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The Carinthian grass hybrid *Helictotrichon* ×*krischae* (Poaceae tribe Aveneae) – epitome of a hybrid zone

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Abstract: Heuchert, B. & Röser, M. 2004: The Carinthian grass hybrid *Helictotrichon* ×*krischae* (Poaceae tribe Aveneae) – epitome of a hybrid zone. Schlechtendalia **12**: 69–83.

Results of micromorphological, anatomical and morphometrical analyses are reported for *Helictotrichon parlatorei* (widespread in the Alps), *H. setaceum* subsp. *petzense* (endemic to the Karavanke Range) and their hybrid *H.* ×*krischae* which is only known from the Petzen Mountains in the Karavanke Range. The hybrid origin of *H.* ×*krischae* is confirmed by intermediate characters of the laminas of the leaves. Several specimens macroscopically not identified as hybrids are shown to display a mosaic of parental and intermediate characters in leaf architecture and are actually also hybrids. This is discussed with reference to current ideas about natural hybridisation and its evolutionary significance.

Zusammenfassung: Heuchert, B. & Röser, M. 2004: The Carinthian grass hybrid *Helictotrichon* ×*krischae* (Poaceae tribe Aveneae) – epitome of a hybrid zone. Schlechtendalia **12**: 69–83.

Die Ergebnisse mikromorphologischer, anatomischer und morphometrischer Untersuchungen werden für die Gräser-Taxa *Helictotrichon parlatorei* (weit verbreitet in den Alpen), *H. setaceum* subsp. *petzense* (endemisch in den Karawanken) und deren Hybriden *H.* ×*krischae* (bekannt nur von der Petzen in den Karawanken) vorgestellt. Die hybridogene Entstehung von *H.* ×*krischae* kann anhand der gefundenen intermediären Merkmale im Aufbau der Blattspreiten bestätigt werden. Mehrere Individuen, die sich makroskopisch nicht als Hybriden identifizieren lassen, zeigen in den untersuchten mikromorphologischen Merkmalen eine Kombination von elterlichen und intermediären Merkmalen, so daß es sich bei ihnen ebenfalls um hybridogene Pflanzen handelt. Dieses Ergebnis wird im Zusammenhang mit gegenwärtigen Vorstellungen über Hybridisierungen zwischen Pflanzenarten und die evolutionäre Bedeutung von Hybridzonen diskutiert. Die mikromorphologischen und anatomischen Resultate werden detailliert dargestellt.

Introduction

The Alps harbour a rich assemblage of tall perennial oatgrass taxa currently ascribed to the genus *Helictotrichon* Besser [(including *Avenula* (Dumort.) Dumort. or *Avenochloa* Holub)], some of which belong to *Helictotrichon* subg. *Helictotrichon*. These are *H. parlatorei* (Woods) Pilg., *H. sempervirens* (Vill.) Pilg., *H. setaceum* (Vill.) Henrard with subsp. *setaceum* and subsp. *petzense* (H. Melzer) Röser, and *H. sedenense* (DC.) Holub. The latter occurs in the Western Alps, but also in the higher mountain ranges of western Europe and the southwestern Mediterranean, i.e. the Massif Central, Pyrenees, the Cantabrian Mountains, Sierra Nevada, and the Moyen and Grand Atlas in Morocco.

Taxonomically, *H. parlatorei*, *H. sempervirens*, and *H. setaceum* represent a clearly defined monophyletic group and share a common derived character which is otherwise

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absent in taxa of subg. *Helictotrichon*, i.e., disarticulation of the rachilla of the spikelet only above the glumes and not below each lemma. Diaspores are therefore not single florets, but compound structures consisting of all florets per spikelet.

The ranges of this species complex are confined to the Alps, only *H. setaceum* subsp. *setaceum* extends to the western Préalpes of France and the Mt. Ventoux. The main range of *H. setaceum* subsp. *setaceum* comprises the outmost southwestern Alps and is largely congruent with that of *H. sempervirens*. Both are comparatively rare and only locally frequent. *Helictotrichon parlatorei* is the most widespread taxon of the species complex and occurs in most parts of the arc of the Alps except the Swiss Alps and regions of the Central Alps with prevailing base-poor bedrock. It seems to be especially abundant along the southern Alps and more scatteredly distributed in the northern Alps. The sister of *H. setaceum* subsp. *setaceum*, i.e. subsp. *petzense*, was discovered in the sixties of the last century by the Austrian botanist H. Melzer on the Petzen Mountain in the Karavanke Range, the border between Carinthia and Slovenia (southeastern Alps) and this was one of the most surprising recent discoveries in the comparatively well-studied vascular plant flora of the Alps. The taxon was originally described as a separate species, *H. petzense* H. Melzer (Melzer 1967), and became transferred later to *H. setaceum* in subspecific rank (Röser 1996). *Helictotrichon setaceum* thus has two partial ranges with subsp. *setaceum* in the outmost southwestern and subsp. *petzense* in the outmost southeastern Alps. The partial ranges are separated by a distance of approximately 600 km. This discovery stimulated floristic research and further stands of subsp. *petzense* came to knowledge from the Karavanke Range. Further stands were found c. 25 km SW of the Petzen Mountain in Carinthia, i.e., on the Kärntner Storschitz Mountain and the Felsentore of the Uschowa Mountain (Erlberg, in Sloven. Olšewa) and in Slovenia c. 10 km S the Petzen Mountain on the Raduha Mountain (cf. Hartl et al. 1992, Jogan 2001). The entire range of subsp. *petzense* is still minute. Distribution patterns of *H. setaceum* with both of its subspecies and of *H. sempervirens* seem to imply that they were shaped during glacial periods, because the southwestern and southeastern Alpes served as important refuge areas. This may apply as well to *H. parlatorei*, although its entire distribution has not been mapped in detail. Maps are available for the few stands of this species in the German and Slovenian Alps (Schönfelder & Bresinski 2001, Jogan 2001), but only for parts of the western Alps (Röser 1989, Chas 1994) and of Austria (Hartl et al. 1992, Maier et al. 2001).
The species has a discontinuous distribution in the northern flank of the arc of the Alps since it is absent in the Swiss Alps (Hess et al. 1967, Welten & Sutter 1982). It occurs east of the Lechtaler Alps eastwards to the Wiener Schneeberg (Lower Austria). The distribution appears to be much more closed in the southern calcareous flank of the Alps (Pignatti 1982). In addition to the glacial refuge areas already encountered in *H. sempervirens* and *H. setaceum* the large refuge areas in the southern and the minor ones in the northern margin of the Alps, respectively, have obviously played some role for *H. parlatorei*.

In describing *H. petzense* it was already noted by Melzer (1967) that intermediates occurred between such plants and *H. parlatorei* which is also present on the Petzen

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Tab. 1: Macroscopical diagnostic characters of *Helictotrichon parlatorei*, *H. setaceum* subsp. *petzense* and *H. ×krischae* according to MELZER (1967), CONERT (1979–1997). Question marks denote character states not indicated.

	H. parlatorei	*H. setaceum* subsp. *petzense*	*H. ×krischae*
Length of ligule in leaves of sterile shoots	3–6 mm, papery, acute	0.2–0.5 mm, truncate and ciliolate	1.0–1.5 mm
Lamina of leaves of sterile shoots	flat to slightly involved in life, 2–3 mm wide	permanently infolded, 0.7–0.8 mm in diameter	not infolded in life, after desiccation 1 mm in diameter
Culm beyond the inflorescence branches	glabrous	pubescent	?
Glumes	?	longer than entire spikelet (awns included)	?
Lower glume	?	?	shorter than entire spikelet (awns included)

Mountain (Tab. 1). This hybrid with characters intermediate between the parental taxa was named *H. ×krischae*. During a field trip of the second author in 1998 the impression was obtained, that in addition to strictly intermediate *H. ×krischae* also other individuals with closer resemblance to either *H. setaceum* subsp. *petzense* or *H. parlatorei* occurred on the Petzen Mountain. On the occasion of a students excursion through the eastern Alps in 2001, populations of the concerned parental taxa and their intermediates were studied in the field more detailed and were sampled for later laboratory morphological/anatomical and DNA analyses in order to sort out whether there is actually a continuous transition between *H. setaceum* subsp. *petzense* and *H. parlatorei* (hybrid zone) or not. Results of morphological and anatomical studies are reported here.

Material and methods

Samples of *H. parlatorei*, *H. setaceum* subsp. *petzense*, *H. ×krischae*, and further intermediates were collected in the Trebnik-Kar which is one of the northwards stretching glacial cirques of the Petzen Mountain at an altitude of 1700–1800 m (Tab. 2). *Helictotrichon parlatorei* forms extensive stands there on limestone screes while the almost vertical and bare rocks are inhabited by *H. setaceum* subsp. *petzense*. Intermediates are found in the contact zone between them, namely at the base of rocks and the upper edges of screes. Material of *H. setaceum* subsp. *petzense* was collected for comparison also on the Kärntner Storschitz Mountain, some 25 km SW of the Petzen Mountain, where *H. parlatorei* is absent. Further material of *H. parlatorei* was collected on the Wiener Schneeberg (Lower Austria) where *H. setaceum* subsp. *petzense*

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Tab. 2: Collection details of the accessions studied for leaf anatomy. Vouchers are kept at the herbarium HAL.

	Number	Locality			Phenology	N/E	Exposition	Altitude [m]	Collector
H. parlatorei	0401, 0403, 0408, 1101, 1102, 1103, 1104,1201, 1204	Austria, Carinthia, Karavanke Range	Petzen Mountain, near Bleiburg, Trebnik-Kar	scree, limestone	1101 sterile, other fertile	46°30'39"/ 14°46'9"	SE	1696	B. Heuchert
'	10647 a,b,c, T3, T4	'	'	bolder-covered slope/ limestone	fertile			ca.1800	M. Röser
'	1501	Austria, Lower Austria	Wiener Schneeberg	scree, limestone	'	47°45'26"/ 15°50'10"	S	1756	B. Heuchert
'	1601	'	'	'	'	47°45'26"/ 15°50'17"	'	1715	'
'	1701, 1702	'	'	'	'	47°45'23"/ 15°50'17"	SE	1705	'
'	1802, 1807, 1901	'	'	'	'	47°45'14"/ 15°50'15"	'	1589	'
H. setaceum* subsp. *petzense	0206, 0601, 0803,	Austria, Carinthia, Karavanke Range	Petzen Mountain, near Bleiburg, Trebnik-Kar	limestone rock	'	46°30'38"/ 14°46'13"	S	1788	'
'	0902	'	'	'	'	46°30'36"/ 14°46'20"	E	1776	'
'	1302, 1303	'	Kärntner Storschitz Mountain	'	'	46°25'43"/ 14°31'25"	SE	1676	'
'	1402, 1403	'	'	'	'	46°25'46"/ 14°31'27"	'	1719	'
'	10646T1, T4	'	Petzen Mountain, near Bleiburg, Trebnik-Kar	'	'			ca.1800	M. Röser
H. ×krischae	0501	'	'	base of limestone rock	0501, 0503 sterile, 0502 fertile	46°30'38"/ 14°46'13"	SE	1785	B. Heuchert
'	10648-1B, T1b, T2	'	'	'	1B sterile, other fertile			ca.1800	M. Röser
H.* cf. *×krischae	10649T1,a,b	'	'	limestone rock	sterile			ca.1800	'

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is absent. A specimen of *H. ×krischae* from the Petzen Mountain which had been cultivated for five years under greenhouse conditions in the Botanical Garden of the Martin Luther University was also included for comparison (accession no. 10648-1B). Plants were identified according to the macroscopical diagnostic features listed in Tab. 1. Intermediate plants between *H. parlatorei* and *H. setaceum* subsp. *petzense* that could not be unambiguously ascribed to *H. ×krischae* were termed *H.* cf. *×krischae*. For a first quantitative analysis of transitional characters between these taxa we selected characters of the leaves and measured them individually per plant irrespectice of the presumed taxonomic identity. Anatomical investigation of leaf blades in transverse section was carried out on herbarium material except the greenhouse specimen where fresh material was used. The dried material was softened in boiling water for 3–5 min. Transverse sections were made in the lower half of fully developed leaves of sterile, non-flowering shoots either by hand using a razor blade or with a cryotome LEICA CM 1900 (thickness of sections 30–40 µm). Sections were transferred to microscopical slides and were embedded either without staining and dehydration directly in „Kaisers Glyceringelatine" (MERCK) or were stained with safranine and astra blue to identify the composition of cell walls. Cell walls with only cellulose are stained blue, lignified cell walls are stained red (GERLACH 1984). Subsequent to dehydration in ethanol such preparations were made permanent with „Merckoglas" (MERCK) as embedding medium. Microscope ZEISS Axioskop 2 served for microscopical examination, ZEISS AxioCam HR for digital photographs, and software ZEISS AxioVision for measuring quantitative characters and image processing. Quantitative data were transferred to software Microsoft Excel and analysed further with software package SPSS version 11.5.1 (SPSS Inc. 2002). The width of the lamina is indicated for one half. In case of asymmetrical leaves the wider half was measured. The number of vascular bundles refers also to one half of the lamina and includes the median vascular bundle. The length of trichomes (specialised epidermal cells) was determined in randomly selected 8 to 28 trichomes per plant specimens. Prickles and macro-hairs were included in the measurement, but not papillae. Technical terms in grass anatomy follow ELLIS (1976, 1979) and PRAT (1932, 1960).

Results

Leaf blades in transverse section of *Helictotrichon parlatorei*, *H. setaceum* subsp. *petzense*, *H. ×krischae*, and further intermediates have a basically similar structure. Leaf architecture is typically pooid (festucoid), because vascular bundles have two sheaths, an outer parenchyma and an inner mestome sheath (endodermis) with typically asymmetrically thickened cell walls (Figs 1 A, C, E; 2 B, F). Chlorenchyma cells of the mesophyll have almost equal size and shape, are not arranged in definite patterns, and two-celled microhairs are absent (Fig. 1 A).

In addition to this general pattern of leaf blade architecture in Poaceae subf. Pooideae, the taxa in question share some peculiarities, i.e., presence of prominent ribs and deep furrows at the adaxial surface of the leaf blades and a continuous layer of subepidermal

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sclerenchymatous tissue at the abaxial side which is a comparatively rare character in Pooideae: Aveneae. This structure of leaves induced VIERHAPPER (1906, 1914) to term it *Stipavena* or *Stipavenastrum* leaf type, respectively.

In safranine/astra blue-stained sections, cell walls composed of cellulose are stained blue, notably the phloem elements and the bulliform cells at the bottom of the adaxial longitudional furrows of the lamina. Cell walls of the mestome sheath, bundle fibres and metaxylem vessels are stained red, i.e. they are lignified. Cells of the girders which connect the vascular bundles with the adaxial and the abaxial surface of the lamina are also lignified and thus reveal sclerenchymatous, but not collenchymatous as previously assumed (CONERT 1979–1997, RÖSER 1989, LANGE 1995).

Outline and shape of the lamina in transverse section

In *H. parlatorei*, *H. setaceum* subsp. *petzense*, and intermediates *H.* ×*krischae* and *H.* cf. ×*krischae*, the two halves of the lamina are curved upwards on either side of the median bundle (canaliculate).
The degree of curvature is variable in *H. parlatorei* and ranges from a broad and wide to a narrow U (Fig. 1 B), equivalent to character states 118, 119, 153 described by ELLIS (1976), respectively. This corresponds to the shape of the leaf blades in living plants of *H. parlatorei* since they are usually flat and only slightly curved inwards. Under water stress they become inrolled more strongly (MELZER 1967 and pers. observ.). The two halves of the lamina in *H. parlatorei* are sometimes asymmetrical on either side of the median vascular bundle.
In *H. setaceum* subsp. *petzense*, the two halves of the leaves are curved similarly, but in form of a reduced U (cf. ELLIS 1976: character state 154). Since the leaf blade is thicker than in *H. parlatorei* the outline of the transverse section becomes almost circular. The leaves are setaceous, permanently infolded, and the two halves of the lamina are usually symmetrical on either side of the median vascular bundle (Fig. 1 D).
Leaf blades of typical *H.* ×*krischae* (Figs 2 A, B) and of *H.* cf. ×*krischae* are intermediate in shape and thickness. The halves of the lamina form a narrow U. The transverse section is elliptical in outline and corresponds largely to character state 153 in ELLIS (1976).

Adaxial surface of the lamina

In each of the samples, prominent ribs of the upper leaf surface are formed above the median and the major lateral vascular bundles, minor ones above the 2nd order lateral bundles. In *H. parlatorei*, the prominent ribs are flat-topped square ribs (Fig. 1 B), with base equal to or even narrower in relation to the apex (characters 217 and 221, respectively, in ELLIS 1976). In *H. setaceum* subsp. *petzense* the prominent ribs above the median and major lateral bundles have a rounded apex (Figs 1D, E; character 214 in ELLIS 1976). The intermediates *H.* ×*krischae* and *H.* cf. ×*krischae* have both shapes of prominent ribs and transitional forms between them (Figs 2 A, B). Ribs above the 2nd order bundles are always much shorter and apically rounded in all taxa and specimens studied (Figs 1, 2).

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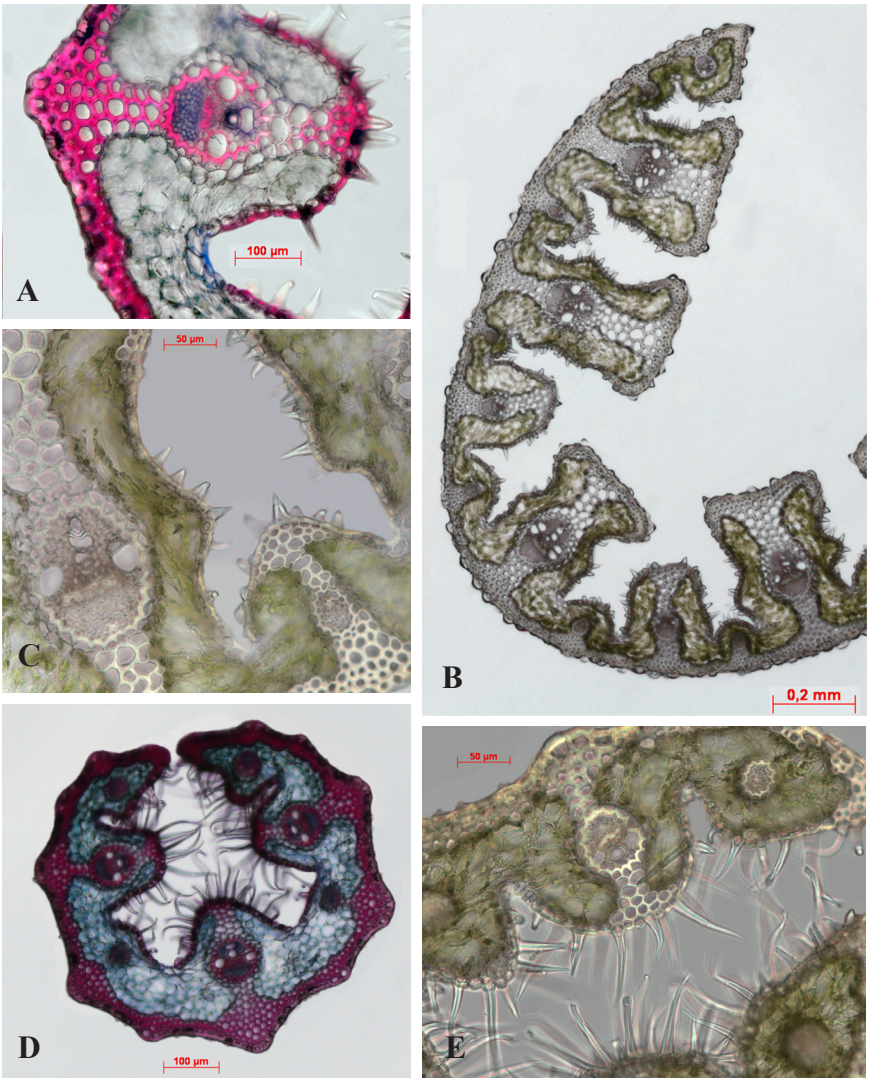

Fig. 1 (above): Median vascular bundle of *H.* cf. ×*krischae* (no 0601) in transverse section stained with safranine/astra blue (A); leaf lamina of *H. parlatorei* (no 1101) in transverse section (B) and trichomes (C); leaf lamina of *H. setaceum* subsp. *petzense* (no 1302) stained with safranine/astra blue (D) and (E) trichomes (no 0803).

Fig. 2 (p. 76): Leaf laminas of *H.* ×*krischae* (no 0502, 10648-1B) in transverse section (A, C) and (B) trichomes (no 10648T2); leaf laminas of hybrids macroscopically resembling *H. setaceum* subsp. *petzense* (no 10646a, 0601) in transverse section (D, E) and (F) trichomes (no 10646b). – A and E stained with safranine/astra blue.

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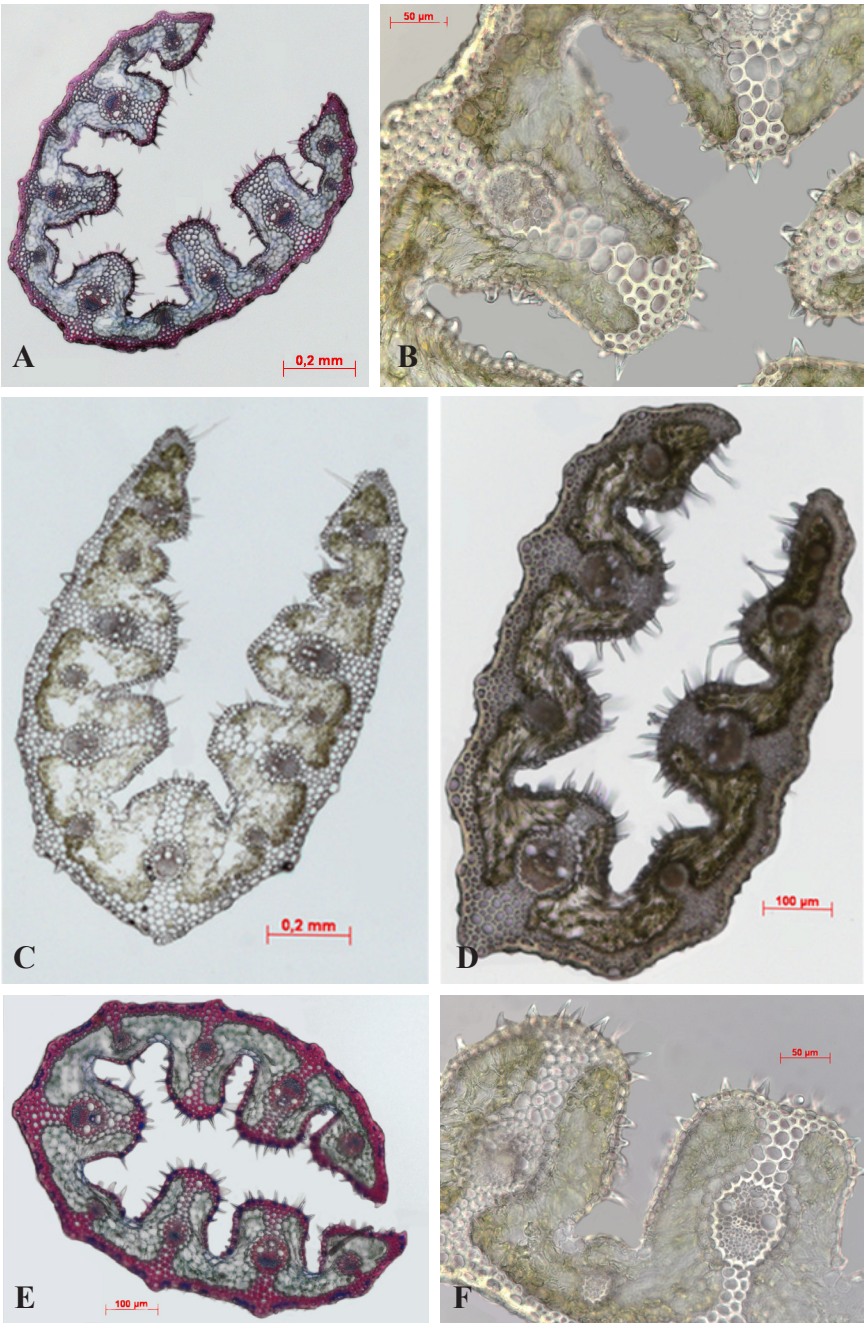

Fig. 2: Legend on p. 75.

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Abaxial surface of the lamina

The abaxial surface of the lamina has no prominent keel. The surface is smooth in *H. parlatorei* (Fig. 1 B), but distinctively ribbed in *H. setaceum* subsp. *petzense* (Fig. 1 D). Ribs are situated in *H. setaceum* subsp. *petzense* opposite vascular bundles and are usually developed additionally in the intercostal zones on both sides of the main vascular bundle (Fig. 1 D). *Helictotrichon ×krischae* and *H.* cf. *×krischae* are intermediate, i.e., small ribs and shallow furrows are present (Fig. 2 A).

Width of the lamina

The widths of one half of the laminas are indicated in Table 3 and Fig. 3. *Helictotrichon parlatorei* has the widest leaves. 50 % of the values range between 1,035 and 1,340 µm, 25 % are larger than 1,340 µm. The maximum width of the leaf half is 1,634 µm. *Helictotrichon setaceum* subsp. *petzense* has narrower leaves, 50 % of the values range between 608 and 782 µm per one half of the leaf. *Helictotrichon ×krischae* and *H.* cf. *×krischae* are intermediate with 50 % of the values ranging between 750 and 1,000

Tab. 3: Width of halves of the leaf laminas.

		H. parlatorei	*H. setaceum* subsp. *petzense*	*H. ×krischae*	*H.* cf. *×krischae*
Mean (µm)		1197.8	709.5	935.2	925.0
Median (µm)		1170.0	702.6	940.7	925.0
Minimum (µm)		930.0	521.9	665.6	920.0
Maximum (µm)		1634.0	954.1	1280.0	930.0
Percentile (µm)	25	1035.0	608.5	750.3	920.0
	50	1170.0	702.6	940.7	925.0
	75	1340.0	782.0	1000.0	930.0

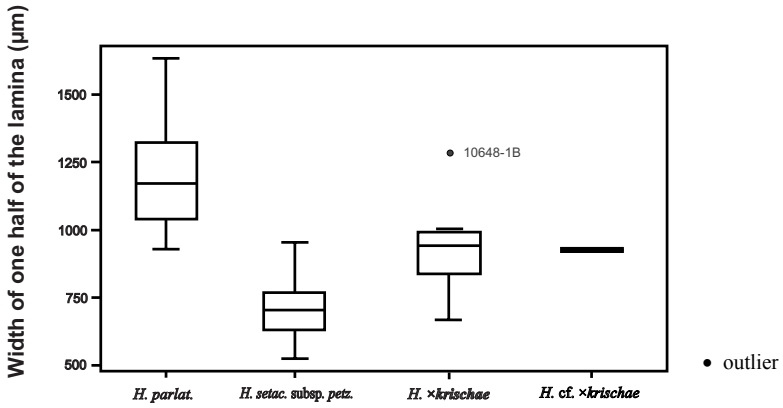

Fig. 3: Width of one half of the leaf lamina (boxplot).

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µm or 920 and 930 µm, respectively. 1,000 µm is the maximum width in *H. ×krischae* except the greenhouse plant (no. 10648-1B) where 1,280 µm is reached (Fig. 2 C; outlier in Fig. 3). The t-test confirmed that the differences are significant (confidence interval 95 %).

Number of vascular bundles

The number of vascular bundles varies between 11 and 18 in *H. parlatorei* (one half of the leaf including the median bundle). In *H. setaceum* subsp. *petzense* 7 bundles are present almost invariably, only specimens nos. 0601, 10646a, b (all from the Petzen Mountain) deviate in having 8, 9, and 10 vascular bundles, respectively (Fig. 4). *Helictotrichon ×krischae* shows, comparable to *H. parlatorei*, a higher variation of the number of bundles which ranges between 8 and 14. The two specimens of *H.* cf. *×krischae* studied each have 9 bundles. The number of vascular bundles is obviously directly correlated with the width of the lamina (cf. Figs 1B, D; 2 A, C, D, E; 3; 4) and cannot be treated as an independent character in further analysis.

Length of trichomes

Trichomes are present on the adaxial surface of the lamina in all acessions studied. They are localised in *H. parlatorei* mainly along the flanks of the ribs, in *H. setaceum* subsp. *petzense*, *H. ×krischae*, and *H.* cf. *×krischae* additionally on the apices of the ribs (Figs 1 B, C, D, E; 2 A, B). The length of trichomes is strongly different among the specimens and taxa. In *H. parlatorei*, 50 % of the trichomes are between 11 and

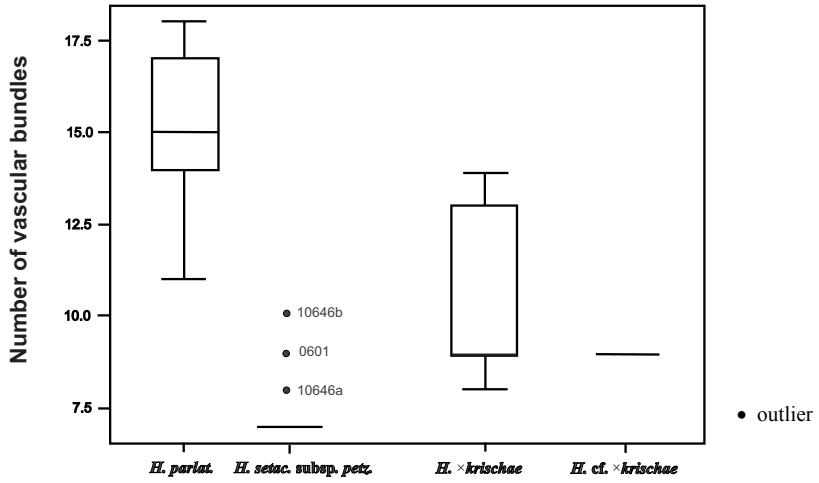

Fig. 4: Number of vascular bundles per one half of the leaf lamina including the median bundle (boxplot).

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19 µm long. The entire variation of lengths is comparatively small (Table 4; Figs 5; 6). *Helictotrichon setaceum* subsp. *petzense* has a wider variation of trichome lengths and on average c. twice as long trichomes than *H. parlatorei* (36 µm *vs*. 16 µm). 50 % of the trichomes are between 22 and 47 µm long (Tab. 4; Figs 5; 6). The median value (50 % percentile) is 29.9 µm in *H. setaceum* subsp. *petzense* vs. 15.4 µm in *H. parlatorei*. Accessions of *H. setaceum* subsp. *petzense* from the Kärntner Storschitz Mountain (no. 1302a) are similar to those from the Petzen Mountain. Three specimens of subsp. *petzense* from the Petzen Mountain, however, do not show the characteristic length of trichomes and variation of lengths, i.e., accession nos. 0601, 10646a, b (cf. above the number of vascular bundles). They have comparatively short trichomes with rather small variation of lengths (Figs 2 D, E, F; 5; 6).

Tab. 4: Length of trichomes of the leaf laminas.

		H. parlatorei	*H. setaceum* subsp. *petzense*	*H. ×krischae*	*H.* cf. *×krischae*
Mean (µm)		16.0	36.0	24.4	29.5
Median (µm)		15.4	29.9	21.9	25.4
Minimum (µm)		1.4	8.9	10.5	15.5
Maximum (µm)		38.9	83.1	83.4	80.7
Percentile (µm)	25	11.9	21.7	16.2	20.7
	50	15.4	29.9	21.9	25.4
	75	19.4	47.4	28.7	33.7

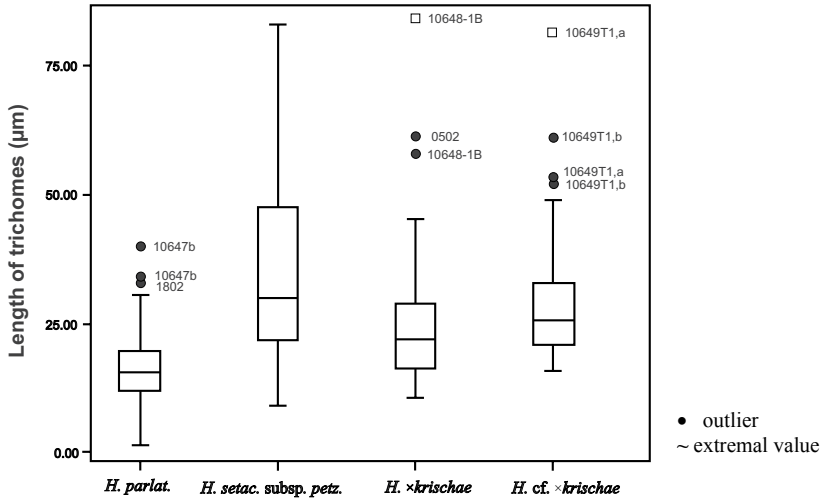

Fig. 5: Length of trichomes of the leaf laminas in the taxa studied (boxplot).

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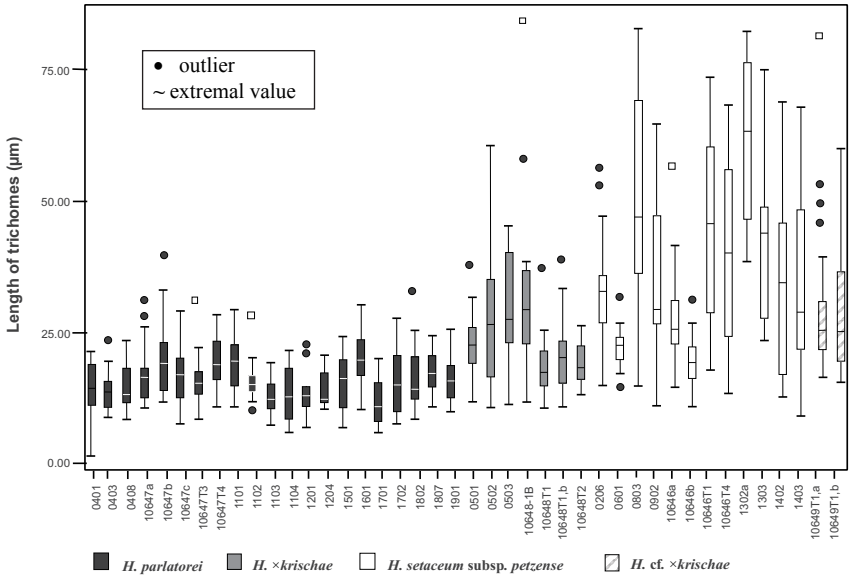

Fig. 6: Length of trichomes of the leaf laminas per specimen studied.

The trichomes of *H.* ×*krischae* and *H.* cf. ×*krischae* are intermediate in length between *H. parlatorei* and *H. setaceum* subsp. *petzense* (Tab. 4; Figs 5; 6). 50 % of the trichomes in *H.* ×*krischae* are 16 to 29 µm long, with a median value of c. 22 µm. Trichomes of the two accessions of *H.* cf. ×*krischae* studied are similar to each other with 50 % of the values ranging between 21 and 34 µm in length.

Thickness of the abaxial subepidermal layer of sclerenchyma

The abaxial surface of the leaves is characterized by a continuous subepidermal layer of sclerenchyma fibres which is connected with the major vascular bundles by girders (Figs 1 A, B, D; 2 A). Stomata, consequently, are absent in the abaxial epidermis. The sclerenchyma is strongly developed in *H. setaceum* subsp. *petzense* and consists with the inclusion of the lignified epidermis of a three- to five-celled layer in the intercostal zones (Fig. 1 D). The layer in *H. parlatorei* is usually only two-celled (Fig. 1B). *Helictotrichon* ×*krischae* and *H.* cf. ×*krischae* are intermediate (Figs 2 A, B).

Discussion

The micromorphological and anatomical characters of leaf laminas studied in *H. parlatorei* and *H. setaceum* subsp. *petzense* confirm the hybrid origin of *H.* ×*krischae*. *Helictotrichon* ×*krischae* is intermediate between the parental taxa *H. parlatorei* and

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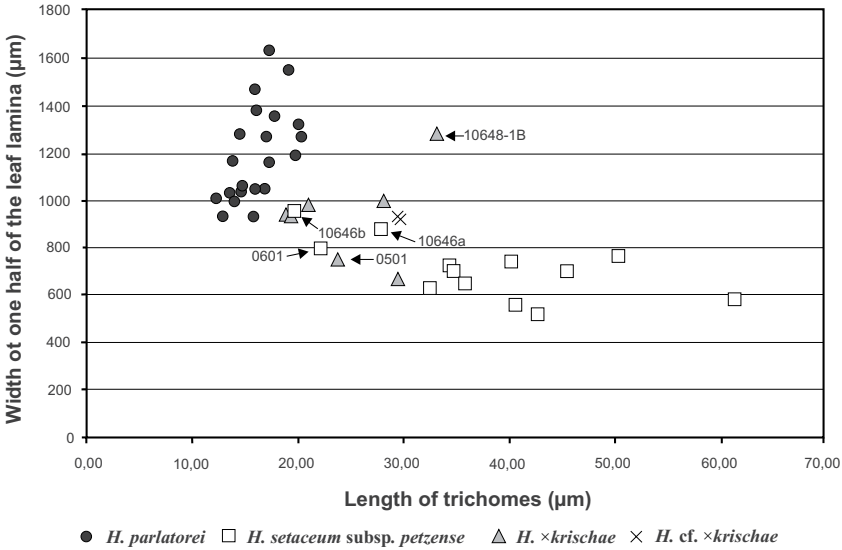

Fig. 7: Length of trichomes plotted against the width of one half of the leaf laminas.

H. setaceum subsp. *petzense* with reference to the outline and shape of the lamina in transverse section, the shape of the ribs on the abaxial leaf surface (Figs 1 B, D; 2 A, C), the width of the lamina (Fig. 3), the number of vascular bundles (Fig. 4), the length of trichomes on the adaxial surface (Figs 5; 6), and the thickness of the subepidermal layers of sclerenchymatous fibres on the abaxial side of the laminas.

The results indicate that further intermediates between *H. parlatorei* and *H. setaceum* subsp. *petzense* occur on the Petzen Mountain. They are different from *H. ×krischae* which is strictly in-between the parental taxa. Such specimens, termed *H.* cf. *×krischae*, resemble more strongly either *H. parlatorei* or *H. setaceum* subsp. *petzense* in macroscopical features, but have intermediate characters in the anatomy and micromorphology of the leaves which are comparable to *H. ×krischae* (Figs 3–6).

Three specimens identified on macroscopical features unambiguously as *H. setaceum* subsp. *petzense* have characters intermediate between *H. parlatorei* and *H. setaceum* subsp. *petzense* in the structure of the leaf laminas (Figs 2 D, E, F; 6; 7). They appear to be further hybrids or to have hybrid origin.

These findings suggest the presence of a hybrid zone between *H. parlatorei* and *H. setaceum* subsp. *petzense* on the Petzen Mountain. Specimens such as *H. ×krischae* with characters strictly in-between the parental taxa *H. parlatorei* and *H. setaceum* subsp. *petzense* are part of this hybrid zone, but are not representative.

In the scatter diagram of leaf characters (Fig. 7), the accessions of *H. parlatorei* form

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a neatly defined cluster irrespective of their particular provenances (Petzen Mountain, Wiener Schneeberg). Accessions of *H.* ×*krischae* and *H.* cf. ×*krischae* (Petzen Mountain) deviate and have characters intermediate between *H. parlatorei* and most accessions of *H. setaceum* subsp. *petzense* (Petzen Mountain, Kärntner Storschitz). An exception is the greenhouse plant no. 10648-1B (marked in Figs 3; 7) that has been cultivated for five years under greenhouse conditions in the lowland. It produces much broader and fleshier (cf. Fig. 2 C) leaf laminas than its hybrid relatives on the natural site. The shape of the ribs (Fig. 2 C) and the length of trichomes (Fig. 6), however, has not become much altered under greenhouse conditions.
The specimen which fit macroscopically *H. setaceum* subsp. *petzense* (nos. 0601, 10464a, b; marked in Fig. 7), but deviate with respect to micromorphological characters of the laminas (Fig. 4), are nested within the cluster of hybrids.
Typical specimens of *H. setaceum* subsp. *petzense* are clearly separated from *H. parlatorei* in Fig. 7. In contrast to *H. parlatorei* they are characterised by a comparatively small variation of leaf widths and a huge variation of trichome lengths.

From the morphometric data presented here it can be concluded that the hybrid plants between *H. setaceum* subsp. *petzense* and *H. parlatorei* are not necessarily intermediate in all characters between the parental taxa, since they display a mosaic of parental and intermediate characters. This is a frequent pattern in natural hybridisation (RIESEBERG & ELLSTRAND 1993, ARNOLD 1997). The extent of post-mating reproductive isolation in the concerned taxa of *Helictotrichon* is unknown and it is difficult to estimate from the present data whether the hybrid plants between *H. setaceum* subsp. *petzense* and *H. parlatorei* actually contribute to genetic introgression into the parental taxa or not. Due to the ecologically strongly different adaptations of the parental taxa on the naturally site of the Petzen Mountain a considerable selection against hybrid plants and genetic introgression seems likely.

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References

ARNOLD, M.L. 1997: Natural hybridization and evolution. Oxford, UK: Oxford University Press.

CHAS, E. 1994: Atlas de la flore des Hautes-Alpes. Gap: Conservatoire botanique national de Gap-Charance, Conservatoire des espaces naturels de Provence et des Alpes du Sud, Parc National des Ecrins.

CONERT, H.J. 1979–1998: Poaceae (Echte Gräser oder Süßgräser). In: CONERT, H.J., JÄGER, E.J., SCHULTZE-MOTEL, W., WAGENITZ, G. & WEBER, H E. (eds.): G. Hegi, Illustrierte Flora von Mitteleuropa, Vol. 1 Teil 3. Ed. 3. Berlin: Parey Buchverlag.

ELLIS, R.P. 1976: A procedure for standardizing comparative leaf anatomy in the Poaceae. I. The leaf-blade as viewed in transverse section. Bothalia **12**: 65–109.

ELLIS, R.P. 1979: A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. Bothalia **12**: 641–671.

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GERLACH, D. 1984: Botanische Mikrotechnik. Ed. 3. Stuttgart: Georg Thieme Verlag.

HARTL, H., KNIELY, G., LEUTE, G.H., NIKLFELD, H. & PERKO, M. 1992: Verbreitungsatlas der Farn- und Blütenpflanzen Kärntens. Klagenfurt: Naturwissenschaftlicher Verein.

HESS, H.E., LANDOLT, E. & HIRZEL, R. 1967: Flora der Schweiz und angrenzender Gebiete. Birkhäuser: Basel.

JOGAN, N. (ed.) 2001: Gradivo za Atlas flore Slovenije. Miklavž: Center za kartografijo favne in flore.

LANGE, D. 1995: Untersuchungen zur Systematik und Taxonomie der Gattung *Helictotrichon* Besser ex J. A. Schultes & J. H. Schultes (Poaceae) in Südosteuropa und Vorderasien. Bibliotheca Botanica **144**: 1–238.

MAIER, M., NEUNER, W. & POLATSCHEK, A. 2001: Flora von Nordtirol, Osttirol und Vorarlberg. Vol. 5. Innsbruck: Tiroler Landesmuseum Ferdinandeum.

MELZER, H. 1967: Helictotrichon petzense, spec. nova – ein neu entdeckter Endemit der südöstlichen Kalkalpen. Österreichische Botanische Zeitschrift **114**: 309–319.

PIGNATTI, S.1982: Flora d'Italia. Vol. 3. Bologna: Edagricole.

PRAT, H. 1932: L'épiderme des Graminées, étude anatomique et systematique. Annales des Sciences Naturelles, Sér. 10, Botanique **14**: 117–324.

PRAT, H. 1960: Vers une classification naturelle des Graminées. Bulletin de la Société Botanique de France **107**: 32–79.

RIESEBERG, L. & ELLSTRAND, N.C. 1993: What can molecular and morphological markers tell us about plant hybridization. Critical Revues in Plant Science **12**: 213–241.

RÖSER, M. 1989: Karyologische, systematische und chorologische Untersuchungen an der Gattung *Helictotrichon* Besser ex Schultes & Schultes im westlichen Mittelmeergebiet. Dissertationes Botanicae **145**: 1–250.

RÖSER, M. 1996: Ecogeography of the grass genus *Helictotrichon* (Poaceae: Aveneae) in the Mediterranean and adjacent regions. Plant Systematics and Evolution **203**: 181–281.

SCHÖNFELDER, P. & BRESINSKI, A. (eds.) 1990: Verbreitungsatlas der Farn- und Blütenpflanzen Bayerns. Stuttgart: Verlag Eugen Ulmer.

VIERHAPPER, F. 1906: Zur Systematik der Gattung *Avena*. Verhandlungen der zoologisch-botanischen Gesellschaft in Wien **56**: 369–370.

VIERHAPPER, F. 1914: Zur Systematik der Gattung *Avena*. Verhandlungen der Gesellschaft Deutscher Naturforscher und Ärzte **85**: 670–674.

WELTEN, M. & SUTTER, R. 1982: Verbreitungsatlas der Farn- und Blütenpflanzen der Schweiz. Vols. 1–2. Basel: Birkhäuser.

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