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

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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

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## 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

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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 (Qosja & al. 1996), where it grows in crevices of limestone cliffs and possibly numbers only a few hundred individuals (Frajman & Schneeweiss 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 Jug Dujaković (ZAGR), and Surina (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. trichocalycinum* (Ten.) K. Malý, 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 & Schimann-Czeika in Rechinger (1965) combined the systems of Boissier and Fedorov, dividing *Asyneuma* into *A. sect. Clinocarpium* (Boiss.) Rech. f. & Schiman-Czeika, *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, dehiscent by 3 pores near the base”. When he wrote this, he probably followed Hayek in assuming that the capsule dehiscent 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 & Schneeweiss (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 & Schneeweiss (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 Botani-

cal 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 locations 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 dehiscent 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*

Table 1. Comparison of morphological key features and chromosome numbers of *Hayekia comosiformis*, *Campanula* “isophyllous” group, *Asyneuma* Sect. *Clinocarpium* and *Asyneuma* s.str. (chromosome numbers are based on: Anchev 1975, 1993; Contandriopoulos 1980a, 1980b; Strid & Franzén 1981; Tzanoudakis & Kypriotakis 1987; Lammers & Hensold 1996; Probatova & al. 1998; Park & al. 2006; Probatova 2006; Rice & al. 2015 and references therein).

| Taxon                | <i>Asyneuma comosiforme</i>                                                                                                                                                                                                                                            | <i>Campanula</i><br>“isophyllous” group                                                                                                                                                                                                                                                 | <i>Asyneuma</i> sect.<br><i>Clinocarpium</i>                                                                                                              | <i>Asyneuma</i> s.str.                                                                                                                    |
|----------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------|
| <b>Habit</b>         | Perennial, lax, caespitose, with many erect non-branched stems, up to 30 cm                                                                                                                                                                                            | Perennial, lax, caespitose, with many erect, simple or branched stems, up to 50 cm                                                                                                                                                                                                      | Perennial, non-caespitose, with single, erect, simple or branched stems, up to 90 cm                                                                      | Perennial, non-caespitose, with single or several, erect, simple or branched stems, up to 100 cm                                          |
| <b>Stems</b>         | Very branched, fragile, sub-ligneous, soboliferous, elongated, horizontal or vertical, subterranean rhizomes with many elevated, almost-woody shoots, and herbaceous, flexuous, often scorpioid, above-ground stems. Shoots glabrous, with longitudinal papillate rows | Rarely with very branched, fragile horizontal rhizomes, repent or with elevated shoots, or soboliferous with strong, divided caudex (e.g. in <i>C. poscharskyana</i> ); persistent, often woody at base); flexuous, herbaceous stems. Shoots hairy, without longitudinal papillate rows | Herbaceous stems arising directly from carrot-shaped root; not divided on caudex or soboliferous. Shoots subglabrous, without longitudinal papillate rows | Herbaceous stems arising directly from carrot-shaped root, not divided on caudex or soboliferous                                          |
| <b>Leaves</b>        | Quadrangular, to almost rhombic, rarely lanceolate with long, narrowly winged petioles; basal leaves not in rosettes; withered at anthesis, sometimes semi-succulent                                                                                                   | Cordate to ovate with long unwinged petioles; basal leaves arranged in rosettes, persistent at anthesis                                                                                                                                                                                 | Ovate to lanceolate, sessile or subsessile; basal leaves not arranged in rosettes, withered at anthesis                                                   | Linear to linear-oblongate, oblong, spatulate, ovate to lanceolate, often undulate, sessile or subsessile; basal leaves in dense rosettes |
| <b>Inflorescence</b> | Monochasial in lower part (with a single main axis) and corymbose in terminal part; round-topped; flowers solitary                                                                                                                                                     | Many flowered racemes, elongated and unilateral; flowers solitary                                                                                                                                                                                                                       | Many-flowered, simply or sparingly branched racemes; flowers solitary or in clusters                                                                      | Many-flowered, simply or sparingly branched racemes, flowers solitary or in clusters                                                      |
| <b>Pedicel</b>       | Slender, equal or longer than ovary, erect at anthesis, elongated and recurved in fruit, without bracteoles                                                                                                                                                            | Slender, equal or longer than ovary, erect or recurved, often with linear or setiform bracteoles                                                                                                                                                                                        | Slender, much longer than ovary, recurved both at anthesis and in fruit, with linear or setiform bracteoles                                               | Absent, or very short, much shorter than ovary                                                                                            |
| <b>Calyx lobes</b>   | Narrowly triangular to almost linear, dentate, with one, rarely two, teeth on each side                                                                                                                                                                                | Narrowly triangular to linear, sometimes dentate, with few teeth on each side                                                                                                                                                                                                           | Linear to setaceous, without teeth on each side                                                                                                           | Triangular, without teeth on each side                                                                                                    |
| <b>Corolla</b>       | Rotate, divided nearly to base into 5 deflexed long linear strap-like lobes                                                                                                                                                                                            | Campanulate to rotate with triangular lobes never divided to base in strap-like lobes                                                                                                                                                                                                   | Rotate with narrowly triangular or strap-like lobes divided to base                                                                                       | Rotate with narrowly triangular or strap-like lobes divided to base                                                                       |
| <b>Capsule</b>       | Pendent, opening by medial, V-shaped, translucent, upward-curving and persistent valves                                                                                                                                                                                | Pendent, opening by basal pores or rarely with medial valve ( <i>C. poscharskyana</i> ) or capsule without pores or valves ( <i>C. aureliana</i> )                                                                                                                                      | Pendent, opening by basal pores                                                                                                                           | Erect, opening by apical pores                                                                                                            |
| <b>2n</b>            | <b>34</b>                                                                                                                                                                                                                                                              | 32, <b>34</b>                                                                                                                                                                                                                                                                           | 24, 32, 48, 56, 64                                                                                                                                        | 20, 22, 24, 28, 32, <b>34</b> , 48, 56, 64, 68, 102                                                                                       |

and *Campanula* species, but also in other genera, such as *Adenophora*, *Feeria* Buser, *Michauxia* 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 & Kypriotakis 1987; Lammers & Hensold 1996; Probatova & al. 1998; Park & al. 2006; Probatova 2006; Rice & al. 2015, and references therein).

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

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. ( $\equiv$  *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; Contandri-

poulos 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 herbaceous 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 cauline leaves, much longer than pedicels. *Capsule* pendent, dehiscent by 3 clearly protruding, recurved axicorns, pushing fruit wall (pericarp), and opening medially by V-shaped, translucent, upward-curving, persistent valves.

***Hayekia comosiformis* (Hayek & Janch.) Lakušić ex D. Lakušić, Shuka & Eddie, *comb. nov.*** (Fig. 1–3) = *Asyneuma comosiforme* Hayek & Janch. in Oesterr. Bot. Z. 70: 20. 1921 = *Campanula comosiformis* (Hayek & Janch.) Frajman & Schneew. in Syst. Bot. 34: 599. 2009. – Lectotype (designated by Frajman & Schneeweiss 2009: 599): [Albania, Shija gorge, east of Bicaj] “Nordost-Albanien: Felsen am unteren Beginn der Šija-Schlucht bei Bicaj, ca 400 m”, 15 Jun 1918, H. Zerny (GB-004 7108 [photo!]; isotype: W [photo!]).

**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* soboliferous, 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 corymb, 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 cauline 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. Hallaçi (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  $\times$  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  $\frac{1}{3}$ , 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  $\times$  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-curving valves (Fig. 2A, B). *Seeds* shiny reddish to dark brown, 0.8–0.9 mm long  $\times$  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  $\mu\text{m}$  long (Fig. 4).

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

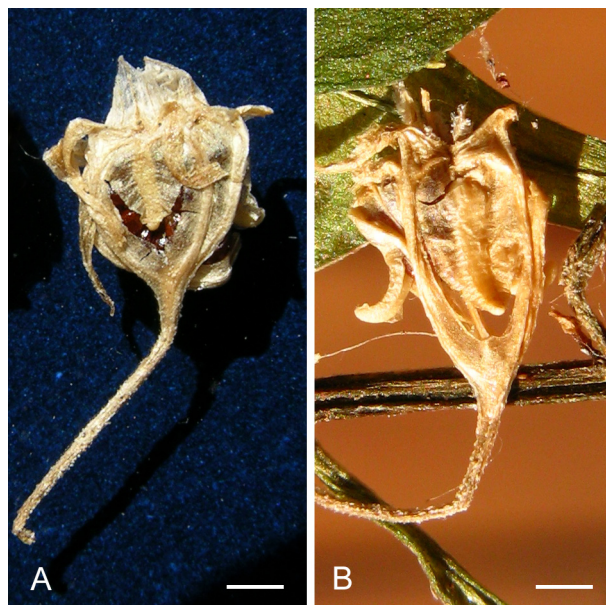


Fig. 2. *Hayekia comosiformis*, capsules with recurved axicorns and V-shaped, upward-curving valves. — Scale bars: A, B = 1 mm. — Origin: Bicaj canyon (Shija gorge).

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

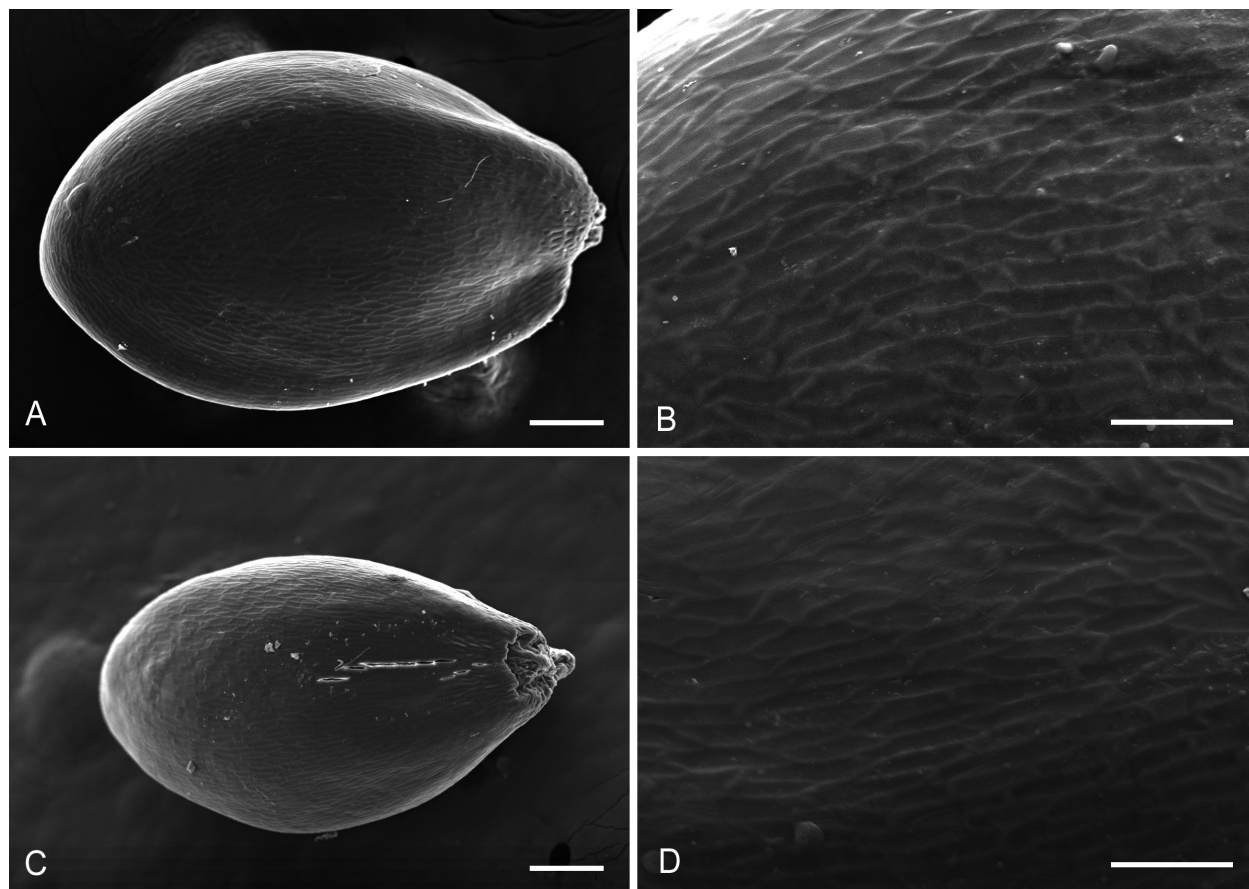


Fig. 3. *Hayekia comosiformis* — A, B: flattened seed; C, D: ellipsoid seed. — Scale bars: A, C = 100  $\mu\text{m}$ ; B, D = 50  $\mu\text{m}$ . — Origin: Bicaj canyon (Shija gorge)..

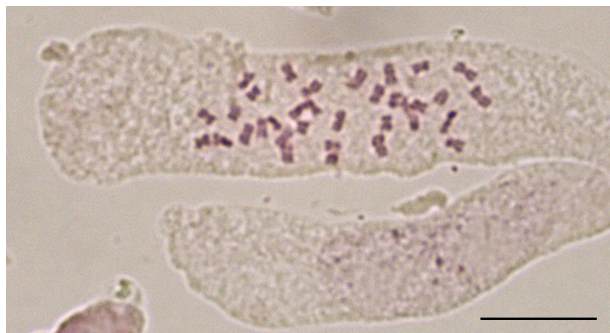


Fig. 4. *Hayekia comosiformis* – metaphase chromosome plate,  $2n = 2x = 34$ . – Scale bar = 10  $\mu\text{m}$ . – Origin: plants collected in Mali i Dejës and grown in Botanical Garden “Jevremovac” in Belgrade.

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 chasmophytic vegetation in cracks and crevices of small ledges or terraces. It is currently 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 *Pinus heldreichii* Christ. Geologically, the rocks are upper Triassic to lower Cretaceous, and composed of homogeneous 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 deltoides* 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 scutellaris* 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* Cyr., *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 & Dörfel.) D. A. Webb and *Sedum telephium* subsp. *maximum* (L.) Krocke 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., *Amphoricarpus autariatus* Blečić & E. Mayer, *Asperula doerfleri* Wettst., *Carex kitaibeliana* Degen ex Bech., *Edraianthus 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.) Jáv., *Pinus heldreichii*, *Potentilla apennina* Ten., *Saxifraga paniculata*, *Sedum dasyphyllum* 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 according to the criteria and categories of the IUCN (IUCN Standards and Petitions Subcommittee 2017). It is included in the Red List of protected species of Albania and assessed as Endangered (EN A1b) (MoE 2013). It occurs in only eight localities, with an area of occupancy of 44 km<sup>2</sup> extending over 394.2 km<sup>2</sup>. The population size was estimated between 1500 and 2000 mature individuals. Because the localities at higher altitudes and within canyons are subject to the same threats from climate change, and there is a reduction in available habitat in three other localities, mainly due to water course deviation for hydropower construction or quarrying activities, *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 University 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.

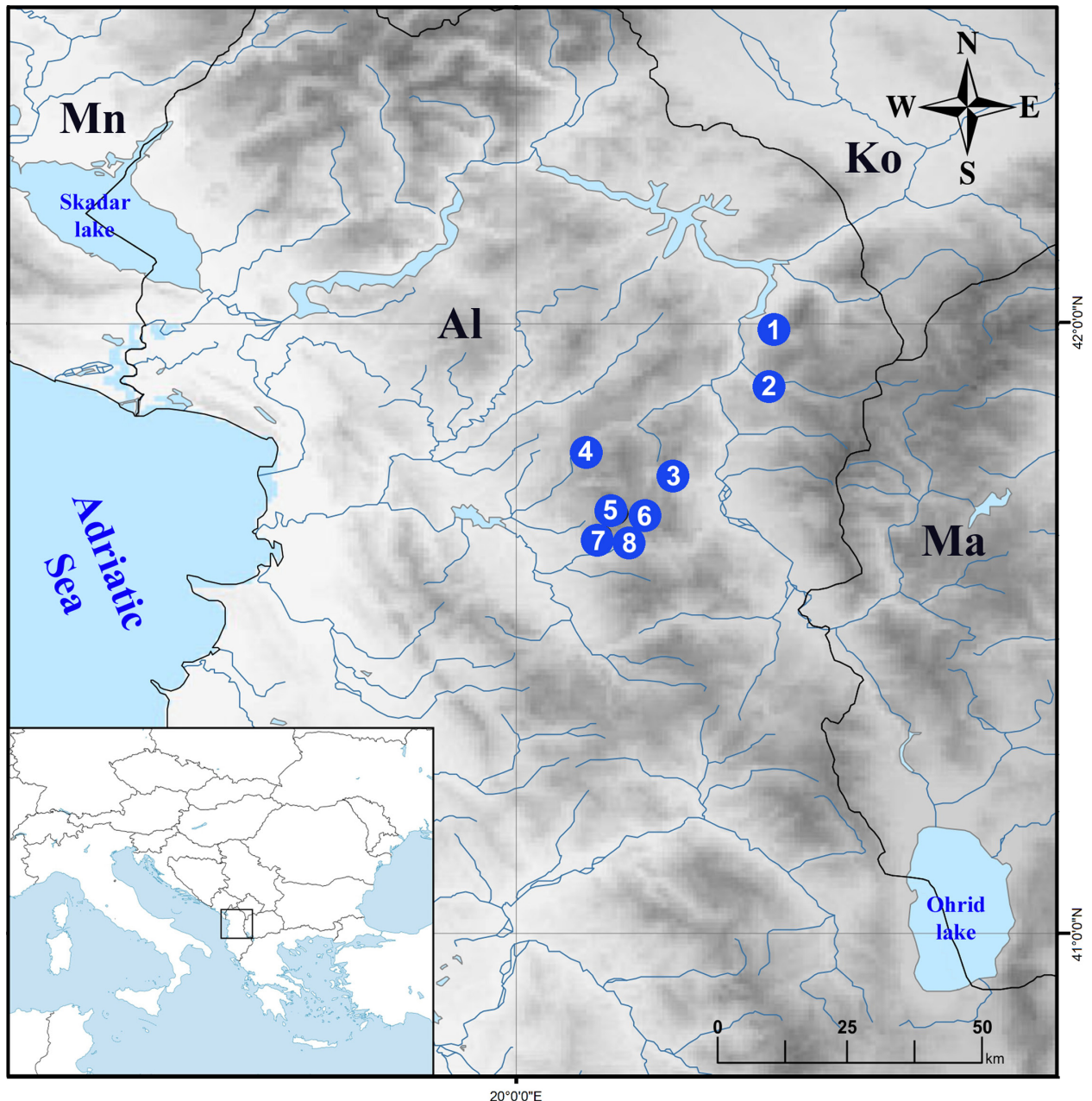


Fig. 5. Distribution of *Hayekia comosiformis* – numbers on map correspond with numbers of sites listed under Material studied. – Country codes: Al = Albania; Ko = Kosovo; Ma = North Macedonia; Mn = Montenegro.

**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** — Bicaç 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 (Rreth 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

sides of the road Kalimash–Morinë, Kukesi district” (Hallaçi 2008) refer to the same site: the Shija gorge E of Bicaj (site 1).

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