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A REVERSAL TO HYPOGYNY IN *CAMPANULA ALPINA* AND ITS IMPACT ON CAPSULE DEHISCENCE: EVIDENCE FROM MORPHO-ANATOMY OF THE FRUITING OVARY

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Introduction. *Campanula alpina* is a perennial herbaceous bellflower grown in the Eastern Alps, Carpathians, and Balkans. Fruit in *Campanula* species opens by the hipocrepiform slits in the fruit wall, which are formed by axicorns, elongated structures inside the ovary composed of lignified parenchyma cells. Our objectives were to reveal the fruit structure and dehiscence mode in *C. alpina* and compare it with *C. latifolia*, a type species of the genus *Campanula*.

Materials and methods. Flowers and fruits at different stages of morphogenesis of *C. alpina* subsp. *alpina* were examined. Plant materials were sampled in two plots in the Chornohora massif of the Ukrainian Carpathians.

Results. Contrary to other *Campanula* species, in *C. alpina* only the basal part of the ovary is fused with the calyx forming the flattened ovary base. The placentation is axile, the fruit wall and septas are parenchymatous, only axicorns are lignified. Dehiscence of the hanged fruit proceeds by the curving of axicorns outside by drying. In the dehiscent capsule viewed from above, hollow openings in the horizontal ovary base are exposed, and the curved axicorns attached to the crumpled fragments of the ovary wall are visible inside the ovary.

Discussion. The dehiscence of the fruit in *C. alpina* proceeds through septifragal and hipocrepiform slits like in *C. latifolia*. The main differences are that the ovary is mostly superior, openings are located on the horizontal ovary base, and valves together with axicorns curve inside the ovary. The semi-inferior or nearly superior ovary insertion could be traced in illustrations in digital databases and researches for some taxa of *Campanula* section Medium. No issues have been made on the evolution of the ovary position in Campanuleae, since only the inferior ovary was referred for this tribe before



the present article. The functional implications of shifts in the ovary position in *C. alpina* could be a result of selection of the pollination mechanism, or dissemination mode.

Conclusions. The peculiarity of the fruit in *C. alpina* is the axicorns curving inside the ovary during the dehiscence. It is expected that deviation from the inferior ovary will be confirmed in other related species of the *Campanula* with pendent fruits. No argumentation about the evolution of secondary hypogyny in *Campanula* has been proposed so far.

Key words: bellflower family, gynoecium, capsular fruit, morphogenesis, axicorn

INTRODUCTION

The inferior ovary and capsular fruits are the common features of the Campanulaceae family (Eichler, 1875; Schönland, 1894; Lammers, 2007; Takhtajan, 2009; Stevens, 2017). Inferior capsules dehiscing with valvate pores in the fruit wall are characteristic of the tribe Campanuleae of the subfamily Campanuloideae (Schönland, 1894; Eddie *et al.*, 2003; Lammers, 2007; Roquet *et al.*, 2008; Andreychuk & Odintsova, 2020). The arrangement of the pores near the fruit base or above its middle-height is correlated with fruit spatial orientation and assumed to be an adaptation for ballistochory (Candolle de, 1830; Kindermann, 1911; Roth, 1977; van der Pijl, 1982; Leins & Erbar, 2010; Niu *et al.*, 2016). Specifically, erect capsules dehisce at their upper half, while hanged fruits have pores near the fruit base. This fact was used in diagnosis of *Campanula* sections *Rapunculus* Boiss. and *Medium* Tourn., correspondingly (Boissier, 1875; Schönland, 1894). No deviation of the ovary position from the inferior ovary has been reported for the *Campanula* taxonomy so far (Schönland, 1894; Visiulina, 1961; Lammers, 2007; Roquet *et al.*, 2008; Dremluga, 2009; 2013; Mansion *et al.*, 2012; Crowl *et al.*, 2016; Liveri *et al.*, 2019).

Fruits in *Campanula* and the related genera of Campanulaceae open by hippocrepiform slit in the fruit wall, which is formed by a special tissue on the inside of the fruit (entitled „die Sklerenchymmassen” in German) which moves as it dries and perforates the fruit wall, thus allowing the dispersal of the seeds (Beck, 1885; Kindermann, 1911). This strand of lignified tissue was named an axicorn by A. Kolakovsky, who supposed it to be an elongated organ inside the ovary (between the central column and septa) composed of lignified parenchyma cells (Lakoba, 1986).

In our previous investigation of the fruit anatomy and dehiscence in the type species of the genus *Campanula* – *C. latifolia* L. (section *Medium*), we found axicorns as longitudinal bands of lignified parenchyma of the septas of the ovary (Andreychuk & Odintsova, 2019). Axicorns disjunct from the central column by septifragal slits and make hippocrepiform slits in the fruit wall by their lower beak.

In the flora of Ukraine, 31 species of *Campanula* were referred (Mosyakin, Fedoronchuk, 1999), arranged into sections *Rapunculus* and *Medium* (Visiulina, 1961; Dremluga, 2009). We assumed that all members of the *Campanula* section *Medium* have the same dehiscence mode conditioned by long axicorns and basal openings, however only a few species were previously investigated anatomically (Beck, 1885; Kindermann, 1911; Lakoba, 1986). Our present objectives were to compare morpho-anatomical structure and dehiscence of the fruit in *C. latifolia* with another species of the section *Medium* – *C. alpina* Jacq. which is distinct from other *Campanula* species by growth in high-mountain habitats.

Campanula alpina is a perennial herbaceous bellflower grown in the Eastern Alps, Carpathians, and Balkans, in alpine, subalpine and subnival grasslands (Schönland, 1894;

Visiulina, 1961; Ronikier *et al.*, 2008; Dremluiga, 2013). In Balkans, *C. alpina* subsp. *orbelica* inhabits, is also entitled as *Campanula orbelica* Pančić (Ronikier & Zalewska-Galosz, 2014). This subspecies (or species) has triangular calyx appendages wider than half of calyx teeth width, spreading shoots, therefore the whole plant is not compact; corolla is smaller than in *C. alpina* Jacq. subsp. *alpina*. In *C. alpina* Jacq. subsp. *alpina* calyx-appendages are ligulate, additional shoots mostly absent, branches erect, appressed to the main stem, therefore the whole plant is compact.

Fruits of *C. alpina* are large (9–11 mm × 12–14 mm), spherical, pendent on curved pedicels, dehiscent at the base; the pubescence composed of scattered rough trichomes (Dremluiga, 2013). The species is well differentiated from the other *Campanula* species by their leaves, shoot system and rocky alpine localities (Dremluiga, Zyman, 2013), that is why no taxonomical significance was considered to the fruit features.

MATERIALS AND METHODS

We examined flowers and fruits of *Campanula alpina* Jacq. subsp. *alpina* (*C. alpina* s. str.) at different stages of post-anthesis. Plant materials were sampled in two plots in the Chornohora massif of the Ukrainian Carpathians: (1) Zakarpattia oblast, Rakhiv district, Petros mnt, near the summit (2022 m a.s.l.), 5.07.2018; leg. R. Andreychuk; (2) Ivano-Frankivsk oblast, Nadvirna district, Vorokhta village, Pozhyzhevsk mnt, summit (1822 m a.s.l.), and a hollow between Pozhyzhevsk and Breskul mnts., 9.08.2023; leg. A. Odintsova.

Materials were partly examined in fresh condition and the rest of materials were fixed in 70% ethanol for storage and subsequent study. Fruits were sectioned with razor blade by free hand. Sections were stained with phloroglucinol and chloride acid in order to evaluate the presence of lignin (Liljegren, 2010; Pradhan Mitra & Loqué, 2014). Totally, about 50 fruits were investigated. Photographs were made by digital camera SIGETA M3CMOS 10000 10.0MP USB 3.0 and light microscopes XS-2610 and SIGETA MB-303. Total samples of fruits were examined with stereomicroscope MBS-10.

For examination of the anthetic and post-anthetic ovary, we followed an original guideline (Odintsova, 2023). According to this approach, we described subsequently exomorphological, micromorphological, anatomical features of the flower and fruit, and then, the process of fruit dehiscence. We considered the merosity of the gynoecium, placentation and seed number, which were examined in the sectioned fruits, to be micromorphological features, while the anatomy of the fruit wall and vascular anatomy of the ovary were considered anatomical features that refer to tissue structure. We characterized dehiscence of the fruit with regard to all types of slits developed for seed releasing.

RESULTS

Exomorphological structure of the flower and fruit. Flowers and fruits are pendent, about 2.0 cm in height (**Fig. 1A–E**). Calyx lobes 5–6, lanceolate, directed along the corolla, 2 cm in length, 2–3 mm in width, pubescent, persistent in fruit. The corolla is bell-shaped, 11–12 mm in diameter, blue, its lobes are widely triangular. Filaments at the base are expanded and pubescent, blue (**Fig. 1B**). Calyx-appendages are ligulate, declined, 1–2 mm in length, 1 mm in width, pubescent on margins (**Fig. 1C**). During fruit ripening, corolla, stamens and style are twisted, desiccated and persist in fruit for a long time (**Fig. 1D,E**).

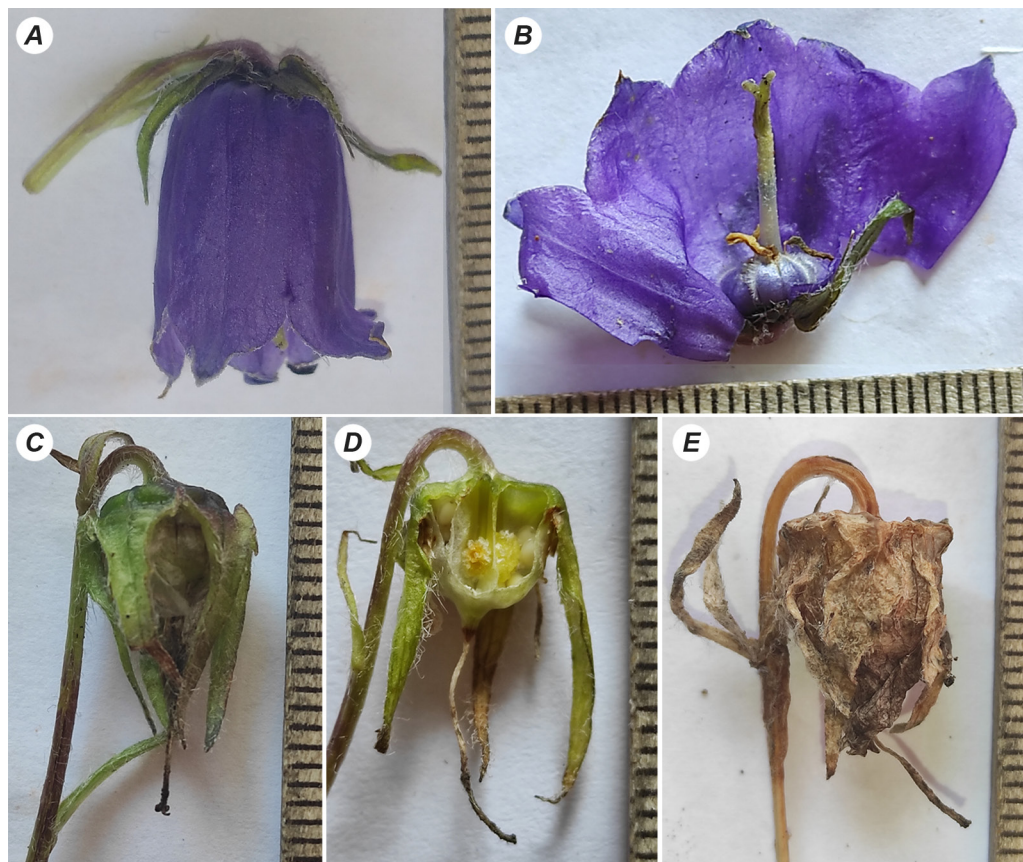


Fig. 1. Morphological structure of the flower (**A–B**) and fruit (**C–E**) of *Campanula alpina* (fresh material): flower at the late anthetic stage from exterior (**A**), and with dissected corolla (**B**); green unripe fruit lateral view (**C**), longitudinally dissected unripe fruit (**D**), dry fruit (**E**)

Ovary at pre-anthesis and anthesis is inconspicuous from the exterior beneath calyx lobes (**Fig. 1A; 2A**). The calyx lobes are arranged at the right angle to the flattened ovary base. From the interior of the corolla, ovary is largely free of the calyx, covered by extensions of the filaments (**Fig. 1B**). At pre-anthesis and anthesis, ovary from interior is hemispheric, bearing terminal erect style (**Fig. 2B,C**). At post-anthesis, ovary becomes larger, spherical or oval (**Fig. 2D–F**). Only basal part of the ovary is fused with the calyx forming at first a slightly convex and then flattened ovary base (**Fig. 1C–E**). The length of the ripe fruit (with the persistent calyx and corolla) is about 2 cm, the fruiting ovary length and diameter is about 1 cm. The capsule is pendent, light-yellow to light-brown color. Capsule surface in the infrasepalous part (which is fused with the calyx) is ridged, pubescent on ridges, with prominent branched veins and flat depressions between veins predicting the upcoming openings (**Fig. 4A,B**). The capsule surface in the suprasepalous part (above the level of calyx attachment) is smooth, glabrous (**Fig. 2D–F**).

Micromorphology of the fruiting ovary. In transversal section, the capsule is roundish, thin-walled, 3–4 locular, with thin septas. Among fruits collected on the location

of Pozhyzhevskaya mnt, there were 11 fruits with four locules, 16 fruits with three locules, and one fruit with five locules (in total 28 fruits). In the center of the fruit there was a cylindrical central column divided by ventral slits of the carpels at the upper part of the locules above the placenta (Fig. 3A–D). Septas in this part of the ovary remain connected forming a strand of transmitting tissue (Fig. 3A,B). In each locule, a bilobate wide-ovate placenta is found in the upper portion. It attaches to the carpel blade with a narrow stalk (Fig. 3C). The placenta bears numerous seeds (about 60) in many rows (Fig. 4A). A seed set per fruit is 177 seeds ($n = 10$), from 168 to 189, in the location of Petros mnt. Seeds are ovate or elliptic, biconvex, lustrous, 1.5–2.0 mm in length, 1.0–1.5 mm in width, narrowly winged (Fig. 4C).



Fig. 2. External and internal morphology of the ovary of *Campanula alpina* (fixed material): pre-anthetic flower general view (A) and with partly removed corolla (B); anthetic flower sectioned longitudinally (C); unripe fruiting ovary with style remnant (D), tangentially sectioned unripe fruiting ovaries with placenta (pl) visible (E), and with axicorns (ax) (F). Level of calyx insertion to the ovary is marked with a white arrowhead. Scale bar: 2 mm

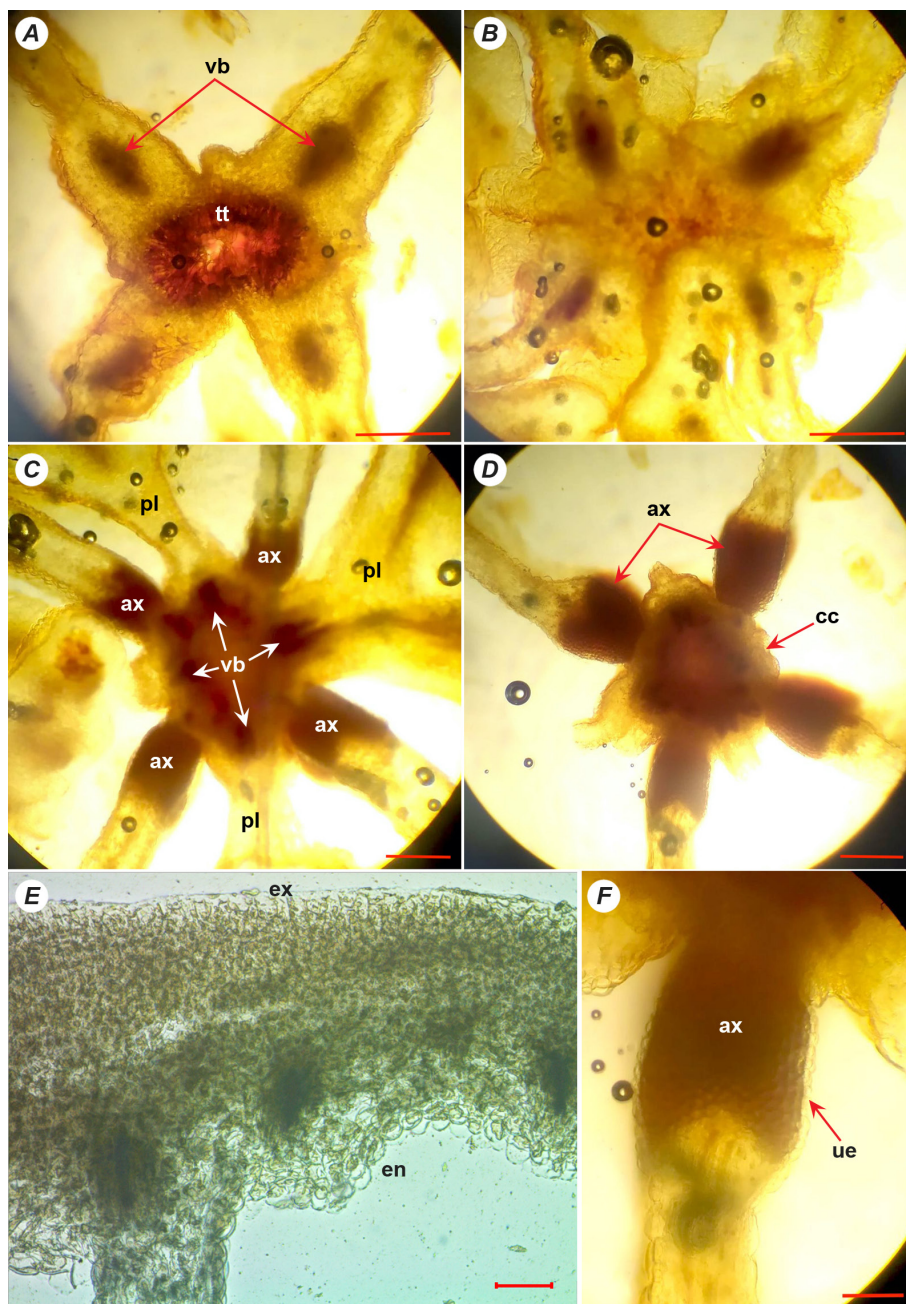


Fig. 3. Micromorphology and anatomy of the tetramerous fruiting ovary of *Campanula alpina* in descending sections: upper part of the ovary, vascular bundles (vb) occur in the proximal ends of septas, transmitting tissue (tt) in the center (A); ovary just above placentas level (B); level of placentas (pl) insertion, axicorns (ax) and vascular bundles (vb) in the central column are visible (C); axicorns attached to the central column (cc) in the lower part of the ovary (D); parenchymatous fruit wall, exocarp (ex) and endocarp (en) are unligified (E); an axicorn with unligified epidermis (ue) of the septum (F). Scale bar: 0.3 mm (A–D), 0.1 mm (E, F)

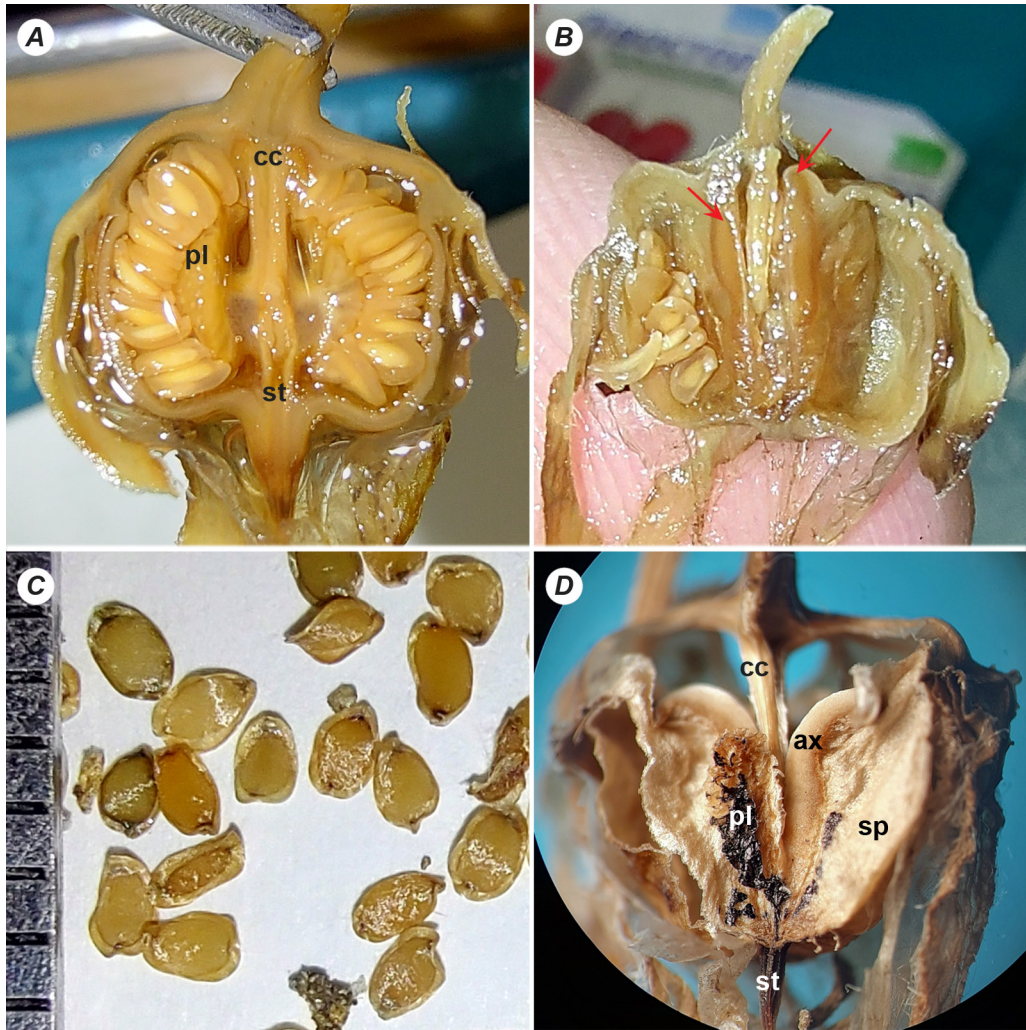


Fig. 4. Fruit of *Campanula alpina* during the dehiscence in longitudinal section, fixed fruits (**A**, **B**), dry fruits (**C**, **D**): radially sectioned unripe fruit in the locule plane (**A**); radially sectioned unripe fruit in the septum plane at the beginning of opening, axicorns marked with arrow (**B**); seeds (**C**); dehiscence fruit with axicorns half detached from the central column (**D**): axicorns (ax), central column (cc); placenta with seeds (pl), septum (sp), style remnant (st)

Anatomical structure of the fruiting ovary. The fruit wall and septas in the green fruit are parenchymatous (**Fig. 3E**). Exocarpium is composed of unligified layer of cells, with unicellular trichomes in ridges. Mesocarpium has 10–12 cell layers, unligified, thickened in ridges where the vascular bundles appear. Endocarpium is unligified, unlayered. In the transversal section of the fruiting ovary, three (or four depending of the number of locules) axicorns are visible, attached to the central column (**Fig. 2F**; **4B**). Axicorns are composed of lignified parenchyma cells and extend from the very base of the ovary to the upper edge of the placenta (**Fig. 4B**). The epidermal cells that cover axicorns are not lignified (**Fig. 3F**).

The vascular system of the inferior (infrasepalous) portion of the fruiting ovary is composed of 3–5 ascending vascular bundles which branch into two-three bundles each and give rise to the sepal, petal and stamen traces (**Fig. 5A–D**). When 5 vascular bundles occur, three of them are more prominent than the other two. Proximally, ascending bundles give numerous small bundles entering the free (superior) portion of the ovary. These bundles arrange in the ovary wall in such a mode that 5–7 bundles are located between septas. Some of them give rise to branches into septas. From the pedicel, the vascular cylinder enters the central column. It breaks into 3 (or 4) bundles entering placentas where seed traces are formed from them (**Fig. 3C–D**). Above placentas, these bundles divide in halves and fuse with halves of the other pair, thus forming septal bundles (**Fig. 3A,B**).

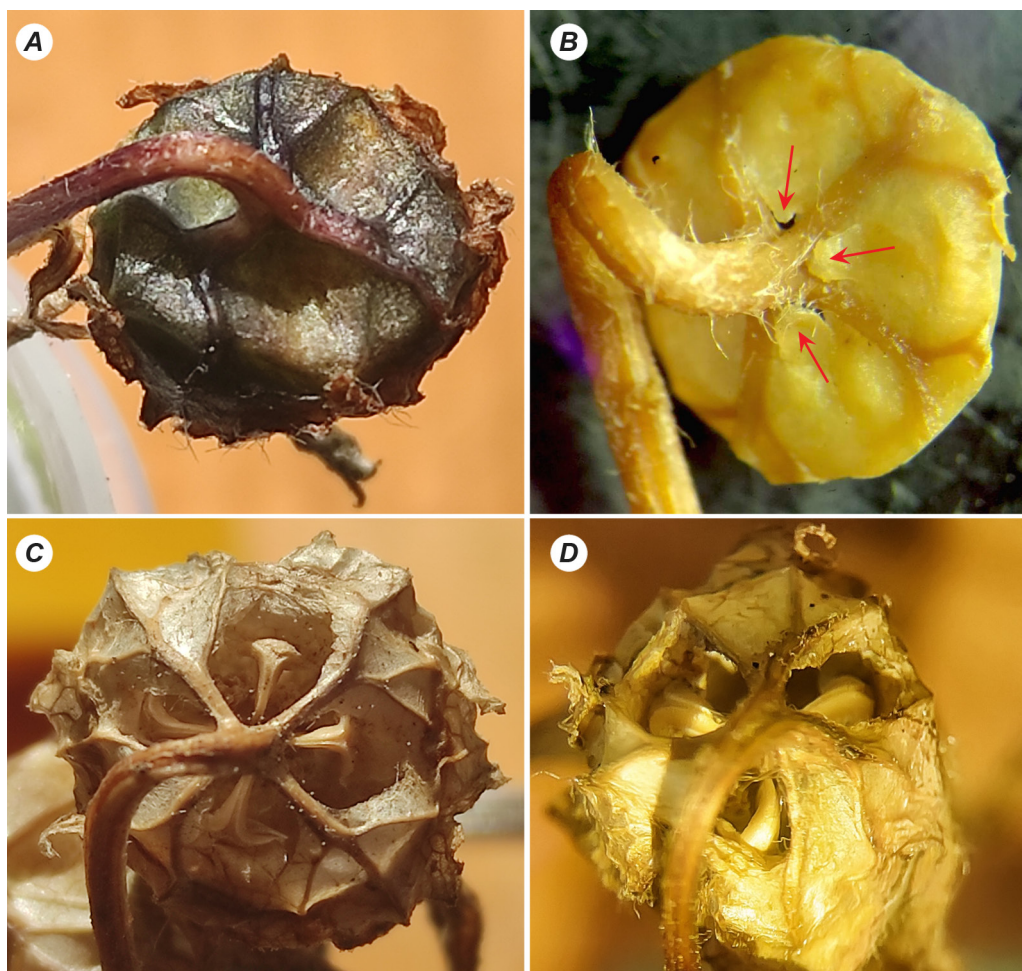


Fig. 5. Fruit of *Campanula alpina* during the dehiscence viewed from the pedicel: fixed fruit (**B**), dry fruits (**A**, **C**, **D**): ripe fruit with three depressions in place of upcoming openings (**A**); the beginning of opening formation (arrows) in tetramerous fruit (**B**); dehiscent fruits with four (**C**) and three (**D**) openings where axicorns are visible inside the ovary; note groove in axicorns' proximal surface

Dehiscence of the fruit. The depressions of upcoming openings are slightly expressed on the flat horizontal surface of the inferior portion of the ovary between veins (**Fig. 5A**). The hippocrepiform slit is formed on the proximal edge (closer to the pedicel) of each depression (**Fig. 5B**). The openings are initiated by the curving of axicorns outside by drying (**Fig. 4D**). As a result, septa is destroyed by the septifragal slit between axicorn and central column (**Fig. 5B–D**). The axicorn beak, which is attached to the ovary wall, pulls the fragment of the ovary wall to the interior of the ovary. In the dehiscent capsule one can see from above the openings in the horizontal ovary base and curved axicorns attached to the crumpled fragment of the ovary wall (the valve). A longitudinal groove can be seen on the surface of the axicorn freed from the central column (**Fig. 5C,D**).

DISCUSSION

Fruit structure and dehiscence in *Campanula* species with inferior and superior ovaries. The opening mechanism of fruit in *Campanula* was studied in detail (Beck, 1885; Kindermann, 1911; Roth, 1977; Lakoba; 1986). Bending of the axicorn is provided by differently oriented arrangement of lignified cells which shrink in different directions (Roth, 1977). Fruit in *C. latifolia* was characterized as inferior trilocular capsule with septifragal-hippocrepiform dehiscence (Andreychuk & Odintsova, 2019). In *C. latifolia* and *Adenophora liliifolia*, as in most members of the Campanuleae, three (rarely four, depending of the carpels' number) depressions in the ovary wall in place of upcoming opening are formed at the pre-anthetic stage (Andreychuk & Odintsova, 2019; 2021). There is a principal similarity of the fruit structure and opening in *C. alpina* and *C. latifolia* in the following aspects: flower and fruit are pendent; ovary has three (in *C. alpina* also four) locules; axile placenta is above the middle-height of the locule; septas are thin; longitudinal axicorns on the inner border of the septas which touch the central column; axicorns extend from the very capsule base to the upper placenta edge; openings in the capsule wall are roundish, they develop between veins nearby the pedicel by means of the axicorn curving outwards. The dehiscence of the fruit in *C. alpina* proceeds through septifragal and hippocrepiform slits, too.

The main differences between capsules in *C. alpina* and *C. latifolia* are the ovary position and turning of the fruit wall fragment surrounded by the hippocrepiform slit (**Fig. 6**). Namely, in *C. alpina*, ovary is in the most part superior, openings are located on the horizontal ovary base, and valves curve inside the ovary thus crumpling the septum (**Fig. 6A,B**). In *C. latifolia*, as in most *Campanula* species, ovary is fully inferior, openings are located on the convex-vertical ovary wall, and valves curve outside the ovary during the dehiscence (**Fig. 6C,D**).

In both species, *C. alpina* and *C. latifolia*, as in most Campanuleae, openings occur in the inferior portion of the ovary that evidences a high level of the epigyny, when dehiscence mechanism is formed in the tissues of the complex identity (carpels and adnated calyx) (Odintsova, 2016). During fruit morphogenesis in *C. alpina* we can observe at first a slightly convex ovary base which turns out to be flat in late stages of fruit ripening. That could be a recapitulation of a more advanced level of epigyny in the early fruit onto-morphogenesis in *C. alpina* (Odintsova, 2022). Hence, the hypogynous (or nearly hypogynous) condition in *C. alpina* is supposed to be a reversion from the epigynous one.

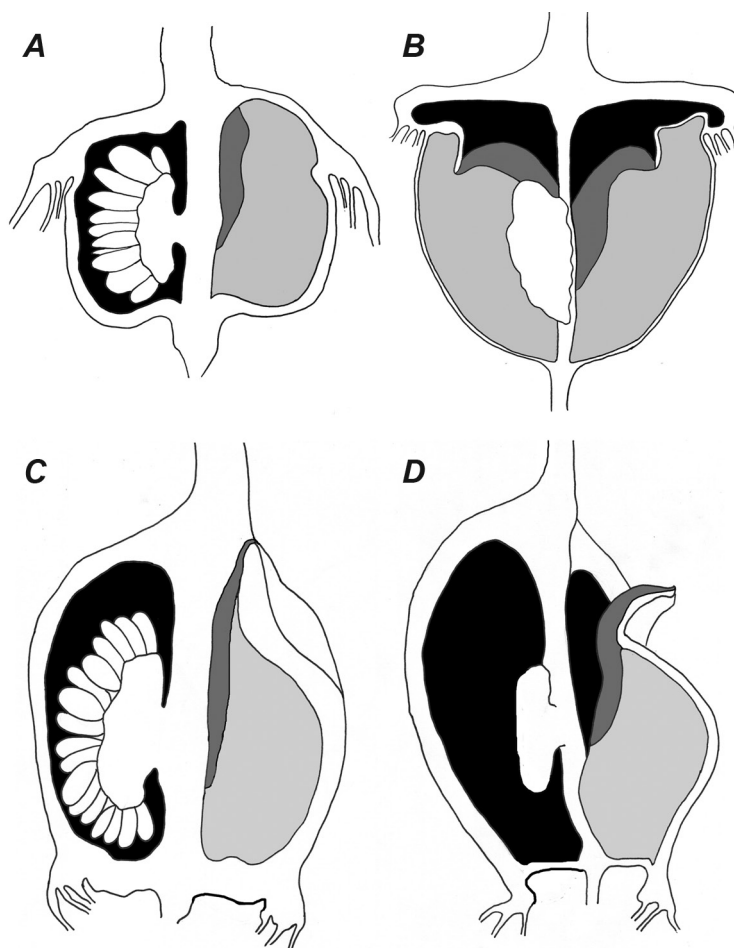


Fig. 6. Dehiscence of the hanged capsule in *Campanula alpina* (**A, B**) compared to *C. latifolia* (**C, D**): capsule before dehiscence (**A, C**), dehiscing capsule (**B, D**); in **B** capsule is tetramerous; axicorn is dark grey, septum is light grey. Fruit in *C. latifolia* is reconstructed according to the materials presented in Andreychuk & Odintsova (2019) and to the re-examination of fixed fruits from the abovementioned research

The fruit in *C. alpina* can be defined as septifragal-hippocrepiform capsule, as in *C. latifolia* and other Campanuleae. Previously, it was entitled as capsule dehiscant by pores or valves (Lammers, 2007; Takhtajan, 2009; Mansion *et al.*, 2012), or even ceratium, a capsular fruit dehiscing by separation or breaking of pericarp layers, or dehiscing endocarp, with persistent parts, septas, placentas, style, replum etc. (Spjut, 1994). Another fruit type, according to Spjut (1994), a septifragal capsule, has a central column, no replum, and septas that break near the central column. Thus, the definition of septifragal capsule better fits the *Campanula* fruit, if one examines the fruit structure and dehiscence accurately.

Taxonomic significance of the ovary position in *Campanula* species. The hypogynous condition of *Campanula alpina* subsp. *alpina* revealed by the present

study might be relevant to *C. alpina* subsp. *orbelica*, a closely related taxon (Fig. 6B in Ronikier & Zalewska-Galosz, (2014). The superior ovary in the fruiting stage in *C. alpina* is well evident in drawings of the botanists of the 18th to early 19th centuries (Jacquin *et al.*, 1773; Sturm, 1830); it was also described by N. Jacquin: “*Capsula supera, subrotunda, obtusa, glabra, trilocularis, in maturitate trifariam perforatur ad basin*” [Capsule superior, subrounded, obtuse, glabrous, three-locular, at maturity with three pores at the base] (Jacquin *et al.*, 1773, p. 12).

The surprising overlooking of the unusual ovary position in the well-known European species *C. alpina* by subsequent researchers might be explained by the absence of taxonomical problems regarding this species. The taxonomists were rather formal in characterizing this species as having “a short calyx tube” (Visiulina, 1961), with no admission that calyx tube is an essential part of the inferior ovary. The other cause of overlooking the ovary position is the appearance of prominent calyx appendages covering the ovary, thus hiding it from the external view. For instance, according to our observations (unpublished data), the ovary in *Campanula sibirica* L. is semi-inferior, covered by calyx appendages. However in the previous research on fruit structure and dissemination in *C. sibirica*, *C. taurica* Juz. and *C. talievii* Juz., fruit was defined as fully inferior capsule (Miroshnichenko, 2014).

In some phylogenetic studies (Borsch *et al.*, 2009), *C. alpina* forms a sister clade to *C. hofmannii* (Pant.) Greuter & Burdet. In another research, an unresolved clade with *C. alpina*, *C. hofmannii*, *C. medium* L., *C. speciosa* Pourr. and *C. alpestris* All. occurs (Mansion *et al.*, 2012). As one can see in GBIF database (<https://www.gbif.org>), the ovary is not very extended beneath the calyx and thus can be prominent above calyx insertion and hidden in the corolla in some *Campanula* species, for example, in *C. speciosa* see <https://www.gbif.org/occurrence/4046497846> (originally stored at <https://www.inaturalist.org/observations/149504268>); in *C. alpestris* see <https://www.gbif.org/occurrence/731858318>; <https://www.gbif.org/occurrence/1935668433> (originally stored at <https://www.jacq.org/detail.php?ID=1350062>); <https://www.gbif.org/occurrence/3963231173> (originally stored in <https://www.inaturalist.org/observations/141302949>), and in *C. hofmannii* see <https://www.gbif.org/occurrence/3768451332>; and <https://www.gbif.org/occurrence/2242414148> (originally stored in https://intermountainbiota.org/imglib/storage/portals/seinet/arizona/DBG_KHD/KHD00053/KHD00053916_lg.jpg). Similar inconspicuous outlines of the ovary could be the evidence of a semi-inferior or nearly superior ovary found in drawings and photos of flowers and fruits of *Campanula speciosa* subsp. *speciosa* (entitled as *C. allionii* Lapeyr.) (Schönland, 1894); *C. speciosa* (Roquet *et al.*, 2008), *C. hofmannii* (Schlatti & Eberwein, 2016).

The closest relatives of *C. alpina*, according to Visiulina (1961) are *C. aucheri* A.DC. (= *C. saxifraga* subsp. *aucheri* (A.DC.) Ogan.) and *C. argunensis* Rupr. (= *C. saxifraga* subsp. *argunensis* (Rupr.) Ogan.). Both species grow in the Caucasus mountains. The Caucasian taxa of *Campanula* are also presented in GBIF database at the anthetic phase, with a weakly expressed ovary beneath calyx: *C. aucheri* A.DC. (= *C. saxifraga* subsp. *aucheri* (A.DC.) Ogan.) (<https://www.gbif.org/occurrence/3439617193>; originally stored in <http://id.luomus.fi/C.383608>); <https://www.gbif.org/occurrence/3439624168>, originally stored in <http://id.luomus.fi/C.383613>), and *C. argunensis* Rupr. (= *C. saxifraga* subsp. *argunensis* (Rupr.) Ogan.) (<https://www.gbif.org/species/5410314>, originally stored in <https://www.jacq.org/detail.php?ID=1878519>). All the abovementioned species belong to the section Medium and could be closely related (Roquet *et al.*, 2008;

Borsch *et al.*, 2009; Mansion *et al.*, 2012). Most of these species have pendent fruits and calyx appendages. The hypogynous or semi-epigynous condition for these taxa may be considered in future as a specific feature or potential synapomorphy for a probable clade.

Evolutionary grounds and adaptive significance of the shift to secondary hypogyny. The main morphological changes of ovaries in angiosperms are carpel fusion, carpel and ovule number reduction, inferiority of the ovary (Xiang *et al.*, 2024). Inferior ovary seems to be synapomorphy for Campanulids clade, and capsular fruit is ancestral for Asterales (Stull *et al.*, 2018). In Campanulaceae, gynoecium is isomeric or oligomeric (3–5-merous), carpels are fused, ovule number is mostly high, and the ovary varies from superior to inferior (Lammers, 2007). Although floral evolution was examined in Campanulaceae from biogeography and genomics perspectives, no issues have been made on the evolution of the ovary position (Crowl *et al.*, 2016). The inferior ovary in Campanulaceae is supposed to be of appendicular origin, the result of the evolutionary fusion of the carpels with synsepalous calyx, as was evident from floral morphology, vascular anatomy and organogenesis in *Downingia bacigalupii* Weiler (Kaplan, 1967). Semi-inferior or superior ovaries were found in members of the Wahlenbergiaeae and Platycodoneae (Schönland, 1894; Lammers, 2007), as well as in the subfamily Lobelioideae of Campanulaceae. Interestingly, in *Cyclocodon* Griff. ex Hook. f. & Thomson and *Campanumoea* Blume (= *Codonopsis* Wall.) from the tribe Platycodoneae, sepals inserted at the ovary base and fruit is a berry (Wilde *et al.*, 2012). In contrast, in Campanuleae, only the inferior ovary was referred until the present article (Schönland, 1894; Lammers, 2007; Roquet *et al.*, 2008).

The evidence of the reversal from epigyny to hypogyny is rare in angiosperms. One of the first records of reversal of the ovary position from inferior to superior for *Tetraplasandra gymnocarpa* (= *Polyscias gymnocarpa* (Hillebr.) Lowry & G. M. Plunkett) (Araliaceae) suggested two possible causes of this evolutionary event: (a) isolation of the ancestors from flower-eating predators and (b) selection for increased outcrossing (Eyde & Tseng, 1969). Reversal to hypogyny in *Wachendorfia* Burm. ex L. (Haemodoraceae) is supposed to be related to a shift in the pollination mechanism (Simpson, 1998). In *Lithophragma* (Nutt.) Torr. & A. Gray (Saxifragaceae) nearly superior ovary was referred which was named “pseudosuperior” (as mimic of superior ovary which is not developmentally homologous with truly superior ovary produced via a hypogynous ground plan). This ovary results from the bidirectional evolution of ovary position and its shift toward greater superiority in some species (Kuzoff *et al.*, 2001).

Diverse variants of ovary positions in *Lithophragma* arise through allometric shifts in the rate of vertical growth in the inferior versus superior regions of the ovary (Soltis & Hufford, 2002). One reason for this shift to the extent of the superior region may be a selection by pollinators that insert an ovipositor into the superior region of the ovary when visiting an anthetic flower (Soltis & Hufford, 2002). A shift to a more pronounced superiority of the ovary may be referred in *Melaleuca* L. (Myrtaceae) as a reaction on the general flower and fruit reduction (Stepanova, 2002).

A number of families with various ovary positions from fully inferior to superior, treated as secondary hypogynous, were referred, viz Araliaceae, Asphodelaceae, Begoniaceae, Bromeliaceae, Campanulaceae, Dichapetalaceae, Flacourtiaceae, Haemodoraceae, Memecylaceae, Melastomataceae, Rhamnaceae, Rhizophoraceae, Rubiaceae, Saxifragaceae, Vochysiaceae (Soltis *et al.*, 2003; Basso-Alves *et al.*, 2017).

In Melastomataceae, the functional implications of variation in the ovary position remain poorly understood, as from the selection of pollinators or fruit dehiscence (Basso-Alves *et al.*, 2017).

In *C. alpina*, ripe capsules opened in the flat upper surface are exposed to the wind and rain, the common natural events in the high-mountain regions. Although anemochory was referred for Campanulaceae in general (Lammers, 2007), seed dispersal in *C. alpina* may also occur by means of rain outflow from the capsule, i. e. ombrochory with winged floating seeds. The evidence from images of ripe and opened fruits could be very useful for examination of the dehiscence mechanism but such cases are rather solitary (see https://ukrbin.com/show_image.php?imageid=126339; https://ukrbin.com/show_image.php?imageid=263428; https://ukrbin.com/show_image.php?imageid=121592).

CONCLUSIONS

The fruit in *Campanula alpina* is a nearly superior (pseudosuperior) tri-tetramerous dry multi-seeded capsule with septifragal-hippocrepiform dehiscence provided by the long axicorns. The peculiarity of the fruit is curving of the axicorns inside the ovary during the dehiscence. The unusual dehiscence of the fruit is affected by hypogynous condition in this species, which is supposed to be a reversal from epigynous condition, typical of the tribe Campanuleae. It is expected that the deviated position from the inferior ovary will be confirmed in other related species of the *Campanula* section Medium with pendent fruits. This feature of the gynoeceum can be regarded as a common trend of the species of the section Medium or potential synapomorphy. No argumentation about the evolution of secondary hypogyny in *Campanula* has been proposed yet since it is the first record of hypogyny in this genus. Like in other angiosperms with reversal to hypogyny, the functional significance and selective benefit of the changed ovary position in *C. alpina* remain poorly understood.

COMPLIANCE WITH ETHICAL STANDARDS

Human Rights. This article does not contain any studies with human subjects performed by any of the authors.

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Conceptualization, [A.O.]; methodology, [A.O.]; investigation, [A.O.; Y.Kh.; R.A.]; resources, [A.O.; R.A.]; data curation, [-]; writing – original draft preparation, [A.O.; R.A.]; writing – review and editing, [A.O.]; visualization, [A.O. (fig. 1; fig. 5 A, C; fig. 6); Y.Kh. (fig. 3E; fig. 4; fig. 5 D; fig. 6); R.A. (fig. 2; fig. 3 A–D, F; fig. 5B)]; supervision, [A.O.]. All authors have read and agreed to the published version of the manuscript.

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РЕВЕРСІЯ ДО ВЕРХНЬОЇ ЗАВ'ЯЗИ У *CAMPANULA ALPINA* ТА ЇЇ ВПЛИВ НА РОЗКРИВАННЯ КОРОБОЧКИ: СВДЧЕННЯ МОРФО-АНАТОМІЇ ЗАВ'ЯЗИ НА СТАДІЇ ПЛОДУ

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Вступ. *Campanula alpina* – це багаторічний трав'яний вид дзвоників, поширений у Східних Карпатах, Альпах і на Балканах. Плід у роді *Campanula* розкривається півмісяцевими щілинами в оплодні, які формуються завдяки аксикорнам, – видовженим структурам усередині зав'язі, які сформовані зі здерев'янілих паренхімних клітин. Нашою метою було з'ясувати структуру та спосіб розкривання плоду в *C. alpina* й порівняти дані з *C. latifolia*, типовим видом роду.

Матеріали та методи. Досліджували квітки і плоди *C. alpina* subsp. *alpina* на різних стадіях морфогенезу. Матеріал зібрано у двох локалітетах хребта Чорногора в Українських Карпатах.

Результати. На відміну від інших видів *Campanula*, у *C. alpina* лише базальна частина зав'язі є зрослою з чашечкою, формуючи розширену основу зав'язі. Плацентія центрально-кутова, оплодень і перегородки паренхімні, лише аксикорни є здерев'янілими. Розкривання повислого плоду здійснюється завдяки вигинанню

аксикорнів назовні під час їхнього підсихання. У розкритому плоді в горизонтальній основі зав'язі згори видно отвори, крізь які помітні зігнуті аксикорни, що приєднані до загорнутих фрагментів оплодня.

Обговорення. Розкривання плоду в *C. alpina* здійснюється через утворення септифрагальних і півмісяцевих щілин, так само як в *C. latifolia*. Головна відмінність полягає в тому, що зав'язь більшою частиною верхня, отвори розміщені в горизонтальній базальній ділянці зав'язі, а клапани оплодня з аксикорнами загинаються всередину зав'язі. Напівнижню або майже верхню зав'язь можна простежити на ілюстраціях у цифрових базах даних і опублікованих дослідженнях інших таксонів *Campanula* секції *Medium*. Немає жодних припущень щодо еволюції положення зав'язі серед *Campanuleae*, оскільки до нашої статті для цієї триби було наведено лише нижню зав'язь. Функціональне значення зміни положення зав'язі в *C. alpina* може бути пов'язане з добором на механізм запилення або спосіб дисемінації.

Висновки. Особливістю *C. alpina* є згинання аксикорнів усередину зав'язі під час розкривання плоду. Відхилення положення зав'язі від нижньої може бути згодом підтверджено і для інших споріднених видів роду *Campanula* з повислими плодами. Досі не запропоновано припущень щодо еволюції вторинної гіпогінії у роді *Campanula*.

Ключові слова: родина дзвоникових, гінецей, коробчастий плід, морфогенез, аксикорн