Trichome morphology of eleven genera of the tribe Alysseae (Brassicaceae) occurring in Bulgaria

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Abstract

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The leaf and silicule trichomes of 18 species of Alyssaeae were studied by scanning electron and light microscopy. Four trichome types are distinguished: (1) simple, (2) stalked 2- to 5-armed, (3) stellate and (4) dendritic trichomes. (1) Simple trichomes cover the leaves of Lunaria rediviva and, mixed with stalked 2- to 3-armed ones, compose the leaf indumentum of Camelina sativa. The simple trichomes on the silicules of Clypeola jonthlaspi subsp. microcarpa are columnar with transverse furrows. (2) Stalked 2-5-arm ed trichomes are present on the leaves of Draba korabensis, D. muralis, D. siliquosa and Erophila verna subsp. spathulata. Peculiar stalked trichomes with swollen globular base occur on the lower leaf surface of D. muralis. (3) Stellate trichomes cover the leaves of Alyssoides utriculata subsp. bulgarica, Aurinia saxatilis subsp. orientalis, A. uechtritziana and Clypeola jonthlaspi and the leaves and silicules of Alyssum cu neifolium s. str., A. orbelicum, A. pirinicum and Fibigia clypeata. (4) Dendritic trichomes co-occur with stellate ones on the silicules (but rarely on the leaves) of Berteroa species and Fibigia clypeata. The trichomes may be smooth (some stellate trichomes), minutely warty (simple and dendritic trichomes) or tuberculate (most of the stellate trichomes). The trichomes of the morphologically related species Alyssum pirinicum, a new combination validated here, and A. cuneifolium provide additional reliable features to distinguish them.

Key words: angiosperms, Cruciferae, indumentum, micromorphology, scanning electron microscopy.

Introduction

Trichome morphology has been used by many authors as a character in the classification of the Brassicaceae (Hayek 1925, Nyárády 1955, Dudley 1964, Greuter 1974, Rollins & Shaw 1973, Rollins & Banerjee 1976, Ančev 1991, Rollins 1993), especially in the tribe Alyssaeae (Janchen 1942, Al-Shehbaz 1987), where trichomes are widely present. In the Bulgarian flora Alyssaeae are represented by c. 45 species in 11 genera, the largest being Alyssum with 23 species. Scanning electron and light microscopy studies of the trichomes of 61 Alyssum species, including members of all its six sections (see Dudley 1964), distributed in Europe, SW Asia and the Mediterranean,
demonstrated a large morphological diversity at the species and the section level, as well as the presence of patterns of variability within these groups (Ančev 1991, 2000). The present study aims at expanding the knowledge of the trichome diversity in Alyssum and the remaining 10 genera of the tribe Alysseae in Bulgaria.

**Material and methods**

The morphology of the trichomes on the lower leaf surface of 17 species of the tribe Alysseae was studied by scanning electron microscopy (SEM), using a Joel-JSM-35 at 20 kV, and in Schivereckia doerfleri by light microscopy. The trichomes were investigated on the basal (rosette) leaves or the lower cauline leaves. The indumentum of the upper leaf surface of all studied species was examined by light microscopy. In addition, the trichomes of the silicules in eight of the species were studied. Trichome description and classification follows the system of Theobald & al. (1979). The investigation is based on herbarium material deposited in BRA, SO and SOM (herbarium abbreviation according to Holmgren & Holmgren 1998-), as listed in Table 1.

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<th>Species</th>
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<th>Year</th>
<th>Collector(s)</th>
<th>Herbarium Abbreviation</th>
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Results and Discussion

*Lunaria rediviva* L.

*Leaf trichomes* (Fig. 1A) simple, rather minutely papillose, straight or curved, flattened in the lower part, rounded and tapering above, long on the midrib and veins, otherwise shorter with straight or hooked tips.

*Alyssoides utriculata* subsp. *bulgarica* (Sagorski) Hartvig

*Leaf trichomes* (Fig. 1B, C) stellate, tuberculate, angulate, with mounded, massive, coarse-tuberculate centre. Rays simple or once forked, with 6-7 subpatent, non-appressed, smooth tips.

The stellate leaf trichomes of this taxon are characteristic by their regularly subpatent, non-appressed rays and delimit it clearly from subsp. *utriculata* (Hartvig 2002).

*Alyssum cuneifolium* Ten.

*Leaf trichomes* (Fig. 1D, E) stellate, rounded, smooth or sparsely tuberculate, with narrow, slightly swollen centre. Rays 2(-3)-forked, with 22-23 tips, straight, tapering. *Silicule trichomes* (Fig. 1F, 2A) appressed, stellate, densely tuberculate, with narrow, mounded, coarsely tuberculate or almost smooth centre and massive primary arms at an angle of 35-45°. Rays 2(-3)-forked, with 16-18 tuberculate, mostly straight, tapering tips.

*Alyssum pirinicum* (Stoj. & Acht.) Ančev, *comb. & stat. nov.*


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Table 2. Trichome types of 18 *Alysseae* species on leaf (L) and silicule surface (S): Stalked = stalked 2-5-armed; Sta-gb = stalked 3-4-armed with globular base; stel-1 = appressed-stellate; stel-2 = stalked-stellate; den-1 = stalked with simple and forked branches, den-2 = terminally stellately branched; den-3 = fasciculately branched. The dominant types are in bold.

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Leaf trichomes (Fig. 2B, C) stellate, rounded and angulate, almost smooth to sparsely tuberculate, with narrow flat centre. Rays 1-3-forked, with 20-26 straight or curved tips, shorter than in Alyssum cuneifolium. Silicule trichomes (Fig. 2D, E) stellate, not appressed, at least some of them on short stalks, sparsely minutely tuberculate, with narrow flat centre and delicate primary rays at an angle of c. 60-70°. Rays 3-forked, with 16-22 smooth or almost smooth, straight or curved tips.

Alyssum pirinicum is a diploid local endemic with $2n = 16$, restricted to the alpine area of the N Pirin Mt (Ančev 1991). Stojanov & Achtarov (1939) distinguished it from A. cuneifolium at subspecies level, but both taxa are very well separated by their trichome morphology. Besides, A. cuneifolium is hexaploid with $2n = 48$ (Küpfner 1974, for Italy), although Hartvig (2002) reported...
2n = 32 with question mark from Greece. Jalas & al. (1996) treated *A. cuneifolium* subsp. *pirinicum* as a synonym of *A. scardicum*, a tetraploid species with 2n = 32. *A. scardicum*, however, differs clearly from the diploid *A. pirinicum* in the indumentum of appressed, symmetric, rounded, stellate, densely tuberculate trichomes with 33-34 ultimate rays (Ančev 2000: fig. 6B).

*Alyssum orbelicum* Ančev & Uzunov

Leaf trichomes (Fig. 2 F, 3A) stellate, rounded, densely minutely tuberculate, with narrow, swollen to umbonate centre. Rays long, often curved or crooked, with 16-23 tips. Silicule trichomes (Fig. 3B, C) with coarse, tuberculate, massive centre with large almost smooth umbo. Primary rays 10-12, short, partly fused at the base, with (16-)21-25 long, tapering, smooth tips, densely tuberculate.

Fig. 2. Trichomes of *Alyssum* species – A: *A. cuneifolium*, stellate trichome on silicule surface, close up of mounded, tuberculate centre; B-E: *A. pirinicum*, leaf indumentum of stellate trichomes (B), close up of flat centre (C), indumentum on silicule surface, with stalked, stellate trichome with ascending rays, at upper left (D), close up of stellate silicule trichome with narrow centre (E); F: *A. orbelicum*, leaf indumentum of stellate trichomes. – Scale bars: A, C, E = 50 µm; B, D, F = 100 µm.
The coarse, tuberculate silicule trichomes marked by a massive centre and short, partly fused primary rays well delimit this species, in addition to the inflorescence and flower characters, from the related *A. nebrodense* and *A. alpestre* (Ančev 2000, Ančev & Uzunov 2002).

Leaf trichomes (Fig. 3D, E) not appressed, stellate, angulate, smooth. Rays slender, 1-2-forked, with short additional side branches and long, tapering tips.

*Aurinia uechtritziana* (Bornm.) Cullen & T. R. Dudley
Leaf trichomes (Fig. 3F, 4A) appressed, stellate, tuberculate, rounded, with narrow, coarsely tuberculate, slightly swollen centre. Primary rays short, with 10-13 smooth tips.

Fig. 3. Trichomes of *Alyssum* and *Aurinia* species – A-C: *Alyssum orbelicum*, stellate leaf trichome with umbonate centre (A), silicule indumentum of appressed, stellate trichomes (B), close up of massive centre of stellate silicule trichome with large umbo and fused primary rays (C); D-E: *Aurinia saxatilis* subsp. *orientalis*, leaf indumentum of stellate trichomes with short, thorn-like side branches (D), close up central portion of leaf trichome (E); F: *A. uechtritziana*, leaf indumentum of appressed, stellate trichomes. – Scale bars: A, C = 50 µm; B, D, F = 100 µm; E = 10 µm.

The coarse, tuberculate silicule trichomes marked by a massive centre and short, partly fused primary rays well delimit this species, in addition to the inflorescence and flower characters, from the related *A. nebrodense* and *A. alpestre* (Ančev 2000, Ančev & Uzunov 2002).

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*Aurinia uechtritziana* (Bornm.) Cullen & T. R. Dudley
Leaf trichomes (Fig. 3F, 4A) appressed, stellate, tuberculate, rounded, with narrow, coarsely tuberculate, slightly swollen centre. Primary rays short, with 10-13 smooth tips.

Fig. 3. Trichomes of *Alyssum* and *Aurinia* species – A-C: *Alyssum orbelicum*, stellate leaf trichome with umbonate centre (A), silicule indumentum of appressed, stellate trichomes (B), close up of massive centre of stellate silicule trichome with large umbo and fused primary rays (C); D-E: *Aurinia saxatilis* subsp. *orientalis*, leaf indumentum of stellate trichomes with short, thorn-like side branches (D), close up central portion of leaf trichome (E); F: *A. uechtritziana*, leaf indumentum of appressed, stellate trichomes. – Scale bars: A, C = 50 µm; B, D, F = 100 µm; E = 10 µm.
**Berteroa incana** (L.) DC.

Leaf trichomes (Fig. 4B) stellate and dendritic. Stellate trichomes tuberculate, sessile or almost sessile, with wide, flat or slightly swollen centre; primary rays shortly forked, with 6-7, long, unequal tips, often with short side arms. Dendritic trichomes smaller, with unequal branches. Sili-cule trichomes (Fig. 4C) almost sessile or stalked, branched, with forked and simple branches, mixed with dendritic, minutely warty trichomes with long central and short side branches.

**Berteroa mutabilis** (Vent.) DC.

Leaf trichomes (Fig. 4D) spaced, variable, 5- and 6-armed, tuberculate, stalked or almost sessile, with slightly swollen centre, sometimes approaching the stellate type. Primary arms short, forked, with 5-6 long, unequal tips. Sicule trichomes (Fig. 4E, F) stellate, mostly spaced, sessile, ter-
minally branched to stellate-like branched with unequal arms and short side branches; among them some single, minutely warty, dendritic trichomes with long central and short side branches.

**Berteroa obliqua** (Sm.) DC.
Leaf trichomes (Fig. 5A, B) stellate, sessile, minutely tuberculate, with slightly swollen centre. Primary rays short, forked, with 6-8 unequal tips, mixed with stalked, terminally branched trichomes with unequal arms. Silicule trichomes (Fig. 5C) of two types: almost sessile, terminally branched stellate trichomes with unequal arms, often with short side branches, mixed with stalked ones with ascending rays, and dendritic ones (upper right) (F). – Scale bars: A, C, D, F: 100 µm; B, E = 50 µm.

**Fibigia clypeata** (L.) Medik.
*Fibigia clypeata* has a characteristic, heteromorphic leaf and silicule indumentum, composed of stellate, stellate-like and dendritic trichomes. Leaf trichomes (Fig. 5D, E) mostly stellate, moder-
ately to scarcely minutely tuberculate, with narrow, slightly swollen centre. Primary rays short, forked, with 6-9 long, unequal tips. Mixed with few dendritic trichomes (Fig. 8A). Silicule trichomes (Fig. 5F) simple, stellate, stalked or almost sessile with massive, simple rays and rays forked at a short distance from the centre, mixed with stalked stellate-like trichomes with thick, ascending, unequal, smooth rays and single, dendritic trichomes with smooth branches (Fig. 8B).

_Clypeola jonthlaspi_ subsp. _microcarpa_ (Moris) Arcang.

_Leaf trichomes_ (Fig. 6A) stellate, tuberculate, with narrow and slightly protruding central part. Primary rays short, 1-2-forked and with 12-16 straight tips. _Silicule indumentum_: central part (Fig. 6B-D) covered by small papillae and coarse tuberculate outgrowths, mixed with dispersed,
Fig. 7. Trichomes of Draba and Erophila species – A-B: Draba muralis, stalked, 4-armed leaf trichomes with swollen globular base; C: D. siliquosa, stalk 4-armed trichome with flattened stalk; D: Erophila verna subsp. spathulata, stalked Y-shaped trichomes on the leaf surface. – Scale bars: A, C, D = 100 µm; B = 50 µm.

Fig. 8. A-B: Fibigia clypeata, dendritic leaf trichome (A), dendritic silicule trichome (B); C-F: Schivereckia doerfleri, stalked, Y-shaped trichome (C), simple trichome (D), stalked, 5-armed trichome (E), all from leaf indumentum; stalked, 3-armed silicule trichome (F). – Magnification: x 126.
short, simple trichomes with mounded surface with transversely furrowed appearance and rounded to swollen tips. Silicule wing trichomes long, rounded or clavate at the apex.

The presence of clavate trichomes on the silicules, few or very few on the disc and numerous on the wing, together with the spathulate leaves and smaller silicules, well delimit it from C. jonthlaspi subsp. jonthlaspi, with silicule disc and wing covered by rounded trichomes or such tapering into a sharp, long, simple point (Runemark 2002).

**Draba korabensis** Kümmerle & Degen

*Leaf trichomes* (Fig. 6F) stalked (2-)3- to 4-armed, almost smooth or finely tuberculate, stalk flattened at the base, arms unequal, tapering, straight or slightly curved.

**Draba muralis** L.

*Leaf trichomes of the lower surface* spaced, 3- and 4-armed with long, tuberculate, tapering arms and very short stalk on swollen globular base (Fig. 7A, B). *Trichomes of the leaf margin* simple and 2-armed, Y-shaped, and on *the upper leaf surface* stalked, (2-)3- to 4-armed, of the same type as in *D. korabensis* (Fig. 6F). Stalked trichomes with swollen globular base were not observed on the upper leaf surface.


**Draba siliquosa** M. Bieb.

*Leaf trichomes* (Fig. 7C) stalked, 3- to 4-armed, minutely warty, with more or less flattened stalk with thickened margins; arms unequal, tapering, straight or with curved or hooked tips. Some of the trichomes with side branches along the stalk demonstrate a transition to the dendritic type.

**Erophila verna** subsp. *spathulata* (Láng) Walters

*Leaf trichomes* (Fig. 7D) stalked, 2-armed, Y-shaped, mixed with 3-armed and very few 4-armed trichomes, with long, straight or curved, tapering arms with minutely warty surface.

**Camelina sativa** (L.) Crantz

Leaf trichomes (Fig. 6E) spaced, simple, long, minutely tuberculate, flattened in the lower part, rounded and tapering above, mixed with shorter, stalked, 2-armed, Y-shaped, and stalked, 3-armed trichomes.

**Schivereckia doerfleri** (Besser) Andrz.

*Leaf trichomes* (Fig. 8C, D, E) stalked, variable, mostly 4-armed, mixed with dispersed 3- or 5-armed ones. *Silicule trichomes* (Fig. 8F) spaced, short, simple, mixed with stalked, 2-armed Y-shaped and few sessile, dispersed, 3-armed trichomes.

**Acknowledgements**

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