The evolving “fate” of Asyneuma comosiforme: validation of Hayekia, a new monotypic genus of Campanulaceae from Albania

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Source: Willdenowia, 49(1) : 81-93

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: https://doi.org/10.3372/wi.49.49110
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Abstract: An account of the discovery of the Albanian stenoendemic Asyneuma comosiforme and brief nomenclatural history of the genus Asyneuma provide a background for the re-assessment of recent molecular findings, which advocate the transfer of A. comosiforme to the genus Campanula. Objections to this transfer are raised, and additional morphological details and arguments are provided, highlighting the uniqueness of this taxon, in order to support a proposal to recognize and validate the monotypic genus Hayekia. A full generic diagnosis, and an expanded species description are provided, in addition to chromosome number, ecological and conservation data. Comments about cladistic analyses and general-purpose Linnaean classifications are made, as well as a recommendation for the recognition of monotypic genera for a better understanding of Campanulaceae evolution.

Key words: Albania, Asyneuma, Campanula, Campanulaceae, capsule dehiscence, character combination, floral morphology, Hayekia, new genus, nomenclature, systematics

Introduction

The transfer of Asyneuma comosiforme Hayek & Janch. to Campanula L. (Frajman & Schneeweiss 2009) has highlighted a well-known taxonomic problem that is particularly prevalent in the Campanulaceae. Many of the genera cannot be diagnosed explicitly by single characters, but instead by a combination of them, or by overall appearance (Gestalt), often in combination with geographic distribution. If we were to adhere to a narrow character-diagnosis, then several large genera such as Adenophora Fisch., Asyneuma Griseb. & Schenk and Campanula probably would have to be merged. From this perspective, Edraianthus A. DC. is only weakly separable from Campanula based on capsule dehiscence mechanisms, while similar “minor” criteria exist for other small genera. Yet, with a little experience of the Campanulaceae as a whole, these so-called “satellite” genera are readily separable. With the transfer of A. comosiforme, the already weak circumscription of Campanula (Eddie & al. 2003) is rendered even more impractical. Despite these difficulties, we present data to support the contention that...
a combination of morphological characters of this species differs significantly from that of the isophyllous species of *Campanula* (Park & al. 2006) and *Asyneuma*, and that, together with molecular sequence data, warrants the recognition of a new monotypic genus to accommodate *A. comosiforme*. We support this proposal by arguments that advocate the separation of monotypic genera in a Linnaean taxonomic classification, rather than an inclusive, “all-embracing” concept of the genus *Campanula*, and that such an arrangement better enhances our understanding of *Campanulaceae* evolution.

**The discovery of Asyneuma comosiforme**

*Asyneuma comosiforme* was first described from the lower reaches of the Šija (Shija) gorge near the border with Kosovo in the foothills of the Mt Jalica (Gjalica) region of northeastern Albania, which is part of the northwestern Scardic mountains (Šar planina) of the Scardo-Pindian mountain system. The type (designated lectotype) is in the University of Gothenburg Herbarium (GB-0047108). *Asyneuma comosiforme* is a stenoendemic species with a highly localized distribution. Until recently, it was known only from the type locality (Nosja & al. 1996), where it grows in crevices of limestone cliffs and possibly numbers only a few hundred individuals (Frajman & Schnee weiss 2009), but it has now been recorded from several other localities in the region (Barina & al. 2017) and therefore may be more widespread than originally thought. It has recently been collected by Frajman (WU-11089), Bogdanović and Jov Dujaković (ZAGR), and Nirina (NHMR-1093), whose material provided the molecular analyses to be carried out. Considered as a narrow endemic of northeastern Albania, and distributed in only one European country. *A. comosiforme* is defined as a “target species” or “species of European concern” (Ozinga & Schaminée 2005).

When describing this species, Hayek (1924) wrote: “Certainly the most outstanding find that Zerny has made, and one of the most interesting plants of the whole yield. Of all known species of the genus *Asyneuma*, it differs habitually and with respect to the inflorescence, so that it would be absolutely necessary to put it in another genus. But a closer examination of them did not reveal absolutely any feature which would justify such a separation… In habit, the plant is most reminiscent of *Synotoma comosum* (L.) R. Schulz (*Phyteuma comosum* L.), with which it also inhabits similar sites, which is why the name ‘comosiforme’ was chosen for it.” (Translated from the original German by W.M.M.E.) Hayek was probably basing his initial impression on the overall appearance of this species, but, when attempting to classify it using individual characters, he ran into difficulties. At that time, the mature capsules were unknown and Hayek assumed the dehiscence to be basal.

Referring to Bornmüller (1921), Hayek considered the possibility that *Asyneuma comosiforme* might be related to *A. trichocalycticum* (Ten.) K. Maly, but, with his experience of *Campanula*, he recalled that the species with nodding capsules, which open at the base, are generally not separable from those with an upright capsule opening toward the apex. This cautioned him with respect to *Asyneuma* and so the new plant remained in that genus.

**A brief nomenclatural history of Asyneuma**

The following is a loose translation and condensation from Damboldt’s Einleitung (Introduction) in his *Revision der Gattung Asyneuma* (Damboldt 1970): Many of the species that currently belong in the genus *Asyneuma* were originally included in a separate section (sectio III), of the genus *Phyteuma* L. by Alphonse de Candolle (1830) in his *Monographie des Campanulées*, but George Don united them in his *Phyteuma* sect. *Podanthum* G. Don (1834), a move which was adopted by Boissier (1849). Subsequently, Boissier (1875), ignoring or unaware of the work of Ruprecht (1867), who had already raised the section to the rank of a genus, as *Podanthum* (G. Don) Boiss., similarly placed the species in *Podanthum* and subdivided it into two sections: *Podanthum* sect. *Eupodanthum* (with the diagnosis “Capsula erecta poris versus apicem vel ad medium dehiscens”, but the name not validly published, Turland & al. 2018: Art. 21.3, 32.1(c)) and *Podanthum* sect. *Clinocarpium* Boiss. (with the diagnosis “Capsula nutans poris basilaribus dehiscens”). However, Grisebach & Schenk (1852) had already established *Asyneuma* as a genus distinct from *Campanula* and *Phyteuma*, and it was Janchen (1906) who first pointed to the priority of *Asyneuma* over *Podanthum*. Therefore, Bornmüller (1921), in his revision, transferred Boissier’s species of *Podanthum* to *Asyneuma*. Fedorov (1957) subdivided the genus into two sections, A. sect. *Eupodanthum* Fed. and A. sect. *Sceptrum* Fed., and emended the description of the former. In *Flora iranica*, Rechinger & Schimmann-Czech in Rechinger (1965) combined the systems of Boissier and Fedorov, dividing *Asyneuma* into A. sect. *Clinocarpium* (Boiss.) Rech. f. & Schiman-Czechka. A. sect. *Eupodanthum* and A. sect. *Sceptrum*.

**Asyneuma comosiforme and its “fate”**

Recognizing the uniqueness of *Asyneuma comosiforme*, Radomir Lakušić (2001), transferred it to the new genus *Hayekia*. However, he did not provide a description or diagnosis, leaving this name not validly published (Turland & al. 2018: Art. 38.1(a)). In his projected but unpublished *Flora dinarica*, he provided the following description for the new genus: “Flowers distinct thinly stalked. Petals 5, free curved linear, 12–15 mm long.
and 1.5–2.5 mm wide, violet-blue to lilac blue. Ovary 3-celled. Capsule nodding, dehiscing by 3 pores near the base”. When he wrote this, he probably followed Hayek in assuming that the capsule dehisced basally, which led him to include A. trichocalycinum as Hayekia trichocalycina and A. pichleri (Vis.) D. Lakušić & F. Conti as H. malyana in his new genus (neither name validly published, Turland & al. 2018: Art. 35.1). The most recent revision of Asyneuma is by Damboldt (1970), who, unlike Lakušić (2001), claimed that Hayek was in error to have suspected A. comosiforme to have a closer relationship with A. trichocalycinum, which he excluded from Asyneuma (together with A. sect. Clinocarpium) on account of its pendent capsules with basal pores, and despite having the corolla divided to the base. He retained A. comosiforme, reserving judgement until mature capsules were available. Also excluded by Damboldt were Campanula psilostachya Boiss. & Kotschy, C. strigillosa Boiss., Phyteuma regelii Trautv. [= Sergia regelii (Trautv.) Fed.] and Podanthum scoparium Boiss. & Hausskn., all of which were included in Asyneuma by Bornmüller (1921). Since then, depending on the author, A. trichocalycinum has been included either in Campanula or Asyneuma (Lammers 2007). Recently, a molecular analysis has shown conclusively that A. trichocalycinum and A. pichleri are correctly placed with Asyneuma and form a sister group to the rest of the genus (Stefanović & Lakušić 2009), although it remains debatable whether they should be accorded full generic status (if so, a new generic name is required).

Independently, Frajman & Schneeweis (2009) and Stefanović & Lakušić (2009) presented a surprising finding for Asyneuma comosiforme. Their results suggest that A. comosiforme belongs neither in Asyneuma nor close to the A. trichocalycinum–A. pichleri complex. Instead it apparently has a closer relationship with the isophyllous species of Campanula, which prompted these authors to transfer A. comosiforme to the genus Campanula. These results were corroborated by Bogdanović & al. (2014, 2015). Asyneuma comosiforme was inferred by Frajman & Schneeweis (2009: 596) as belonging to the isophyllous Campanula species of the Garganica clade (in the circumscription of Park & al. 2006). Frajman & Schneeweiss also stated (2009: 596) that “Asyneuma comosiforme is clearly nested within the Rapunculus clade of Campanula and is not closely related to Asyneuma” (our emphasis). They cited Damboldt (1970) to support this contention.

### Material and methods

This study is based on the herbarium material deposited in the herbaria BEOU, BP, GB, JE, NHMR, TIR, W, WU and ZAGR (herbarium codes follow Thiers 2017+), personal field investigation (field. obs.) in all known sites, and living plants cultivated in the Botanical Garden Jevremovac, University of Belgrade. Names of taxa and taxonomic information and data are taken from the Euro+Med PlantBase (Euro+Med 2006–2017) and Lammers (2007). Abbreviations for the author(s) of scientific names follow the authors database of the International Plant Names Index (http://www.ipni.org/ipni/authorsearchpage.do). Special emphasis was placed on the type materials and the descriptions in protologues. These materials are cited under Material studied. The localities for occurrences of the species in the field were recorded with a GPS (Garmin eTrex Legend HCx and Garmin eTrex Vista C).

Seeds and type of hairiness of leaves, corolla, pistil and fruits were examined under a LEICA stereo-binocular microscope. For the investigation of fine micromorphological structure of seeds, samples were coated with gold and studied with a scanning electron microscope (JEOL JSM-6460).

Root tips obtained from plants grown in pots were used for the analyses of mitotic chromosomes. They were pre-treated with 0.002M 8-hydroxyquinoline for 3 h at 4°C, fixed in cold 3:1 (v/v) absolute ethanol/glacial acetic acid for 48 h and stored in 70% ethanol at 4°C for further use. Hydrolysis was performed in 1N HCl for 12 min at 60°C and staining in Schiff reagent for at least 2 h (Feulgen & Rossenbeck 1924), followed by squash in acetic carmin. Chromosome plates were observed under a Leica DMLS light microscope (Leica Microsystems, Wetzlar, Germany) and photographed with Leica DCF 295 camera (Leica Microsystems). The chromosome number was determined from at least five individuals and from at least 10 cells per root tip.

### Results

We provide new insights on the morphology of Asyneuma comosiforme based on detailed studies of living plants in all vegetative stages from different habitats and localities. Details are shown on Table 1, Fig. 1–3 and in the Expanded species description of the Taxonomy section.

The data in Table 1 should highlight the diagnostic characters for Asyneuma comosiforme and its separation from Asyneuma and the isophyllous species of Campanula, but, taken individually, most of these key features also occur in diverse genera of the Campanulaceae (Table 2), none of which can be diagnosed by a single character alone, but by a combination of them. We conclude that (1) linear corolla lobes, (2) corymbose inflorescence, (3) capsule dehiscing by lateral, medial valves and (4) rhombic leaves represent a combination of key features that clearly differentiate A. comosiforme from the other taxa.

The chromosome number $2n = 2x = 34$, was determined here for the first time in Asyneuma comosiforme (Fig. 4). Given that this number is a common number in the bellflower family, not only in many Asyneuma
and Campanula species, but also in other genera, such as Adenophora, Feeria Buser, Michaelia L’Hér., Physoplexis (Endl.) Schur, Phyteuma and Trachelium L. (Table 2), it cannot be used as an exclusive character for the segregation or conjugation of the genera within the Campanulaceae.

Discussion

A more rigorous, in-depth morphological examination of Asyneuma comosiforme reveals it to be enigmatic with respect to both Asyneuma and Campanula. Hayek (1921, 1924) thought the plant was closer to Asyneu-
Table 2. Distribution of morphological key features and chromosome number of *Hayekia comosiformis* in comparison with other European genera of the Campanulaceae (chromosome numbers are based on: Rice & al. 2015, and references in: Anchev 1975, 1993; Contandriopoulos 1980a, 1980b; Strid & Franzén 1981; Tzanoudakis & Kyriakakis 1987; Lammers & Hensold 1996; Probato & al. 1998; Park & al. 2006; Probato 2006; Rice & al. 2015, and references therein).

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Linear corolla</th>
<th>Corymbous inflorescence</th>
<th>Lateral medial valves</th>
<th>Rhomboid leaves</th>
<th>Capsule dehiscence 2n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asyneuma comosiforme</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3 lateral, medial valves 34</td>
</tr>
<tr>
<td>Campanula</td>
<td>0</td>
<td>0/1</td>
<td>0/1</td>
<td>0/1</td>
<td>all combinations of lateral dehiscence: pores or valves (proximal, medial, distal) 14, 16, 17, 18, 20, 22, 24, 25, 26, 28, 30, 32, 33, 34, 35, 36, 40, 46, 48, 50, 51, 52, 54, 55, 56, 58, 68, 80, 90, 96, 102, 154</td>
</tr>
<tr>
<td>Asyneuma</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3 lateral, distal pores 20, 22, 24, 28, 32, 34, 48, 56, 64, 68, 102</td>
</tr>
<tr>
<td>Phyteuma</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0/1</td>
<td>2 or 3 lateral, medial pores 16, 18, 20, 22, 24, 26, 28, 34, 36</td>
</tr>
<tr>
<td>Petromarula</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3 lateral, medial pores 30</td>
</tr>
<tr>
<td>Physoplexis</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2 or 3 lateral, medial pores 34</td>
</tr>
<tr>
<td>Trachelium</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2 or 3 lateral, proximal pores 32, 34</td>
</tr>
<tr>
<td>Legousia</td>
<td>0</td>
<td>0/1</td>
<td>0</td>
<td>0</td>
<td>3 lateral, distal valves 20, 26</td>
</tr>
<tr>
<td>Jasione</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2 short, apical valves 12, 14, 24, 26, 36, 60</td>
</tr>
</tbody>
</table>

*ma,* although perhaps not comfortably so, which was also our conclusion. In overall appearance, *A. comosiforme* resembles *Asyneuma* marginally more than the isophyllous bellflowers. It even bears a superficial resemblance to *Diosphaera rumeliana* (Hampe) Bornm. (= *C. rumeliana* (Hampe) Vatke), perhaps less so to *Physoplexis comosa* (L.) Schur. Despite the corroboration of the three molecular studies (Frajman & Schneeweiss 2009; Stefanović & Lakušić 2009; Bogdanović & al. 2014, 2015), the taxonomic status of *A. comosiforme* remains questionable. If this species is transferred to *Campanula,* it becomes even more difficult to find characters to clearly separate *Asyneuma* and *Campanula* on morphological grounds, but we disagree with the notion that most morphological characters are highly plastic and not suitable to delineate natural groups (Bogdanović & al. 2014: 1250, referring to Roquet & al. 2008, 2009). Bogdanović & al. (2014) provided a key to the species of *C. ser. Garganicae* Trinajstić, which included *A. comosiforme* (as *C. comosiformis* (Hayek & Janch.) Frajman & Schneew.), but most of the characters used in the key are equivocal. Within a group of species, discontinuously variable character states are not explicitly definable, and have tendencies towards one expression or another, but they can be used in combination to provide perfectly adequate diagnoses. Both the above-mentioned studies have influenced the respective authors to conclude that the deeply divided corolla is unreliable as the sole character to differentiate *Asyneuma* from *Campanula.* Bogdanović & al. (2014: 1250) stated “There have been several attempts of classification (De Candolle 1830; Boissier 1875; Gadella 1966a, 1966b; Contandriopoulos 1984; Kolakovsky 1994), but none of them have been confirmed by any phylogenetic studies available to date…” However, Eddie & al. (2003: 565) concluded “Overall, there is a remarkable congruence between the ITS tree and traditional ideas on species relationships within the Campanulaceae (Eddie, 1999). The insights of early workers such as De Candolle and Boissier have proved to be remarkably clear, and their classification systems have, on the whole, been logically consistent with our findings on phylogeny.” Despite this, a cladogram is not synonymous with a classification and should not be used simply as a template for one. It is a useful means of data exploration and can provide phylogenetic insight, but should be interpreted with great care.

While the newly recovered “phylogenetic” position of *Asyneuma comosiforme* by Frajman & Schneeweiss (2009), Stefanović & Lakušić (2009) and Bogdanović & al. (2014) is strongly supported, the cladograms obtained by those authors invite explanation. Although the topology of a cladogram can highlight close phylogenetic relations, this is not always the case and it can vary greatly depending on the parameters selected for the analysis. Frajman & Schneeweiss’s interpretation of the topology of their trees lacks the latitude necessary to obtain a broad vision of the inter-relationships within these lineages.

In fact, *Asyneuma comosiforme* is not as remote from *Asyneuma* as Frajman & Schneeweiss (2009) implied. It is not nested within the Garganica clade but is actually consistently sister to it. This may simply indicate that its molecular signature has diverged significantly from the bulk of species in *Asyneuma,* and therefore its position...
is perhaps not so surprising because both lineages are likely to have descended from a common ancestor anyway. There is no doubt that the genus Asyneuma and the isophyllous campanulas are closely related sister lineages within the Rapunculus clade of Campanula s.l. (Eddie & al. 2003; Park & al. 2006), or within the large clade CAM02-12 (Mansion & al. 2012; Jones & al. 2017). The apparent, closer relationship of A. comosiforme with the isophyllous campanulas on the molecular cladogram may be due to evolutionary stasis of its genome and/or differential rates of mutation. Asyneuma comosiforme may be ancestral to the isophyllous campanulas. How we classify A. comosiforme is another question because, from a morphological perspective, it is clearly “out of phase” with both Asyneuma and Campanula. This is the most important point at issue in this paper.

In the proposed taxonomic treatment of Asyneuma comosiforme, we have been guided by the recommendations or principles advocated by McVaugh (1945), for example: “The most important criterion of any supposed genus is not the width of the gap between it and another, but its own biological unity. Homogeneity of many characters, regardless of the degree of overlapping of these characters with those of other genera is the best indicator of this unity.” (Recommendation 3, in part).

Such segregation is hardly a new precedent. In early classifications, Phyteuma embraced all the segregate taxa that are now assigned to Asyneuma, Cryptocodon Fed., Cylindrocarpa Regel, Petromarula Vent. ex R. Hedw., Physoplexis and Sergia Fed. The western North American Campanula prenanthoides Durand has also been transferred to Asyneuma (McVaugh 1944, 1945; Gadella 1966b). The recognition of unique evolutionary grades of organization as mono/oligotypic genera should help us better understand the evolutionary history of the Campanulaceae, especially the rapunculoid bellflowers, because this assemblage is a major stumbling block in the reclassification of the family. Asyneuma comosiforme is isolated and unique within the Asyneuma/isophyllous lineages and therefore it is fitting for it to be given proper recognition in the genus Hayekia.

**Taxonomy**

Taking the above comparisons and discussion into account, we support the opinion of Radomir Lakušić (2001), who transferred Asyneuma comosiforme to the separate genus Hayekia. Based on additional morphological, karyological, chorological and ecological details provided here, which further highlight its taxonomic uniqueness, we propose the following.

**Hayekia** Lakušić ex D. Lakušić, Shuka & Eddie, gen. nov.

Type: *Hayekia comosiformis* (Hayek & Janch.) Lakušić ex D. Lakušić, Shuka & Eddie.

**Generic diagnosis** — Hayekia resembles Asyneuma, but differs as follows. Rhizomes subligneous and fragile, divergently branched, elongate and soboliferous, giving rise to many flexuous (often scorpioid), vertical herbaeous shoots; shoots glabrous with longitudinal papillate rows. Leaves ovate to rhomboid, with winged petiole. Flowers long pedicellate, clustered in a head-like, terminal raceme (corymb), with bracts of lower and middle flowers same as cauleine leaves, much longer than pedicels. Capsule pendent, dehiscing by 3 clearly protruding, recurved axicorns, pushing fruit wall (pericarp), and opening medially by V-shaped, translucent, upward-curving, persistent valves.


**Expanded species description** — Given that Hayek (1921) described this species on the basis of a few specimens collected in the flowering stage from a single locality, the following is an expanded description of living plants from different habitats and localities, and representing all vegetative stages.

Caespitose perennial. Rhizomes subligneous, elongated and very branched, subligneous; stems many, erect, non-branched, 20–30 cm long, subligneous, becoming herbaceous, lax and leafy, fragile, often with a flexuous (sometimes scorpioid) (Fig. 1B): shoots glabrous with longitudinal papillate rows. Leaves ovate to rhomboid, sometimes semi-succulent, glabrous; petiole long, narrowly winged; blade of basal leaves orbicular-ovate, small, withered at anthesis; blade of cauline leaves quadrangular, nearly rhombic, with obtuse lateral angles, rarely lanceolate, base triangular, cuneate, margin serrate with sharp teeth pointing forward (Fig. 1C, D), apex tapering to a point, ± acute. Inflorescence axis normally terminating in a loose, head-like, flat- or round-topped node, with lower pedicels longer than upper ones (Fig. 1C, D); occasionally inflorescence axis lacking a terminal corymb and then single flowers borne in leaf axils; bracts of lower and middle flowers same as cauleine leaves, much longer than pedicels (Fig. 1C, D); bracts of upper flowers narrowly lanceolate, very small; pedicels slender, erect at anthesis (Fig. 1C, E, F), but elongated and recurved in fruit (Fig. 1D). Calyx green, ovoid, glabrous; calyx lobes narrowly triangular to almost linear-lanceolate, 2–3 × as long as ovary, with 1 (rarely 2) prominent, curved tooth on each margin (Fig. 1F). Corolla blue to dark lilac, rotate, divided nearly to...
Fig. 1. *Hayekia comosiformis* – A: habit; B: soboliferous, subligneous rhizomes; C: inflorescence at flowering stage; D: inflorescence at fruiting stage; E: flower showing linear, strap-like lobes, filaments with narrowly deltoid filament base, anthers and style; F: flower showing calyx and calyx lobes with a tooth on each margin. – Photographs: A by B. Hallaći (Shija gorge, 29 May 2012); B, C, E, F by L. Shuka (Shija gorge, 2 Jun 2017); D by B. Surina (Cape of Skanderbeg, 26 Jul 2012).
base into 5 deflexed, long linear, strap-like lobes (Fig. 1A, C, E, F), each 12–20 mm long × 1.5–2.5 mm wide. **Filaments** blue, with narrowly deltoid base (Fig. 1E); **anthers** dirty green to dirty yellow, several times longer than distal, filiform part of filament. **Ovary** 5-ribbed, trilocular; **style** slender, as long as or longer than corolla lobes; **collector hairs** in upper ⅓, often encrusted with translucent, saffron-coloured pollen, usually curved backward in female phase (Fig. 1E). **Capsule** ovoid to deltoid, 2.7–3.8 mm long × 1.6–3.1 mm wide, 5-ribbed, glabrous; dehiscing by 3 clearly protruding, recurved axicorns pushing fruit wall (pericarp) and opening in medial part with V-shaped, translucent, persistent, upward-curling valves (Fig. 2A, B). **Seeds** shiny reddish to dark brown, 0.8–0.9 mm long × 0.5–0.6 mm wide, differentiated into flattened (Fig. 3A) and ellipsoid (Fig. 3C) types, both with similar striate testa with elongate, fibriform cells and slightly raised and anastomosed, radial and anticlinal walls forming a distinct, rugose, linear lumen (Fig. 3B, D).

**Chromosome number** — $2n = 2x = 34$, chromosomes 0.805 to 1.856 μm long (Fig. 4).

**Phenology** — Flowering from mid-May (at lower altitudes) until mid-July (at higher altitudes).

**Distribution and ecology** — Northeastern Albania, stenoendemic, monotypic (Fig. 5); 400–1985 m; crevices and scree of limestone cliffs and gorges.

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Fig. 2. *Hayekia comosiformis*, capsules with recurved axicorns and V-shaped, upward-curving valves. – Scale bars: A, B = 1 mm. – Origin: Bicaj canyon (Shija gorge).

Fig. 3. *Hayekia comosiformis* – A, B: flattened seed; C, D: ellipsoid seed. – Scale bars: A, C = 100 μm; B, D = 50 μm. – Origin: Bicaj canyon (Shija gorge).
Korab – Gjalica and Deja – Pas Deja mountain groups.
Currently known from eight sites (four canyons and four cracks and crevices of small ledges or terraces. It is cur-
ing relatively low temperatures and high air humidity.

in Mali i Dejës and grown in Botanical Garden “Jevremovac” = 34. – Scale bar = 10 μm. – Origin: plants collected

Fig. 4. Hayekia comosiformis – metaphase chromosome plate, 2n = 2x = 34. – Scale bar = 10 μm. – Origin: plants collected

in Mali i Dejës and grown in Botanical Garden “Jevremovac” in Belgrade.

Generally, Hayekia comosiformis is restricted to steep, rocky slopes along semi-shaded canyons, providing relatively low temperatures and high air humidity. Here, it grows with other chasmosphatic vegetation in cracks and crevices of small ledges or terraces. It is cur-
ingly known from eight sites (four canyons and four localities in open screes or at the upper tree line) of the Korab–Gjalica and Deja–Pas Deja mountain groups.

Two localities have a northwesterly aspect and are located in the tributaries of the right bank of the Black Drin, at 520 m (Bicaj canyon, site 1) and 630 m (Çaja canyon, site 2), respectively, whereas the third locality in the Seta canyon (Çidhna e Poshtme, site 3), occurs in the left bank of the Black Drin at 550 m and has an easterly aspect. The locality in the canyon of Kepi i Skënderbeut (site 8) is at the altitude of 1080–1150 m with a southeasterly aspect. Other localities of the Deja–Pas Deja mountains where H. comosiformis occur are not situated in canyons. They are found at altitudes of 1250–1985 m and 3.5–12.5 km from the canyon of Kepi i Skënderbeut, in semi-shady rock crevices and on open, stony and rocky pastures, with shallow soil, within the zone of forests of Fagus sylvatica L. and Pin-
us heldreichii Christ. Geologically, the rocks are upper Triassic to lower Cretaceous, and composed of homoge-
neous limestone in the Bicaj, Seta, Kepi i Skënderbeut and Guri i Vashës (site 6) localities, but of a mixture of limestone and thin, granitic tiles at the Lapaj bridge of the Çaja canyon. All the other localities of the Deja–Pas Deja mountains are on limestone substrates.

The tree flora of the upper parts of the rocky slopes in the three lowest localities comprises principally Carpinus orientalis Mill. and Juniperus deltooides R. P. Adams, rather than Fagus sylvatica and Pinus heldreichii, which occurs in the two localities above 1000 m, and Juniperus communis subsp. nana Syme in the Deja mountains above 1500 m. Associated vegetation on the rocky slopes of all the canyons is generally sparse, but includes Allium flavum L., Asperula scutel-
laris Vis., Athamanta turbith subsp. haynaldii (Borbás & R. Uechtr.) Tutin, Campanula korabensis F. K. Mey., Clinopodium thymifolium (Scop.) Kuntze, Moehringia

bavarica (L.) Gren., Moltkia petraea (Tratt.) Griseb., Ramonda serbica Pančić, Saxifraga paniculata Mill., Scabiosa crenata Cyt., Silene multicaulis Guss. and Teucrium arduini L. In addition, Heliosperma nikolicii (A. Seliger & Wraber) Niketić & Stevan., Hieracium waldsteinii Tausch, Saxifraga federici-augusti subsp. grisebachii (Degen & Dörfl.) D. A. Webb and Sedum telephium subsp. maximum (L.) Krocker were noted in the Bicaj and Çaja canyons, while Crepis macedonica Kitan. was observed in the Seta and Kepi i Skënderbeut canyons. In the Kepi i Skënderbeut canyon, Saxifraga federici-augusti subsp. grisebachii is replaced by S. sempervivum C. Koch. In the Deja–Pas Deja mountains localities, Hayekia comosiformis is associated with Alchemilla velebitica Borbás ex Janch., Amphoricar-
pos autarius Blečić & E. Mayer, Asperula doerfleri Wettst., Carex kitaibehiana Degen ex Bech., Edraian-
thus graminifolius (L.) A. DC., E. serpyllifolius (Vis.) A. DC., Euphorbia myrsinites L., Hieracium villosum Jacq., Juniperus communis subsp. nana, Laserpitium siler L. subsp. zernyi (Hayek) Tutin, Leucanthemum vulgare Lam., Minuartia graminifolia (Ard.) Tav., Pinus heldreichii, Potentilla apennina Ten., Saxifraga panicu-
lata, Sedum dasiphyllum L., Sesleria interrupta Vis., Stachys recta L., Thalictrum minus L., etc.

Conservation status — The estimation of the potentially threatened status of Hayekia comosiformis was made ac-
cording to the criteria and categories of the IUCN (IUCN Standards and Petitions Subcommittee 2017). It is in-
cluded in the Red List of protected species of Albania and assessed as Endangered (EN A1b) (MoE 2013). It oc-
curs in only eight localities, with an area of occupancy of 44 km² extending over 394.2 km². The population size was estimated between 1500 and 2000 mature in-
dividuals. Because the localities at higher altitudes and within canyons are subject to the same threats from cli-
mate change, and there is a reduction in available habi-
tat in three other localities, mainly due to water course deviation for hydropower construction or quarrying ac-
tivities, H. comosiformis is assessed as Endangered EN B1ab(iii)+2ab(ii,iv,v).

Etymology — The generic name Hayekia is feminine and therefore the specific epithet is comosiformis. The name Hayekia was chosen by Prof. Radomir Lakušić in honour of Prof. Dr August von Hayek (1871–1928), who was an Austrian botanist and associate professor at the Univer-
sity of Vienna, and who is particularly remembered for his phytogeographical investigations in the Balkans and the southeastern Alps. Prof. Lakušić (1933–2005) was a Yugoslavian botanist, a biogeographer and a vegetation biologist, whose field of work included, in particular, the subalpine and alpine high-mountain vegetation of the southeastern Dinarides in Bosnia and Herzegovina, and Montenegro. He was a professor at the Universities of Sarajevo and Banja Luka.
Material studied — This includes herbarium specimens examined or plants observed in the field. The site numbers correspond with the numbers on the distribution (Fig. 5). Because the species is listed as endangered, more precise locality data are omitted. This information could be supplied on request to any bona fide researcher.

District of Kukës (Rrethi i Kukësit):

**Site 1** — Bicaj canyon (Shija gorge): BP524980!, BP589744!, BP768765!, GB-004 7108!, NHMR-1093!, TIR!, W 1958-0010312!, WU-4884!, ZAGR-32597!

**Site 2** — Çaja canyon: TIR!, ZAGR-32598!

District of Peshkopi (Rrethi i Peshkopisë):

**Site 3** — Seta canyon (Çidhna e Poshtme): TIR!

District of Mirditë (Rrethi i Mirditës):

**Site 4** — Kurbnesh: BP-22449!

District of Mat (Rreth i Matit):

**Site 5** — Mali i Dejës: BEOU-46886!, BP-21607!

**Site 6** — Guri i Vashës: TIR!

**Site 7** — Maja e Butrojes: Z. Barina & al., field. obs.

**Site 8** — Kepi i Skënderbeut (Cape of Skanderbeg): JE5075!, NHMR-1982!, TIR!

Note: three literature records: “Gjallica–Koritniku” (Shuka & al. 2008), “ALBANIA. Gjalica, Mustafe” (Bogdanović & al. 2014) and “a 4 km territory in both

Fig. 5. Distribution of *Hayekia comosiformis* — numbers on map correspond with numbers of sites listed under Material studied. — Country codes: Al = Albania; Ko = Kosovo; Ma = North Macedonia; Mn = Montenegro.
sides of the road Kalimash–Morinë, Kukesi district” (Hallaçi 2008) refer to the same site: the Shija gorge E of Bicaj (site 1).

Acknowledgements

The work of the first and fourth authors was realized by the financial support provided by the Serbian Ministry of Education, Science and Technological Development (project No. 173030). We thank Besnik Hallaçi (National Agency of Protected Areas, Albania), Boštjan Surina (Natural History Museum Rijeka), Božo Frazierman (University of Innsbruck) and Sandro Bogdanović (University of Zagreb) for providing locality data, Miloš Bokorov (University Novi Sad) for the SEM photos, Sanja Kovačić (University of Zagreb, Botanical Garden) for facilitating correspondence and helping with translations, and Thomas G. Lammers (University of Wisconsin–Oshkosh) and Evgeny V. Mavrodiev (Florida Museum of Natural History) for their comments on an earlier version of this article.

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