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Biological flora of Central Europe *Himantoglossum adriaticum* H. Baumann

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Abstract

Himantoglossum adriaticum H. Baumann is a long-lived perennial orchid with an adriato-mediterranean distribution. The species-level separation of this species from the more geographically widespread *H. hircinum* has only recently been confirmed via a combination of molecular and morphometric techniques, which are further developed here. To provide a comprehensive overview of its autecology we integrated previously published information with extensive unpublished data derived mainly from populations in the Keszthely Hills of Hungary. In this paper we assess the distribution, habitat preferences, life history and seed germination (ex situ and in situ) of *H. adriaticum*, with special emphasis on its reproductive biology.

Keywords:
Orchidaceae; dormancy; genetic and morphological variation, life cycle; pollination; reproductive biology;

Contents

Introduction

The genus *Himantoglossum* W.D.J. Koch includes some of the most conspicuous orchids native to central Europe. Its large and showy flowers are characterized by a greatly elongated central labellar lobe that emerges from the bud in circinnate form but, once extended, transforms into a sinistral spiral (Bateman et al., 2013). The species-level separation of *H. adriaticum* H. Baumann from the more geographically widespread *H. hircinum* has only recently been cemented via a combination of molecular and morphometric techniques applied across Eurasia (Sramkó et al., 2014; Bateman et al., 2017). Here, we have assembled an international team to bring together diverse data, both published and unpublished, with the aim of generating a data-rich review of this increasingly well-understood species.

To provide a comprehensive overview of topics such as morphology and taxonomy, distribution and habitat requirements, life history, phenology, growth patterns and floral biology, we used previously published information as well as unpublished data. Observations of the species' ecology were conducted across nearly the whole of its distribution area, but the majority of our previously unpublished data were collected in Hungary, mainly in the Keszthely Hills close to Keszthely town. Data were collected from sites along a minor road (approximately 1.8 km in length); from 1992 until 2007, 154 tagged plants were surveyed individually, and from 1999 until 2014, 0.5 × 0.5 m wire-grid plots were established in areas of high juvenile density to capture adult as well as seedling and juvenile data.

The growth stage of an individual was recorded as seedling (seedling1: single-leaved individuals with leaf width equal to or less than 0.5 cm; seedling2: single-leaved individuals with leaf width of 0.6–1.0 cm), juvenile (single-leaved individuals with leaf width of 1.1–1.5 cm or two-leaved individuals), sterile adult (two-leaved individuals with largest leaf width equal to or greater than 1.6 cm or with three or more leaves), flowering adult (individuals that produced an inflorescence), dormant (individuals that disappeared in one year but re-appeared in a subsequent year) or dead (individuals confirmed dead or typically invisible for three or more years).

Morphological observations included number of leaves, plant height (cm), and length and width of the largest leaf (cm). For reproductive individuals, length of inflorescence (cm), number of flowers and number of seedpods produced were also recorded.

Furthermore, the five largest populations in Hungary (Sümeg, Kőszeg, Nagytevel, Keszthely, Harka) were censused between 2012 and 2014. All vegetative rosettes were counted and measured in March. They were classified by life-stages according to the width of the largest leaf. The census of reproductive individuals was made in June.

Unless otherwise stated, data given without a published literature source refer to these localized but intensive investigations.

Morphology and taxonomy

Nomenclature and taxonomy

Himantoglossum adriaticum H. Baumann – Die Orchidee (Hamburg) 29(4): 171. 1978. Synonym: *Himantoglossum hircinum* (L.) Spreng. subsp. *adriaticum* (H. Baumann) H. Sund. – Eur. Medit. Orch. ed. 3: 40. 1980. Colloquial names: Croatian: Remenojezična kozonoška, Jadranska kozonoška, English: Adriatic Lizard Orchid, German: Adriatische Riemenzunge, Hungarian: Adriai sallangvirág, Italian: Barbone adriatico, Slovakian: Jazýčkovec jadranský, Slovenian: Jadranska smrdljiva kukavica. Specific epithet refers to the species' distribution being centred on the Adriatic Sea.

Recent detailed phylogenetic and morphometric analyses showed that the genus *Himantoglossum* Spreng. consists of nine species apportioned among three subgenera (Sramkó et al., 2014; Bateman et al., 2017). *Himantoglossum adriaticum* belongs to the largest subgenus *Himantoglossum.* This species and its closest relative, *H. hircinum* (L.) Spreng., form sect. *Hircinum*, characterized morphologically by labellar lateral lobes greater than 3 mm, labellar 'abdomen' greater than 20 mm, spur less than 4 mm and gynostemium less than 4.5 mm (Bateman et al., 2017).

Morphology

Himantoglossum adriaticum H. Baumann (Fig. 1) is a perennial, tuberous, photoautotrophic orchid with an over-wintering rosette that consists of (1–)2–5(–12), lanceolate, pale green basal leaves. The mature plants have rosette leaves (6.6–)7.5–17.5(–24.7) cm long and (1.5–)2.5–4.5(–12.8) cm broad. The mean±SD number of basal leaves in individuals of five Hungarian populations are 2.6±1.7 (range: 1–12) (Fig. 2). The generative shoots are (14–)40–80(–120) cm tall. The inflorescence is elongate and lax, composed of (4–)15–40(–115) flowers and typically 14–24 cm in length.

The lower bracts are 19.2–71.5 mm long, whereas the upper bracts are shorter than the flowers. The hood is greenish-pinkish-white, bordered purple outside, sometimes broadly so, veined purple inside. The sepals are oval, (6.8–)7.1–10 mm long and 3.7–5.3 mm broad, whereas the petals are linear-lanceolate, 4.4–7 mm × 1.2–1.8 mm. The labellum is deeply 3-lobed, spotted with purple papillae (Fig. 3B), margins intensely coloured, usually reddishbrown or dark purple (rarely olive green). The median lobe is 28–61 mm × 1.3–2.3 mm, incised at the tip by a notch 2.4–12.4(–18) mm deep. The lateral lobes are linear, acute, 2.9–10(–25) mm long. The spur is sack-like, curved (1.6–)2.1–3(–3.7) mm long and lacks nectar (Delforge, 2006; Molnár V., 2011). The spur entrance is reduced by long papillae and there is a single common viscidium (Claessens and Kleynen, 2011; Fig. 3A). The colourless papillae are osmophores (floral fragrance glands; Vöth, 1999). Flowers have a slight, sweetish, aromatic smell (Vöth, 1999). Fruit capsules are (10–)12–16(–20.5) mm long and (2.3–)3–4(–4.8) mm wide. The thousand-seed weight is 0.0013 g (Sonkoly et al., 2016). Mature seeds consist of a dead fusiform testa 0.35–0.53 × 0.15–0.21 mm, containing an embryo 135–160 × 82–160 μm (Mrkvicka, 1994) (Fig. 3D).

Aberrations observed in Hungary included hypochromatic and twin flowers, as well as yellow-striped chlorotic specimens (Appendix 1).

Is H. adriaticum *a genuine species distinct from* H. hircinum*?*

The epithet *adriaticum* was first used by Baumann (1978), who immediately treated this new taxon as a full species. However, *adriaticum* was rapidly demoted to a subspecies of *H. hircinum* by Sundermann (1980) and Wood (1983). Thereafter, most authors have chosen to view *H. adriaticum* as a *bona fide* species, albeit on the basis of severely limited systematic data; only recently has *adriaticum* been examined using modern systematic techniques. Sramkó et al. (2014) generated three molecular data-sets from numerous samples that encompassed the full taxonomic and geographic range of the genus *Himantoglossum sensu lato*, employing *Steveniella satyrioides* as outgroup. They generated sets of trees from (a) the high-copy nuclear region ITS (Appendix 2), (b) the low-copy nuclear gene *LEAFY* (Fig. 4A) and (c) four concatenated plastid regions (*accD-psaI*, *atpF-atpH*, gene *rps16*, *trnH-psbA* and *trnL-ndhF*, including the genes *rpl32* and *ycf1*) (Fig. 4B).

Their results clearly showed that European species of *Himantoglossum sensu stricto* showed low molecular divergence and were therefore of comparatively recent origin (certainly within the last one million years; see also fig. 8 of Sramkó et al., 2014). ITS and plastid data also showed that lizard orchids to the west of a north–south zone passing through the Adriatic Sea, the former Yugoslavia and Hungary were readily molecularly distinguished from those to the east, thereby delimiting the *hircinum* and *caprinum* groups, respectively (Sramkó et al., 2014; Bateman et al., 2017).

The westerly *hircinum* group consisted only of *H. hircinum* in western Europe plus *H. adriaticum* in central Europe, the two species rarely being found in sympatry. ITS data were unable to reliably distinguish between the two putative species (Appendix 2), suggesting either conspecificity or very recent separation, whereas the plastid data consistently placed samples in separate monophyletic *hircinum* and *adriaticum* groups that received strong statistical support, suggesting the existence of two distinct species (Fig. 4B). The *LEAFY* phylogeny also implied that the two taxa should be treated as separate species (Fig. 4A). However, *LEAFY* clustered two samples of the eastern *H. calcaratum jankae* alongside *H. adriaticum*, which Sramkó et al. (2014) interpreted as sign of gene-flow between *adriaticum* and *jankae* within the overlap of their distribution areas.

Bateman et al. (2017) gathered *in situ* morphometric data for 45 quantitative and semi-quantitative morphological characters from 152 individual plants encompassing all widely recognised species of the genus *Himantoglossum sensu lato*. Their results supported the DNA-based inference that *H. adriaticum* is more similar to *H. hircinum* than to members of the eastern *caprinum* group, particularly if pigmentation characters are ignored. Observed similarities included small sepals, short gynostemia, and on the labellum a short ‘thorax’ (the region of the labellum separating the spur entrance from the lateral lobes), short ‘legs’ and small labellar spurs. Nonetheless, sufficient morphological differences were noted to conclude that *adriaticum* merits full species status.

Here, we have abstracted from Bateman et al.'s (2017) matrix the information on *H. hircinum* (three populations: two from England and one from Morocco) and *H. adriaticum* (two populations, both from Hungary) and re-analysed the data in order to (a) determine via this more focused analysis whether the two taxa are sufficiently morphologically distinct for convincing recognition as separate species and (b) to identify those morphological characters that best distinguish between the two species (note that three of the original 45 characters were rendered invariant by subsampling to produce the reduced data-matrix).

The resulting principal coordinates plots (Fig. 5, Table 1) show a typical pattern when two *bona fide* species are compared. The first coordinate accounts for an unusually large proportion of the total variation and reliably separates *H. adriaticum* from *H. hircinum* (Fig. 5A). It reflects substantial differences in the distribution of purple markings across the labellum, the width of the labellum, and the colour of the adaxial (external) surface of the sepals. The much weaker second coordinate is a typical ‘vigour’ coordinate; it largely represents variation in plant size, which is in turn primarily a manifestation of both ontogenetic variation and ecophenotypic influences rather than of genetics *per se* (Bateman and Denholm, 1989; Bateman, 2001). This coordinate largely separates the comparatively small plants sampled in Newmarket from the other two populations of *H. hircinum*, on the basis of its smaller numbers of flowers per inflorescence (<35) that possess shorter labella (<45 mm; Table 1).

The yet weaker third and fourth coordinates (Fig. 5B) also serve primarily to distinguish between conspecific populations. The third coordinate distinguishes between the two Hungarian populations of *H. adriaticum*. Compared with Kőszeg, Nyirád has on average more strongly down-curved labellar spurs, longer labellar ‘legs’ (>5 mm) and slightly wider petals (>1.3 mm), whereas Kőszeg has darker (reflectivity <20%) purple-coloured sepals (Table 1). The fourth coordinate distinguishes the Ifrane population of *H. hircinum* on the basis of the absence of both purple spots on its sepals and purple-brown pigmentation on the upper part of its stem, together with less recurved labellar ‘arms’. A corresponding minimum spanning tree (results not shown) based on application of the Gower (1971) similarity coefficient succeeded in resolving individuals from all five populations into potentially monophyletic groups. This is an unusual outcome for closely related orchid species – an outcome that demonstrates that these *Himantoglossum* populations have cohesive rather than hyper-variable morphologies, though populations of *H. adriaticum* appear somewhat more internally variable than do those of *H. hircinum*.

Returning to consider the species-distinguishing first coordinate in greater detail (Table 1), it highlights the more localised distribution of purple-stained papillae on the labella of *H. hircinum* (particularly in the Ifrane and Newmarket populations) relative to those of *H. adriaticum*, in which the markings reliably extend distally well beyond the emergence of the ‘arms’ (lateral labellar lobes). Other characters that distinguish the two species with at least 90% reliability include the much paler and greener sepals (typically yellowish-green to green in *H. hircinum*, mauve to purple in *H. adriaticum*), denser inflorescence (>2.0 flowers per cm), and longer floral bracts (>20 mm) of *H. hircinum*. Its labellum is broader (shoulder width >6 mm, torso width >1.5 mm) and averages a width : length ratio of *ca* 1.7, compared with *ca* 1.0 in *H. adriaticum* (Fig. 6).

In summary, our morphological data support our molecular data in demonstrating that modest but nonetheless reliable differences exist between the two taxa, and the *in situ* morphometric data have identified the most effective diagnostic characters (though obviously, larger and more geographically comprehensive studies remain desirable). Certainly, the status of *H. adriaticum* as a full species, sister to – but nonetheless distinguishable from – *H. hircinum*, should no longer be viewed as equivocal.

Evolutionary origin of H. adriaticum

The ITS, plastid and morphometric data all indicate that *H. adriaticum* is the sister species of *H. hircinum* (Sramkó et al., 2014; Bateman et al., 2017) – a conclusion further supported by cytogenetic similarities and their juxtaposed geographical distributions in western and central Europe, respectively. Although the genus *Himantoglossum* is likely to have originated in the Caucasus, Sramkó et al. (2014) estimated from plastid data an equal probability that *H. adriaticum* originated in western or central-southern Europe. But which of the two sister species gave rise to the other?

The *LEAFY* tree (Fig. 4A) could be viewed as evidence for a hybrid origin of *H. adriaticum* between *H. hircinum* and *H. calcaratum jankae* in their contact zone immediately east of the Alps. Certainly, artificial crossing of several other *Himantoglossum* species (dominantly allogamous) has demonstrated that intrinsic sterility barriers are weak (Bateman et al., 2017; Malmgren, 2018). However, as neither ITS nor plastid nor morphometric data-sets indicate a strong influence from *H. calcaratum*, it seems to us more likely that there has been recent and recurrent gene-flow from *H. adriaticum* into *H. calcaratum*, at least within Hungary (Sramkó et al., 2014). Although *H. adriaticum* and *H. hircinum* show approximately equal variation in *LEAFY* sequences and in morphometric data (Bateman et al., 2017), *H. hircinum* is more variable in plastid and ITS data (Bateman et al., 2013; Sramkó et al., 2014), tentatively indicating that *H. adriaticum* is more likely to be the species that evolved more recently. One factor potentially complicating genetic interpretation but not yet adequately studied is the supposed distributional outlier of *H. hircinum* in southern Italy, though the divergent ribotype of these populations (Sramkó et al., 2014) suggests that they represent an unlikely ancestor of *H. adriaticum*.

If *H. adriaticum* is indeed derived from *H. hircinum*, it may partly owe its origin to mild floral paedomorphosis, as the labellum of *H. adriaticum* more closely resembles the juvenile labellar shape of *H. hircinum* (Fig. 6, inset). Pollinator specificity is an unlikely underlying cause of speciation, as both of these species attract via food deceit several shared pollinator species, most commonly (but not confined to) bees (Claessens and Kleynen, 2011; Bódis et al., 2015).

Distribution and habitat requirements

Geographical and altitudinal distribution

Himantoglossum adriaticum is an adriato-mediterranean species (Fig. 7, Appendix 3). Populations are known from Italy and Croatia (Baumann, 1978), Slovenia (Ravnik, 2002), Austria (Mrkvicka, 1990), Czech Republic (Rybka et al., 2005), Slovakia (Vlčko et al., 2003), Hungary (Molnár V. et al., 1995), Bosnia and Herzegovina (Milanović et al., 2015) and Albania (Barina and Pifkó, 2009).

Two localities are conspicuously outlying from the main part of distribution: one in Albania and one in central Romania. The locality in Albania should be treated as an ambiguous occurrence data as the voucher specimen seen by one of the authors (GS) at BP is in fruit, and therefore is unsuitable for adequate determination. The collector of the species based his identification on previous, brief visual examination of the species in flower, but failed to collect it in that crucial phenological stage (Barina Z. *ex verb.*) Therefore, we must consider the Albanian occurrence as uncertain; it could easily represent a mistakenly identified *H. calcaratum* specimen. Another satellite occurrence is represented by a single herbarium specimen collected by F. Schur in the mid-19th century near Sibiu (C Romania). As this specimen (examined by us as an unnumbered sheet in the herbarium of the Institute of Botany, Vienna – WU) unequivocally belongs to this species, it indicates a potential (extinct?) occurrence in Romania.

Himantoglossum adriaticum occurs from sea level up to 1600 m (Delforge, 2006: 356). Based on 102 locations, the mean altitude of its populations is 463±308 m (Fig 8, Appendix 3, range: 69–1530 m). On the southern part of its distribution range the species occurs at higher altitudes, thereby mirroring its sister-species *H. hircinum* (Bateman et al., 2013). A significant negative correlation was observed between geographic latitude and altitude (Spearman's correlation test, $\rho=-0.585$, $p<0.001$) but no correlation was found between geographic longitude and altitude (Spearman's correlation test, $\rho=-0.277$, $p=0.005$).

Substratum

Himantoglossum adriaticum inhabits dry, usually shallow rocky soils with neutral or basic reaction (Rybka et al., 2005; Delforge, 2006: 256). According to our data, pH varies between 6.3 and 7.5, although $CaCO_3$ content can vary greatly, as can nitrogen, phosphorous and potassium contents (Table 2).

Habitats and associated plant communities

Himantoglossum adriaticum is a species of light or semi-shaded habitats (Rybka et al., 2005; Delforge, 2006). Baumann reported the species as a calcicole of dry grasslands and open forests (Baumann and Künkele, 1982). According to Delforge's (2006) summary reflecting its ecological preferences across its entire distribution, *H. adriaticum* occurs in short, poor grassland, banks, thickets, woodland margins and open woodlands.

Habitat preferences in specific countries are: Central Italy: roadside (34.3%), scrubby hillside or scrubby grassland (31.3%), grassy hillside or meadow (21.9%); also below the city walls and abandoned quarries (Klaver, 2011). Croatia: sunny to mid-shade dry, mostly calcareous habitats, abandoned grasslands, south- and west-facing slopes, woodlands with open canopy and their margins, scrublands (Čičmir et al., 2015). Slovenia: network of small patches of semi-dry grasslands and scrubby hillsides (Kaligaric et al., 2004; Trčak et al., 2006), scattered olive trees and other woody species on a warm hillside (Glasnovic et al., 2013). Bosnia-Herzegovina: secondary thermophylous grasslands, which were formed after being clear cut (Milanović et al., 2015). Austria: dry grasslands with *Stipa* spp. and *Bromus erectus* and calcareous open rocky grasslands on dolomite (Mrkvicka, 1990). Hungary: calcareous rock steppes, xero-mesophilous grasslands, scrub woodlands and thermophilous woodland fringes; however, a greater number of individuals are usually found on secondary habitats, such as traditional orchards, abandoned vineyards and mown grassy verges alongside public roads (Neilreich, 1866: 66; Molnár V., 2011; Bódis et al., 2014). Slovakia: warm grasslands and forest steppes, on bushy hillsides and in sparse forests (Šefferová Stanová et al., 2015). Czech Republic: edges of open pubescent oak forests and on sunny hillsides with shrubs (Rybka et al., 2005).

An investigation of 84 phytocoenological relevés that encompassed every country of the distribution area except Albania concluded that the species had no strong phytocoenological preferences; it could persist in a wide range of habitats from mesic grasslands to dry scrublands. The primary habitats of *H. adriaticum* could be open forests with a mosaic of fully sunny and shaded patches, where the species grows in small groups (Bódis et al., 2018). Large, extensive populations can be found on secondary habitats (i.e. roadsides or abandoned vineyards) that offer similar ecological conditions (Fekete et al., 2017).

Himantoglossum adriaticum occurred in 10 phytocoenological classes according to the system of Mucina et al. (2016). Grasslands most characteristic for *H. adriaticum* are secondary habitats with *Bromus erectus* and *Brachypodium pinnatum*. The phytocoenological class Festuco-Brometa was reported from Italy, Slovenia, Croatia, Bosnia and Herzegovina, Hungary, Austria and Slovakia. The most important Natura habitat is 6210 – Semi-natural dry grasslands and scrubland facies on calcareous substrates (Festuco-Brometalia), which is formally recognised as important for orchid sites in general. The number of habitats of community interest is 13 (Appendix 4; Bódis et al., 2018).

Life cycle, phenology and growth

Phenology and growth

The phenology of *H. adriaticum* is similar to those of other orchid species that are centred on the Mediterranean region and have 'winter-green' leaves (e.g. *Anacamptis pyramidalis*, *A. morio*, *Neotinea ustulata*, *N. tridentata*, *Ophrys insectifera*). The leaves of the larger plants appear after autumn rainfall; in Hungary, usually in September (rarely late August or October). All individuals undergo an intensive growth period after their autumn appearance, lasting until November. Thereafter, the growth patterns of individuals in different size categories diverge: large plants (4 or more rosette leaves) show stasis or only slight growth until the end of March. During this period the leaf area is often reduced because of damage caused by frosts and/or herbivores. Leaf growth of large plants is rapid from the end of March until the arrival of the first warm period, typically in May. By the end of the growing period, individuals have leaf areas of 40–110 cm^2. In contrast, in the case of medium- (3 rosette leaves) and small-sized plants (2 leaves) growth is characterized by an almost constant rate; no substantial differences could be observed between the autumn, winter or spring phases. Only about 10% of individuals increased their leaf number year-by-year. For *H. adriaticum* the most interesting status is that of the four-leaved plants, which is the threshold for a large, potentially flowering size in this species (Bódis and Botta-Dukát, 2008). Leaf area and leaf traits were assessed on the basis of basal leaves from five plants in the Keszthely Hills (Table 3).

In the case of *H. adriaticum* the size threshold for flowering appears to be a leaf area of 50 cm^2, which is usually reached in the four-leaf stage of the rosettes. Above that size the probability of flowering rises with increase in leaf number (Fig. 9). Increase in the leaf number and the leaf area of flowering plants had already been greater for two years before flowering took place, compared with equivalent plants that remained sterile. The cost of a single phase of reproduction is usually two leaves during the following season; we did not distinguish the cost of flowering and fruiting. The mean number of leaves of flowering plants was 5.1, irrespective of whether plants flowered after a reproductive or vegetative year. In the year following flowering, vegetative plants had on average 3.2 leaves, a reduction of almost two leaves. The cost of reproduction related to plant size, initially increasing with plant size but smallest (0.43 leaves) in case of the largest individuals bearing more than six leaves (Table 4; Bódis, 2010).

Individuals of *H. adriaticum* flower from early May to late July, depending on latitude, altitude, microclimate and weather during the given year. The overall period of anthesis is wide. As calculated from 141 precisely dated herbarium records, photographic documents and field observations (Appendix 3), the average Julian date of flowering is 161.9±15.7 (11 June); in Austria it is 169.4±13.1 (n=33) whereas in Italy it is 153.5±15.8 (n=53). The earliest observation of flowering was made in Italy (Ca' La Lagia), on 1 May, whereas the latest observation was made in Austria (Vienna) on 23 July. This is an extreme value but not unique; equivalent observations are in Slovakia 18 July, in Italy 16 July and in Hungary 14 July. Nonetheless, flowers typically appear between 30 May and 19 June (Fig. 10).
The capsules mature for 4–6 weeks, after which the seeds are shed rather quickly, during a few sunny days in July or August. Thereafter, the plants remain at rest for a few months.

Life cycle and dormancy

Himantoglossum adriaticum is a long-lived orchid; the average life span is 8 years and one tenth of plants live for at least 15 years. Based on our observations (Keszthely Hills, 1993–2005, 154 plants) the average half-life is 5.5 years (determined using the methodology of Silvertown, 1982). The half-life of *H. hircinum* populations was estimated at 3.5–6.3 years and the maximum observed life span of individuals was 19 years (Pfeifer, 2004). These figures are intermediate between unusually short-lived European orchids such as *Ophrys sphegodes*, which has a half-life of 1.5–2.3 years and an observed maximum life-span of 10 years (Hutchings, 1987), and unusually long-lived species such as *Orchis purpurea*, which yielded estimated half-lives of 44 and 66 years (Jacquemyn et al., 2010).
The majority (60%) of the individuals observed in five Hungarian populations had 1 or 2 leaves (Fig. 2). According to our observations on the Keszthely Hills population (1108 records made between 1993 and 2005; Fig. 11), 1-leaved or 2-leaved plants flower only rarely; inflorescences are produced by 10% of 3-leaved plants, 30% of 4-leaved, 64% of 5-leaved, 77% of 6 leaved, 86% of 7-leaved, 90% of 8-leaved and all rosettes of 9 or more leaves. During our 3 years of monitoring of all populations in Hungary the proportion of flowering individuals per population varied between zero and 19% (Table 5). Only 20 plants flowered in Hungary in 2012, when there was a drought during the winter and spring before the flowering time; in contrast, we counted 537 reproductive individuals in 2014, when the preceding autumn and winter were much wetter. During this period, fluctuation in the total number of individuals was much smaller (2466 plants in 2012 and 5019 plants in 2014) (Table 5).

During long-term monitoring (1999–2007) of the population in the Keszthely Hills, the ratios of contrasting stages of the recruitment (seedling1 : seedling2 : juvenile) varied greatly among our plots. Some plots were dominated by seedlings, and others by juvenile stages, for several successive years. Recruitment has also been shown to vary among plots in the same year in *H. hircinum* populations (Carey et al., 2002; Pfeifer et al., 2006).
The mortality of seedlings and juveniles depended on their size; unsurprisingly, the smallest seedlings had the highest mortality rate. The transition from recruitment to adult stage was only 4.5% from all transitions (Fig. 12). Although there were many seedlings in an Austrian *H. adriaticum* population, the number of adults did not increase in response (Mrkvicka, 1990). About 80% of *H. hircinum* plants died before their adult stage in a German population subjected to long-term monitoring (Pfeifer et al., 2006). We detected dormancy of recruitment, restricted to only one year (Fig. 12). The proportions of dormant plants were 9–10% in seedlings and 19% in the juvenile state.

During a 14-year period the majority of the Keszthely population reliably (53.5–76.9% yearly) consisted of sterile plants, typically having only one or two leaves. The proportion of flowering plants per population per annum varied between 4.1% and 34%. Reproduction occurred mainly (62%) after a sterile year. Nearly one-third (31%) of flowering plants flower again in the subsequent year. Out of 154 plants monitored between 1993 and 2007, only one individual flowered in 75% of the relevant years (nine flowering years out of 12). A further three plants flowered in 54–57% of studied years and a further 3 individuals had a 50% flowering record, whereas 15 plants did not flower during the observation period; one of the 15 plants produced a leaf rosette in every year but the remainder had at least one dormant year. About half (52%) of all reproductive stages happened without consecutive flowering. Only four plants flowered continuously for five years – the longest flowering period without interruption. After the flowering year 56% of plants are sterile, 10% dead and 3% dormant.

The annual proportion of dormant plants varied between 1.6 and 12.3%. The probability of dormancy immediately after a dormant stage is as high as after the sterile stage (46% vs. 46%), but much lower (8%) after flowering. After dormancy, the probability of a consecutive dormant stage is higher (52%) than a sterile stage (44%). Flowering immediately after a dormant year was rare (4%). In the case of adult plants, the dormant period lasted between one and six years, one third of the dormancies lasting only one year. The annual mortality rate of adults varied between 5.7% and 20.6%. We detected a sterile life stage immediately before death in 72% of cases.

On the basis of the observed stage-transition probabilities (Fig. 12), stasis and retrogression proved to be the most important features in the stage structure of our investigated population. Stasis means survival from one year to the next in the same stage class, whereas retrogression means plants decreasing in size during the year or reverting from the previous stage (e.g. from flowering status to a vegetative one or becoming dormant) (Silvertown et al., 1993).

Seed production and dispersal

Wind-dispersed seeds (Fig. 1D) are numerous, the estimated number of seeds per capsule ranging from 1119 to 23740 (Table 6).

*Seed germination (*ex situ *and* in situ*) and seedling morphology*

According to Mrkvicka (1990), new plants first create a protocorm, then develop a shoot above the soil surface and only then develop the first root and tuber. Seeds germinate in the first year (in sterile garden culture) and the first leaf reaches the surface of the substrate. However, Rasmussen (1995) argued for an alternative ontogenetic pattern for *Himantoglossum* species of protocorm→tuber with roots→shoot (above ground). Based on our results in *ex situ* situations the protocorm developed first a shoot apex, then the tuber. Next, we detected the first leaf and the adventitious roots from the tuber. During *ex situ* germination, the first protocorm appeared nine months after sowing on modified Fast media (pH 5.5), whereas at pH 7.5 the first protocorm appeared after seven months. The seeds needed 8–11 months after sowing to germinate in their natural habitats. At the Hungarian sites of Keszthely and Sümeg respectively the germination rate was 50.3% and 39.9% in close proximity to the living plants but only 19.4% and 3.5% respectively in the control packets, which were placed 10 m from the living plants (Fig. 13; Gilián et al., 2018).

According to microscopic observation, the symbiosis between the fungi and the orchid protocorm starts soon after the appearance of the white protocorm bearing rhizoid hairs but before shoot initiation (Gilián et al., 2018). While the symbiosis is established the seed coat decays and the protocorm enlarges. Shoot development commences when the protocorm can be seen by eye.

Most of the seedlings emerge around the mother plants (rarely more distant than 30–40 cm); most seeds fall in that area (Jersáková and Malinová, 2007) and the fungal partners are also more likely to be present (Jacquemyn et al., 2007). According to our investigation in the Keszthely Hills, seedlings emerged in large numbers in the third year after the adult plants had flowered; the seeds must spend two years within the soil before they are able to develop their first green leaf. The emergence of the seedlings was continuous during the vegetative period. According to our personal observations, recruitment is encouraged by a wet, cool autumn but discouraged by cold winters.

In the emergence of the seedlings, besides the meteorological factors, an important role is also played by the current year's status of the parent plant (i.e. dormant vs vegetative vs reproductive). The seedlings behave similarly to the maternal parent plant; when the seed-parent is dormant, the seedlings also remain below the soil surface. The status of the seed-parent in the previous year does not influence the number of emergent seedlings (Bódis, 2010).

Seedlings have been cultured in vitro by germinating seeds asymbiotically to produce protocorms. Protocorms of *H. adriaticum* needed 3 months in constantly dark conditions at 4 ^{o}C then a further 4 months on pH 6.5 and 7.5 in the dark at 24 ^{o}C before they appeared above the substrate. In natural light, the seedlings needed 3–4 months to reach 5 cm in height. When seedlings were transferred to a fresh substrate, they grew at a comparable rate (Gilián et al., 2018).

Mycorrhizae

The symbiotic mycorrhizal partners of *H. adriaticum* have been little studied. As in most other tuberous orchids, it is possible that the genera of *Rhizoctonia*-like fungi are also mycorrhizal on *H. adriaticum* (Rasmussen, 2002; Dearnaley, 2007). *Rhizoctonia versicolor* (Ceratobasidiaceae, Cantharellales) was isolated from root sections of *H. hircinum* growing in France (Hardegger et al., 1963; Urech et al., 1963).

Fungal diversity in ten adult *H. adriaticum* plants collected from two geographically distinct protected areas of Central Italy was analysed by means of molecular methods. Six out of ten individuals, from both investigated areas, were colonised by fungi belonging to *Tulasnellaceae*. Three of the remaining plants were colonised by *Fusarium* sp. and the fourth by *Exophiala salmonis* (Pecoraro et al., 2013). We analysed samples taken from the protocorms (*in situ* germination at Keszthely and Sümeg, Hungary) and they yielded a fungal sequence similar to that published by Pecoraro et al. (2013) (Gilián, 2015).

Spatial distribution of plants within populations

Occasionally, populations consist of only one or two flowering individuals – termed satellite populations by Carey et al. (2002) in their parallel study of *H. hircinum*. Satellite populations were reported from Hungary (Vajda, 1956; K. Lájer, M. Óvári, R. Szilaj, A. Mészáros, pers. obs.) and from Italy (Klaver, 2011). Klaver (2011) reported a recent increase of the species in the province of Pesaro-Urbino, where he found at 10 localities only one flowering plant, at 20 localities small groups of 2–20 flowering plants, but only two populations that exceeded this number: one with 36 inflorescences and the other with at least 60.

In Slovenia, close to the border with Italy above Klariči, small groups are similarly characteristic (Glasnovic et al., 2013). In the Medvednica Mountains of Croatia, 57 flowering individuals of *H. adriaticum* occupied a 20 m^2 plot in 2013 (Zadravec et al., 2014). During our survey we detected 8–9 flowering plants of *H. adriaticum* in Croatia (in the Istrian Peninsula), 6–7 in Slovenia (Mala Varnica), 13 in Austria (Lobau), 9 in Slovakia (Stupava), 23 in Hungary (Kőszeg) within 4 m^2 in 2016, but 24–25 inflorescences within 4 m^2 in Bosnia-Herzegovina (Suvaja) in 2017. Seedlings and juvenile plants are often crowded in small areas (Fig. 1B). Our observations of a 25 cm × 25 cm fixed plot at Keszthely identified 19–83 individuals (mainly juveniles and seedlings) when monitored between 1999 and 2013.

Responses to abiotic and biotic factors

Response to climate factors

As in *H. hircinum* (Good, 1936; Füller, 1981; Heinrich and Voelckel, 1999), photosynthetic area – concentrated mainly on the first-formed leaves – is often reduced by winter frosts in Hungary (Appendix 5A, B; Bódis and Botta-Dukát, 2008). Hot, dry springs and early summers leading to insufficient water supply can cause abortion of inflorescences (e.g. in *H. hircinum*: Carey and Farrell, 2002; *Dactylorhiza sambucina*: Inghe and Tamm, 1988; *Ophrys apifera*: Wells and Cox, 1989).

We examined the effects of meteorological factors on the number of observed reproductive individuals, height of flowering stem, mean number of flowers and fruit set by multiple linear regression. Explanatory factors were summer, autumn, winter and spring precipitation in the current vegetation period and annual temperature and number of frost days in the preceding vegetation period. Variables were selected adapting to the vegetation period of *H. adriaticum*. Hence, August was included with autumn and summer was restricted to June. We used the number of frost days instead of the annual average temperature, because in the latter case winter and summer extremes are levelled out. The number of frost days is also more relevant to the biology of the species because the plant is sensitive to winter frosts. Mean height of shoots and arcsin-transformed fruit-set were analyzed through general linear regression, while the number of flowering individuals and the number of flowers in inflorescences were analyzed with Poisson generalized linear models with log-link.

A positive correlation was confirmed between the annual precipitation of the previous vegetative period and both the number of flowering individuals and mean number of flowers in inflorescences. These reproductive traits were negatively correlated with the number of frost days in the previous vegetative period and with spring temperature in the current vegetative period. Mean number of flowers were also related the mean temperature for June (Table 7; Bódis, 2010).

Response to competition and management

Himantoglossum adriaticum prefers semi-shaded habitats, often growing along the margins of forests or in scrubby grasslands. After abandonment of traditional land-use practices (mowing or grazing) the scrubby vegetation eventually overgrows and overwhelms the orchid. Plants of *H. adriaticum* can survive under the shrubs for several years, because they can assimilate resources during the winter. Such plants also occasionally bloom, though the inflorescence becomes etiolated and the resulting fructification is unusually weak (Zadravec et al., 2014). In 2013 at one abandoned vineyard at Kőszeg, 12 plants flowered in deep shade, under the closed canopy layer, where fruit set was 2.5% (12 fruits/479 flowers). In contrast, 38 flowering plants in adjacent herbaceous vegetation set 55.1% fruits (709 fruits/1285 inflorescences) (Sándor, 2013).

Slaviero et al. (2016) argued that *H. adriaticum* is consistently found very close to open areas, even in cases where it occurs under a tree canopy in Italy. Their results revealed that local herbaceous vegetation cover and height is negatively related to the cover of *H. adriaticum,* whereas neither the total cover nor the cover and height of the shrub layer exhibited significant effects. They found that the number of fruits was positively correlated with the height of *H. adriaticum* plants. We also identified a positive correlation of fruit set with inflorescence height, whereas we found a negative correlation with cover of woody species (Biró et al., 2015a). It is not known whether populations found under a shrub canopy represent residual individuals of former open dry grasslands invaded by shrubs after the abandonment of traditional management practices or whether this reflects present ecological requirements (Slaviero et al., 2016).

Scrub clearance has a positive effect on fruit set, though in rocky habitats covered with thin soil, the consequences can instead be negative. Exposure to full sun can desiccate the plants to a point where they abort the inflorescence and rapidly wither. Complete clearance is damaging, because the resulting bare soil and strong sunshine dry the orchids; only a percentage of the shrubs present should be cut.

Herbivores and pathogens

Because the rosettes are winter-green, during a mild winter the leaves can suffer from herbivory. We observed *Meloe* (*M. proscarabeus, M. violaceus*) imagoes and *Epilecta linogrisea* (*Noctuidae*) caterpillars chewing the leaves in early spring in the Keszthely Hills (Appendix 5D–E). We also noticed unidentified caterpillars on the inflorescences that eat the flowers, sometimes consuming every flower on the shoot. Vertebrates do not graze the rosettes but can grub out (Appendix 5C) or trample them; for example, in some years, horses destroy inflorescences in the Keszthely population.

No data are available on fungal or viral pathogens.

Floral biology

Pollination

Known pollinators of deceptive (non-rewarding) flowers of *H. adriaticum* are mainly Hymenoptera species, though the inflorescences are also visited by some Coleoptera (Table 8). Geitonogamous pollination (i.e. pollinaria transferred from a flower to another flower on the same plant) was conclusively observed in Zala county in 2007 (M. Óvári, pers. obs.) and in Veszprém county in 2018 (A. Mészáros, pers. obs.), where the only inflorescence present in that summer nonetheless ripened fruits.

Pollinator spectra differ locally. Teschner (1980) reported only *Andrena* and *Colletes* species as pollinators in the Istria Peninsula of Croatia, but when he transferred some *H. adriaticum* inflorescences to Germany, small, medium and large bees and bumblebees also pollinated the flowers. According to Vöth (1990), the main pollinator in Austria is *Apis mellifera*. The honeybees visit *H. adriaticum* mainly after finding no reward in nearby *Salvia* flowers.

Several Hymenoptera species have since been observed as pollinators (Table 8). *Dinoptera* (*Acmaeops*) *collaris* (Coleoptera) also carry the pollinaria, though removal could be random, simply reflecting the beetle's size (Table 8); hoverflies, bugs and bumblebees seemed unsuitable as pollinators. Floral visits are short (only a few seconds) by wild insects, but honeybees visit up to six flowers on the same inflorescence, inadvertently collecting numerous pollinaria on their head (Appendix 6A; Claessens and Kleynen, 2011).

The flowers of *H. adriaticum* are typical 'bee-flowers' (Cingel, 1995; Claessens and Kleynen, 2011). However, the phenological adaptation of the plant is not optimal for bees, because its flowering period is earlier than the swarming periods of most potential pollinators (Cingel, 1995). *Himantoglossum adriaticum* appears more generalized for pollinators than was expected by some observers based on its phenotype (a relatively short spur, pale colours and presence of marked guides), which caused the plant to be assigned by some observers to the syndrome of short-tongue bees (Fantinato et al., 2017).

Little information is available about the floral signals that attract insects. The long papillae and hairs located toward the bottom of the spur entrance secrete emitting minute quantities of cell fluid (Fig. 3A) and are reputedly attractive to *Colletes* species. The colourless papillae are osmophores (Vöth, 1990). Teschner (1980) showed that the spur of *H. adriaticum* (similar to its sister species *H. hircinum* and *H. calcaratum*) may contain small quantities of glucose, though Bateman et al. (2013) questioned the functional significance of these inferences.

While probing the flowers for nectar, insects will touch the bursicle that encloses the single fused viscidium (Fig. 3C). After removal of the pollinaria, the caudicle starts to bend and move gradually into a position suitable for contacting the stigmatic cavity, ideally that of a different flower after the pollinator has moved on to visit another plant, thereby increasing the possibility of allogamy. The mean bending time of caudicles is 82±44 seconds (our observations: n=36, min=33, max=197).

Based on our investigation of 13 flowering individuals (on 19 June 2013 in Sümeg, between 06:00–21:00 hours), a mean of 2.9 flowers/individual had pollinaria removed (min=0, max=9) – 10.7%±12.7% (min=0, max=43.8%) of the open, intact flowers. Pollinator activity (visit, pollinia removal and deposition) was highest in the early morning (between 06:00–08:00 hours) and the late afternoon (between 15:00–18:00 hours). Although the two pollinaria share a single viscidium (Fig. 3C), in a few cases (19%) the visiting insect removed only one pollinarium from the flower. We were able to investigate this intriguing phenomenon only in one individual. During one day 1.5±1.5 flowers/individual were pollinated (female reproductive success), constituting 3.7±4.9% of the open, intact flowers.

Fruit set

The reproductive success of *H. adriaticum* is generally low. According to our observations, nearly half of the flowering individuals produced only 0–5 capsules and a further 30% produced 5–15 capsules (Fig. 14). About half of the flowering plants had fruit-set lower than 30%, whereas fruit-set greater than 70% characterized only 1% of the observed reproductive plants.

Based on our data (collected between 1992 and 2016, 58 observations in 5 countries; Appendix 7), fruit-set of the populations fluctuates between 3.7% and 61.7% (Fig. 15). Previously published fruit-set data varied between 4.5% and 44% in Austria (Vöth, 1990), and between 5.4% and 23.3% in Hungary (Bódis and Molnár, 2009). The fruit-set of 61.7% observed at Nagytevel is the highest reproductive success ever recorded for this species (Biró et al., 2015b). More than half of our observations showed 10–30% fruit-set at the population level, reflecting the significant variation observed among individuals (Fig. 14).

Factors affecting fruit set

Biotic factors

Two factors play important roles in the fruit-set of *H. adriaticum*: there was positive correlation with the length of inflorescences, implying greater attractiveness and/or extensive geitonogamy as a result of increased pollinator residence periods (Kropf & Renner, 2008), whereas there was a negative correlation between the cover provided by woody species (trees and shrubs) and fruit set (Biró et al., 2015a; Fekete et al., 2017). Fruit set decreased significantly in later blooming flowers (Biró et al., 2015a).

Abiotic factors

Fekete et al. (2017) found that close proximity to roads negatively affects reproductive success of three lizard orchid species (including *H. adriaticum*).

Our observations suggest that the meteorological conditions at flowering time may affect the fruit set. On hot days the blooming flowers wither and dry after only 3–4 hours. On wet days we found mildew fungi inside the flower that coated the gynostemium and gradually destroyed the underlying tissues.

Physiological and biochemical information

Physiological data

Ziegenspeck (1936) reported about 7560 stomata per cm^2 in case of *H. hircinum*. According to our investigation there are no stomata on the upper (adaxial) leaf surface of *H. adriaticum*, though the mean density on the lower (abaxial) surface was 5330±1760 per cm^2 (mean±SD, n=70) of the basal leaves of five plants (Keszthely Hills) plus the stem leaves of a further two plants (Istria, Croatia and Keszthely Hills) (Appendix 8).
Differences were also noted among the individuals investigated (5 specimens, Keszthely Hills) and among regions of the leaf (base, middle region and apex of the leaf blade). Stomatal density of the rosette leaves was significantly lower (Tukey HSD) near the base (mean±SD=43.7±10.2 per mm^2; n=15) than in the middle (mean±SD=63.8±15.0 per mm^2; n=18) or near the apex (mean±SD=60.7±18.8 per mm^2; n=17).

Biochemical data

Strack et al. (1989) reported the distribution of anthocyanins in flower of *H. adriaticum* (% of total anthocyanin content) as chrysanthemin (2.2%), cyanin (5.5%), seranin (15.5%), ophrysanin (1.6%), orchicyanin II (7.2%), serapianin (20.4%) and orchicyanin I (3.7%); unfortunately, 43.9% of the recovered anthocyanins were categorised as unknown. They documented 0.6% anthocyanin of petal dry weight of extracted petal residues (insoluble material). The anthocyanin patterns of *H. adriaticum* resembled those of *H. robertianum* and *H. metlesicsianum* (Strack et al., 1989).

Genetic data

Chromosome number

A chromosome number of 2*n*=36 has been reported for *H. adriaticum* from Slovakia (as *H. hircinum*; Murín and Májovský *in* Löve 1976) and Italy (Capineri and Rossi, 1987; D'Emerico et al., 1993). The species shows a similar karyomorphology to *H. hircinum* (D'Emerico et al., 1990); meiotic studies revealed 18 bivalents at metaphase I (D'Emerico et al., 1993). The karyotype of material collected on Monte Pollino (Italy) was 20m + $8m^s$ + 8sm (D'Emerico et al., 1993). Aneuploidy with chromosome number 2*n* = 37 has also been reported (D'Emerico et al., 1993).

Conservation

Himantoglossum adriaticum is listed in Annex II and IV of Council Directive 92/43/EEC (the 'Habitats Directive'). The Habitats Directive, despite its title, specifies particular animal and plant species within its two appendices. Appendix II lists species requiring special territorial protection, which is implemented in the form of a so-called 'special area of conservation'. Appendix IV stipulates species requiring strict protection, for which reason they are to be included in the list of Endangered and Critically Endangered species and provided with the necessary conservation requirements (Trčak et al., 2006; Čičmir et al., 2015).
Himantoglossum adriaticum is protected by national law in most of the countries where it occurs, mainly as a result of listing in the Appendices of the Habitats Directive. Its conservation status varies among countries, either the protected or strictly protected category, or anywhere on the spectrum from province level to whole country (Table 9). Note than any orchid species is, by definition, included in the Appendix II of Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).
Himantoglossum adriaticum has 'least concern' conservation status on European Red List of Vascular Plants (Bilz et al., 2011) and also on the IUCN Red List (Dostalova et al., 2011). National Red Data Books include *H. adriaticum* in most of the countries where it occurs, treated by different conservation status ranging from 'least concern' to 'critically

endangered'. Its conservation status has changed to a less vulnerable category in both Croatia and Slovakia in recent years (Table 9).

Himantoglossum adriaticum is often present in habitats of community interest (Bódis et al., 2018), specifically in *Bromus erectus* dominated dry grasslands (Natura 2000 code 6210). Long-term, low-intensity management (mowing or grazing) is an important contributor to maintaining a favourable state of that habitat (Trčak et al., 2006; Slaviero 2016). Decline of dry grasslands due to their abandonment is the most serious current threat to *H. adriaticum.* Large populations can be found in secondary habitats such as mown roadside verges or abandoned vineyards, offering welcome refuges in today's rapidly changing environment (Fekete et al., 2017).

As is the case with *H. hircinum* (Carey et al., 2002; van der Meer et al., 2016), *H. adriaticum* has not (yet) suffered noticeably from climate change (Molnár V. et al., 2012). It appears that, at least across a significant part of its distribution area, long-term survival is likely despite the rapid changes in climate and land use. Molnár V. et al. (2012) showed that deceptive (or autogamous), long-lived and early flowering terrestrial orchids with dominantly Mediterranean distributions follow climate change more closely that the remainder. The recent expansion of the species in both Hungary (Óvári, 2017) and Slovenia (Trčak et al., 2006) is also documented. Additionally, the number of individuals is growing in the monitored Hungarian populations.

During our fieldwork we found large (more than 100 flowering individuals) populations in Hungary, Croatia, Italia, Slovenia and Bosnia–Herzegovina. There are many individuals on roadside verges, which clearly have become an important habitat for the species (details in Fekete et al., 2017).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at xxxxxxxxxx

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Fig. 1 Habitus of *Himantoglossum adriaticum*. (A) Seedling. (B) Mass of winter rosettes of individuals with different ages. (C) Winter rosette of a juvenile (left) and adult individual. (D) Flowering individual. (E) Inflorescence. (F) Infructescence. Photos A & F by J. Bódis, B–E by M. Csábi.

Fig. 2 Distribution of number of basal leaves of individuals in five Hungarian populations of *H. adriaticum* (n=11687, 2012–2014).

Fig. 3 Reproductive organs of *H. adriaticum*. (A) Gynostemium (frontal view). (B) Basal part of labellum. (C) Pollinaria. (D) Seeds. Photos A–D by M. Csábi.

Fig. 4 Molecular phylogenetic trees for *Himantoglossum sensu lato* constructed using parsimony from DNA sequence data for (A) the low-copy nuclear gene *LEAFY* and (B) four concatenated plastid regions. Statistical support values represent boostrap values and posterior probability respectively. Reproduced from Figs. 5 and 6 respectively of Sramkó et al. (2014).

Fig. 5 Bivariate scattergrams of the first versus second (A) and third versus fourth (B) principal coordinates for 20 plants of *H. adriaticum* (two populations, closed symbols) and 23 plants of *H. hircinum* (three populations, open symbols). UK = United Kingdom, Mo = Morocco, Hu = Hungary.

Fig. 6 Bivariate scattergram regressing the ‘shoulder’ width versus overall length of labella in the studied plants, illustrating the contrasting ratios in *H. adriaticum* (*ca* 0.10 : 1) versus *H. hircinum* (*ca* 0.17 : 1; weaker r^2 value). Inset: Average dimensions of labellar features in the two species, abstracted from Fig. 18 of Bateman et al. (2017); scale bar = 10 mm.

Fig. 7 Natural distribution range of *H. adriaticum* based on references in Appendix 3. Full circles – recent records (after 1990), open circles – older than 1990, question mark – uncertain data, see detailed in text.

Fig. 8 Altitudinal distribution of *H. adriaticum* populations based on 102 locations, including literature sources, field observations, herbarium records and photographic documents (Appendix 3).

Fig. 9 Ratio of reproductive (R) versus vegetative (V) individuals in relation to the leaf number in a *H. adriaticum* population (1993–2007, 1108 observations, Keszthely Hills, Hungary).

Fig. 10 Julian days of flowering. Based on 141 precisely dated herbarium records, photographic documents and field observations (Appendix 3).

Fig. 11 Number of basal leaves in the Keszthely population (Hungary, n=1108, 1993–2005).

Fig. 12 Transition probalities (in %, the sum of the transition values 100%) between life stages from year t to year t+1 in a *H. adriaticum* population in the Keszthely Hills (Hungary). Pooled data from 7 years of observations (2000–2007) and 577 transitions.

Fig. 13 In situ germination rates in control packets (C), and near to the mother plants (M) after eleven months in Hungary.

Fig. 14 Frequency distribution of individual number of flowers and fruits in 3038 individuals of *H. adriaticum*.

Fig. 15 Frequency distribution of population fruit set (n=58) of *H. adriaticum.*

Table 1

Characters contributing to the first four principal coordinates for individual plants of the *adriaticum–hircinum* clade only, based on 42 morphometric variables measured for five populations (see Fig. 13). Characters in roman lettering increase in value in parallel to the value of the coordinate, whereas characters in italics decrease in value as the value of the coordinate increases.

Coordinate	PC1	PC2	PC3	PC4
Percentage of variance accounted for	31.4	13.3	11.1	8.4
Demographic significance	Separates *adriaticum* from *hircinum*	Distinguishes the Newmarket *hircinum* population	Separates the two *adriaticum* populations	Distinguishes the Ifrane *hircinum* population
Contributory characters, listed in order of decreasing contribution	*Lip marking distribution* Sepal exterior colour y Lip shoulder width Lip torso width Floral bract length Lip limb colour x Sepal exterior colour x Column width	*Lip maximum length* *Ovary length* *Basal bract length* *Inflorescence length* *Lip torso length* *Number of flowers* *Stem diameter* *Stem height*	*Spur curvature* *Sepal exterior colour Y* *Lateral petal width* *Lip leg length*	Sepal interior dots Stem pigmentation Lip arm–torso position

Table 2 Properties (Mean±SD and range) of the parameters of soils that support *H. adriaticum* populations.

	n	**pH_{KCl}**	**Total salt (m/m)%**	**$CaCO_3$ (%)**	**Organic matter (%)**	**Nitrogen (N) (mg/kg)**	**P_2O_5 (mg/kg)**	**K_2O (mg/kg)**
Croatia	9	7.03±0.26 6.4–7.3	0.02±0.01 0.01–0.03	24.8±18.8 0.05–64.1	7.8±4.1 2.8–16.3	13.0±10.0 3.5–32.2	50±37 27–146	308±108 164–467
Hungary	16	7.01±0.23 6.7–7.4	0.01±0.01 0.01–0.05	3.1±6.2 0.05–22.8	8.0±7.6 1.5–26.92	18.8±18.0 2.1–54.1	192±167 31–513	258±154 82–557
Italy	15	7.15±0.18 6.6–7.5	0.03±0.02 0.01–0.08	34.8±18.4 0.05–57.7	7.8±5.0 4.77–19.9	23.1±23.6 2.5–79,7	92±59 37–269	326±128 164–556
Austria, Slovenia, Slovakia	6	7.08±0.4 6.3–7.4	0.04±0.04 0.01–0.1	7.1±15.7 0.05–14.5	5.3±2.5 3.5–9.1	61.8±61.3 2.4–148.0	75±19 46–93	152±74 110–302
All occurrences	46	7.07±0.25 6.3–7.5	0.02±0.02 0.01–0.1	18.2±19.6 0.05–64.1	7.5±5.6 1.5–26.9	25.2±31.2 2.1–148.0	116±119 27–513	276±138 82–557

Table 3 Leaf traits were counted on the base of 5 basal leaves from the Hungarian Keszthely Hills population. Leaf area was determined using Image J, version 1.4.3.67.

		Mean	SD
Specific leaf area (SLA)	m^2/kg	14.4	1.3
Leaf area (LA)	mm^2	2386	1552
Leaf dry-matter content (LDMC)	mg/g	168.8	12.4

Table 4 Costs of reproduction related to plant size (based on the Keszthely Hills population)

No. of leaves year *t*	Status in year *t*	N	No. of leaves year *t+1*	No. of leaves *(t+1)-t*	Cost of reproduction (no. of leaves)
3	vegetative	229	3.48±1.08	+0.48	0.96
	reproductive	23	2.52±0.95	-0.48	
4	vegetative	131	4.46±1.33	+0.46	1.38
	reproductive	50	3.08±1.08	-0.92	
5	vegetative	46	5.52±1.64	+0.52	1.78
	reproductive	82	3.71±1.26	-1.23	
6≤	vegetative	23	5.13±1.58	-1.13	0.43
	reproductive	89	4.94±1.53	-1.70	

Table 5 The number of total and flowering individuals in 5 Hungarian populations, between 2012–2014.

Locality	Total number of individuals			Number of flowering individuals			Proportion of flowering individuals (%)		
	2012	**2013**	**2014**	**2012**	**2013**	**2014**	**2012**	**2013**	**2014**
Harka	48	57	63	0	1	4	0	1.75	6.35
Kőszeg	618	873	939	2	50	178	0.32	5.73	18.96
Nagytevel	386	607	516	3	41	85	0.78	6.75	16.47
Sümeg	1058	2192	2984	10	63	214	0.95	2.87	7.17
Keszthely	356	482	517	5	34	56	1.40	7.05	10.06
TOTAL	**2466**	**4211**	**5019**	**20**	**189**	**537**	**0.81**	**4.49**	**10.69**

Table 6 Number of seeds per capsule in Hungarian populations of *Himantoglossum adriaticum.*

No. of capsules	No. of seeds			Reference
	Mean	Min.	Max.	
14	4222 ± 1499	1795	6978	Bódis, 2010
52	7996 ± 5638	1119	23740	Sándor, 2013
22	10686 ± 1550	NA	NA	Sonkoly et al., 2016

Table 7 Relationship between flowering characteristics and meteorological factors. *** p<0,001; ** p<0,01; * p<0,05; ns: not significant

reproductive traits	**current vegetation period**		**previous vegetation period**	
	temperature	*precipitation*	*temperature*	*precipitation*
number of flowering individuals	(-) spring ***	ns	(-) number of frost days ***	(+) annual ***
mean height of shoots	ns	(+) June*	(-) number of frost days **	ns
mean number of flowers in inflorescences	(-) spring * (-) June**	(-) spring *	(-) number of frost days **	(+) annual **
fruit-set	ns	ns	ns	ns

Table 8 Insect pollinators and potential pollinators (asterisced) of flowers of *Himantoglossum adriaticum*. (m): male, (f): female insect

Species	Location	Reference
Hymenoptera		
Osmia caerulescens (L., 1758) (m)	Hungary: Keszthely Hills	Bódis (2010)
Osmia bicornis (L., 1758)	Italy: Fermignano	unpublished record of authors (Appendix 6)
Andrena sp.	Croatia: Istria Peninsula	Teschner (1980)
Andrena haemorrhoa (Fabricius, 1781)		Claessens and Kleynen (2011)
Andrena carbonaria sensu lato		Claessens and Kleynen (2011)
Andrena nigroaenea (Kirby, 1802)		Claessens and Kleynen (2011)
Andrena potentillae (Panzer, 1809)		Claessens and Kleynen (2011)
Anthidium manicatum (L., 1758)	Italy: Euganean Hills	Fantinato et al. (2017)
Apis mellifera (L., 1758)	Austria	Vöth (1990) Claessens and Kleynen (2011)
Apis mellifera (L., 1758)	Hungary: Bakony Hills	Biró et al. (2015)
Apis mellifera (L., 1758)	Italy: Euganean Hills	Fantinato et al. (2017)
Colletes daviesanus (Smith, 1846)	Italy: Euganean Hills	Fantinato et al. (2017)
Colletes similis (Schenck, 1853)	Austria	Vöth (1990)
Colletes similis (Schenck, 1853)	Hungary: Sümeg	Sulyok et al. (1998)
Colletes similis (Schenck, 1853)	Hungary: Keszthely Hills	Bódis 2010
Colletes sp.	Croatia: Istria Peninsula	Teschner (1980)
Colletes sp.	Hungary: Kőszeg	unpublished record of authors (Appendix 7)
Bombus sp.	Germany - translocated inflorescences	Teschner (1980)
Bombus sp.	Hungary: Sümeg	Sulyok et al. (1998)
Lasioglossum (*Evylaeus*) *morio* (Fabricius, 1793) (f)	Hungary: Keszthely Hills	Bódis (2010)
Lasioglossum (*Evylaeus*) *lucidulum* (Schenck, 1861) (f)	Hungary: Keszthely Hills	Bódis (2010)
Megachile melanopyga (Costa, 1863) (f)	Hungary: Keszthely Hills	Bódis (2010)
Eristalis arbustorum (L., 1758)	Italy: Euganean Hills	Fantinato et al. (2017)
Coleoptera		
*Cteniopus sulphureus** (L., 1758)	Italy: Monte Pollino	Dura (2015)
Dinoptera (*Acmaeops*) *collaris* (L., 1758)	Hungary: Sümeg	Nagy (2013) (Appendix 7)
Tropinota squalida (Scopoli, 1783)	Italy: Euganean Hills	Fantinato et al. (2017)

Table 9 Current conservation status of *Himantoglossum adriaticum* across Europe.

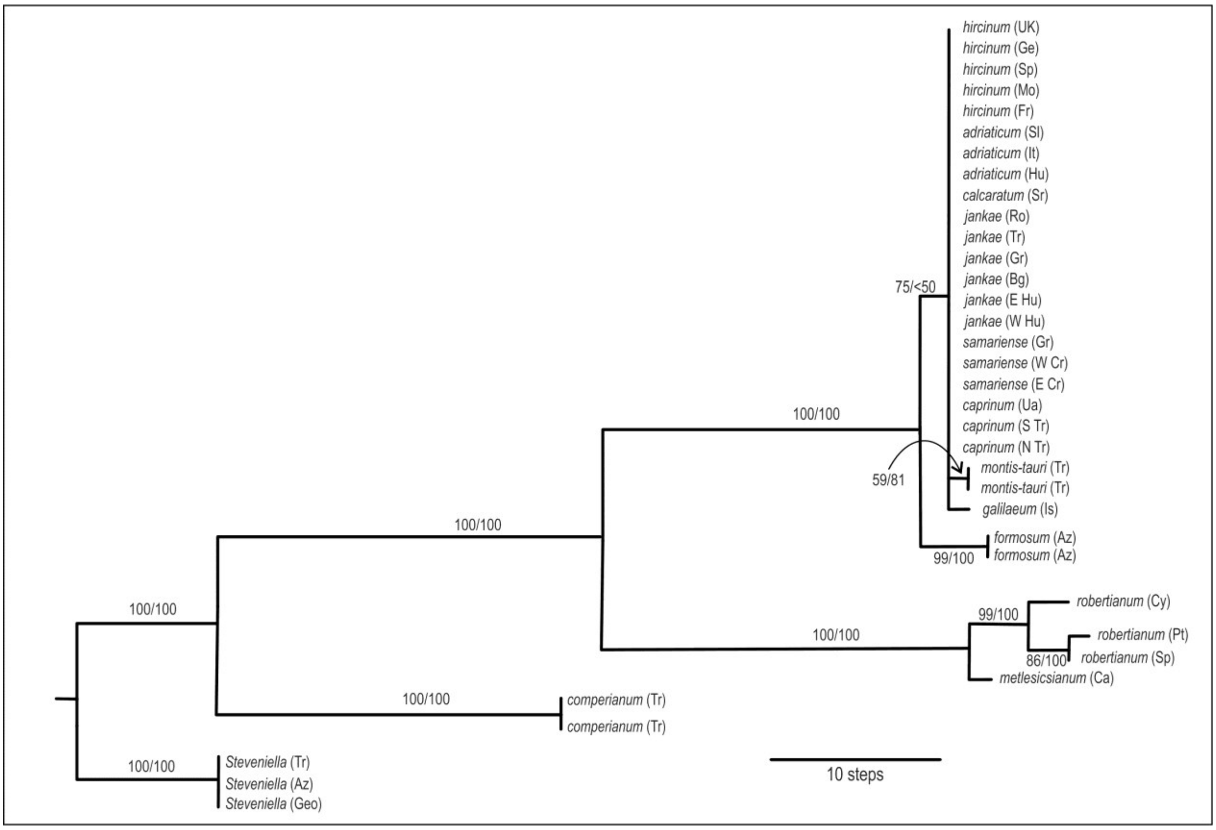
Country	**Legal protection**	**Conservational status**	**Reference**
Italy	Protected	Least Concern (LC)	Conti et al., 2005 Rossi et al., 2013
Croatia	Strictly protected	Least Concern (LC) (earlier Nearly Threatened (NT)*)	Borovečki-Voska et al., 2014 Anonymous, 2016 (*Vuković and Nikolić, 2006)
Slovenia	Protected	Vulnerable (VU)	Anonymous, 2002, 2004 Trčak et al., 2006
Austria	Protected	Endangered (EN) Stark gefährdet (Kat. 2)	Niklfeld et al., 1999
Czech Republic	Protected	Critically Threatened (CR)	Grulich, 2012

Slovakia	Protected	Endangered (EN) (earlier Critically threatened (CR)*)	Anonymous, 2003 Eliáš et al., 2015 (*Feráková, Maglocký and Marhold, 2001)
Hungary	Strictly protected	Endangered (EN)	Király et al., 2007
Bosnia and Herzegovina	New species	Not yet assessed	Milanović et al., 2015
Albania	New species	Not yet assessed	Barina and Pifkó, 2009
Romania	New species – no recent data	Treated as *H. hircinum* Endangered (EN) (*Periclitate. Specii în pericol de extincţie*); treated as *H. hircinum* ssp. *caprinum* – Gusterita Vulnerable (VU)	Boşcaiu et al., 1994 Oprea, A., 2005

Appendix 1

Aberrations. A. Individual with hypochromatic flowers. B–C. Twin flowers and their fruits. D. Variegated leaf rosette. All photographs: by J. Bódis.

Appendix 2



Phylogenetic relationships within the genus Himantoglossum as depicted by a phylogenetic tree based on the nuclear ribosomal internal transcribed spacer (nrITS) region displayed as a phylogram adapted from the study of Bateman et al. (2017). The topology of the tree is drawn from a maximum parsimony analysis of the nrITS region. The same topology of the tree was found by Bayesian phylogenetic reconstruction, and therefore only support values (Bayesian posterior probability) from that analyses are displayed next to the corresponding branches displayed after the bootstrap support values coming from the parsimony analysis (lack of support is indicated by '<50').

Appendix 3

List of sources indicating the geographical distribution. Some sources were used for altitudinal distribution (marked with *) as well as date of flowering (marked with **).

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Unpublished observation

Cemetery, Óbudavár, Hungary: A. Mészáros & P. Simon 2018

Appendix 4

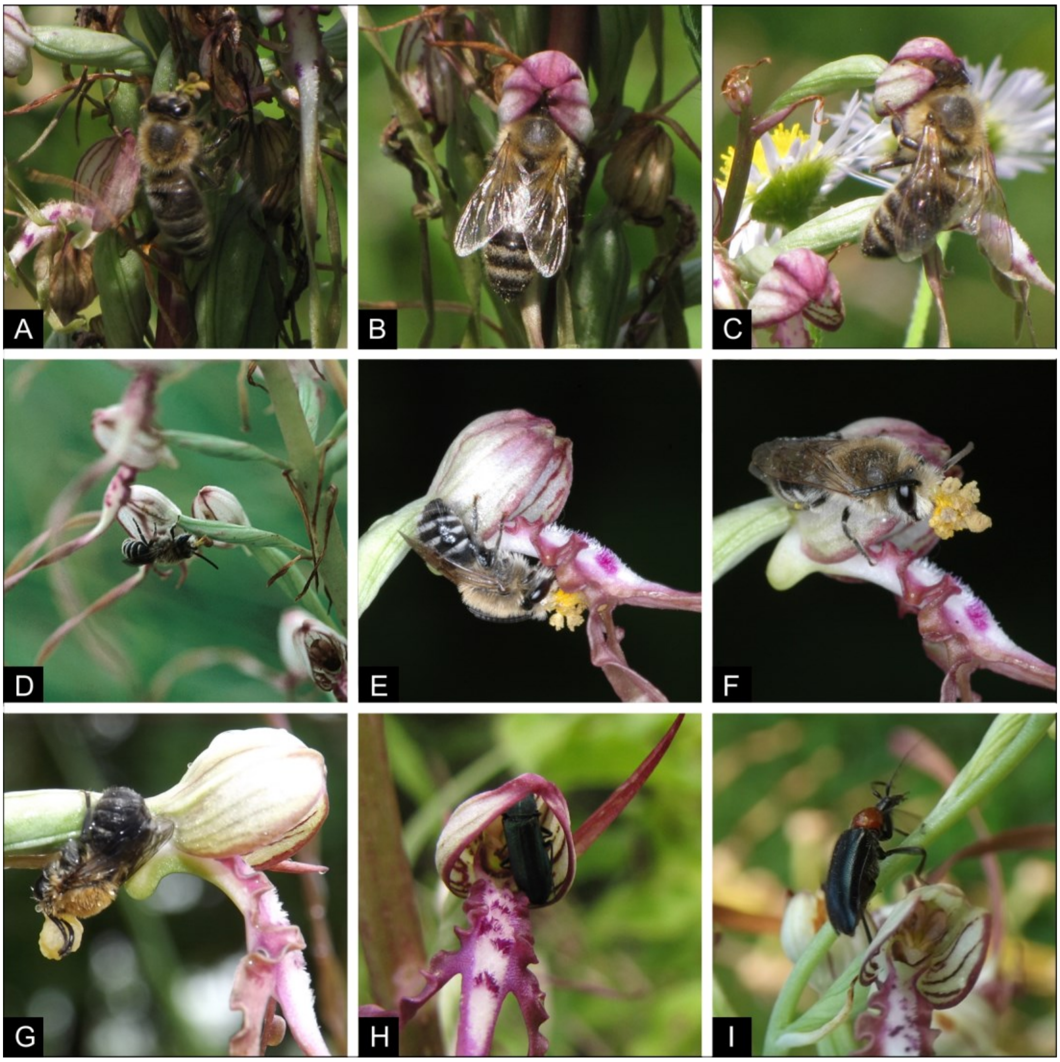
List of Natura 2000 vegetation types where *H. adriaticum* occurred. These habitats are listed in Annex II of Council Directive 92/43/EEC (the 'Habitats Directive') of the European Commission. Detailed habitat list of the species (with references) can be found in Bódis et al. 2018.

40A0 Subcontinental peri-Pannonic scrub
6110 Rupicolous calcareous or basophilic grasslands of the Alysso-Sedion
6190 Rupicolous pannonic grasslands (Stipo-Festucetalia pallentis) (H)
6210 Semi-natural dry grasslands and scrubland facies on calcareous substrates - important orchid sites (Festuco-Brometalia)
6220 Pseudo-steppe with grasses and annuals of the Thero-Brachypodietea
6240 Sub-pannonic steppic grasslands (H)
62A0 Eastern sub-mediteranean dry grasslands (Scorzoneratalia villosae)
6510 Lowland hay meadows (Alopecurus pratensis, Sanguisorba officinalis)
8140 Eastern Mediterranean screes
91H0 Pannonian woods with Quercus pubescens (H)
91L0 Illyrian oak – hornbeam forests (Erythronio-Carpinion)
91M0 Pannonian-Balkanic turkey oak- sessile oak forests (H)
9340 Quercus ilex and Quercus rotundifolia forests

Appendix 5

Damages and conservation. A–B. Effect on frost on winter leaf rosettes (Hungary: Keszthely Hills). C. Adult individual grubbed by wild boar (Hungary: Bakony Hills). D. Chewed winter leaf rosette (Hungary: Keszthely Hills). E. *Epilecta linogrisea* (*Noctuidae*) caterpillar chewing a leaf (Hungary: Keszthely Hills). F. Flowering individuals which were saved from mowing in a private garden (Hungary: Kőszeg). Photographs: A–F by J. Bódis.

Appendix 6



Pollinator and visitor insects of *H. adriaticum*. A–C. *Apis mellifera*; D–F. *Colletes similis*. G . *Osmia rufa*. H. unidentified Buprestidae (Coleoptera). I. *Dinoptera* (*Acmaeops*) *collaris*. Photographs: A–C, G. by J. Bódis, D by A. Molnár V., E, F by T. Markovics, G–I by T. Nagy.

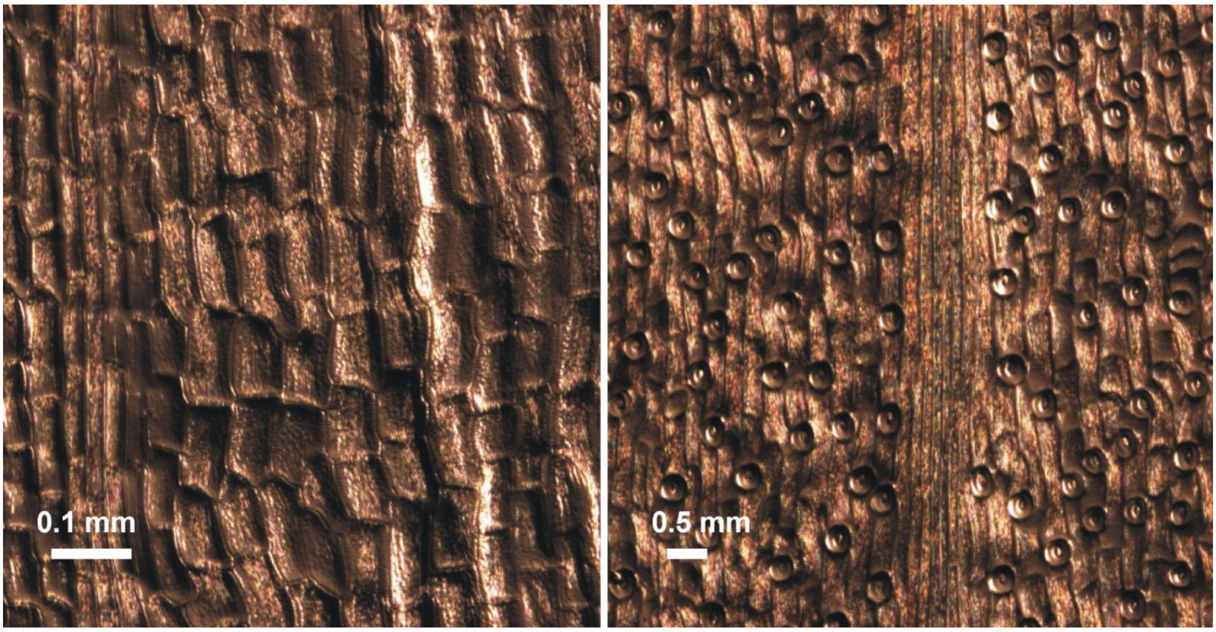
Appendix 7

Fruit-set of the populations. Data were collected by the authors

Locality	Country	Year	n	No. of flowers	No. of fruits	Fructification rate (%)
Suvaja	BIH	2017	54	2236	598	26.7
Nagytevel	HU	2017	42	1576	692	43.9
Sümeg	HU	2017	88	2799	578	20.7
Kőszeg	HU	2017	147	5604	3129	55.8
Keszthely	HU	2017	76	2525	404	16
Nagytevel	HU	2016	68	2345	1005	42.9
Sümeg	HU	2016	135	4063	873	21.5
Kőszeg	HU	2016	142	5545	1544	27.8
Keszthely	HU	2016	90	3206	598	18.7
Vienna, Lobau	A	2016	64	1407	292	20.8
Stupava	SK	2016	62	1330	643	48.3
Nagytevel	HU	2015	77	3074	1649	53.6
Sümeg	HU	2015	170	5400	1045	19.4
Kőszeg	HU	2015	128	4873	2141	43.9
Keszthely	HU	2015	76	2835	817	28.8
Apecchio	I	2015	120	3874	673	17.4
Citta di Castello	I	2015	50	1162	329	28.3
Urbania-Acqualagna	I	2015	65	2559	508	19.9
Nagytevel	HU	2014	81	2981	1712	57.4
Sümeg	HU	2014	179	5278	1262	23.9
Kőszeg	HU	2014	171	5883	2211	37.6
Keszthely	HU	2014	53	1862	408	21.9
Učka	CRO	2014	84	2557	285	11.1
Letaj I,	CRO	2014	64	1809	253	14
Letaj II	CRO	2014	20	952	178	18.7
Paz	CRO	2014	19	551	46	8.3
Nagytevel	HU	2013	41	1477	911	61.7
Sümeg	HU	2013	54	1721	403	23.4
Kőszeg	HU	2013	50	1764	721	40.9
Keszthely	HU	2013	34	1197	110	9.2
Učka	CRO	2013	100	2965	411	13.9
Letaj I,	CRO	2013	14	410	64	15.6
Letaj II	CRO	2013	12	422	77	18.2
Paz	CRO	2013	7	210	44	21
Nagytevel	HU	2011	41	1101	166	15.1
Sümeg	HU	2011	49	1337	281	21
Kőszeg	HU	2011	18	406	92	22.7
Keszthely	HU	2011	29	738	61	8.3
Nagytevel	HU	2010	11	227	118	52
Sümeg	HU	2010	25	640	179	28
Kőszeg	HU	2010	33	1300	549	42.2
Keszthely	HU	2010	12	267	10	3.7
Sümeg	HU	2009	29	849	358	42.2
Keszthely	HU	2009	23	579	61	10.5
Sümeg	HU	2008	32	1009	242	24
Keszthely	HU	2008	33	1040	128	12.3
Keszthely	HU	2007	21	530	187	35.3
Keszthely	HU	2006	21	601	207	34.4

Keszthely	HU	2005	55	1736	297	17.1
Keszthely	HU	2004	20	524	286	54.6
Sümeg	HU	2003	19	486	256	52.7
Keszthely	HU	2003	19	642	161	25.1
Sümeg	HU	2002	76	2326	633	27.2
Keszthely	HU	2002	32	912	156	17.1
Keszthely	HU	2001	10	315	21	6.7
Keszthely	HU	2000	12	333	19	5.7
Keszthely	HU	1999	31	971	96	9.9
Keszthely	HU	1998	30	975	197	20.2
Keszthely	HU	1997	23	686	58	8.5
Keszthely	HU	1996	67	2130	342	16.1
Keszthely	HU	1995	73	2758	219	7.9
Keszthely	HU	1994	19	671	36	5.4
Keszthely	HU	1993	17	544	51	9.4
Keszthely	HU	1992	25	909	171	18.8

Appendix 8



There are no stomata on the upper (adaxial) leaf surface of *H. adriaticum* (left), only on the lower (abaxial) surface (right). Photographs: J. Bódis