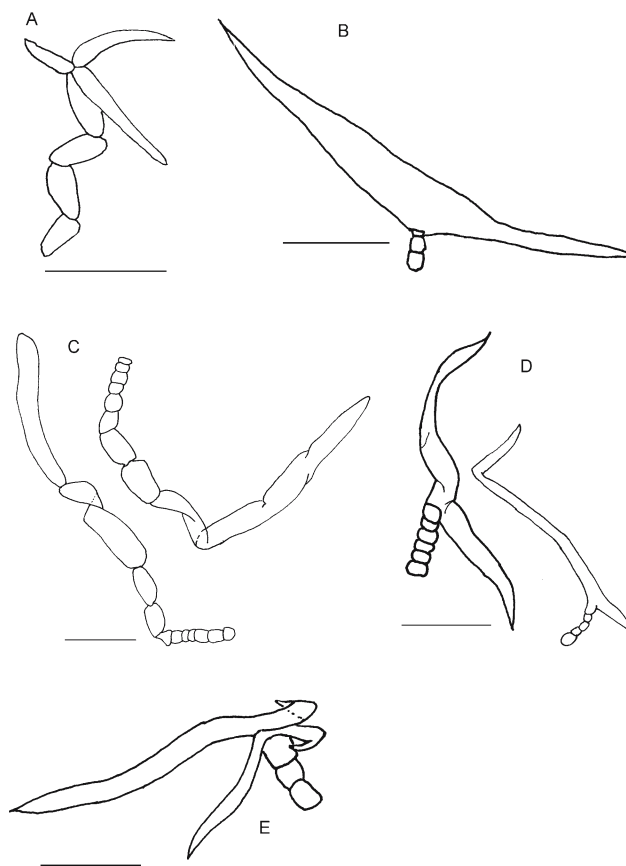


Fig. 3. A – Uniseriate filiform branched trichome; *Scorzonera hispanica* (scale bar 100  $\mu\text{m}$ ). B – Uniseriate filiform trichomes with elongated apical cell; *Koelpinia linearis* (scale bar 100  $\mu\text{m}$ ). C – Uniseriate filiform trichomes with elongated apical cells; *Crepis bocconeii* (scale bar 200  $\mu\text{m}$ ). D – Uniseriate filiform trichomes with elongated apical cells (T-shaped); *Crepis alpestris* (scale bar 200  $\mu\text{m}$ ). E – Stellate trichome; *Malacothrix crepoides* (scale bar 100  $\mu\text{m}$ ).

#### B. Uniseriate glandular trichomes with multiseriate base and unicellular head

Base multiseriate, stalk multicellular and uniseriate with unicellular glandular head on the apex (Fig. 2A).

#### C. Bi- or multiseriate glandular trichomes

Usually long, with broad base and multicellular stalk, narrowing towards the apex. Neck cells usually arranged in two rows, rarely more. Head always multicellular (Fig. 2C; Fig 4A).

#### D. Long conical trichomes

Composed of a short basal cell and a very elongated, conical apical cell (Fig. 4B)

#### E. Short conical trichomes

Composed of three to more than ten, roughly equally long cells arranged in one row. Presence of cuticular micropapillae and thick cell walls are characteristic for this type (Fig. 4F).

#### F. Multiseriate eglandular trichomes

Broad-based, conical, with cells arranged into two or more rows. Variable in size. Because of variable shape of the apical part of the trichome and variable shape of cells, we recognize three subtypes (within this type):

##### *F1. Trichomes with projecting cell apices*

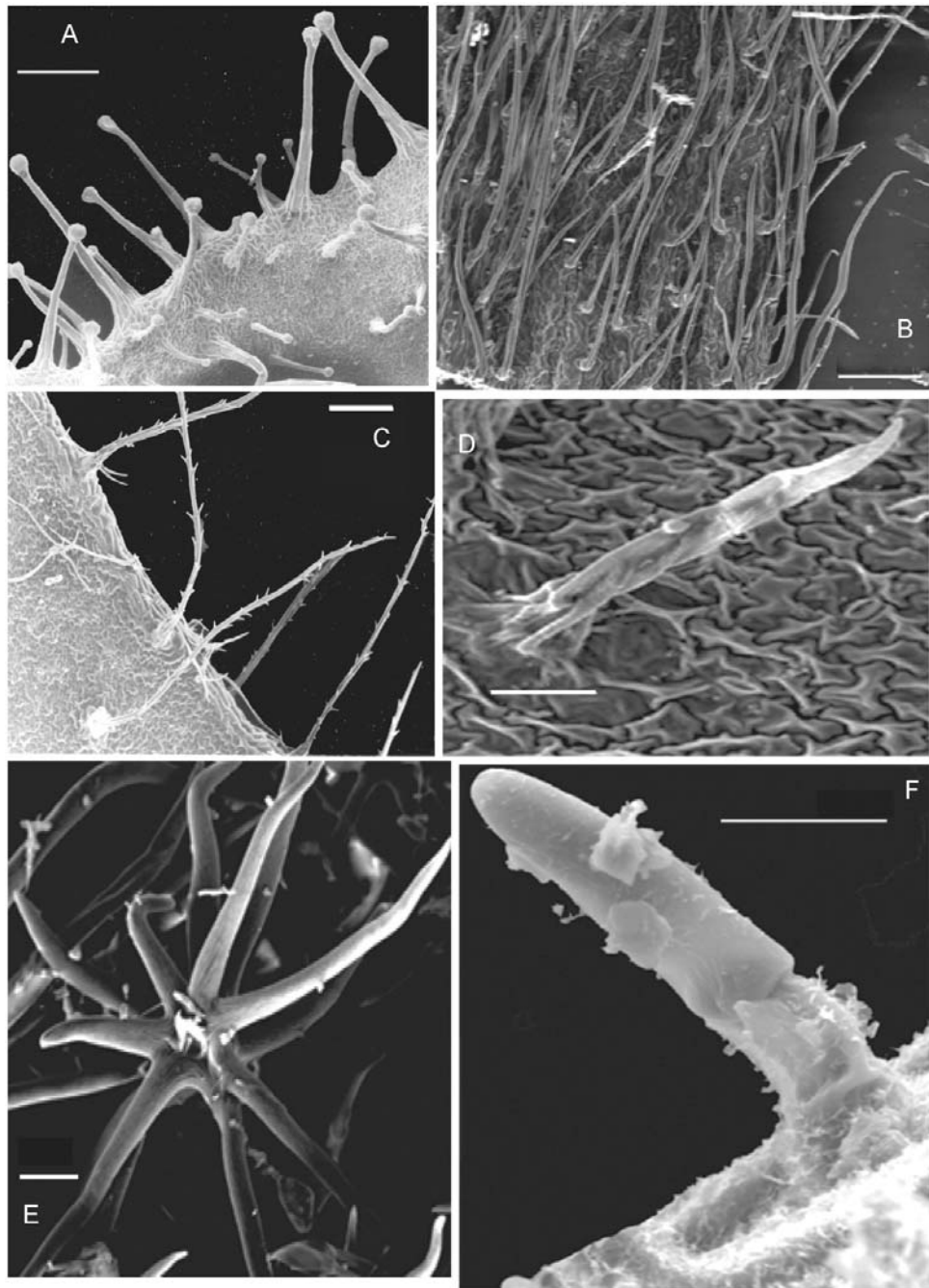


Fig. 4. A – Multiseriate glandular trichomes; *Hieracium amplexicaule* (scale bar 100  $\mu\text{m}$ ). B – Long conical trichomes; *Catananche caerulea* (scale bar 200  $\mu\text{m}$ ). C – Multiseriate eglandular trichomes with projecting cell apices; *Pilosella officinarum* (scale bar 100  $\mu\text{m}$ ). D – Multiseriate eglandular trichomes with non-projecting cell apices; *Hypochaeris uniflora* (scale bar 50  $\mu\text{m}$ ). E – Stellate trichome; *Andryala aghardii* (scale bar 20  $\mu\text{m}$ ). F – Short conical trichome; *Stephanomeria panniculata* (scale bar 20  $\mu\text{m}$ ).

Usually very long, composed of elongated cells with more or less pronounced apical parts. Projecting parts can differ in their length. If the length of the free ends of the cells are once or twice the diameter of the rachis, they may be termed barbellate, or coarsely barbellate, possibly tending to be subplumose (Fig. 1E; Fig. 4C). If the free ends are three times the diameter of the rachis then the hair may be considered plumose (Fig. 1D).

**F2. Trichomes with non-projecting cell apices**

Apical parts of trichome cells not pronounced. Trichome apex composed of two, rarely one cell. These

trichomes widely differ in their length (Fig. 4D).

**F3. Trichomes with branched apices**

Apex branched, composed of 2–4, sometimes more cells of variable shape (straight, hooked) (Fig. 5A, C).

**G. Uniseriate eglandular trichomes with multiseriate base**

Base multiseriate, trichome body uniseriate. Apical cell markedly elongated in most taxa (Fig. 2B)

**H. Uniseriate filiform trichomes**

Uniseriate, forming a fine sparse or dense filamentous reticulum (net) on different organs. In some taxa



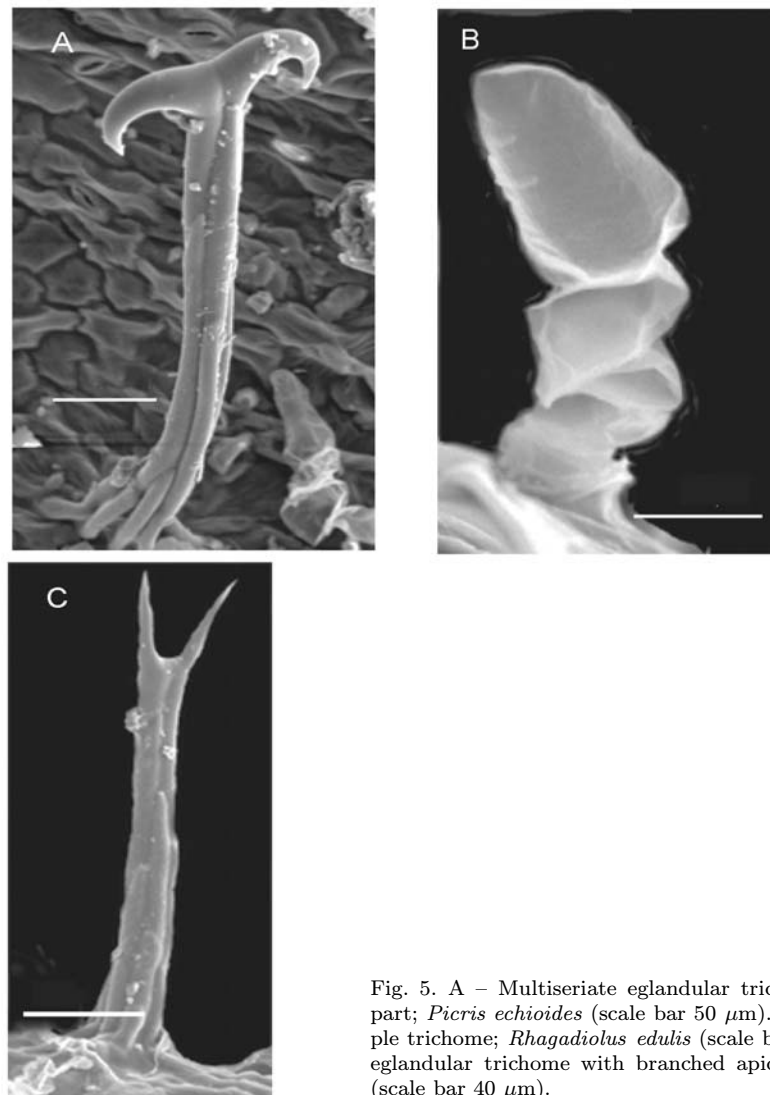


Fig. 5. A – Multiseriate eglanular trichome with branched apical part; *Picris echiooides* (scale bar 50  $\mu\text{m}$ ). B – Uniseriate filiform simple trichome; *Rhagadiolus edulis* (scale bar 20  $\mu\text{m}$ ). C – Multiseriate eglanular trichome with branched apical part; *Picris hieracioides* (scale bar 40  $\mu\text{m}$ ).

present on young organs only. According to cell shape and differences between the apical and basal part, we recognize four subtypes (within this type).

*H1. Uniseriate filiform simple trichomes*

Filamentous structures, very variable in length, composed of cells more or less equal in size and shape (Fig. 1B; Fig. 5B).

*H2. Uniseriate filiform branched trichomes*

Filamentous, randomly branched. Number of branches variable, three being the most common. Composed of more or less equally long cells (Fig. 2D; Fig. 3A)

*H3. Stellate trichomes*

Trichomes with a multicellular stalk, with cells usually arranged in one row (stalk base occasionally bi- or multiserial). One or two branched apical cells. Number of branches varying mostly from 7 to 12 (Fig. 3E; Fig. 4E).

*H4. Trichomes with elongated apical cells*

Trichomes composed of uniseriate multicellular stalk and one or more apical cell(s), the latter considerably elongated in comparison with the stalk cells (usually longer than the whole stalk), in some cases forming

two branches (T-shaped trichomes) (Fig. 1C; Fig. 3 B,C,D)

The distribution of the trichomes in the analysed taxa is given in Table 1, their description in the studied genera is given in Appendix 1.

*Generic affinities based on the presence and absence of trichome types*

The complete absence of pubescence is not informative for assessing the resemblance among the analyzed genera. According to preliminary analyses, the glabrous genera form an unresolved group besides the other 'hairy' Lactuceae and were excluded from further analyses.

Trichomes unique for one genus (types B and G for *Prenanthes*) or for only one taxon (type A for *Stephanomeria exigua* subsp. *daneii* or type D for *Catananche caerulea*) have been observed. Uniseriate filiform simple trichomes (type H1) were the most frequent (recorded in 21 out of 42 hairy genera) and therefore are taxonomically less informative.

For 8 out of 9 'hairy' American genera, the absence of multiserial eglanular trichomes (type F) is charac-

Table 1. Trichome types in the analysed taxa.

Taxon	Stem	Leaves	Taxon	Stem	Leaves
<i>Agoseris alpestris</i>	H1	–	<i>Koelpinia linearis</i>	H4	H4
<i>Agoseris gaspensis</i>	H1	H1	<i>Krigia amplexicaulis</i>	C	–
<i>Andryala agardhii</i>	C, H3	H3	<i>Krigia montana</i>	H1	H1
<i>Andryala integrifolia</i>	C, H3	F1, H3	<i>Lactuca perennis</i>	–	–
<i>Andryala laevitomentosa</i>	C, H3	H3	<i>Lactuca saligna</i>	–	–
<i>Andryala pinnatifida</i>	C, H3	F1, H3	<i>Lactuca serriola</i>	–	–
<i>Andryala ragusina</i>	H3	H3	<i>Lapsana communis</i>	C, F2	F2
<i>Aposeris foetida</i>	H1	F2	<i>Launaea pumila</i>	–	–
<i>Arnoseris minima</i>	–	E	<i>Launaea stenocephala</i>	–	H1
<i>Catananche caerulea</i>	D	D	<i>Launaea taraxacifolia</i>	H1	–
<i>Cephalorrhynchus picridiformis</i>	–	–	<i>Leontodon autumnalis</i>	F3, H1	F3, H1
<i>Cephalorrhynchus soongoricus</i>	–	–	<i>Leontodon hispidus</i>	F3, H1	F3, H1
<i>Cephalorrhynchus polycladus</i>	–	–	<i>Leontodon montanus</i>	F2, H1	F2, H1
<i>Chondrilla canescens</i>	H2	H2	<i>Lygodesmia rostrata</i>	E	–
<i>Chondrilla juncea</i>	H2	–	<i>Lygodesmia spinosa</i>	E, H1	E, H1
<i>Chondrilla pauciflora</i>	–	–	<i>Macrorhynchus troximoides</i>	H1	H1
<i>Chondrilla chondrilloides</i>	–	–	<i>Malacothrix crepoides</i>	C, H3	C, H3
<i>Chondrilla ramosissima</i>	F2	H2	<i>Malacothrix obtusa</i>	H1	H1
<i>Chondrilla yosii</i>	–	–	<i>Malacothrix saxatilis</i>	H1	H1
<i>Chlorocrepis staticifolia</i>	H1	H1	<i>Microseris douglasii</i>	–	–
<i>Cicerbita alpina</i>	C	C	<i>Microseris linearifolia</i>	H1	H1
<i>Cicerbita panicii</i>	–	–	<i>Microseris troximoides</i>	H1	H1
<i>Cichorium intybus</i>	C, F2	C, F2	<i>Mycelis muralis</i>	–	–
<i>Crepis alpestris</i>	C, F2, H4	H4	<i>Nothocalais cuspidata</i>	H1	H1
<i>Crepis aurea</i>	C, F2, H1, H4	–	<i>Paraixeris denticulata</i>	–	–
<i>Crepis biennis</i>	F2, H4	F2	<i>Picris hieracioides</i>	F3, H4	F3
<i>Crepis bocconi</i>	F2, H4	F2, H4	<i>Picris echiioides</i>	F3	F3
<i>Crepis bulbosa</i>	C	–	<i>Pilosella echiioides</i>	F1, H3	F1, H3
<i>Crepis diversifolia</i>	H1, H4	–	<i>Pilosella macrantha</i>	C, F1, H3	F1, H3
<i>Crepis foetida</i>	F2, H4	F2, H4	<i>Pilosella officinarum</i>	C, F1, H3	H3
<i>Crepis jacquini</i>	H1	H1	<i>Podospermum canum</i>	H2	–
<i>Crepis pannonica</i>	F2	F2, H4	<i>Podospermum laciniatum</i>	H2	H2
<i>Crepis praemorsa</i>	F2, H1	F2	<i>Prenanthes albus</i>	–	F2
<i>Crepis pulchra</i>	F2	F2, H1, H4	<i>Prenanthes barbata</i>	B, G	B, G
<i>Crepis pyrenaica</i>	F2, H4	F2	<i>Prenanthes crepidinea</i>	B, G	B, G
<i>Crepis sibirica</i>	F2, H4	F2	<i>Pyrrhopappus multicaulis</i>	–	–
<i>Crepis tenuifolia</i>	–	–	<i>Reichardia macrophylla</i>	–	–
<i>Crepis viscidula</i>	C, F2, H4	F2, C	<i>Rhagadiolus stellatus</i>	F2, H1	F2
<i>Crepis zacintha</i>	F2, C	F2	<i>Scolymus hispanicus</i>	–	E, H1
<i>Crepidiastrum keiskeanum</i>	–	–	<i>Scolymus maculatus</i>	–	E
<i>Crepidiastrum lanceolatum</i>	–	–	<i>Scorzonera hispanica</i>	H2	H2
<i>Crepidiastrum platyphyllum</i>	–	–	<i>Scorzonera rosea</i>	H2	–
<i>Dendroseris pruinata</i>	–	–	<i>Sonchus arvensis</i>	C	–
<i>Dubyaea hispida</i>	–	C, H1	<i>Sonchus asper</i>	–	H1
<i>Haenselereia granatensis</i>	–	H1	<i>Sonchus oleraceus</i>	–	H1
<i>Hedypnois cretica</i>	F3	F3	<i>Sonchus palustris</i>	C	–
<i>Hieracium amplexicaule</i>	C, H3	C	<i>Stephanomeria cichoriacea</i>	H1	H1
<i>Hieracium eriophorum</i>	F1	F1	<i>Stephanomeria exigua</i>	A	–
<i>Hieracium japonicum</i>	H3	F1	<i>Stephanomeria minor</i>	H1	–
<i>Hieracium lanatum</i>	F1	F1	<i>Stephanomeria paniculata</i>	E	–
<i>Hispidella hispanica</i>	F1, H3	F1, H3	<i>Taraxacum sect. Ruderalia</i>	–	H1
<i>Hololeion maximoviczii</i>	–	–	<i>Taracum sect. Erythrosperma</i>	–	H1
<i>Hololeion krameri</i>	–	–	<i>Tolpis barbata</i>	E, H4	E
<i>Hymenonema graecum</i>	–	E	<i>Tolpis capensis</i>	H4	E
<i>Hymenonema laconicum</i>	–	E	<i>Tolpis coronopifolia</i>	H4	H4
<i>Hyoseris radiata</i>	F2	F2	<i>Tolpis laciniata</i>	H1	H1
<i>Hyoseris scabra</i>	–	F3	<i>Tolpis lagopoda</i>	–	E, H4
<i>Hypochaeris acaulis</i>	–	–	<i>Tolpis macrorhiza</i>	H4	H4
<i>Hypochaeris elata</i>	H4	F2, H4	<i>Tolpis succulenta</i>	H4	–
<i>Hypochaeris glabra</i>	–	F1	<i>Tolpis virgata</i>	–	–
<i>Hypochaeris incana</i>	H1	F2	<i>Tolpis webbii</i>	–	–
<i>Hypochaeris maculata</i>	F2, H4	F2	<i>Tragopogon orientalis</i>	H1	–
<i>Hypochaeris setosus</i>	–	F2	<i>Urospermum daleschampii</i>	F2	F2
<i>Hypochaeris variegata</i>	F2	F2	<i>Urospermum picroides</i>	F2	F2
<i>Hypochaeris uniflora</i>	F2, H1, H4	F2	<i>Willemetia stipitata</i>	C	–
<i>Ixeridium gramineum</i>	–	–	<i>Youngia japonica</i>	E	–
<i>Ixeris dentata</i>	–	–	<i>Youngia racemifera</i>	F2	F2
<i>Ixeris polycephala</i>	–	–			
<i>Ixeris stolonifera</i>	–	–			

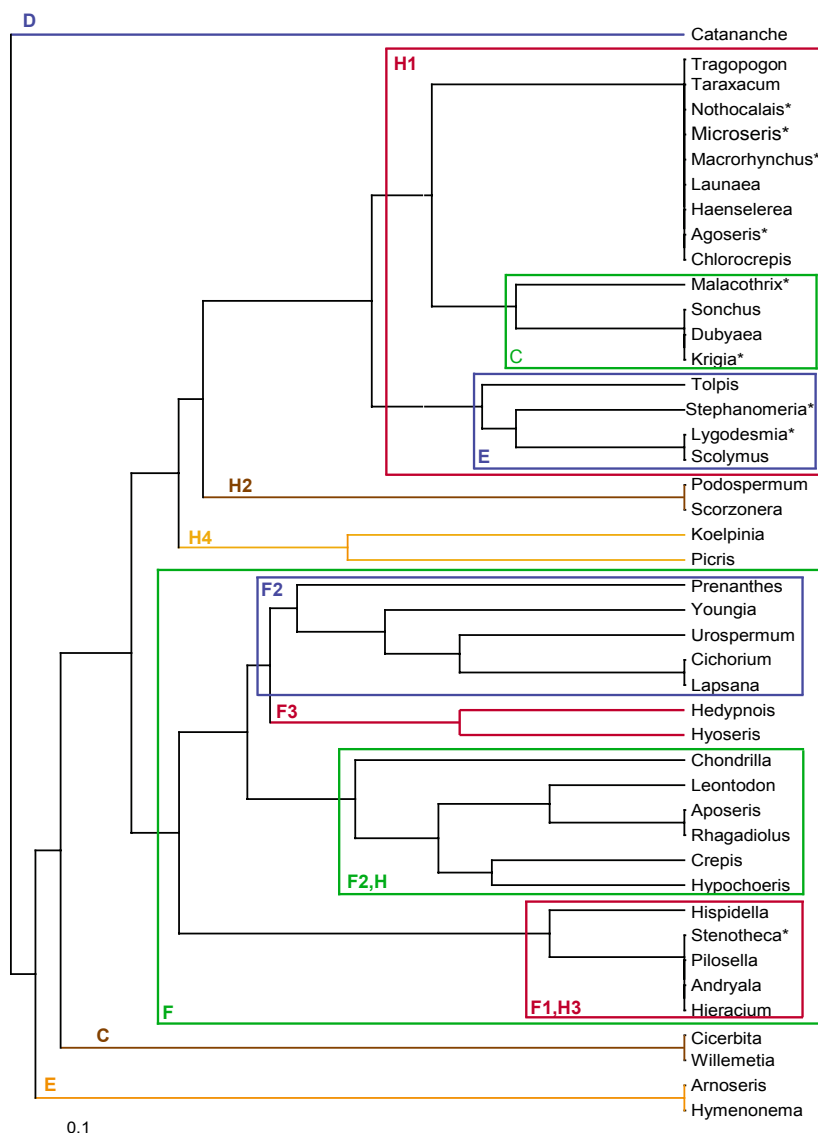


Fig. 6. Tree based on the distribution of the trichome types among the analysed “hairy” genera. Groups of genera characterised by the presence of particular trichome type(s) are marked by coloured rectangles and branches, the coloured characters are the abbreviations of these trichome types (see Results – trichome classification). American genera are marked by asterisk.

teristic. It seems that the presence of F type trichomes is often correlated with co-occurrence of multiserial glandular hairs (Type C) and that the latter type is very rare in New World genera for that reason.

*Catananche* is basal to the rest of the Lactuceae. Its position is due to the uniqueness of the D-type. In *Arnosseris* and *Hymenonema* only the type E was found. Similarly *Cicerbita* and *Willemetia* are characteristic by the occurrence of the type C. Although these types were observed in other genera as well, the lack of other types in the *Arnosseris-Hymenonema* and *Cicerbita-Willemetia* sets them apart of the other genera.

The remaining Lactuceae are subdivided into two groups. For one of them the presence of the type F is characteristic (Fig. 6, green rectangle marked as F). This type is missing in the genera belonging to the other branch with, exception of *Picris* (types F3 and H4). This genus is grouped together with the genus *Koelpinia* (only H4) due to the occurrence of the H4

type. Although it was observed in *Tolpis*, *Crepis* and *Hypochoeris* as well, they have other types that place them together with other genera. In *Tolpis* they co-occur with the E and H1, in *Crepis* and *Hypochoeris* with F2 and H1 types. *Podospermum* and *Scorzonera* cluster together due to the occurrence of the H2 type. The rest of the F-type lacking group is characterised by the presence of the H1 type and is further subdivided due to its co-occurrence with the types C or E.

The F-type bearing group is composed of 18 genera that are further subdivided. The genera *Hieracium*, *Pilosella*, *Stenotheca*, *Hispidella* and *Andryala* are separated from the core of the group by the co-occurrence of the F1 and H3 types. The core group possess the two other subtypes of the type F and within this cluster two groups are separated by the presence or absence of the H-type. In the H type-lacking group *Hedypnois* and *Hyoseris* are apart the rest of the genera. They are characterised by the presence of the F3 type that is the



only type observed in *Hedypnois* and co-occurring with the F2 in *Hyoseris*.

## Discussion

In comparison with a coarse classification of only four Lactuceae trichome types (Stebbins 1953), our more detailed categories correspond to his as follows: (i) our uniseriate filiform trichomes (type H with four subcategories) were described by him as ‘slender trichomes that may form fine or coarse and arachnoid tomentum’, (ii) his ‘spreading hairs’ comprise our multiserial eglanular trichomes (type F with three subcategories) and our uniseriate long conical trichomes (type D), (iii) we included his ‘coarse spreading trichomes with forked or stellate apex’ into our subtype F3 (multiserial eglanular trichomes with branched apical parts), (iv) his ‘coarse spreading trichomes with glands at the apex’ correspond to our multi- or biserial glandular trichomes (type C).

Additionally, we recognize two further types of glandular trichomes, uniseriate glandular ones without or with multiserial basis (types A and B, respectively). Whether Stebbins did not recognize our trichome types E and G or whether they are included into one of his four categories cannot be decided, because he did not study their morphological and anatomical differences in further detail.

Although one of the aims of the present study was searching for affinities between the analyzed genera, it would be misleading to consider it as a classification system of the Lactuceae. The reason for including resemblance analysis in this work was the assessment of the contribution of trichomes to the clarification of relationships in the tribe at generic level.

For the analysed American genera the lack of the F- type is characteristic, the only exception is *Stenotheca*. This genus is closely related to genus *Hieracium*. In some taxonomic concepts, it is included into *Hieracium* (as *Hieracium* subgen. *Chionoracium* Sch. Bip. (e.g. Zahn 1921–1923; Guppy 1978; Beaman 1990)). The absence of the F type in the remaining 8 exclusively American genera is not surprising. Stebbins (1953) found that his “spreading hairs” are present in the majority of Old World genera, but absent in nearly all genera endemic to the New World. This finding is in concordance with the results obtained from cpDNA (Whitton et al. 1995) and ITS sequence data (Lee et al. 2003) according to which the American Lactuceae are monophyletic with the exception of the monotypic genus *Phalacroseris*.

The genera *Hieracium*, *Pilosella*, *Stenotheca*, *Andryala* and *Hispidella* (unique combination of F1 and H3 types observed) were, together with *Tolpis*, *Hololeion* and *Arnoseris*, included by Bremer (1994) in the subtribe Hieraciinae (he treated the *Stenotheca* as a subgenus of *Hieracium*). In genus *Tolpis*, uniseriate short conical eglanular trichomes (type E), uniseriate filiform simple trichomes (type H1) and uniseriate trichomes with elongated apical cells (type H4) were

observed. For genus *Arnoseris*, the E-type is characteristic, and our representatives of *Hololeion* are glabrous. The dissimilarity between these three and the above-mentioned genera was revealed by other characters as well. *Arnoseris* and *Hololeion* have clearly different fruit morphology compared to the rest of Bremer’s Hieraciinae (Sennikov & Illarionova 2002). *Arnoseris* also differs from *Hieracium*, *Andryala* and *Pilosella* in respect to pollen architecture (Blackmore 1984). According to cypsel anatomy, *Tolpis* was considered to be the most primitive member of the Hieraciinae (Sennikov & Illarionova 2002). However, pollen grains of *Tolpis* are rather similar to those of *Arnoseris* (Askerova 1970; Blackmore & Jarvis 1986). The distinction between *Tolpis* and our *Hieracium-Pilosella-Andryala-Hispidella* group is further supported by *ndhF* chloroplast gene sequences (Park et al. 2001). Although the pollen grains of the monotypic genus *Hispidella* are similar to those of *Tolpis* and *Arnoseris*, Jeffrey (1966) found a close relationship of *Hispidella* with *Pilosella*, *Andryala* and *Hieracium* based on other morphological characters, that is in concordance with cpDNA and ITS sequence data (Fehrer et al. 2007). According to these results the removal of the genera *Arnoseris*, *Hololeion* and *Tolpis* from the Hieraciinae sensu Bremer should be reconsidered.

Despite higher number of trichome types and subtypes was described, their contribution to the relationships on generic level is rather small. Apart of the above mentioned, the analysis based solely on trichomes characters did not reveal any other trends, which would be in congruence with results obtained from different data. Even not in the case of such morphologically compact and unambiguously distinguishable structures as the F3 type, which presence suggests strong similarity between the genera *Picris*, *Leontodon*, *Hyoseris* and *Hedypnois*. This relationship is supported by other studies (Stebbins 1953; Jeffrey 1966; Baagøe 1980; Blackmore 1981; Bremer 1994; Blackmore & Persson 1996; Samuel et al. 2003) as well. However due to their co-occurrence with several (and widespread) types from which only the F3 is shared by all four genera, it is not reflected in the resulting tree.

The morphological similarity only, seems to be insufficient criterion for delimitation of trichome types as taxonomic characters. It is likely that the morphology of trichomes, structures that are in immediate contact with the surrounding environment, will rather reflect ecological constraints than phylogenetic relationships. Therefore knowledge of their development and its genetic background may help in the future to distinguish homologous structures from analogous ones of similar morphology, but different origin. Especially in the case of abundant and morphologically overlapping forms (as the type H), the insight to these aspects may increase the taxonomic information carried on them. On the other hand trichomes on the fertile parts of plants may be more variable, therefore the investigation of the involucre and inflorescence may increase the level of resolution of the intergeneric relationships. It

may be useful as well in respect of the genera with absence of trichomes on the vegetative organs.

### Acknowledgements

We are thankful to the curators of herbaria BRA, BP, BEO, PR, M, MAF, SAV, TNS for the possibility to use small pieces of specimens for our study, to I. Turisová (Banská Bystrica), L. Mucina (Stellenbosch) and M. Niketić (Beograd) for providing herbarium specimens, to K. Marhold (Bratislava), M. Bačkor (Košice) and C.E. Jarvis (London) for help with literature, to L.D. Gottlieb (Davis) for his kind help with the identification of some *Stephanomeria* species, to the staff of the Laboratory of Electron Microscopy and Microanalyses at the Institute of Material Research of the Slovak Academy of Science in Košice and the Laboratory of Electron-optic methods at the Comenius University in Bratislava for help with the SEM. Grateful thanks are due to J. Fehrer (Průhonice) for her critical comments on the first draft of the manuscript. Financial support was provided by The Research and Development Support Agency (APVT-51-026404) and Grant Agency of the Ministry of Education of the Slovak Republic and the Slovak Academy of Sciences (VEGA project No. 2/6054/26).

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Received July 6, 2007  
Accepted Jan. 25, 2008

## Appendix 1. Description of the trichome types in the analysed genera

### *Agoseris*

Uniseriate filiform simple trichomes (H1). Composed of more than 10 oblong or ovate cells.

### *Andryala*

(i) Multiseriate glandular trichomes (C). Neck cells always in two rows, head multicellular. (ii) Multiseriate eglandular trichomes with projecting cell apices (F1). (iii) Stellate trichomes (H3). Stalk uniseriate, cells longer in the upper part than at the base. Apical cells 1–2, with 7–12 branches. Branches arranged more or less regularly.

### *Aposeris*

(i) Multiseriate eglandular trichomes with non-projecting cell apices (F2). The apex is composed of two partly overlapping cells. (ii) Uniseriate filiform simple trichomes (H1).

### *Arnoseris*

Uniseriate short conical eglandular trichomes (E). Composed of 5–7(–8) cells, with thick cell walls, covered with cuticular micropapillae. Apical cell rounded or pointed.

### *Catananche*

Uniseriate long conical eglandular trichomes (D). This type was observed only in this genus.

### *Cicerbita*

Multiseriate glandular trichomes (C). Always two neck cells.

### *Cichorium*

Multiseriate glandular trichomes (C) and eglandular multiseriate trichomes with non-projecting cell apices (F2).

### *Crepis*

(i) Multi- or rarely biseriate glandular trichomes (C). Always two neck cells. In *C. viscidula* also biseriate ones observed. (ii) Multiseriate eglandular trichomes with non-projecting cell apices (F2). Very variable in width and length, pale, yellow or dark brown. (iii) Uniseriate filiform simple trichomes (H1). Usually very long, composed of oblong cells. (iv) Uniseriate trichomes with elongated apical cells (H4). Stalk cells usually four or more. Apical cells 1–4, long, curved. In *C. pyrenaica*, *C. biennis*, *C. alpestris*, and *C. foetida* apical cells 1–2, divided into two branches (T-shaped trichomes).

### *Chondrilla*

(i) Multiseriate eglandular trichomes with non-projecting cell apices (F2). (ii) Uniseriate filiform branched trichomes (H2). Very long, composed of 4–10 (or even more) oblong cells.

### *Chlorocrepis*

Uniseriate filiform simple trichomes (H1). Very short, curved, appressed.

### *Dubyaea*

(i) Multiseriate glandular trichomes (C). Always two neck cells. (ii) Uniseriate filiform simple trichomes (H1). Long, composed of eight or more oblong cells. Cells gradually elongating from the base to the apical part of the trichome.

### *Haenselereia*

Uniseriate filiform simple trichomes (H1). Short pressed to the organ surface composed of 4–10 cells.

### *Hedypnois*

Multiseriate eglandular trichomes with branched apical part (F3). Apical part forked, composed of two cells. Apical cells larger, possessing thicker cell walls in comparison with the rest.

### *Hieracium*

(i) Multi- or biseriate glandular trichomes (C). Biseriate trichomes: short, base composed of two cells, stalk composed of (6–)8(–10) cells arranged into two rows, head in most cases bicellular. Multicellular trichomes: long, base composed of at least three cells, stalk cells in three or more rows, head multicellular. (ii) Multiseriate eglandular trichomes with projecting cell apices (F1) In *H. lanatum* plumose-like because of very long projecting apical parts of cells. (iii) Stellate trichomes (H3). Stalk composed of 3–5 (–7) cells. Apical cells one or two. Branches straight, crinkled or forked, irregularly arranged.

### *Hispidella*

(i) Multiseriate eglandular trichomes with projecting cell apices (F1). (ii) Stellate trichomes (H3) with uniseriate stalk, apical cells two, branched into 7–10 regularly arranged branches.

### *Hymenonema*

Uniseriate short conical eglandular trichomes (E). Most frequently composed of five cells with thick cell walls. In some cases, base composed of two cells.

### *Hyoseris*

(i) Multiseriate eglandular trichomes with non-projecting cell apices (F2). Very long, apex composed of 2–3 overlapping cells. (ii) Multiseriate eglandular trichomes with branched apex (F3). Apical part composed of two cells, with very thick cell walls. Apical cells larger in comparison with others.

### *Hypochaeris*

(i) Multiseriate eglandular trichomes with projecting cell apices (F1). The apical ends of cells less embossed than in *Pilosella*, *Andryala*, *Hieracium* and *Hispidella*. (ii) Multiseriate eglandular trichomes with non-projecting cell apices (F2). Very long, curved, in most cases two apical cells. (iii) Uniseriate filiform simple trichomes (H1). Very long, composed of 12–15 cells. Cells arranged in one row, in one case (*H. uniflora*) basal cells in two rows. (iv) Uniseriate trichomes with elongated apical cells (H4). Variable in size. Stalk composed of 4–8(–10) round or tetragonal cells. Apical cells 1 or 2, long, curved.

### *Koelpinia*

Trichomes with elongated apical cells (H4). Stalk composed of two or three cells, apical cell always one, several times longer in comparison with the stalk cells, triangular in shape, with thick cell walls.

**Krigia**

(i) Multiseriate glandular trichomes (C). Neck cells two. (ii) Uniseriate filiform simple trichomes (H1). Small, crisped.

**Launaea**

Uniseriate filiform simple trichomes (H1). Variable in size. In *L. stenocephala* minute, in *L. taraxacifolia* very long, composed of 12 or more cells.

**Lapsana**

(i) Multiseriate glandular trichomes (C). Neck cells two. (ii) Multiseriate eglandular trichomes with non-projecting cell apices (F2), composed of big oblong cells, arranged in two or more rows. Trichome base broad (usually three rows of cells), composed of round cells.

**Leontodon**

(i) Multiseriate eglandular trichomes with non-projecting cell apices (F2). (ii) Multiseriate eglandular trichomes with branched apices (F3). Variable in size. Apex branched, composed of 2–7 elongated cells with thick cell walls. (iii) Uniseriate filiform simple trichomes (H1). Cells oblong, their length moderately increasing from base to apex.

**Lygodesmia**

(i) Uniseriate short conical eglandular trichomes (E). Composed of 2–3 cells with thick cell walls with cuticular micropapillae. (ii) Uniseriate filiform simple trichomes (H1). Very long, cells longer in the upper part than at the base. Cuticular micropapillae observed only in the lower part of trichomes.

**Macrorhynchus**

Uniseriate filiform simple trichomes (H1). Composed of more than 10 cells, sparsely covered by cuticular micropapillae.

**Malacothrix**

(i) Multiseriate glandular trichomes (C). Neck cells two. (ii) Uniseriate filiform simple trichomes (H1). Curved, variable in size. In *M. obtusa* long, composed of more than 10 oblong cells. In *M. saxatilis*, composed of 5–10 (sometimes more) tetragonal or oblong cells 2–3 times smaller than in *M. obtusa*. (iii) Stellate trichomes (H3). Stalk composed of three or more tetragonal cells. Apical cells two, each with two (rarely three) branches.

**Microseris**

Uniseriate filiform simple trichomes (H1). Long, composed of less than 10 oblong cells, covered with cuticular micropapillae.

**Nothocalais**

Uniseriate filiform simple trichomes (H1). Long, composed of more than 10 cells. Densely covered by cuticular micropapillae.

**Picris (incl. Helminthotheca)**

(i) Multiseriate eglandular trichomes with branched apical part (F3). Apex composed of 2–4 elongated, declined or straight cells with thick cell walls. Two apical cells typical for *P. hieracioides*, apical part in *P. echioides* composed of 2–4, most commonly three cells. Apical cells usually hooked. (ii) Uniseriate eglandular trichomes with elongated apical cells (H4). Stalk composed of 3–6 cells. Apical cells ovate, mostly 2–3, with thicker cell walls than the stalk cells.

**Pilosella**

(i) Multiseriate glandular trichomes (C). Neck cells always two. (ii) Multiseriate eglandular trichomes with projecting cell apices (F1). (iii) Stellate trichomes (H3). Stalk cells arranged in one row. Apical cells 1–2 with 8–11(–12) branches. Branches arranged more or less regularly.

**Podospermum**

Uniseriate filiform branched trichomes (H2).

**Prenanthes**

(i) Uniseriate glandular trichomes with multiseriate base (B). Basal cells covered with micropapillae, stalk composed of 5–10 cells, head unicellular. (ii) Multiseriate eglandular trichomes with non-projecting cell apices (F2). (iii) Uniseriate eglandular trichomes with multiseriate base (G). The body of the trichome composed of 7–10 (sometimes more) cells. Basal cells covered with cuticular micropapillae.

**Rhagadiolus**

(i) Multiseriate eglandular trichomes with non-projecting cell apices (F2). Apical part composed of two cells. (ii) Uniseriate filiform simple trichomes (H1). Short, composed of ovate cells. Cells gradually elongating from the base to the apical part of the trichome.

**Scolymus**

(i) Uniseriate short conical eglandular trichomes (E). Composed of 3–5 cells with thick cell walls. (ii) Uniseriate filiform simple trichomes (H1). Very long, composed of more than 10 cell of equal size and shape.

**Scorzonera**

Uniseriate filiform branched trichomes (H2).

**Sonchus**

(i) Multiseriate glandular trichomes (C). Neck cells arranged in more than two rows. (ii) Uniseriate filiform simple trichomes (H1). Long, filamentous, composed of ovate or oblong cells. Cells moderately elongated to the apex.

**Stenotheca**

(i) Multiseriate glandular trichomes (C). (ii) Multiseriate eglandular trichomes with projecting cell apices (F1). (iii) Stellate trichomes (H3).

**Stephanomeria**

(i) Uniseriate glandular trichomes with multicellular head (A). Stalk composed of 5–8 cells, head multicellular. (ii) Uniseriate short conical eglandular trichomes (E). Composed of 4–5 cells with thick cell walls. Densely covered by cuticular micropapillae. (iii) Uniseriate eglandular filiform unbranched trichomes (H1). Very long, composed of more than 10 cells of more or less equal size and shape.

**Taraxacum**

Uniseriate filiform simple trichomes (H1). Long, usually composed of more than 10 ovate or tetragonal cells.

**Tolpis**

(i) Uniseriate short conical eglandular trichomes (E). Composed of 4–10(–12) cells. Rarely covered by micropapillae. (ii) Uniseriate filiform simple trichomes (H1). Fine, short, composed of 3–5 cells. (iii) Uniseriate trichomes with elongated apical cells (H4). Stalk composed of 1–3 cells, apical cells usually long and curved. T-shaped trichomes: stalk longer, apical cells 1–2, very long, narrow, usually curved. Observed in *T. barabata* and *T. succulenta*.

**Tragopogon**

Uniseriate filiform simple trichomes (H1). Present just sparsely.

**Urospermum**

Multiseriate eglandular trichomes with non-projecting cell apices (F2). Narrowing towards the apex, apex composed of a single elongated cell.

**Willemetia**

Multiseriate glandular trichomes (C). Neck cells two.

**Youngia**

- (i) Multiseriate eglandular trichomes with non-projecting cell apices (F2). Short, apical part composed of two cells.  
 (ii) Uniseriate short conical eglandular trichomes (E). Composed of 5–10 cells. Without cuticular micropapilae.

**Appendix 2. List of studied material**

- Agoseris Raf.** *A. alpestris* Greene; USA, Nevada, Mt. Rose, *Rose*, 26. VII. 1935 (PR 71638). *A. gaspensis* Fernald; Canada, Québec, *Père Louis – Marie, FF. Fabius & Adonis M. Raymond et J. Paquin*, 6. VIII. 1934 (PR 71639).  
**Andryala L.** *A. agardhii* Haens. ex DC.; Spain, prov. Almeria, Sierra de Maimon, *Reverchon*, VI. 1895 (PR 611836). *A. integrifolia* L.; France, St. Étienne, *Hervier*, VII. 1983 (BRA s.n.); France, Ajaccio, *Nábělek*, VII. 1938 (SAV s.n.). *A. levitomentosa* (Nyár. ex. Sennikov) Greuter; Romania, Mșii. Bistrișei Mts, Mt. Bogolin, *Mráz*, 20. VII. 2000 (Herb. Mráz s.n. and cultivated plant no. 858). *A. pinnatifida* Ait.; Spain, Tenerife, *Hillebrand*, VI. 1879 (BRA s.n.). *A. ragusina* L.; Spain, prov. Almeria, *Ross & Jury*, 1. II. 1990 (SAV s.n.); Spain, prov. Almeria, Las Negros, *Marhold*, 1. IV. 1991 (SAV s.n.).  
**Aposeris Cass.** *A. foetida* (L.) Less.; Romania, Munșii Padișului, *Mráz*, 4. VIII. 2002 (Herb. Mráz s.n.).  
**Arnosseris Gaertn.** *A. minima* (L.) Schweigg. & Köörte; Germany, Bavaria, *Mayer & Petzi*, 29. VI. 1904 (PR 611832, PR 13222).  
**Catananche L.** *C. caerulea* L.; France, St. Crépin, *Mráz*, 2. VII. 2003 (Herb. Mráz s.n.); France, Vercors, *Futák*, 25. XI. 1967 (SAV s.n.); France, Hérault, Mas de Londres, *Zahradníková*, 21. VI. 1964 (SAV s.n.).  
**Cephalorrhynchus Boiss.** *C. picridiformis* (Boiss.) Turisl; Afghanistan, prov. Parwan, Salang – Tail bei Samedá, *Podlech*, 25. VII. 1969 (M 0080865). *C. polycladus* (Boiss.) Kirp.; Afghanistan, distr. Wakhan, *Roemer*, VIII. 1964 (M 0080867). *C. soongoricus* (Regel) S. Kovalevsk.; Afghanistan, prov. Baghlan, *Podlech*, 7. V. 1971 (M 0080866).  
**Cicerbita Wallr.** *C. panicii* (Viss.) Beauverd; Montenegro, Mt. Durmitor, *Niketić*, 26. VII. 1989 (BEO, dupl. Herb. Mráz s.n.). *C. alpina* Wallr.; Slovakia, Slovenský raj Mts, *Mráz*, VI. 2004 (Herb. Mráz s.n.).  
**Cichorium L.** *C. intybus* L.; Slovakia, Košice, Botanical Garden of the P. J. Šafárik University, *Mráz*, VI. 2002 (Herb. Mráz s.n.).  
**Crepis L.** *C. alpestris* (Jacq.) Tausch; Austria, Algäuern Alpen, *Mráz*, 17. VII. 2002 (Herb. Mráz s.n.). *C. aurea* (L.) Cass.; Austria, Algäuern Alpen, *Mráz*, 18. VII. 2002 (Herb. Mráz s.n.). *C. biennis* L.; Slovakia, Košice, Botanical Garden of the P. J. Šafárik University, *Mráz*, VII. 2001 (Herb. Mráz s.n.). *C. bocconi* P. D. Sell; France, Les Hautes Alpes, *Mráz*, 4. VII. 2003 (Herb. Mráz s.n.). *C. bulbosa* (L.) Tausch [ut. *Aethorisa bulbosa* (L.) Cass.]; France, Corse, Propiano, *Nábělek*, 1938 (SAV s.n.). *C. diversifolia* Walp.; ???, 8. VII. 1986 (M 0080862). *C. foetida* L.; France, Briançon, *Mráz*, 1. VII. 2003 (Herb. Mráz s.n.). *C. jacquini* Tausch; Slovakia, Muránska planina Mts, *Turis*, 1. VIII. 2000 (Herb. Turisová s.n.). *C. pannonica* (Jacq.) C. Koch; Slovakia, Salka, Sovie vinohrady, *Turisová*, 5. V. 2001 (Herb. Turisová s.n.). *C. praemorsa* (L.) Tausch; Slovakia, *Mráz*, 13. VII. 2002 (Herb. Mráz s.n.). *C. pulchra* L.; Slovakia, Kováčovské kopce, *Turisová*, 5. V. 2001 (Herb. Turisová s.n.). *Crepis pyrenaica* (L.) Greuter; Austria, Algäuern Alpen, *Mráz*, 13. VII. 2002 (Herb. Mráz s.n.). *Crepis sibirica* L.; Slovakia, Nízke Tatry Mts., Donovaly, *Turisová*, 26. VII. 1994 (Herb. Turisová s.n.). *Crepis tenuifolia* Willd.; ???, *Beljaeva & Gavrilenko*, 21. VII. 1979 (M 0080861). *Crepis viscidula* Froel.; Romania, Munții Țarcu, *Mráz*, VII. 2002 (Herb. Mráz s.n.). *Crepis zacintha* (L.) Babç. [ut. *Zacintha verrucosa* Gaertn.]; Croatia, Istria, in siccis supra Abbazia *Kümmerle & Moesz*, 20. V. 1907 (BP s.n.).  
**Crepidiastrum Nakai** *Crepidiastrum keiskeanum* Nakai; TNS 375651; TNS 426341; TNS, Loan No. A – 18 – 36. *Crepidiastrum lanceolatum* Nakai; TNS 402058. *Crepidiastrum platyphyllum* (Franch. & Sav.) Kitam.; TNS, Loan No. A – 18 – 35.  
**Chondrilla L.** *Chondrilla juncea* L.; Slovakia, Bratislava, *Mráz*, V. 2002 (Herb. Mráz s.n.); Slovakia, Košice, *Mráz*, VI. 2003 (Herb. Mráz s.n.); *Chondrilla canescens* Kar. et Kir., ???, *Androsov*, 30. VI. 1909 (M – 0080872). *Chondrilla pauciflora* Ledeb.; ???, (M – 0080873). *Chondrilachondrilloides* (Ard.) Karst. [ut *Chondrilla prenanthoides* (Scop.) Vill.]; Greece, Peloponnes, *ignt.* (M – 0080869). *Chondrilla ramosissima* Sibth. & Sm.; Greece, Korinthia, *Merxmüller & Wiedmann*, 17. IV. 1954 (M – 0080870). *Chondrilla yossii* Kitam.; Afghanistan, prov. Parwan, *Podlech*, 6. X. 1970 (M – 0080868).  
**Chlorocrepis Griseb.** *Chlorocrepis staticifolia* Griseb. [= *Tolpis staticifolia* (All.) Sch. Bip.]; France, Briançon, Bois de L'ours, *Mráz*, 1. VII. 2003 (Herb. Mráz s.n.).  
**Dendroseris D. Don** *Dendroseris pruinata* (Johow) Skottsb.; Chile, Juan Fernandes Island, Santa Clara: Mora Spartan, *Stuessy & Sanders*, 6. XI. 1980 (M – 0080881).  
**Dubyaea DC.** *D. hispida* DC., TNS 641402.  
**Haenselerea Boiss. ex DC.** *Haenselerea granatensis* Boiss. ex DC.; Spain, Sierra Nevada, *ignt.*, 6. V. 1895 (PR 611859); Spain, Sierra Nevada, *ignt.*, 1 – 23. VII. 1879 (PR 611851); Spain, Sierra Nevada, *ignt.*, 3. VII. 1895 (M – 0080878).  
**Hedypnois Miller** *Hedypnois cretica* (L.) Dum.; France, Corse, Ajacio, *Nábělek*, IV. 1938 (SAV s.n.).  
**Hieracium L.** *Hieracium amplexicaule* L.; France, Les Hautes Alpes, La Grève, *Mráz*, 3. VII. 2003 (Herb. Mráz s.n.). *Hieracium eriophorum* St.-Amans; France, sables maritimes á Contis, *Gareaud*, 22. VIII. 2000 (Herb. Mráz s.n.). *Hieracium japonicum* Franch. & Sav.; TNS 637501; TNS, Loan No A – 18 – 43. *Hieracium lanatum* Vill.; France, Briançon, *Mráz*, 8. VII. 2003 (Herb. Mráz s.n. s.n.).  
**Hispidella Barnades ex Lam.** *Hispidella hispanica* Barnades ex Lam.; Spain, Sierra de Quadavuama, *Villoso*, 14. VII. 1933 (GAT 827).  
**Holeleion Kitam.** *Holeleion krameri* (Franch. & Savat.) Kitam.; TNS, Loan No. A – 18 – 45. *Holeleion maximowiczii* Kitam.; TNS, Loan No. A – 18 – 46.  
**Hymenonema Cass.** *Hymenonema graecum* (L.) DC.; Greece, *Reiser*, 18. VI. 1894 (PR 611848, 611849); Greece, Syros, *Kabát*, 4. VII. 1889 (PR 611850, 611851); Greece, Anaphi, *Leonis*, 3. VII. 1898 (PR 611856); ???, *ignt.*, 10. VII. 1897 (M – 0080880). *Hymenonema laconicum* Boiss. & Heldr. ex Boiss.; Greece, Laconia, *Zahn*, 5. VI. 1896 (M 0080879).  
**Hyoseris L.** *Hyoseris radiata* L.; France, Nice, *Nábělek*, IV. 1938 (SAV s.n.). *Hyoseris scabra* L.; France, Corse, Ajacio, *Nábělek*, IV. 1938 (SAV s.n.); France, Agay, *Nábělek*, IV. 1938 (SAV s.n.).  
**Hypochaeris L.** *Hypochaeris acaulis* (Remy) Reiche; Chile, prov. Curicó, *Grau & Grau*, 29. III. 1975 (M 0080876). *Hypochaeris elata* Griseb; Argentina, prov. De Jujuy, *Cabrara*, 15. II. 1963 (M 0080876). *Hypochaeris incana* (Hook. & Arn.) MacLoskie; Argentina, Espinazo del Zorro (Yao – Yao), *Schajovskoy*, 6. XII. 1965 (M 0080875). *Hypochaeris glabra* L.; France, Corse, Ajacio, *Nábělek*, IV.



- 1938 (SAV s.n.). *Hypochaeris maculata* L.; Slovakia, Vyšný Klatov, Mráz, 12. VI. 2002 (Herb. Mráz s.n.). *Hypochaeris setosus* Rusby; ???, Gaviria & Muller, 16. VIII. 1991 (M 0080874). *Hypochaeris uniflora* Vill.; Slovakia, Úhorná, Mráz, 14. VI. 2002 (Herb. Mráz s.n.). *Hypochaeris variegata* Baker; Argentina, prov. Buenos Aires, Sierra de Curramala, Fabris & Schwabe, ??? (M 00808873).
- Ixeridium** (A. Gray) Tzvelev *Ixeridium gramineum* (Fisch.) Tzvelev; TNS, Loan No. A – 18 – 27.
- Ixeris** (Cass.) Cass. *Ixeris dentata* Nakai; TNS, Loan No. A – 18 – 28. *Ixeris polycephala* Cass.; TNS, Loan No. A – 18 – 29. *Ixeris stolonifera* A. Gray; TNS, Loan No. A – 18 – 30.
- Koelipinia** Pallas *Koelipinia linearis* Pallas; Russia, Artamatskij rayon, Podnozhie, Nazarova, 25. VII. 1975 (SAV s.n.); Turkey, Paphlagonia, Wilajet Kasambuli, Freyn, 21. V. 1892 (PR 611846); Cyprus, ad vias inter Nikosia et Kythrea, *ignt.*, 5. IV. 1890 (PR 611846); Turkmenia, Aschabat, Bornmüller, 26. IV. 1900 (PR 611847).
- Krigia** Schreb.  
*Krigia amplexicaulis* Nutt.; USA, New Jersey, Milltown, Johnson, 1. VI. 1933 (PR 611842).  
*Krigia montana* Nutt.; USA, North Carolina, Craggy Mountain, Biltmore, 8 – 13. VII. 1897 (PR 611843, 611844, 611845).
- Lactuca** L. *Lactuca perennis* L.; Slovakia, Zádielska dolina valley, Krak, VII. 2003 (Herb. Mráz s.n.). *Lactuca saligna* L.; Slovakia, Košice, Botanical garden of the P. J. Šafárik University, Krak, VII. 2003 (Herb. Mráz s.n.). *Lactuca serriola* L.; Slovakia, Košice, Botanical Garden of the P. J. Šafárik University, Krak, VII. 2003 (Herb. Mráz s.n.).
- Lapsana** L. *Lapsana communis* L.; Slovakia, Košice, Botanical Garden of the P. J. Šafárik University, Mráz, VII. 2001 (Herb. Mráz s.n.).
- Launaea** Cass. *Launaea pumila* (Cav.) Kuntze; Spain, de Albacete, Boger, Grau & Lopez, 19. V. 1983 (M 0080857). *Launaea stenocephala* Burkill; Afghanistan, prov. Nanghar, Podlech, 19. IV. 1977 (M 0080857). *Launaea taraxacifolia* (Willd.) Amin ex C. Jeffrey; Tanganika Greenway, 28. VI. 1961 (M 0080853).
- Leontodon** L. *Leontodon autumnalis* L.; Slovakia, Biele Skaly, Mráz, 14. VI. 2002 (Herb. Mráz s.n.). *Leontodon hispidus* L.; Slovakia, Košice, Botanical Garden of the P. J. Šafárik University, Mráz, IX. 2003 (Hrb. Mráz s.n.). *Leontodon montanus* Lam.; France, Briançon, Mráz, 2. VII. 2003 (Herb. Mráz s.n.).
- Lygodesmia** D. Don *Lygodesmia rostrata* A. Gray; USA, North Dakota, Leonard Richard Co., Stevens, 20. VIII. 1937 (PR 113117). *Lygodesmia spiniosa* Nutt.; USA, Nevada, Steamboat Springs, Rose, 26. VII. 1935 (PR 113118).
- Macrorhynchus** Less. *Macrorhynchus troximoides* Torr. & A Gray; USA, Rocky Mountains, Hall & Harbour (PR 611852).
- Malacothrix** DC. *Malacothrix crepoides* A. Gray; USA, Eastern Oregon, Howell, V. 1880 (PR 611838). *Malacothrix obtusa* Benth.; USA, California, Monterey County, Priest Valley, Rose, 8. IV. 1937 (PR 133099). *Malacothrix saxatilis* Torr. & A. Gray [= *Malacothrix saxatilis* var. *tenuifolia* (Nutt.) A. Gray]; USA, California, Monterey County, Greenfield, Rose, 18. III. 1933 (PR 113118).
- Microseris** D. Don *Microseris douglasii* Sch. Bip.; USA, California, San Luis Obispo County, Rose, 8. IV. 1937 (PR 133099). *Microseris linearifolia* Sch. Bip.; USA, California, san Bernardino, Parish, V. 1882 (PR 611841). *Microseris troximoides* A. Gray; USA, Eastern Washington, Howell, IV. 188? (PR 611389); USA, Oregon, Galles, Howell, IV. 1882 (PR 611840).
- Mycelis** L. *Mycelis muralis* (L.) Dumort.; Slovakia, Košice, Botanical Garden of the P. J. Šafárik University, Mráz, 20. VII. 2003 (Herb. Mráz s.n.).
- Nothocalais** Greene *Nothocalais cuspidata* Greene; USA, Nebraska, Minden, Hapeman, 8.V. 1933 (PR 71637).
- Paraixeris** Greene *Paraixeris denticulata* (Houtt.) Nakai; Japan, Honshu, pref. Junimagari, Yamanakako – mura, *Togashi*, 7. X. 1983 (M 0080864).
- Picris** L. *Picris echiooides* L. [ut *Helminthia echiooides* (L.) Gaertn.]; Slovakia, Bratislava, Valenta, 5. VIII. 1938 (BRA s.n.). *Picris hieracioides* L.; France, Briançon, Mráz, 1. VII. 2003 (Herb. Mráz s.n.).
- Pilosella** Hill *Pilosella echiooides* (Lumn.) F. W. Shultz & Sch. Bip.; Slovakia, Streda nad Bodrogom, Mráz, 2001 (Herb. Mráz s.n.). *Pilosella macrantha* (Ten.) F. W. Shultz & Sch. Bip.; Slovakia, 2001, (Herb. Mráz s.n.) *Pilosella officinarum* F. W. Schultz & Sch. Bip. Slovakia, 2001, (Herb. Mráz s.n.).
- Podospemum** *Podospemum canum* (C. A. Meyer) O. Hoffm.; Bulgaria, Alibotuš, Nábělek, VIII. 1938 (SAV s.n.); Slovakia, Kamenín, slanisko, Grebensčikov, 27. V. 1955 (SAV s.n.); Slovakia, Kamenín, Futák & Hlaváček, 31. V. 1958 (SAV s.n.). *Podospemum laciniatum* DC.; Slovakia, Devínska Kobyla, Houbová & Flašíková, 19. V. 1979 (SAV s.n.).
- Prenanthes** L. *Prenanthes alba* L.; ???, *ignt.*, 3. IX. 1934 (M 0080858). *Prenanthes barbata* (Torr. & A Gray) Milstead; USA, Alabama, Kral, 1. X. 1971 (M 0080860). *Prenanthes crepidinea* Michx.; USA, Ohio, *ignt.*, 1840 (M 0080859).
- Pyrrhopappus** DC. *Pyrrhopappus multicaulis* DC.; Mexico, State of Coahuila, Rio Grande Valley near Diaz, Pringle, 25. IV. 1900 (PR 611853).
- Reichardia** Roth *Reichardia macrophylla* Vis. & Pančić; Serbia and Montenegro, Mt. Tara, Niketć, 8. VII. 1989 (BEO s.n., dupl. Herb. Mráz s.n.).
- Rhagadiolus** Scop. *Rhagadiolus stelatus* (L.) Gaertn. [incl. *Rhagadiolus edulis* Gaertn.]; Cultivated in the Botanical garden of the P. J. Šafárik University in Košice, Slovakia (origin, Index seminum BG Göttingen 2002); ad muros P. Teresatto, s.d. Müller (BP 184164).
- Scolymus** L. *Scolymus hispanicus* L.; Croatia, Velebit Mts., Kümmerle, 19. XI. 1911 (BP 183857); Italy Fiume, Eördégh – Bíró, 1872 (BP 183857). *Scolymus maculatus* L.; Italy, Capri, Nábělek, IV. 1938 (SAV s.n.).
- Scorzonera** L. *Scorzonera hispanica* L.; Slovakia, Prakovce, cultivated in the garden of J. Mráz (Herb. Mráz s.n.). *Scorzonera rosea* Waldst. & Kit. [= *Scorzonera purpurea* subsp. *rosea* (Waldst. & Kitt.) Nyman]; Ukraine, Mt. Pikuy, Mráz 21. VII. 2002 (Herb. Mráz s.n.).
- Sonchus** L. *Sonchus arvensis* subsp. *uliginosus* (M. Bieb.) Nyman; Slovakia, Košice, Račí potok, Mráz, IX. 2003 (Herb. Mráz s.n.). *Sonchus arvensis* subsp. *arvensis* L.; Slovakia, Košice. Mráz, IX. 2003 (Herb. Mráz s.n.). *Sonchus asper* (L.) Hill; Slovakia, Košice, Botanical Garden of the P. J. Šafárik University, Krak, 24. VII. 2003 (Herb. Mráz s.n.). *Sonchus oleraceus* L.; Slovakia, Košice, Botanical Garden of the P. J. Šafárik University, Krak, 24. VII. 2003 (Herb. Mráz s.n.). *Sonchus palustris* L.; Slovakia, Turňa nad Bodvou, Mráz, 3. X. 2003 (Herb. Mráz s.n.).
- Stephanomeria** Nutt. *Stephanomeria cichoriacea* A. Gray; USA, California, Cucomonga Mts., Parish. & Parish, VIII. 1881 (PR 611835). *Stephanomeria exigua* Nutt. subsp. *daneii* (MacBride) Gottlieb [ut. *S. paniculata* Nutt., rev.:



Gottlieb]; USA, California, Colton, *Pringle*, 30. V. 1882 (PR 611833). *Stephanomeria minor* Nutt.; SAV s.n. *Stephanomeria paniculata* Nutt.; USA Oregon, Eagle Valley, *Chusick*, 12. VII. 1900 (PR 611834).

**Taraxacum Webber** *Taraxacum* sect. *Erythrosperma* Dahlst.; Slovakia, Slovenský Kras, Zádielska dolina, *Mráz*, 3. X. 2003 (Herb. Mráz s.n.). *Taraxacum* sect. *Ruderalia* Kirschner, H. Řllg. & Štěpánek; Slovakia, Košice, Botanical Garden of the P. J. Šafárik University, *Mráz*, V. 2002 (Herb. Mráz s.n.).

**Tolpis Adanson** *Tolpis barbata* (L.) Gaertn.; Cultivated in the Botanical Garden of the P. J. Šafárik University in Košice (origin: index seminum BG Mainz 2001). *Tolpis capensis* (L.) Sch. Bip.; South Africa, Golden Gates Highlands N. P., *Mucina*, 25. XII. 2002 (Herb. Mráz s.n.). *Tolpis coronopifolia* (Desf.) Biv.; Spain, Tenerife, *Cuatrecasas*, 25. IV. 1935 (MAF s.n.). *Tolpis macrorhiza* (Hook.) DC.; Portugal, Ribeiro Frio, *Van Buggenhout*, VI 1989 (MAF 146127). *Tolpis laciniata* (Sch. Bip. ex Webb & Berthel.) Webb; Spain, La Palma, *Pérez de Paz*, 6. IV. 1990 (MAF 139548). *Tolpis lagopoda* C. Sm. ex Link; Spain Tenerife, *Santos*, 29.

VII. 2001 (MAF161355). *Tolpis succulenta* (Dryand.) Lowe; Portugal, Madeira, *Menezes & Dias Ferreira*, 7. XI. 2001 (MAF 161367). *Tolpis virgata* Bertol.; France, Corse, Ajaccio, *Nábělek*, IV. 1938 (SAV s.n.). *Tolpis webbii* Sch. Bip. ex Webb & Berthel.; Spain, Tenerife, *Santos*, 10. VI. 1969 (MAF 76124).

**Tragopogon** *Tragopogon orientalis*; Slovakia, Košice, Botanical Garden of the P. J. Šafárik University, *Mráz*, 2002, (Herb. Mráz).

**Urospermum Scop.** *Urospermum daleschampii* (L.) Scop. ex F. W. Schmidt; Croatia, Split, *Nábělek*, VI. 1938 (SAV s.n.). *Urospermum picroides* (L.) Scop. ex F. W. Schmidt; France, Garonne, *Nábělek*, V. 1938 (SAV s.n.).

**Willemetia Cass.** *Willemetsia stipitata* (Jacq.) Schinz & R. Keller; Austria, Algäuern Alpen, *Mráz*, 20. VII. 2002 (Herb. Mráz s.n.).

**Youngia Cass.** *Youngia japonica* (L.) DC.; USA, Texas, Harris Co., Bellare, SW – Houston, *Nelson*, 17. II. 1988 (M 0080863).

*Youngia racemifera* (Hook. f.) Babc. & Stebbins; TNS, Loan No. A – 18–25.