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HEDERA CREBRESCENS (ARALIACEAE) A NEWLY IDENTIFIED DIPLOID TAXON AND TRIPLOID IVIES FROM HUNGARY

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Abstract: *Hedera crebrescens*, a newly identified species in Hungary is described here. This diploid ivy is not identical with the diploid *H. helix*. It grows vigorously, is invasive, and has spread into most parts of the country and adjacent regions. We also present two triploid species of hybrid origin, which were known formerly as selected varieties of *H. helix*. Triploids differ from the presumed diploid and tetraploid parents based on their reproductive morphological traits and also based on their ecological demands.

Key words: *Hedera crebrescens*, invasive, new species, nomenclature, triploids

INTRODUCTION

Hedera is the only genus of the woody Araliaceae family native to Europe. It occurs along the northern hemisphere including Europe, the Macaronesian islands, Northwest Africa, and East Asia (Lammermayr 1930). Pierot (1974) mentioned 14 species, Rutherford *et al.* (1993) listed 12 species and later (McAllister and Rutherford 1997) 11, while Valcárcel and Vargas (2010) recognized 13 species. The most recently published European Garden Flora reports 12 *Hedera* taxa (McAllister and Marschall 2017: 141). In Hungary and East Central Europe only *Hedera helix* (Linnaeus 1753) is considered native (Soó and Jávorka 1951, Soó 1966). It is widespread in most parts of the country but it is less frequent in the Great Hungarian Plain with the exception of an area in the southeastern part (Bényei-Himmer 1994: 12; Bartha and Király 2015: 65).

At the end of the nineteenth century, a lot of *Hedera* cultivars were planted in European gardens (Rose 1996). Most of the cultivated ivies were mentioned as

"*Hedera hibernica*", "*Hedera helix hybernica*" or "*hibernica hort*" (Seyderhelm 1875). They originated primarily in the British Isles as Scottish, Irish, or English ivies. In France and Belgium cultivated ivies were also referred to as "*H. hibernica*" and this obviously made it difficult later to distinguish this taxon definitively (Koch 1869). Moreover, much confusion has been caused by attributing this name to the planted materials from nurseries. *H. hibernica* (G. Kirchn.) Bean is considered a western European taxon and, in contrast to *H. helix*, is tetraploid (Jacobsen 1954).

In the last decades several morphological (Ackerfield and Wen 2002, 2003, Kost *et al.* 2003, Sulgrove 2004, Valcárcel and Vargas 2010) and molecular studies (Vargas *et al.* 1999, Grivet and Petit 2002, Green *et al.* 2011) were performed on *Hedera* taxa with the aim of revealing phylogenetic relationships and evolution. However, molecular studies followed by cytometric measurements revealed that polyploidy was the major phenomena in the evolution of *Hedera* species, and might have taken place several times independently in different lineages (Green *et al.* 2011). Geographical groups of taxa can include different ploidy levels, diploids, and polyploids. These studies also revealed that formerly used morphological traits such as trichome morphology are not considered evolutionarily stable in ivies (Green *et al.* 2011, Vargas *et al.* 1999).

Recent reports mention that some taxa with different morphological-cytological characters are spreading in semi natural or urban habitats, having escaped from gardens (Clarke *et al.* 2006). By studying ivy diversity in Hungary, we detected an outstanding *Hedera* taxon with a specific habit, bearing a series of distinguishable morphological-phenological traits and with different ecological demands. Earlier, this was considered to be *H. hibernica* (Udvardy and Bényei-Himmer 1999). In the last 15–20 years, we observed that this taxon exhibits invasive behaviour spreading in many semi natural habitats and also in urban ecosystems.

In the course of the detailed study of cultivated ivy specimens based on flow-cytometry, we also detected triploid ivies that were formerly considered *Hedera helix*.

Based on the results of our detailed comparative study of *Hedera* specimens, we consider the need to re-evaluate the taxonomic status of the ivy taxon spreading in Hungary and we propose a new name with the related diagnosis. Accordingly, our aims were (i) to identify, describe, and characterize the *Hedera* taxon that is spreading in Hungarian habitats and formerly misidentified as *H. hibernica;* (ii) to describe and characterize newly identified triploid *Hedera* taxa (2n = 72), which were formerly considered cultivated varieties of the diploid *H. helix*.

MATERIAL AND METHODS

Studied specimens

The specimens described here were collected in the period between 2004 and 2007. Geographical coordinates of the type specimens were recorded using Garmin eTrex Legend GPS. Living material of all taxa is maintained in the ivy collection of the Soroksár Botanical Garden of the Szent István University (Budapest). This garden is situated in the northwestern margin of the Great Hungarian Plain, at the edge of Budapest. It is a lowland area with a continental climate, cold winters, and long-lasting droughts in the summer. In order to test ecological demands and behaviour of the studied *Hedera* taxa we planted 10 test individuals on different sites in the Soroksár Botanical Garden and in particular in a fenced-in area where an oak forest community has been preserved. We also planted 50 individuals in the Buda Arboretum of the Szent István University (Budapest) situated on the southern part of the Gellért Hill, where the climate is milder and the territory is under sub-Mediterranean influence. Recent studies on morphology and ecological demands were preceded by a 20 years observation period (Udvardy and Bényei-Himmer 1999).

Flow cytometry and chromosome counting

To distinguish the different cytotypes in the first approach we used flow-cytometrical analysis with PARTEC I (Partec GmbH, Münster, Germany). Fresh leaves were collected and a 1 cm^2 area was introduced in LB01 isolating buffer according to Doležel *et al.* (1989). After filtration, 1 ml DAPI (conc. 25 ng/ml) was added. Nuclei were stained in 1–5 minutes. We used as control the diploid *Hedera helix* 'Zebegény' (Bényei-Himmer *et al.* 2005*a*, *b*). After we had determined ploidy levels by flow cytometry, chromosome counting was done on altogether 10 specimens. The control was the diploid *H. helix* 'Zebegény'. Chromosomes were revealed from the root tips according to Lengyel *et al.* (2007). Ivy cuttings were rooted in perlite in dark chamber using rooting hormone. Root tips were treated with colchicine, first of 0.05% concentration for 30 min., then again with a concentration of 0.025% for 60 min. Fixing was done with 45% acetic acid, then hydrolysis in 1N HCl at 60 °C for 5 min., pressing under a coverslip. Staining was done with 2% acetocarmine for 24 hours at room temperature.

Morphological study and germination power

To distinguish the new specimens from *Hedera helix* and *H. hibernica*, a morphological study was carried out based on leaf morphometry and detailed

study of other vegetative and reproductive organs. Morphometry was carried out on *H. helix* 'Zebegény', *H. hibernica* 'Hamilton', the new diploid taxon, and the two triploids. Leaves were collected from emerging (orthotrop) vegetative shoots and 30 leaves/taxon were measured. Morphometrical characters were recorded as follows: 1 = Length of petiole, (LPET, mm); 2 = Highest length of a lamina, (LMAX, mm); 3 = Length from the base point to the highest width of a leaf, (WLOC, mm); 4 = Length from the base point to the right apical cut (diagonal length), (DIAG, mm); 5 = Highest width of the leaf, (WMAX, mm); 6 = Length of the vein in the main side lobe of the right side of the lamina, (SVEIN, mm); 7 = Highest length of the leaf measured on the right side of the lamina, (LAMIN, mm); 8 = Highest length of the main central lobe, (MAINL, mm); 9 = Highest width of the main central lobe, (MAINW, mm); 10 = Angle of the side bay of the right side of the lamina (ANGLE, mm) (Fig. 1).

IBM SPSS 2.0 (IBM Corp. 2013) statistical software was used to perform univariate and multivariate statistical analysis. Averages and standard deviations of morphological traits (variables) were used to compare means and statistical significances. The diagrams presented below show variation (standard deviation) and significant differences calculated with ANOVA.

Reproductive power and germination potential were studied by comparing the germination rate of *H. helix* 'Zebegény' and the new diploid taxon. 120 seeds were sewed in a propagation tray in normal garden soil and kept in a green house.

To evaluate the reproductive potential of each taxon involved (*H. helix* 'Zebegény', *H. hibernica* 'Hamilton', and the new diploid taxon) in this study we counted the average number of fruit production/ramet. 3 inflorescences from 5 individuals of each taxon were measured (fruits of altogether 135 inflorescences).

Additional specimens (28 sheets) held in the collection of the Hungarian National History Museum (BP) were also examined for diagnostic characters. These are listed below. Herbarium specimens identified by us as *H. crebrescens*, are marked with an asterisk, all others are *H. helix*: HUNGARY. Kerepes: 207 m, June 1856, Bernátsky, (BP120833); Buda Mountains, Jánoshegy: 528 m, 12 March 1870, L. Szépligeti, (BP120853); Jánoshegy: 528 m, September 1862, J. Tauscher (BP120861)*; Zala, Szentgyörgyhegy: 415 m, 1872, S. Jávorka, (BP120851); Murakeresztúr, Gyurgyácerdő: 25 September 1937, Jávorka and Zólyomi (BP120817); Budapest: Remetehegy: 423 m. 17 December 1916, Á. Boros (BP568834); Kaposújlak, Szarkavár: 153 m, 5 April 1926, Á. Boros (BP444903)*; Rajka, Dunakiliti: 114 m 11 April 1920, Á. Boros (BP444905); Vértestolna, Hajagoshegy: 450 m, 26 April 1931, Á. Boros (BP444931); Vértestolna, Szénáshegy 400 m, 20 September 2001, Z. Barina (BP636676)*; Nyergesújfalu: 103 m, 10 September 2001, Z. Barina (BP636289)*; Nagykovácsi: 139 m, 18 August 1997, L. Felföldy (BP291986); Visegrád: 242 m, 12 June 1921, J.

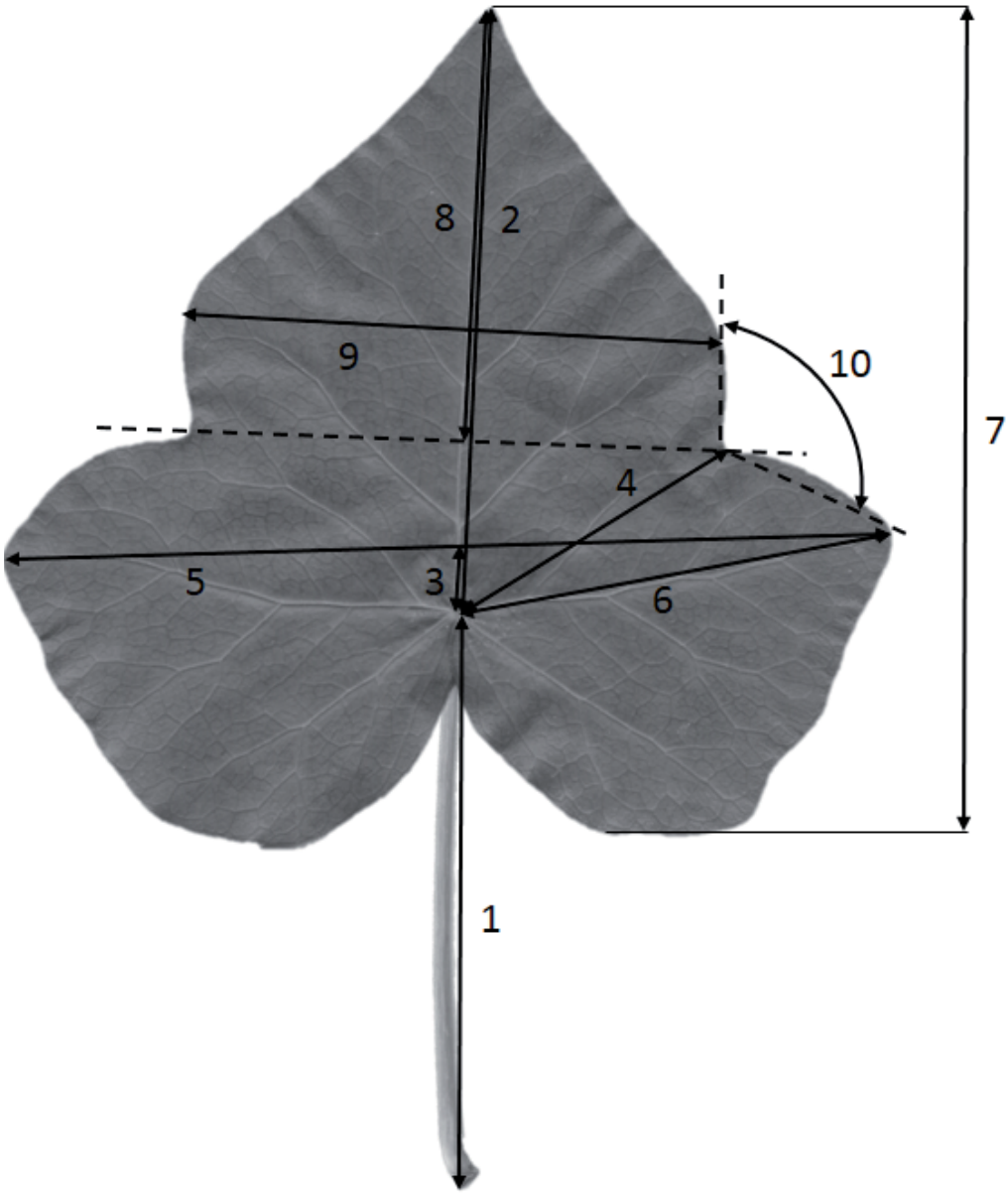

Fig. 1. Measured morphometrical characters of an ivy leaf. 1 = LPET: length of petiole, 2 = LMAX: highest length of a lamina, 3 = WLOC: length from the base point to the WMAX, 4 = DIAG: length from the base point to the right apical cut (diagonal length), 5 = WMAX: highest width of a leaf, 6 = SVEIN: length of the vein in the main side lobe of the right side of the lamina, 7 = LAMIN: highest length of a leaf measured on the right side of the lamina, 8 = MAINL: highest length of the main central lobe, 9 = MAINW: highest width of the main central lobe, 10 = ANGLE: angle of the side bay of the right side of the lamina.

Andrasovszky (BP269647)*; Sármellék, Zalavár: 124 m, 5 April 1952, Á. Károlyi (BP295358)*; Nagyharsány: 166 m, 26 February 1935, A. Pénzes (BP374680); SLOVAKIA. Prenčov Tepličky: 325 m, 1876, Andr. Kmet, (BP120834); Fatra, Likavka valley: 494 m, 22 August 1893, F. Pax, (BP120879); Tatra, Ľubochňa (Fenyőháza): 750 m, 3 August 1906, F. Pax, (BP120872); Chocrscheit, Wald Pocskay: 800 m, 21 May 1899, F. Pax, (BP120878); Bratislava (Pozsony), Thebener Kogel: 18 April 1907, F. Pax (BP120874)*; Jasenová: 700 m, 7 April 1897, F. Pax, (BP 132275); Bratislava (Pozsony): 1909, S. Mágocsy (BP568851); ROMANIA. Portile de fier (Kazanpass): 70 m, 22 August 1901, F. Pax, (BP 120884); Retezat Mt., Cerna valley: 170 m, 28 August 1897, F. Pax, (BP120883); Pojana Ruska: 800 m 15 August 1890, F. Pax, (BP120882); Sibiu (Hermannstadt): 420 m, 15 September 1893, Kimakowicz, (BP120880); Piatra Rosie, Petrosani (Petrozsény): 1000 m, 9 August 1901, F. Pax, (BP120881); Brasov, Cristian (Keresztényfalu): 600 m, 15 March 1906, G. Moesz, (BP120850); CROATIA. Fiume, Musuliensky potok: 2 June 1907, Filarszky, Kümmerle and Moesz (BP5855); Fiume: 16 April 1908, G. Lengyel (BP568856).

Vouchers of the new taxa described here are deposited in BP, while some isotypes are also in private collections at Mária Höhn and Hugh McAllister. The two triploid taxa we describe here were formerly included in two cytological studies, one involving 30 type specimens from the ivy collection of the Soroksár Botanical Garden (Bényei *et al.* 2005a) and another with an extended sample size of 80, also from the collection (Bényei *et al.* 2006, Lengyel *et al.* 2007). Among the ivy samples studied here there were species and also cultivated specimens of commercial origin, cultivars selected by us or cultivars originating in botanical gardens abroad. Research activities and the selection of the ivy collection were performed in the Soroksár Botanical Garden, beginning from the 1970s. Finally, we constructed a key for identification that includes all species mentioned in McAllister and Rutherford (1997) except for *H. cypria* (considered as subspecies based on Valcárcel and Vargas 2010) and including the newly presented taxa.

RESULTS

Taxonomic treatment

Hedera crebrescens M. Bényei-Himmer et M. Höhn, *spec. nov.*

Type: Hungary, Budapest, Gellért Hill, southern slope, 126 m, GPS 47° 28' 50.5"; 19° 02' 25.8", 03.10. 2015. Holotype: BP745240, (Fig. 2), isotype: BP745237

Fig. 2. The holotype specimen of *Hedera crebrescens*.

Diagnosis: Leaf shape on the horizontally creeping shoots is triangular, slightly trilobed, lobes are obtuse and the dense nervation is white. The leaf base is cordate, facing sites overlap (Fig. 4). Leaves on the vertically emerging (orthotrop) shoots are large, 10–16 cm in diameter, with 3–5 lobes and a wider apical lobe. This dome-shaped apical lobe is much larger than the lateral lobes (Fig. 4). The leaves of the flowering, fruiting shoots are cordate. The axis of the inflorescence is short, squat, 3–5 cm, with a few lateral umbels. Under the terminal umbel on the central axis usually there is a solitary flower (Fig. 5). The fruits are dark green, and turn black when ripe. Because of the short peduncules, fruits are densely packed. Fruits have 3–5 mature seeds. Growth is vigorous. *H. crebrescens* is slightly frost sensitive. In cold winters (when temperatures fall below –10° C and cold spells last longer) leaves are damaged, but shoots usually survive and regenerate in the spring. *H. crebrescens* spreads easily by seeds. It is considered to have all the properties of an invasive plant, and it escapes successfully from cultivated areas.

Chromosome number: diploid 2n = 2x = 48 (Fig. 3).

Etymology: The epithet "*crebrescens*" refers to the vigorous growth of the plants.

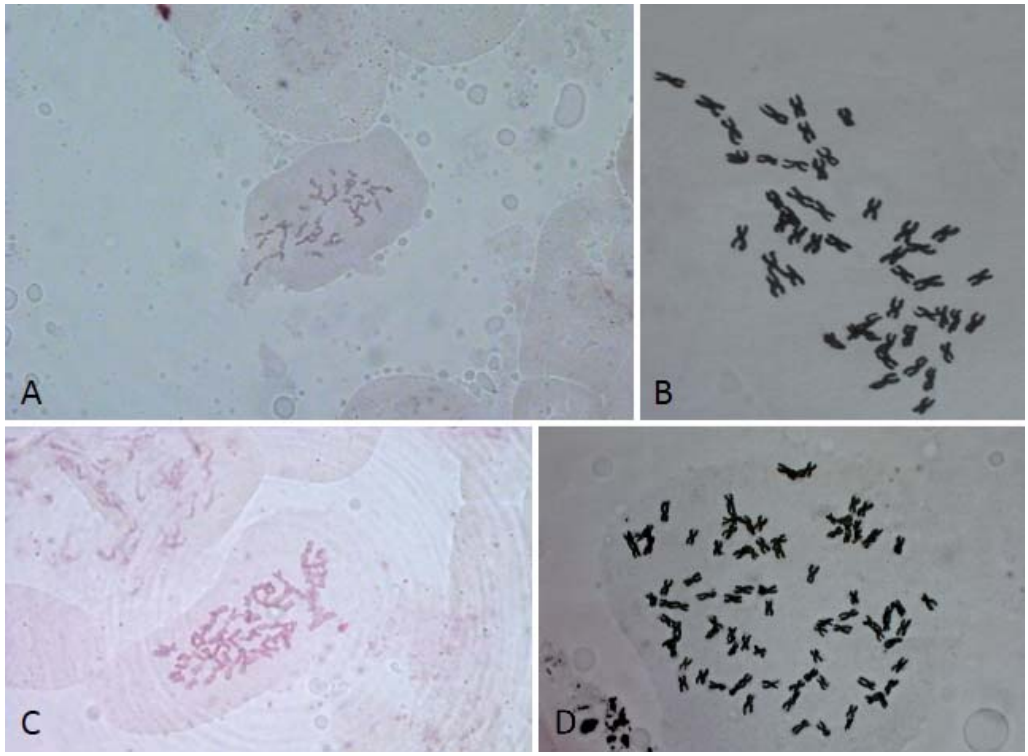

Fig. 3. Chromosome number of *H. crebrescens* (A, B) and *H. hibernica* (C, D). Cytological features were recorded using a 40× objective (magnification of 400× (A, C) and 800× (B, D) in an optical microscope. Photo credit: Pintér I. and Lengyel Sz. (Pintér ined.).

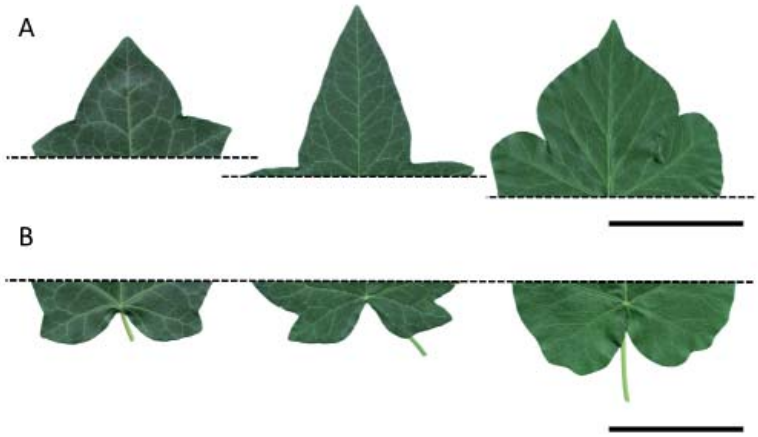

Fig. 4. Leaf characters on the emerging shoots of *Hedera hibernica* (left) *H. helix* (central) and *H. crebrescens* (right), Scale bars=(A, B) 50 mm. A: apical lobe (triangular, elongate, dome-shaped) B: leaf base (open, open, overlapping sites).

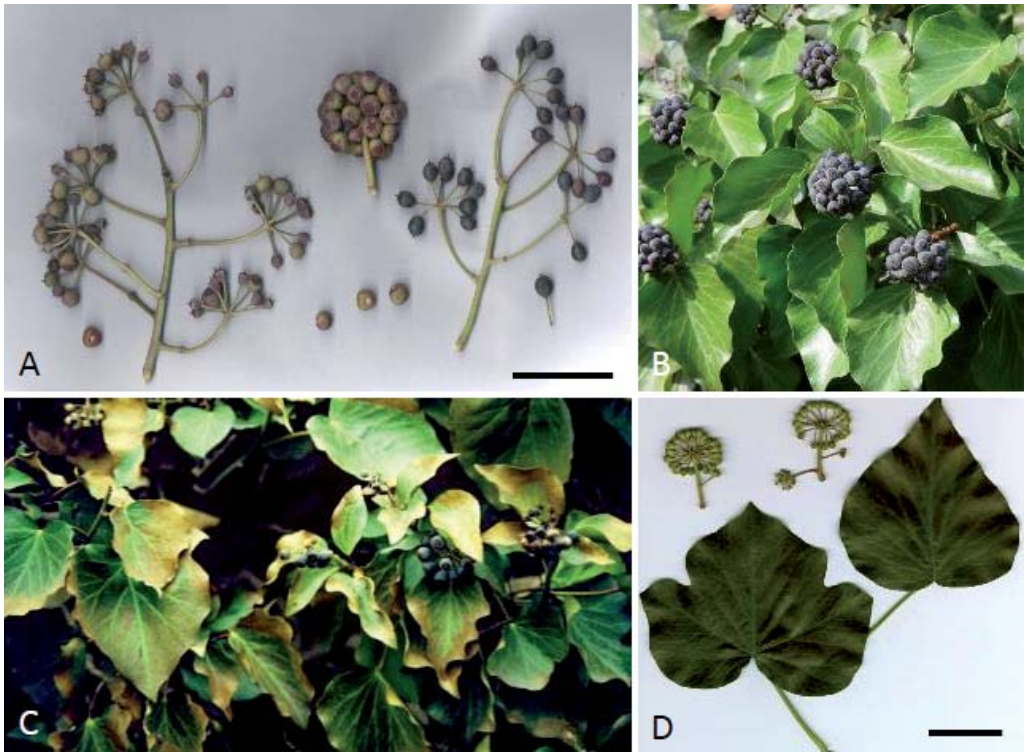

Fig. 5. Morphological characteristics of *Hedera crebrescens* (A: comparison of fruiting shoots of *H. hibernica* (left), *H. crebrescens* (only the apical inflorescence developed) (center) and *H. helix* (right), B: ripening fruits of *H. crebrescens,* and (C): early winter frost damage of *H. crebrescens* D: main morphological characteristics (inflorescence and leaves) of *H. crebrescens.* Scale bars = (A, D) 50 mm.

Distribution: As a fast-growing, easily spreading taxon *H. crebrescens* most frequently grows along railways (from Budapest to Rákospalota-Újpest, Göd, Vác, Kismaros, and Nagymaros towards Zebegény). It can be found also near Lake Balaton and in the area around Szombathely. It often grows in association with *Ailanthus altissima*, *Acer negundo*, *Celtis occidentalis*, *Robinia pseudo-acacia* and *Rubus fruticosus*. It is widespread in cemeteries and their surroundings, such as the Farkasrét Cemetery in Budapest or cemeteries in Eger, Keszthely, and Kecskemét. Other situations in which it can be found are unmaintained gardens, park forests in the Pilis Mountains (Csobánka locality), Kaposvár, Székesfehérvár, gallery forests alongside rivers, for instance in the Bakony Mountains along the Gaja river (Fig. 6). We have detected this taxon outside Hungary in several locations, for instance western Ukraine (in Transcarpathia near Uzhhorod) and in the surroundings of small cities where it has been naturalized. We found it also in Vienna (Austria), southern parts of Slovakia, Germany, and the Netherlands, but occurring mainly in parks.

It is important to consider this new taxon as distinct from *H. helix* and *H. hibernica* not only because of its different morphological traits but also because of

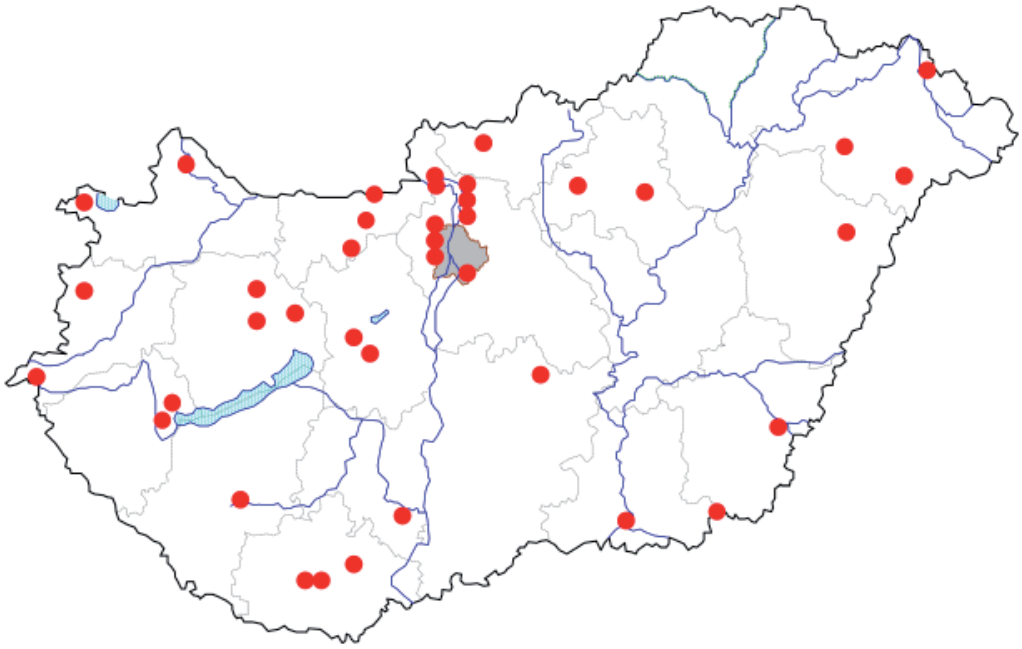

Fig. 6. Geographical sites of the *Hedera crebrescens* records across Hungary: Budapest (János Hill, Sas Hill, Soroksár, Gellért Hill, Rákospalota-Újpest), Csobánka, Debrecen, Eger, Érsekvadkert, Gaja river, Göd, Gyöngyös, Gyula, Kaposújlak, Káloz, Kecskemét, Keszthely, Kismaros, Mezőhegyes, Mosonmagyaróvár, Nagymaros, Nyírbátor, Nyíregyháza, Óbánya, Pécs, Polgárdi, Sióagárd, Sopron, Szeged, Szentgothárd (Pityerszer), Szombathely, Tiszaadony, Vác, Várgesztes, Verőce (further localities are listed in Material and Methods).

its distinct behaviour, specifically that it is capable of becoming invasive because of its successful propagation ability and increased reproductive potential.

Habitat requirements: *H. crebrescens* prefers a semi-humid environment and shady places with an equilibrated water supply. By growing under scrub or hedges, this ivy is able to reduce radiation or frost damage. It may grow in rural environments, filling gaps around houses, in stone cracks, or even in apertures in concrete. It also frequently occupies natural sites where *H. helix* is not present, such as islands along rivers and in gallery forests. On the other hand, it is also a drought tolerant taxon. *H. crebrescens* is slightly frost sensitive. In cold winters (e.g. 1981/1982; 1996/1997 and 2016/2017) when temperature falls below –10 °C and persist for some time, leaves are damaged and decay (Fig. 5C).

Leaf morphometry: Variance analysis was performed on the basis of 10 morphological traits using SPSS statistical method. Accordingly, leaf shape significantly differs both from *Hedera helix* and *H. hibernica* based on morphological traits. Bar charts of the six most discriminant characters are presented in Figure 7.

Hedera crebrescens significantly differs from *H. helix* and *H. hibernica* in six measured parameters: DIAG, SVEIN, LAMIN, MAINL, MAINW, WLOC. All parameters of *H. crebrescens* had higher values than the two triploid specimens (*Hedera* × *soroksarensis* and *H.* × *schmidtii*, see later) and *H. helix*. Moreover at LAMIN, MAINL, MAINW parameters of *H. crebrescens* had the highest value among all taxa studied (Fig. 7).

By comparing *Hedera crebrescens* with *H. hibernica* we found significant differences in two more parameters: WLOC, DIAG, WMAX, SVEIN, LAMIN, MAINL, MAINW, ANGLE. *H. crebrescens* showed the highest length either WLOC, LAMIN or MAINL. Furthermore, *H. crebrescens* had higher values in width, i.e. wider leaves, than *H. hibernica* according to WMAX. The angle of the lateral sinuses of the right side of the lamina (ANGLE) showed that *H. crebrescens* leaves have acute angles, and *H. hibernica* has obtuse angle. *H. crebrescens* significantly differs in all measured parameters from the diploid *H. helix* (Fig. 7).

Nomenclatural notes: Until now, *H. crebrescens* has been identified in Hungary as *H. hibernica* by most gardeners and horticultural experts. *H. hibernica* has been listed in most of the price lists of nurseries from Hungary since 1815. It is documented to have been commercially available since 1875 (Seyderhelm 1875). De Candolle (1830: 261–265) mentioned it as *Hedera helix vulgaris* "*Hybernica hortul*" by adding the comment "*et foliis majoribus*".

Hedera helix var. *hibernica* (as *H. H.* 4. *hibernica*) was described by Georg Kirchner in 1864 (in Petzold and Kirchner 1864). The diagnosis includes statements mostly on the geographical origin of the new taxon (in conflict with Art. 38.3) and a single statement about specific characters referred to its large

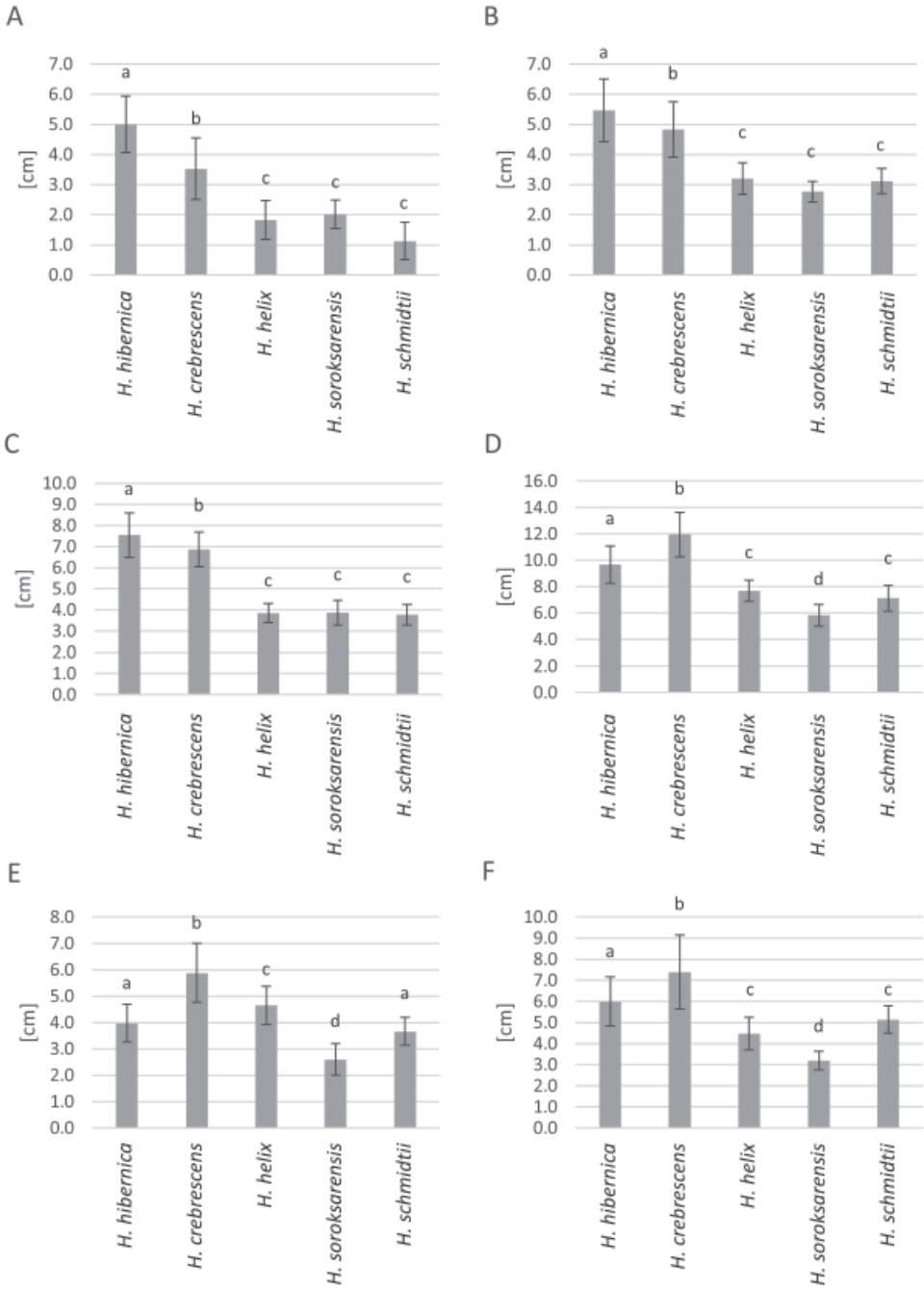

Fig. 7. Main metric characters of the studied *Hedera* taxa, **A**: WLOC = length from the basepoint to the WMAX; **B** = DIAG: length from the basepoint to the right apical cut (diagonal length); **C** = SVEIN: length of the vein in the main side lobe of the right side of the lamina; **D** = LAMIN: highest length of a leaf measured on the right side of the lamina; **E** = MAINL: highest length of the main central lobe; **F** = MAINW: highest width of the main central lobe.

leaves ("Grossblättriger, als der gemeine Epheu"). Later, JÄGER (1865: 176) provided a detailed description for var. *hibernica*.

KOCH (1869) considered this taxon to have originated in Ireland, but to have been cultivated largely in England. According to the nomenclature, Koch concluded that all cultivated garden ivy from Belgium and France should be considered "*Hibernica*". This assumption is probably the origin of the nomenclature used in Hungary for all ivies that differ from the autochthonous *H. helix*. However, Koch mentioned that *H. hibernica* leaves are light-green, plants are fast growing, and are sensible to frost. All these characters fit the taxon we are describing here as *H. crebrescens*.

Under the name *H. hibernica*, Carrière discussed two subtaxa (*H. hibernica aureo-marginata* and *H. hibernica marginata*) without providing a description or diagnosis of *H. hibernica* and without providing a reference to Kirchner's valid description (CARRIÈRE 1890). Doing so, he created a nomen nudum for *H. hibernica* (Art. 38.1). Referring to Kirchner, BEAN (1914) created validly the new combination *H. hibernica* based on the basionym *H. helix* var. *hibernica*. JACOBSEN (1954) mentioned *Hedera hibernica* as a tetraploid ivy.

According to SCHNEIDER (1912), *H. hibernica* is a hybrid between *H. helix* and *H. canariensis* (diploid). The hybrid origin of *H. crebrescens* might be supported by its vigour, fast growth, and high seed production capacity. In its sensitivity to frost also resembles some subtropical taxa, such as the diploid *H. azorica*, *H. nepalensis*, *H. canarensis*, *H. maroccana*, and *H. rhombea*.

TOBLER (1912) notes that leaf petioles of *H. hibernica* grow vertically even on the creeping shoots on the ground. He also mentioned the strong flowering capability and its sensitivity to frost in northern and central Germany. He emphasized that the anthocyanin colouring of the leaves may indicate northern distribution. Based on our observations in the Soroksár Botanical Garden in the winter of 1981–82, when temperatures fell below –20 degrees for a longer period of time, among the ivies growing upwards on tree trunks only *H. crebrescens* suffered frost damage.

Diagnostic characters (from *Hedera helix* subsp. *helix* and *H. hibernica*): *H. hibernica* is a tetraploid taxon (Fig. 3C, D). According to MCALLISTER (1981), for *Hedera hibernica* the most detailed description was given by BEAN (1914).

On the young spring (orthotrop) shoots *H. crebrescens* has very characteristic leaves. The apical lobe is broad, dome-shaped, and widest on the lower third part (not exactly at the lobe base but a little higher). The upper third section begins to narrow sharply towards the tip (Fig. 4 and 5D). Both lateral leaf lobes are obtuse. In *H. hibernica* the apical lobe is not dome-shaped. It has mostly parallel margins or slightly widening margins at the lobe-base (Fig. 4, Table 1). *H. hibernica* has five leaf lobes (Fig. 8).

The texture of the blade is thick with a well-developed mesophyllum that is 20% thicker than that of *H. helix*. The palisade parenchyma is 15–20% broader than in the leaf of *H. helix*. The leaf shape of *H. crebrescens* in most cases is longer than wide, as is the case with *H. hibernica*. The development of lateral shoots with very short internodes bearing small, light green alternating leaves is also characteristic. During the winter, mostly in sunny cold places, leaves of *H. crebrescens* turn yellow or bronze or even claret, but the colour of their veins remains unchanged.

Table 1. Comparison of main morphological traits and conservation status of three *Hedera* species.

	H. crebrescens	*H. helix*	*H. hibernica*
ploidy level	diploid	diploid	tetraploid
shoot	reddish green	brownish green	green
leaves			
– vegetative creeping shoot	leaf blade triangular, leaf base slightly overlapping	nervation white, 3–5 lobed, not overlapping leaf base	5 lobes, not overlapping leaf base
– vegetative emerging shoot	3–5 lobes, lateral lobes obtuse, apical lobe dome-shaped	3–7 lobes, apical lobe elongate	5 lobes, apical lobe triangular or with parallel margins, not dome-shaped
leaves on reproductive shoot	heart shaped, leaf-base cordate	elongate or oval, leaf-base cuneate	triangular-ovate, leaf-base truncate
hairs	white, stellate, always appressed	white, stellate	white, stellate, erect, rays in two directions
inflorescence	main axis thick, 3–5 cm, flowers crowded, one flower below the apical umbel, apical umbel fruiting	main axis 6–9 cm, sparse, third ranking umbels present, lateral umbels fruiting	main axis 8–10 cm, sparse, third ranking umbels present, rarely fruiting
flowering months	September–October	August–October	October–November
fruits	slightly flattened, globose, not protruding discus	reniform, protruding discus	rarely fertile, not protruding discus
seed production	4–5 seeds/fruit, 114 fruits/ramet	1–3 seeds/fruit, 41 fruits/ramet	0–2 seeds/fruit, 51 fruits/ramet
germination	82%	42%	no data available
hardiness	frost sensitive	winter hardy	slightly winter hardy
nature conservation status	propagating, invasive	natural	cultivated

Reproductive shoots may develop close to the ground, as they do not need as much sunlight as the reproductive shoots of *H. helix*. Leaf blades on the reproductive shoots are heart shaped, with a cordate leaf base and acuminate apex, but they are not sharply cuspidate. In contrast, leaves on the reproductive shoots in *Hedera helix* are largely elongate or oval with a cuneate leaf base, while leaves on the reproductive shoots of *H. hibernica* are triangular with a truncated leaf base (Fig. 8).

Inflorescence of *H. crebrescens* develops on a short (3–5 cm) main axis with usually only one umbel (Fig. 5). In the case of *H. helix*, this main axis of the inflorescence is much longer, and it is thin, with lateral branches being distant from one another and developing in August.

On the axis of *H. crebrescens* below the upper umbel there is always a solitary flower (Fig. 5). Flower peduncles in the fruiting umbels are quite short, so the developing fruits are very close to one another and are densely packed like a stuffed ball (Fig. 5). This attribute has ornamental value and cannot be seen in *H. helix* or in *H. hibernica* (Fig. 6A). Moreover, inflorescences of *H. helix* and *H. hibernica* always have third-ranking umbels, while *H. crebrescens* does not. The flowering period of *H. crebrescens* in Hungary starts two weeks later than the flowering period of *H. helix* and usually two weeks earlier compared to *H. hibernica*. Flowers of *H. hibernica* open only in October and November, and often fertilization fails

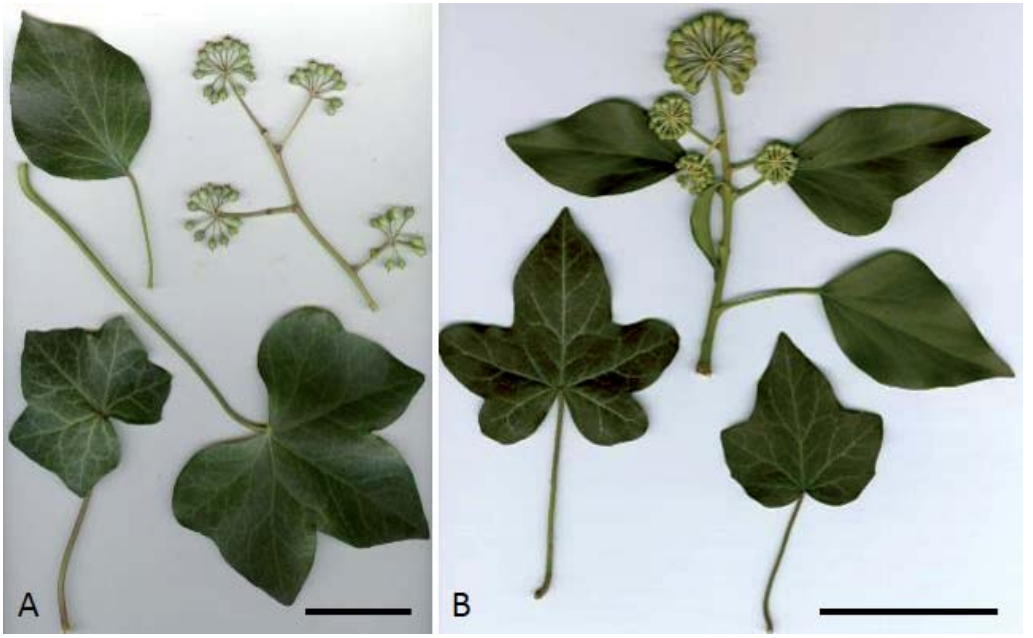

Fig. 8. Morphological variability of leaves of *Hedera hibernica* A: leaf on the creeping shoot (bottom left), vertically emerging shoot (bottom right), generative shoot (top center) and *Hedera helix* subsp. *helix*; B: leaf on the creeping shoot (bottom right), vertically emerging shoot (bottom left), generative shoot (top center). Scale bars = (A, B) 50 mm.

(which is why this taxon could not become invasive). When fertilization is successful, fruiting umbels in *H. hibernica* are big and loose and the inflorescence is a compound cyme (Fig. 5A). In *H. crebrescens* fruits develop from the upper umbel and lateral umbels dry and fall off. Fruits are slightly flattened globose. When ripening, they change color from dark green to black. The disc of the flower does not protrude, as it does in the case of *Hedera helix*. Fruits remain on the plants even into April, and they contain 3–5 rounded-shaped seeds. *H. helix* has 1–3 kidney-shaped seeds/fruit. The fruits of *H. helix* ripen in February and are quickly eaten by birds. The germination rate of seeds is also much higher in *H. crebrescens* compared to *H. helix*.

Our study has revealed that seed production/ramet in *H. crebrescens* is higher than in *H. helix* and *H. hibernica*. The average seed number of one ramet in *H. crebrescens* was 114 seeds, while in the case of *H. helix* it was only 41 and in the case of *H. hibernica* 'Hamilton' was 51.

Seeds of *H. crebrescens* are dispersed by thrushes. In thrush droppings there are sometimes large amounts of viable seeds which can be found germinating in clusters. Cotyledons of the seedlings are more rounded than the seedlings of *H. helix*. The vigorous, rapidly growing plants produce reproductive shoots in a short period of time and yield large amount of fruits with many seeds. The germination capacity is also considerably higher than that of *H. helix*. The general opinion has been accepted up to the present that *H. helix* tends to behave like a weed (Gencsi and Vancsura 1992, Metcalf 1958, Sulgrove 2004, Clarke *et al.* 2006, Udvardy and Bényei-Himmer 1999). On the contrary, we do consider that *H. crebrescens* is the taxon which is spreading behaving like a weed. We performed a germination experiment to study the germination capacity of seeds. The germination test was a case study using 120 seeds/taxa from different clones belonging to *H. helix* and *H. crebrescens*. Based on our observations, the germination capacity of *H. crebrescens* was 82%, which considerably surpasses that of *H. helix*, even of cultivars which had 42% as their highest germination percentage.

By revising herbarium specimens of BP based on diagnostic morphological characters for *H. crebrescens*, such as the dome-shaped apical lobe and obtuse lateral leaf lobes, we identified 7 specimens originating mainly in Hungary and Slovakia beginning in the late nineteenth century. However, herbariums were not accurate for further morphometrical analysis because in most cases both leaf types, i.e. those from the vegetative and reproductive shoots, were not available.

Pharmaceutical use: Because of its chemical compounds, *Hedera* species have pharmaceutical value. Recent studies have revealed biologically active compounds, in particular triterpene saponins, the bidesmosidic glycosides of hederagenin, inositol, carotenes, clorogenic acid, tannins, formic acid, and malic acid,

all of which have medicinal uses. Leaf extracts of ivy have important spasmolytic, antimicrobial, analgesic, anthelmintic, antitrypanosomial, antileishmanial, antitumor, and antimutagenic effects (Lutsenko *et al.* 2010). *H. crebrescens* grows more rapidly, has a higher biomass, and is easier to cultivate than *H. helix*. Target research has not yet been done, but for pharmaceutically active compounds this taxon has already been cultivated in Hungary near Cegléd.

Triploid *Hedera* specimens

In the first decade of this century, we studied the ivy specimens, species, and cultivars growing in the Soroksár Botanical Garden using flow-cytometry. In some cases we found different ploidy levels compared to previous reports, and we detected triploids. In most cases in which flow-cytometry indicated different ploidy levels from what was expected we checked by counting the chromosome number. The triploid specimens of presumably hybrid origin were previously classified as cultivars of *H. helix* or *H. hibernica*. Triploids were also mentioned by Marshall *et al.* (2017). Based on our cytological and morphological results, we describe two triploid cytotypes here.

Hedera* × *soroksarensis M. Bényei-Himmer et M. Höhn in McAllister and Marschall (2017: 401)

Type: Hungary, Budapest: Soroksár Botanical Garden, 100 m. GPS 47° 14' 32.6"; 19° 54' 38.5". Holotype: BP745235 (Fig. 9), isotypes: BP745237, WSY0129182

Chromosome number: triploid: 2n = 3x = 72 (Fig. 10).

Etymology: the epithet '*soroksarensis*' comes from the name of the botanical garden where this taxon was first observed.

Origin: Based on personal observations made in recent decades, a variety of ivy specimens were involved in selection and multiplication of new cultivars. One of these with conspicuous leaf morphology was nominated for national approval in 2001 by Márta Bényei-Himmer as a new variety, with the name *Hedera helix* 'Negro'. In 2004, this variety was registered officially. Based on flow-cytometry and chromosome counting this taxon was shown to be triploid (2n = 72), producing only sterile inflorescences (Fig. 11).

Habitat: Planted individuals are in the botanical garden in Soroksár, Hungary and also in the Buda Arboretum, where vegetative shoots form dense, crowded patches. It has been observed in lowland forests of Hungary, where it grows mainly in association with *Robinia pseudo-acacia*, *Pyrus pyraster*, *Celtis occidentalis*, *Elaeagnus angustifolia*, *Ligustrum vulgare*, *Sambucus nigra*, *Crataegus monogyna* and *Rosa canina*.

Fig. 9. The holotype specimen of the triploid *Hedera* taxa: *H.* × *soroksarensis*.

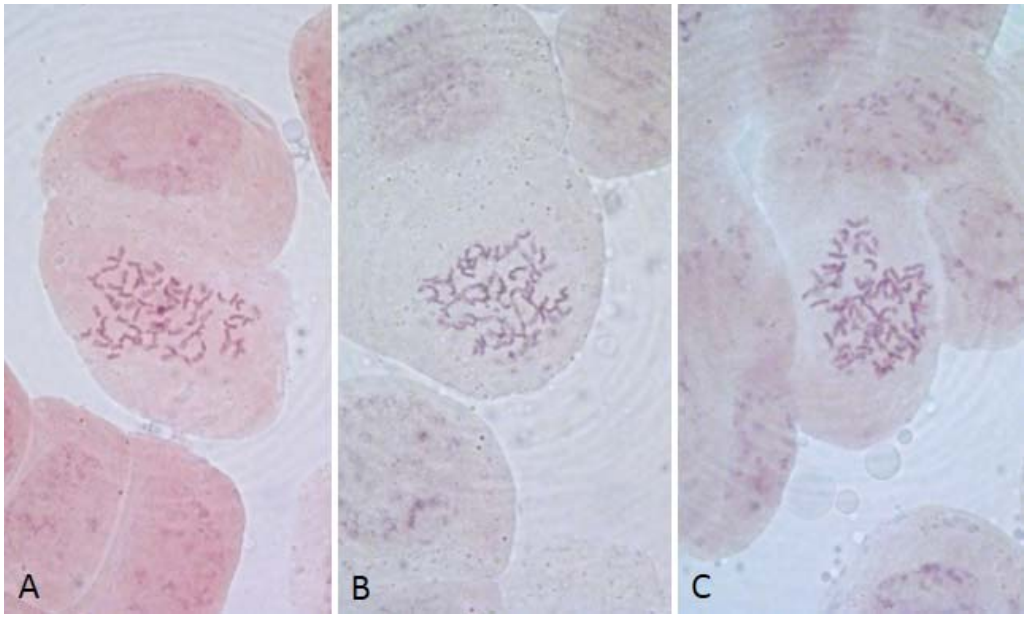

Fig. 10. Chromosome number of the triploid *Hedera* taxa: *H.* × *soroksarensis* ('Negro') (A), *H.* × *schmidtii*. (B) and *H.* × *soroksarensis* ('Woerneri') (C). Cytological features were recorded using a 40× objective (magnification of 400× (A, B, C) in an optical microscope.Photo credit: Pintér I. and Lengyel Sz. (Pintér ined.).

Fig. 11. Sterile inflorescences of *Hedera* × *soroksarensis.*

Diagnostic characters (from *H. helix* subsp. *helix* and *H. hibernica*): Compared to *H. helix*, inflorescences can develop near the ground at the soil surface or at low heights by climbing on tree trunks. Trichomes are more numerous on the veins and in the angles between veins, but they are most dense on the main axis of the inflorescence. Leaves of the creeping shoots most closely resemble those of the tetraploid *H. hibernica* but they are smaller and dark green. The two basal lobes are short. The middle two lobes are wider, while the apical lobe has a wide base tapering to the apex. Most conspicuous is the dark green colour of the leaf blade surface, which on the flowering shoots is pale, not shiny. They measure 5–8 × 7–9 cm and are egg-shaped and slightly asymmetric, tapering toward the apex (Fig. 12). The inflorescences resemble those of *H. hibernica* but the flowers are less developed. The axis of the inflorescence is 4–6 cm (*H. hibernica* is longer up to 6–10 cm), having 2–3 lateral umbels.

Horticultural uses: As it has a moderate growth vigour (around 40–60 cm yearly growth increment) but is not invasive, with its dark green leaves this taxon is one of the best ivies to use as shade-tolerant ground cover to replace lawns or cover bare walls. It can be planted in gardens and parks, as it is not invasive and is resistant to diseases, drought, and frost. There is no need to water, as it is drought tolerant, and the dense shoot network provides an excellent uniform dark-green cover.

Hedera hibernica 'Woerneri' described earlier by Jenny (1964) is also a triploid variety of *H.* × *soroksarensis* (Bényei-Himmer and Höhn 2017: 301).

Fig. 12. Creeping shoots: A: *Hedera* × *soroksarensis* with the dark green leaves, B: *Hedera* × *schmidtii* with slightly triangular emerald leaves with small lobes.

Hedera* × *schmidtii M. Bényei-Himmer, *spec. nov.*

Type: Humgary, Zebegény, northern slope, GPS 47° 47' 50.2"; 18° 54' 44.9". Holotype: BP 745238 (Fig. 13), isotype: BP 745239.

Diagnosis: Shoots are purple-brown with 8–10 cm long internodes. It has mainly creeping shoots, the leaves of which are 7–8 × 8–9 cm, triangular, or slightly trilobed. The leaf base is deeply cordate. On the emerging vertical shoots leaves are more deeply trilobed. The colour of the leaf surface is emerald green with white venation. The main vein with the first rank lateral veins protrudes from the surface. Lateral veins form right angles with the main vein. The underside of the leaf is pale. The leaf is skin-like and medium thick in texture. Leaf margins are usually slightly reflexed. Stellate trichomes are white with mostly 4 rays which both protrude from and lie parallel to the leaf blade. The petiole is purple-brown and 6–9 cm long. This taxon develops flowering shoots at a relatively old age, when it is older than 10 years, at a height of 3–4 m. The main axis of the inflorescence is 5–6 cm, with only a few (3–4) ramifications. The inflorescences and the umbels are loose. Fruits are slightly elongate to globose. We have not yet found germinated seeds.

Chromosome number: triploid: 2n = 3x = 72 (Fig. 10).

Etymology: The epithet "schmidtii" comes from the name of professor Gábor Schmidt, who was the head of the Buda Arboretum where this taxon was preserved.

Origin: This taxon originates from the Börzsöny Mountains (northeastern Hungary). It is maintained *ex situ* in the Soroksár Botanical Garden. It was nominated for national approval in 2001 by Márta Bényei-Himmer as a new variety with the name *Hedera helix* 'Nagybörzsöny'. In 2004, this variety was officially registered.

Habitat: At the original site, the location from which this triploid was first discovered in the Börzsöny Mountains, it occurs in a managed sessile oak forest, where it propagates only vegetatively. The accompanying species are *Acer campestre*, *Pyrus pyraster*, *Robinia pseudo-acacia*, *Sambucus nigra*, *Cornus sanguinea*, *Cornus mas*, *Syringa vulgaris* and *Ligustrum vulgare*.

Diagnostic characters (from *Hedera helix* subsp. *helix* and *H. hibernica*): We have already planted specimens in the botanical garden in Soroksár, Hungary and also in the Budai Arboretum. Our experience shows that vegetative shoots form uniform, medium-crowded patches.

This taxon grows mainly close to the soil surface. Flowering umbels develop only rarely, on 2–3 m high emerging shoots. Like the underside of the leaf, the upper surface and the area among the veins are hairy (*Hedera* × *soroksarensis* has hairs only on the veins and at the edge of vein ramifications). The emerald

Fig. 13. The holotype specimen of the triploid *Hedera* taxa: *Hedera* × *schmidtii*.

green colour of the leaf with white venation is specific to this taxon. Leaves of the flowering (adult) shoots are wide-ovate and triangular, with a truncated leaf base, which is a feature it has in common with *H. hibernica*. The flowering shoots resemble those of *H. hibernica* with their straight, truncated leaf bases, but the leaf apex is not twisted. It grows vigorously (60–80 cm is annual average growth increment), but it is not invasive.

Horticultural uses: As it has a medium growth vigour but is not invasive, with its dark emerald green leaves *H.* × *schmidtii* is suitable to use as a shade-tolerant ground cover to replace lawns or cover bare walls (Fig. 12). It is suitable for planting in gardens and parks, as it is non-invasive and resistant to diseases, drought, and frost.

The triploid cultivars described here differ significantly from *H. hibernica* and *H. crebrescens* in five morphological parameters (WLOC, DIAG, SVEIN, LAMIN, MAINW) (Fig. 7). In the case of *H. helix*, these cultivars significantly differ in only one parameter (MAINL). Only *H.* × *soroksarensis* showed distinct values of LAMIN and MAINW (Fig. 7).

Statistical findings indicated significant differences between the two triploid cultivars in three variables: LAMIN, MAINL, MAINW. At these parameters, *H.* × *soroksarensis* always showed smaller values than *H.* × *schmidtii* (Fig. 7).

Identification key for cultivated and native *Hedera* the taxa in the Carpathian Basin

We consider in the key altogether 11 species including the new taxa and the two triploids. This number is different compared to the 12 species recently published by McAllister and Marschall (2017: 141). We did not consider here the frost sensible Mediterranean species like *H. iberica* and *H. maderensis*, without any importance in Central East Europe, only *H. canariensis* which was several times confused with *H. algeriensis*.

1a Trichomes are greyish, stellate with 4–10 rays 2

1b Trichomes are yellowish brown, flat, scale-like (squamiform), in bundles 5

2a Trichomes are not emerging from the plane of the leaf, rays of the trichomes face two directions (bifurcate). Leaves on the ground creeping shoots are pentagonal with five equal sized lobes. Leaf blades are funnel shaped, 8–10 cm, dark green. The petiole is very long, even 20 cm in length. Leaves does not change colour during winter. The vertically emerging shoots have three to five lobes, and are wider than longer. The leaves of the flowering, fruiting shoots are oval with acuminate apex (pointed) tip. The inflorescence is a loose and compound corymb. The species is flowering in late September or October. The fruits are developing from the lateral umbels, frequently remain immature. Tetraploid species, its cultivars are widely planted ..... *H. hibernica* (Kirschner) Bean (Fig. 8A)

2b Trichomes emerge from the plane of the leaf 3

3a The inflorescence axis is 3–5 cm long, the fruits develop only from the terminal umbel. The lateral umbels decay and fall after flowering. The leaves of the ground creeping shoots are 5–8 cm in diameter and slightly lobed with three lobes at the leaf base (triangular). Leaves are bright green, the veins are light green. The vertically emerging shoots have leaves with 3–5 lobes with a broad central lobe. This dome-shaped broad lobe is much more developed than the lateral lobes (Fig. 4A). The leaves of the flowering, fruiting shoots are heart shaped with cordate leaf base. The leaf blade is large, 10–16 cm long, the trichomes have 7–12 rays. The axis of the inflorescence is short, squat of 3–5 cm with few lateral umbels. Under the terminal umbel on the central axis always one lonely flower develops (Fig. 5D). The pedicel of the flowers are short –1 cm, therefore the ripening fruits are densely packed. Flowering period is from late August to September. The fruits are dark green and becoming black when ripen. Fruits have 3–5 seed. The generative (adult) stage develops early, even on the ground level. In wintertime leaves can change their colour to claret on the sun, but the veins remain green. During very cold winters the leaves freeze and fall, but the shoots survive. Diploid taxon. Widely planted, but spreads also spontaneously and tends to be invasive ..... *H. crebrescens* M. Bényei-Himmer et M. Höhn (Figs 2, 5)

3b The axis of the inflorescence is longer, fruits develop (even) from the lateral umbel 4

4a The leaves of the ground creeping shoots greatly vary. The colour of the leaves can be different from bright green to dark green, often with white veins. Number of leaf lobes can vary between 3–7 and leaf base can be cordate or truncate, with elongate central lobe. Stellate trichomes have 4–10 rays, and multicellular branched trichomes can also appear. The leaves of the generative (adult stage) shoots are elongate, oval with a cuneate leaf base. The length of the inflorescence axis is 6–9 cm long, often third-order branching, in some case with bracts. Flowering period lasts from August until October. Fruits diverse with 1–3 seeds. The protruding discus is frequent. Generative shoots only at elevating age. Leaves do not freeze even during cold winters. Many cultivars are widely planted. Native diploid taxa ..... *H. helix* L. (Fig. 8B)
Triploids considered most probably hybrids between ***H. helix*** and ***H. hibernica***. These triploid specimens were previously treated as ***H. helix*** or ***H. hibernica*** and classified among cultivated ivy varieties.

aa Leaves are triangular, dark green with white veins .... *Hedera* × *schmidtii* M. Bényei-Himmer (Figs 12, 13)

bb Leaves are dark green to black with light green veins having 5 lobes .... *Hedera* × *soroksarensis* M. Bényei-Himmer et M. Höhn (Fig. 9, 12)

4b The leaves of the ground creeping shoots have 5–7 or more equally sized lobes. Leaves are light green. The vertically emerging shoots have leaves of 8 cm or larger. Leaf lobes can appear even on the inflorescence carrying shoots (we met this just few years ago on a flourishing individual). Native species of the Azores, planted as a perennial in horticultural gardens ....*H. azorica* Carr.

5a Broken shoots are fragrant. Leaves are not lobed or not palmately lobed, with dentate margins 6

5b Broken shoots are fragrant or not. Leaves are palmately lobed or triangular 7

6a Leaves are pinnately and slightly lobed, light greyish green, 7–10 cm long. The adult form of leaves is narrow lanceolate and the colour of the fruits is orange ..... *H. nepalensis* Koch

6b Leaves are not lobed, large up to 10–15 cm and skin-like with cordate base. Fruits are black. (Leaf margin is dentate, often 12–18 cm in size. Fast growing cultivar: var. *dentata*. Variegated leaf cultivars are often planted) ..... *H. colchica* (K. Koch) Koch

7a Leaves are small 2–4 cm long, slightly lobed with truncate base. Flat scale-like (squamiform) trichomes, upright emerging hairbundle trichomes are also present on the leaves. In Hungary found only in botanic gardens ..... *H. rhombea* (Miq) Bean

7b Leaves are larger 8

8a Leaves are without lobes, and the blade is elongate triangular or slightly lobed. Colour bright green, 10–12 cm long (subsp. *cypria*). The leaf blade is greyish around the veins. Shoots are often vertically climbing ..... *Hedera pastuchovii* Woronow

8b Leaves are three or five lobed and green or magenta 9

9a Leaves are five-lobed with emerald colour, shoots are magenta. Strong growing capacity. (Develops flowers and fruits in Hungary, on mild winters it is winter-hardy) .... *H. maroccana* McAllister

9b Leaves are elongate triangular-shaped or with three lobes 10

10a Leaves are acuminate, 3 lobed (with pointed tip), leaf blades are longer than their width, leaf bases are rounded. The leaf blade is green with reddish veins. Strong growing and slightly frost tolerant species. Earlier sold and distributed as *H. canariensis*, but this species is different in morphology and ploidy. The 'Gloire de Marengo' is a well-known cultivar, which is planted in open field as well on frost protected areas ..... *H. algeriensis* Hibberd

10b Leaves are barely lobed, mid-sized and wider than longer, pale green. Slow growing and frost sensitive ..... *H. canariensis* Willd.

CONCLUSIONS

Our analysis based on cytological, morphological study and ecological observations indicates that *H. crebrescens* can be considered a distinct taxon among the diploid ivies.

We emphasize that this *Hedera* taxon, spreading in Hungary and formerly treated as *H. hibernica* is not identical with the tetraploid taxon. *H. hibernica* in Hungary has its flowering period later than *H. helix* or *H. crebrescens*, and the late fall frosts damage the seed development and reproductive potential of *H. hibernica*. Moreover, based on Sulgrove (2004), *H. crebrescens* is not identical with *H. hibernica,* the "noxious invasive ivy" taxon spreading in the USA. Based on higher viable seed production, successful propagation by birds, and its high germination rate, we consider *H. crebrescens* as the most invasive ivy taxon in Hungary and most probably in the surrounding countries. We consider that most of the recently reported new occurrences of *H. helix* by the Atlas of Flora Hungariae from the lowland in Hungary refer to *H. crebrescens* (Bartha and Király 2015: 65). In the case of the triploids identified in this study, further study is needed to elucidate the parents.

All the taxa that we have studied exhibited stellate trichome types. However, trichome morphology should not be considered a taxonomically definitive criterion in *Hedera*, as suggested by Krüssmann (1977), because stellate trichomes with four rays emerging in two directions (bifurcate) are present in many *Hedera* taxa. Moreover, when the leaves begin to age, these bifurcate stellate trichomes are able to develop new rays and will become multiangulate.

Studies that include species from the eastern part of the distribution range of the *Hedera* genus, the Caucasus, and the Far East, formerly mentioned by Pojarkova (1951), are necessary in order to explore ivy diversity and relationships.

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Összefoglaló: Az északi mérsékelt égövi, eurázsiai elterjedésű *Hedera* nemzetség mintegy 12 faja közül csak a diploid *Hedera helix* L. tekinthető honosnak a Kárpát-medencében. Kertészeti kultúrából azonban számos faj és azok hibridje, kultúrváltozata ismert. Leggyakrabban találkozhatunk a bizonytalan származású ír borostyánnal, a *H. hibernica*-val, amely egy tetraploid taxon. A különböző ploidia-típusok közötti egyrészt spontán másrészt mesterséges hibridizáció eredményeképpen a borostyánok között morfológiailag változatos génanyag jött létre, mely a taxonok elkülönítését megnehezítette. Morfológiai és citometriai vizsgálatainkkal bizonyítottuk, hogy egy korábban *H. hibernica*-ként számon tartott taxon diploid és nem azonos a szintén diploid, honos *H. helix* fajjal. Ez a taxon félkultúr és kultúr területeken, városi környezetben, vasutak mentén és folyópartokon spontán módon terjed. Összehasonlító morfológiai, fenológiai és kromoszóma vizsgálatok eredményei alapján ezt az új diploid taxont *H. crebrescens* néven írjuk le. Ez a taxon erőteljes növekedésű, mind vegetatív, mind pedig generatív tulajdonságaiban elkülöníthető a *H. helix*-től és a *H. hibernica*-tól is. Terjedési erélyét segíti a nagy maghozam, a magok madarak általi sikeres terjesztése, a magas csírázási arány és gyors növekedése által a honos borostyán élőhelyét veszélyezteti.

A *Hedera* nemzetségből korábban ismert di-, tetra-, hexa- és oktoploid taxonok mellett fajtagyűjteményekben szereplő és spontán előfordulású egyedek átfogó vizsgálatával először azonosítottunk triploid taxonokat. Ezen triploidokat hibrid eredetű fajként tartjuk számon, közöljük a leírást a környezeti igény és kertészeti jelentőség bemutatásával.

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