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***Pinus mugo* and *P. uncinata* as Parents of Hybrids A Taxonomic and Nomenclatural Survey**

By

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With 6 Figures

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Key words: *Pinaceae*, *Pinus mugo*, *Pinus sylvestris*, *Pinus uncinata*, *Pinus* × *ascendens*, *Pinus* × *celakovskiorum*, *Pinus* × *rhaetica*. – Hybridization, nomenclature, taxonomy. – Flora of Europe.

Summary

BUSINSKÝ R. & KIRSCHNER J. 2010. *Pinus mugo* and *P. uncinata* as parents of hybrids. A taxonomic and nomenclatural survey. – *Phyton* (Horn, Austria) 50 (1): 27–57, with 6 figures.

Taxonomy and nomenclature of hybrids among members of the *Pinus mugo* complex (*P. mugo*, *P. uncinata* subsp. *uncinata*, *P. uncinata* subsp. *uliginosa*) and between the *Pinus mugo* complex and *P. sylvestris* are analyzed and summarized. *Pinus* × *rhaetica* nothosubsp. *rhaetica* is identified as a hybrid between *P. sylvestris* and *P. uncinata* subsp. *uncinata*. The previously designated neotype of the name is superseded by a lectotype chosen from the original material (an icon), and an epitype is selected to stabilize the usage of the name. The other hybrids include *P.* × *celakovskiorum* (*P. mugo* × *P. sylvestris*) and *P.* × *rhaetica* nothosubsp. *digenea* (*P.* × *digenea*, *P. uncinata* subsp. *uliginosa* × *P. sylvestris*). For both hybrid names epitypes were selected. The combinations *P. mugo* × *P. uncinata* subsp. *uncinata* and *P. mugo* × *P. uncinata* subsp. *uliginosa* are described as new under the names *P.* × *ascendens* BUSINSKÝ nothosubsp. *ascendens* and *P.* × *ascendens* nothosubsp. *skalickyi* BUSINSKÝ, respectively.

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Zusammenfassung

BUSINSKÝ R. & KIRSCHNER J. 2010. *Pinus mugo* and *P. uncinata* as parents of hybrids. A taxonomic and nomenclatural survey. [*Pinus mugo* und *P. uncinata* als Eltern von Hybriden. Eine taxonomisch-nomenklatorische Übersicht]. – *Phyton* (Horn, Austria) 50 (1): 27–57, mit 6 Abbildungen.

Eine taxonomisch-nomenklatorische Übersicht der Bastarde und Introgressionen innerhalb des *Pinus mugo*-Komplexes (*P. mugo*, *P. uncinata* subsp. *uncinata*, *P. uncinata* subsp. *uliginosa*) und mit *P. sylvestris* wird präsentiert. Es wird gezeigt, dass *Pinus × rhaetica* nothosubsp. *rhaetica* eine Hybride zwischen *P. sylvestris* und *P. uncinata* subsp. *uncinata* ist. Der früher ausgewählte Neotypus wird durch einen Lectotypus (eine Abbildung als ein Element des Originalmaterials) ersetzt und zur Stabilisierung der Nomenklatur durch einen Epitypus ergänzt. *P. × celakovskiorum* (*P. mugo* × *P. sylvestris*) und *P. × rhaetica* nothosubsp. *digenea* (*P. × digenea*, *P. uncinata* subsp. *uliginosa* × *P. sylvestris*) werden ebenfalls besprochen und epitypisiert. Die Bastarde *P. mugo* × *P. uncinata* subsp. *uncinata* und *P. mugo* × *P. uncinata* subsp. *uliginosa* werden neu beschrieben, der erstere als *P. × ascendens* BUSINSKÝ nothosubsp. *ascendens*, der letztere als *P. × ascendens* nothosubsp. *skalicnyi* BUSINSKÝ.

1. Introduction

Hybridization with *Pinus mugo* or *Pinus uncinata* parentage is a widespread and well-known phenomenon (e.g., SZWEYKOWSKI & BOBOWICZ 1983, BOBOWICZ 1990a, BACZKIEWICZ 1995, CHRISTENSEN & DAR 1997, STASZKIEWICZ 2001, SKALICKÝ 1988, BUSINSKÝ 1998). This hybridization may give arguments in favour of treating the whole species group (often referred to as the *P. mugo* complex) as a single, highly variable species. Although this concept was seldom used in the past (e.g., DALLMOR & JACKSON 1948, MARCET 1967, KUOCH & SCHWEINGRUBER 1975), it was more recently accepted by CHRISTENSEN 1987 and followed by several authors, the most important ones being FARJON 1998, 2001, ZOLLER 1981, NEBEL 1990, POLATSCHKEK 1997, GOLDE 2000. Most authors, including GAUSSEN & al. 1993 or FARJON 1984, 2005, accept two species in this group, i. e. *P. mugo* TURRA and *P. uncinata* RAMOND ex DC.

In the present study, we follow previous population and phytogeographical studies (BUSINSKÝ 1998, 2008, 2009, for a summary, see BUSINSKÝ & KIRSCHNER 2006) initiated by R. BUSINSKÝ in the 1980s and continued recently. Our results show that the species complex consists of two species, *P. mugo* TURRA s. str. (= *P. mughus* SCOP., *P. pumilio* HAENKE; mountain pine, Leg-Föhre, Latsche, Krummholz-Kiefer, kleč, kosodrevina) and *P. uncinata* RAMOND ex DC., with two subspecies, the type subsp. *uncinata* (Haken-Kiefer in German sources) in the southwestern and central part of the species' range and subsp. *uliginosa* (NEUMANN) BUSINSKÝ (bog pine, Moor-Spirke, Sumpf-Kiefer, blatka, sosna błotna) in a smaller, northeastern part of the range. Distribution ranges of all these taxa are given in Fig. 1.

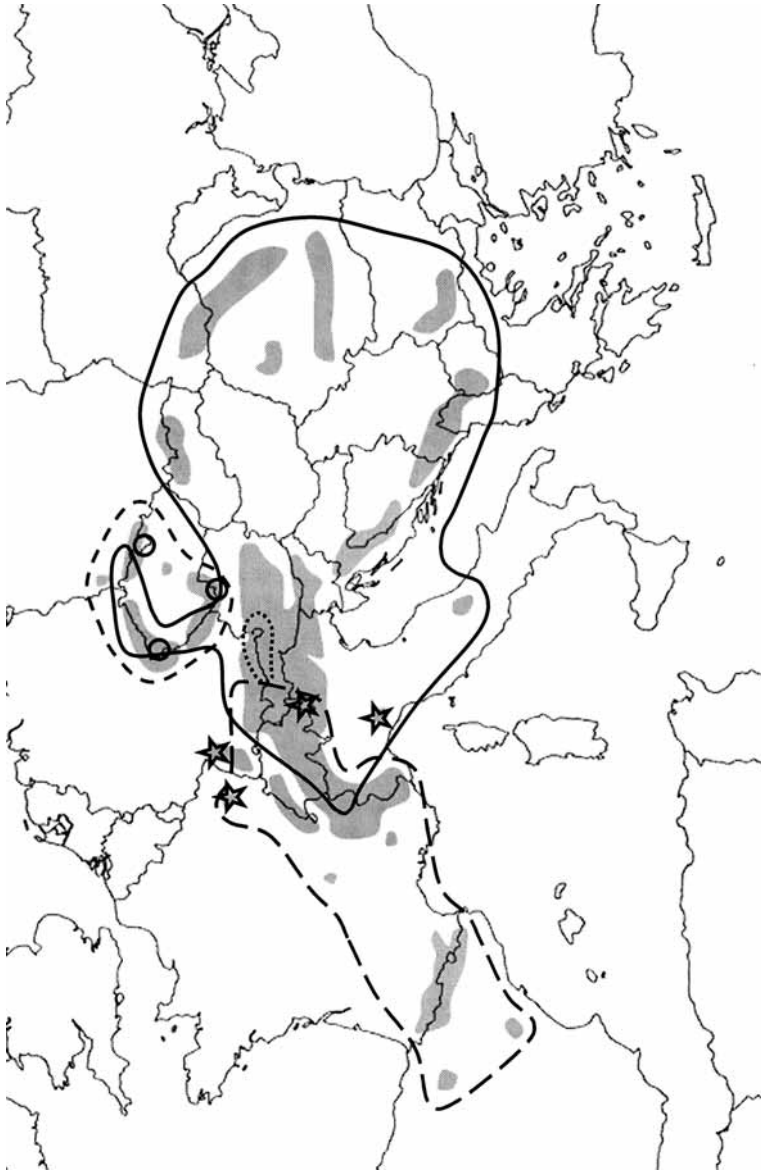


Fig. 1.

Fig. 1. Generalized distribution of the taxa of the *Pinus mugo* complex. Long-dashed line: *P. uncinata* var. *uncinata*; short-dashed line: *P. uncinata* subsp. *uliginosa*; dotted line: *P. uncinata* var. *ancestralis*; solid line: *P. mugo*. Asterisks: Areas of introgressive hybridization between *P. uncinata* subsp. *uncinata* and *P. mugo*. Circles: Areas of introgressive hybridization between *P. uncinata* subsp. *uliginosa* and *P. mugo*.

Note: *Pinus sylvestris* is sympatric or parapatric in the whole range of the *Pinus mugo* complex distribution except in the Abruzzi mountains (Appennino Abruzzese).

Our aim is to summarize the taxonomy and nomenclature of hybrids with *Pinus mugo* or *Pinus uncinata* parentage, with emphasis on the analysis of the name *P. × rhaetica*.

2. Material

The material on which the present conclusions are based consists of population samples of all the taxa of the *P. mugo* complex, covering most of their distribution ranges. A detailed list of populations and their documentation (herbarium specimens, cone samples, photographs) is given in BUSINSKY 2008. The set of samples includes 73 populations of *P. mugo*, 43 localities of *P. uncinata* subsp. *uncinata* and 36 populations of *P. uncinata* subsp. *uliginosa*. Some of the sites were visited repeatedly. Important specimens are deposited in internationally recognized herbaria, mostly BM, G, P, PR and PRA, or documented in the RILOG Herbarium (herbarium of the Silva Tarouca Research Institute for Landscape and Ornamental Gardening, see address of the first author).

3. A Survey of Parental Taxa

In addition to the above three taxa, a relatively common parental taxon of hybrids with *P. mugo* and *P. uncinata* is *P. sylvestris* L. A brief survey of the relevant characters useful for the identification of hybrids is given in Table 1.

We would like to emphasize the importance of the female cone (conelet) orientation for the identification of hybrids with *P. sylvestris*. This character was frequently used in the literature (SHAW 1914, SZWEYKOWSKI & BOBOWICZ 1983, BOBOWICZ 1990a, b, BACZKIEWICZ 1995, CHRISTENSEN & DAR 1997). In *P. sylvestris*, the female cone (conelet) is reflexed on a relatively long peduncle and the cone points downwards, which is unique in the whole subgenus *Pinus*. This character is relevant only from July in the first year of the cone development to about February – March in the second year (under the climatic conditions of Central Europe and mountains of southern Europe). In contrast, in the other two species (*P. mugo* and *P. uncinata*) conelets are erect on a short peduncle during the same stage of development but from the spring months of the second year the cones change their orientation to reflexed during their more rapid growth.

As regards the parental combination of *P. mugo* × *P. uncinata*, there are only two morphological characters useful for the identification of hybrids: general habit of the plants (monocormic tree versus shrub) and symmetry of cones (strongly zygomorphic versus polysymmetric – actinomorphic). The first character state in each pair belongs to *P. uncinata*, the second to *P. mugo*. However, in many populations the correlation between these characters may be suppressed, and it is not easy to identify the hybrids or possible introgressants.

4. Excluded Hybrid Combinations

For the sake of completeness, we provide information on hybrids allegedly involving *Pinus mugo* as one of the parents, with other species than *P. sylvestris* as the other parent. A plant described as *P. × wettsteinii* FRITSCH 1889, reported as a garden hybrid between *P. mugo* and *P. nigra* J. F. ARNOLD, proved to be *P. nigra* (NOVÁK 1953). Another similar case is the reported hybrid between *P. mugo* and *P. leucodermis* ANTOINE (= *P. heldreichii* H. CHRIST). The plant was reported as a hybrid by E. ŠMIDT and annotated by PILÁT 1964. The plant proved to be a dwarf aberrant of *P. heldreichii*, known as cultivar ‘Smidtii’ and originating from Bosnia (first collected in 1926). Further independent records of this hybrid combination were published by FUKAREK 1960 and followed by MIROV 1967. However, this hybrid combination is in general quite improbable (see also BUSINSKÝ 1989) as the parental taxa are phylogenetically and morphologically remote (WANG & al. 1999, GROTKOPP & al. 2004, GERNANDT & al. 2005).

5. Analysis of *Pinus × rhaetica*, the Oldest Name of a Hybrid Between a Member of the *P. mugo* Complex and *P. sylvestris*

5. 1. Valid Publication of the Name

The name *Pinus rhaetica* first appeared as a quotation from a letter sent by Brügger to CHRIST in 1863 (CHRIST 1864). Although several authors (CHRISTENSEN 1987, FARJON 2001) accept the name as *P. × rhaetica* BRÜGGER in CHRIST, Flora [Regensburg] 47: 150 (1864), the name was not published validly at that place. The main argument against the validity of the name *P. rhaetica* there is that the name was not accepted in the latter publication. BRÜGGER gave a good guidance as to the parentage of the hybrid and the locality of his observations: In modern terms the hybrid was considered to belong to the *P. sylvestris* × *P. uncinata* subsp. *uncinata* parentage, and the locality was Plaungood at the foot of Mt. Muotas. There, BRÜGGER (in a letter to CHRIST) did not refer to any description associated with the name *P. rhaetica*. CHRIST himself understood the name as a useful means to cover the whole variation range of *P. sylvestris* at that locality: “(mit diesem Namen fasst Dr. BRÜGGER der Bequemlichkeit halber die diesem Standort eigenth(mlichen Variationen der *Pin. sylvestris* zusammen)” [see quotation below]. In the subsequent part of his paper, CHRIST summarized the complex variation of pines in Oberengadin in numbered paragraphs; most of the forms are illustrated on a plate attached at the end of the journal’s volume. However, none of the descriptions is clearly associated with the name *P. rhaetica*.

For the sake of completeness, we quote BRÜGGER’s letter sent to CHRIST in the late 1863 (CHRIST 1864: 150): “Die bedeutendste und mächtigste Localität is Plaungood (Romanisch ‘Ebener Wald’), eine breite Terrasse am Fuss des Muotas-Berges (rechte Thalseite, Nordwestlage, Granit), 100–200’ [30–60 m] über der Thalebene,

Table 1. – Main morphological and other differences relevant for the identification of hybrids

	<i>P. mugo</i>	<i>P. uncinata</i> subsp. <i>uncinata</i>	<i>P. uncinata</i> subsp. <i>uliginosa</i>	<i>P. sylvestris</i>
growth	shrub*	monocormic tree	monocormic tree	monocormic tree
female cone (conelet) position**	erect	erect	erect	reflexed
cone symmetry	actinomorphic or subactinomorphic	conspicuously zygomorphic, rarely subactinomorphic	± zygomorphic	± zygomorphic or subactinomorphic
colour of apophyses of fully mature cones	glossy, light to chestnut brown	glossy, light to chestnut brown	glossy, light to chestnut brown	dull, pale tawny with greyish tinge
shape of apophyses on the exposed part of the cone	flat, slightly prominent, distally tumid or obliquely low pyramidal	elongated into high, oblique pyramid; rarely only slightly prominent****	obliquely pyramidal with ± rounded apex	slightly prominent to obliquely pyramidal
bark colour and character	blackish or greyish brown, minutely scaly	blackish or greyish brown, with small plates curling up like shavings	blackish or greyish brown, with small plates curling up like shavings	papery thin, flaking and orange-brown on branches and upper trunk, later forming thick grey ribs on lower trunk
needle colour	dark green	dark green	dark to light green	greyish pale green
number of needle resin ducts (and max. number of all resin ducts)	D (1)3–5(6), V (0)1 (7)	D (1)3–5(6), V (0)1(2) (8)	D (1)4–7(8), V (0)1(3) (10)	D 5–13(16), V (1)3–6(7) (5)8–18(23) together
needle epidermis cells in cross section	radially oblong	radially oblong	radially oblong	± square
distance between v. b. as a multiple of v.b. width	usually 0.5–1.2	usually 0.6–1.4	usually 0.7–1.4	usually 1.5–2.5
sclerenchymatic cells along and between v. b.	in thin layer or (almost) absent	in thin layer or (almost) absent	in thin layer or (almost) absent	in multicell bundle of 1 triangular shape on cross section
sclerenchymatic cells along and between v. b. (Fig. 2) ‡	state 1(2–4)	state 1–4(5)	state 1–4(5)	state 4–5

Table 1. Continued

	<i>P. mugo</i>	<i>P. uncinata</i> subsp. <i>uncinata</i>	<i>P. uncinata</i> subsp. <i>uliginosa</i>	<i>P. sylvestris</i>
distribution	The Alps excluding the SW, Appennino Ligure, high mountain ranges of C Europe, Carpathians, Balkan mountains, Abruzzi	from E Spain to NE France, the Schwarzwald Mts., Jura Mts., W, C and N Alps including foothills in Oberbayern	Czech Republic, SW Poland (Kłodzko, Dolny Slask), E Germany (Erzgebirge, Fichtelgebirge, Oberpfalz), N Austria (borderland of S Bohemia)	extensive range from W and N Europe to the Far East
ecology	mountain granitic and limestone rocky or stony slopes up to 2700 m, occasionally peatbogs down to ca. 500 m	mountain granitic and limestone rocky or stony slopes, old scree, limestone alluvia, 800–2350 m, occasionally peatbogs in 610–1820 m	exclusively peatbogs or moorlands, 195–910 m, mostly 450–750 m	ecologically tolerant, preferring open rocky and stony biotopes and sunny woody slopes, up to ca. 2000 m***

Abbreviations used: s.c. = sclerenchymatic cells, v.b. = vascular bundles, D = resin ducts along the dorsal side of the needle, V = resin ducts along the ventral side of the needle.

*) Rare occurrence of monocormic, erect/tree-like individuals up to 8 m tall

**) Timing of observations: late summer to winter (usually August to March)

***) In the European var. *sylvestris*

****) In var. *ancestralis* BUSINSKÝ. This variety was described recently (BUSINSKÝ 2008) and, for the sake of convenience, we provide the protologue of this taxon also here:

Pinus uncinata RAMOND ex DC. subsp. *uncinata* var. *ancestralis* BUSINSKÝ 2008: 7

Diagnosis: Arbores usque 10 vel 15 m altae trunco uno recto usque 40 cm in diametro, strobilis subsymmetricis apophysibus leviter prominentibus vel subplanis.

Type: BUSINSKÝ 35102: Germany, Oberbayern (border with Austria), left side of Isar valley 2 km SW of Vorderriss; sparse pines on grassy moist alluvium of limestone screes along a mountain river, 800 m; tree: 70 cm trunk circumfer., 8.5 m high, 6 m crown diam.; coll. R. BUSINSKÝ, 13.9.1992; holotype: PR, isotypes: herbarium of the RILOG.

Description: Short monocormic trees usually attaining a height of about 10 m (sometimes up to 15 m) and a trunk diameter of 40 cm, with generally subsymmetrical cones, apophyses slightly prominent or almost flat.

Distribution: This variety represents the easternmost disjunct populations of the type subspecies confined to the northern Alps along the border between Tirol (Austria) and Oberbayern (Germany) between 11° and 13° E, above all in upper valley of the Isar River and in Berchtesgaden (Wimbachtal on W side of Watzmann Massif). It occurs there on old fluvioglacial alluvia of limestone screes with species-rich vegetation, mainly between 800 and 1300 m.

‡ Several states used in Tables 1 and 2 for the trait defined as presence of sclerenchymatic cells (s.c.) along and between vascular bundles (v.b.), see also Fig. 2:

(1) S.c. form a thin layer as a narrow bridge along the dorsal side of v.b., or the layer is interrupted, or sometimes s.c. are (almost) absent [“mugo type”]

(2) S.c. form a thick layer as a wide bridge along the dorsal side of v.b.

(3) S.c. form a multicellular bundle in shape of a shallow wedge or a column partly protruding between v.b. from a layer along the dorsal side of v.b. (s.c. are sometimes also scattered along the ventral side of v.b.)

(4) S.c. form a multicellular bundle in 1 whole space between v.b. and along the dorsal side of v.b., whereas s.c. are absent or only scattered along the ventral side of v.b.

(5) The same type as (4), but s.c. form a continuous layer along the ventral side of v.b. [“*sylvestris* type”]

ganz von Wald bedeckt, der am unteren Rande am dichtesten steht und vorzüglich von hohen, schlanken *P. sylv. engadinensis* nebst Arven (*P. Cembra*) gebildet wird. In der Mitte – in der Umgebung einer von der Gemeinde Samaden angelegten Waldbaumschule – wird der Wald lichter, die Arven ziehen sich zurück, und zu den zerstreuten *Pin. sylv.* gesellen sich bei 5450–5500' [1660–1675 m] zuerst einige Exemplare der *P. montana uncinata* mit aufrechtem Stamm, die gegen den oberen Rand der Terasse hin, und an dem daran sich lehrenden Berghang immer zahlreicher werden. Die Waldregion geht von da weg wohl noch 1000–1500' [300–450 m] in die Höhe, d. h. bis an 7000' [2130 m]. – Die *Pin. sylv.* verschwinden bei 6000' [1830 m]; nür *P. uncinata*, Arven und Lärchen gegen höher. – Die Waldlichtung nun, in welcher die Baumschule liegt, is der Standort unserer *Pinus rhaetica* (mit diesem Namen fasst Dr. Brügger der Bequemlichkeit halber die diesem Standort eigenthümlichen Variationen der *Pin. sylvestris* zusammen). – Sie ist dort fast so zahlreich vertreten und ebenso verbreitet als die *P. sylvestris*, jedenfalls zahlreicher als *P. uncinata*."

Another place where the name *P. rhaetica* appeared and was later accepted as validly published (REHDER 1949) is BRÜGGER, Jahresber. Naturforsch. Ges. Graubünden, ser. 2, 23–24: 121 (1880). The name, however, was not published validly at that place either (only the parental combination, references to Flora Curiensis and to BRÜGGER's letter to CHRIST, 1864, and a few additional localities were given). The Flora Curiensis (BRÜGGER 1874) lists the name *P. rhaetica* as a nomen invalidum, too. The name *P. rhaetica* was also mentioned in BRÜGGER 1880: 121 and FOCKE 1881: 419, again without validating diagnosis.

Thus, the first place where all the requirements of the Code (ICBN, Art. 32–45, McNEILL & al. 2006) for a valid publication of the name *P. rhaetica* were fulfilled is BRÜGGER, Jahresber. Naturforsch. Ges. Graubünden, ser. 2, 29 (1884–1885): 173 (1886).

5.2. The Protologue

BRÜGGER 1886 refers to the original meaning of the name as quoted by CHRIST 1864, repeating a substantial part of the above letter to CHRIST, but his conception is substantially broader and includes three "Modifikationen" under the names *P. rhaetica* [unranked] *heerii* BRÜGGER, l. cit., p. 175, *P. rhaetica* [unranked] *pyramidalis* BRÜGGER, l. cit., p. 175, and *P. rhaetica* [unranked] *christii* BRÜGGER, l. cit., p. 176, each with a description, the latter two obviously referred to what we would call *P. mugo* × *P. sylvestris*, the first one confined to the original concept of *P. rhaetica*, i.e., *P. uncinata* subsp. *uncinata* × *P. sylvestris*. As regards the rank assigned to the three infraspecific names, BRÜGGER 1886: 46, 49, 52, 55, 56, 59, 63, 86 etc. systematically used the rank of variety for a number of names but did not use that term for the forms of his *P. rhaetica*. The general term "Modifikation" cannot be treated as a newly proposed rank, and we treat the three names as unranked. CHRISTENSEN 1987 was of a different

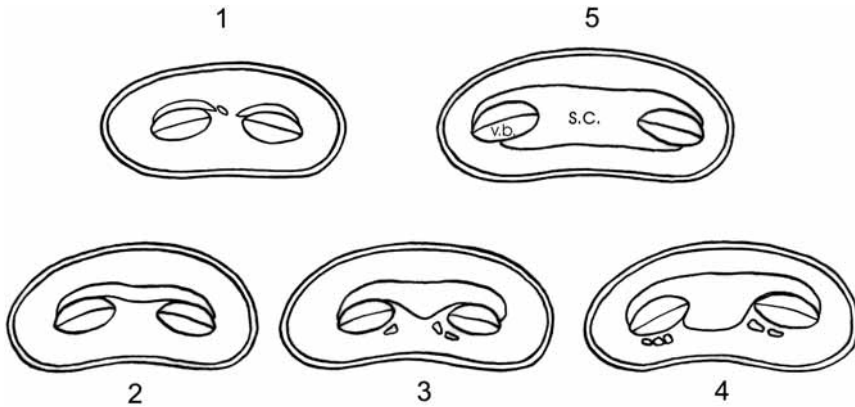


Fig. 2. Types of distribution and mutual position of sclerenchymatic cells and vascular bundles in the leaf of members and hybrids of the *Pinus mugo* complex. 1, “mugo type”; 5, “sylvestris type”. See also Tables 1 & 2. V.b. = vascular bundles, s.c. = sclerenchymatic cells.

opinion and ascribed the rank of variety to the names with the “*P. (rhaetica) Heerii*” form, which we do not consider as well substantiated.

5.3. Original Material

For the purposes of the typification of the name *P. rhaetica*, all the elements of the original material mentioned in the introductory paragraph (BRÜGGER 1886: 173) and under the three infraspecific names are equally eligible for the lectotypification. There is no direct reference to a herbarium specimen that could be understood as a syntype citation. Let us list the possible elements of the original material according to three categories, i.e., herbarium specimens (or localities mentioned in the text), figures and references to protologues of other names.

5.3.1. Herbarium Specimens (or Localities Mentioned in the Text)

First, it should be mentioned that the life work and collections of C. BRÜGGER were studied and annotated by SEILER 1909 who listed all important specimens found in the collection at that time. This helped substantially to trace the specimens, and CHRISTENSEN 1987 also referred to this source.

1. “im Walde Plaungood b. Samaden (1800 m.)” SEILER 1909 not only studied several specimens from this place but also published a figure of transversal section of the leaf of it. However, CHRISTENSEN 1987 did not find any specimen from this locality. With regard to the above material, we did not receive any positive answer from the collections at CHUR and

BAS. This locality was cited for both the original concept of *P. rhaetica* and for *P. rhaetica* [unranked] *heerii* by BRÜGGER 1886: 173, 175.

2. “Am linken Ufer der Albula, in der sog. Weid beim Alvaneuerbad ca. 950 m.” SEILER 1909 did not find any relevant specimen from this locality. Locality cited for *P. rhaetica* [unranked] *pyramidalis* by BRÜGGER 1886: 176.

3. “Camogasker-Thal (O.-Engadin) bei 1950 m.” Collected by H. CHRIST, missing from the BRÜGGER collection (SEILER 1909).

4. “Tegt ob. Savognin, ... 1350 m.” Seen by SEILER 1909 who depicted the needle anatomy (Taf. II). CHRISTENSEN 1987 did not find any specimen from this locality although BRÜGGER 1886: 177 sent cones from this place to H. CHRIST.

5. “Kalkplateau von Padnal, über der alten Kirche Müstail, zwischen Tiefencastel und Alvaschein, ... 1050m.” Seen by SEILER 1909 who depicted the needle anatomy (Taf. III). CHRISTENSEN 1987 did not find any specimen from this locality although BRÜGGER 1886: 177 sent cones from this place to H. CHRIST.

5.3.2. Figures

6. CHRIST 1864: fig. VII. Cited for *P. rhaetica* [unranked] *heerii* by BRÜGGER 1886: 175. The figure (see our Fig. 3) consists of a separate picture of an open cone and a branchlet with a newly developed closed cone, a subterminal female cone, three leaf fascicles from the previous year and several young leaf fascicles. The position of the female cone shows a hybrid origin of the depicted individual of the *P. mugo* complex and *P. sylvestris* parentage. The zygomorphic shape of the closed cone and the apophyse character suggest *P. uncinata* as the most probable parent from the *P. mugo* complex. It should be emphasized that if the name *P. rhaetica* would be treated as validly published in CHRIST 1864, this and the following figures are the only elements of the original material available. SEILER 1909 did not see any specimens of this form (no. 8 in CHRIST 1864) in the BRÜGGER herbarium.

7. CHRIST 1864: fig. VIII. Cited for *P. rhaetica* [unranked] *christii* by BRÜGGER 1886: 176. The figure consists of a separate closed cone and a leaf fascicle. We are unable to interpret this figure in taxonomic terms. SEILER 1909 did not see any specimens of this form (no. 9 in CHRIST 1864) in the BRÜGGER herbarium.

5.3.3. References to Protologues of Other Names or to Descriptions

There are three relevant references, two of them associated with the above two figures published by CHRIST 1864 and connected with the descriptions of forms no. 8 and 9, respectively. According to SEILER 1909, there is no specimen extant that belongs to these forms.

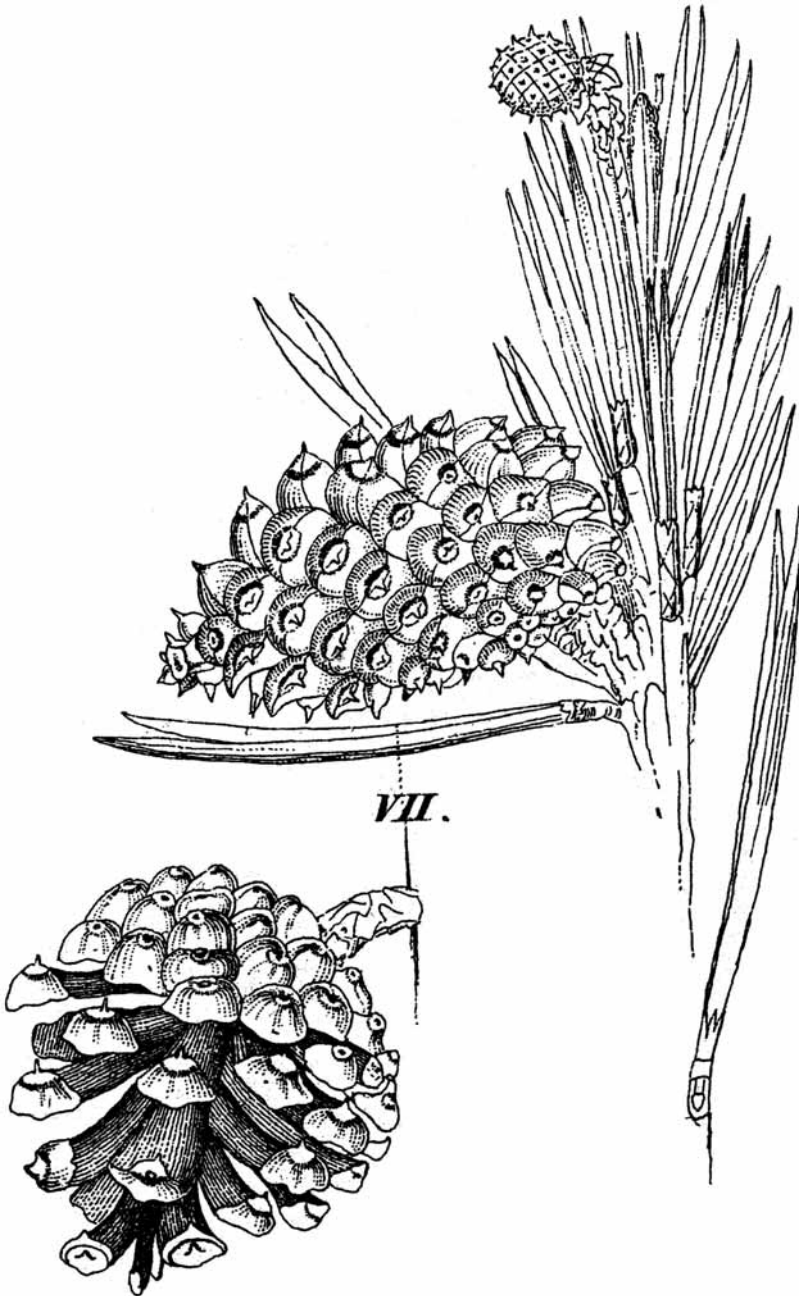


Fig. 3. The lectotype of *P. rhaetica* BRÜGGER; CHRIST 1864: Plate I, Fig. VII. The fertile branchlet in upper part of the figure is chosen as the lectotype.

The third one refers to “*P. sylvestris hybrida* HEER Verhdl. d. Schwz. Nat. Ges. 1862 S. 182” (HEER 1862), which is a validly published infraspecific name in spite of a question mark added after the name, which probably expresses doubts about the hybrid nature of the plants (Art. 34.1, last sentence). The name is based on the material collected by BRÜGGER in “Plaungood bei Samaden”, probably the same material discussed in BRÜGGER’s letter to CHRIST (1864) and mentioned by SEILER 1909. No material was traced by CHRISTENSEN 1987 in the herbarium collections of Z & ZT.

5.4. Typification

From the above list of elements of the original material of *P. rhaetica* it is evident that the neotype of this name selected by CHRISTENSEN 1987: 395 must be superseded by an element of the original material chosen as a lectotype.

In the absence of herbarium material there are two figures to be considered. One of them, i. e. Fig. VII in CHRIST 1864: Plate I, reproduced here as Fig. 3, could be used as the lectotype. In order to avoid future confusion, we select only a part of this figure as the lectotype, and interpret the lectotype by means of an epitype.

5.5. Interpretation of the Type, Selection of an Epitype

The original conception of the name *P. rhaetica* can be inferred from a detailed description of the situation at the original locality mentioned in CHRIST 1864 (a letter from BRÜGGER). The hybrids there belonged to the combination *P. sylvestris engadinensis* × *P. montana uncinata*, which in modern terms means *P. sylvestris* × *P. uncinata* subsp. *uncinata*. In 1886, BRÜGGER had a broader conception of the name that included all the hybrid forms, which we would now classify as *P. sylvestris* × *P. mugo* and *P. sylvestris* × *P. uncinata*.

CHRISTENSEN 1987 accepted the name in this broad sense, i. e. as *P. mugo* sensu latissimo × *P. sylvestris* (in accordance to his extremely broad species conception) and attempted at stabilizing the name by a neotype. He correctly searched the original Oberengadin region for hybrid pines and selected a plant not far from “Plaungood bei Samaden”. Although the neotype is no longer relevant for our nomenclatural consideration, we briefly discuss some aspects of the former neotype specimen. K. I. CHRISTENSEN kindly sent us detailed informations about the collection site of his neotype (not published in CHRISTENSEN 1987, here given as “Switzerland, Graubünden, c. 2 km NE of Pontresina, E of St. Moritz. 46° 31’N 09° 52’E. 1750 m. Substrate acidic. Degenerate bog with *Pinus mugo*, *P. sylvestris*, *P. cembra*, *Larix decidua*, and patches of *Calluna vulgaris*. 27–28/6 1980. Knud Ib CHRISTENSEN. Habit: monocormic tree. Bark: peeling in reddish, papery flakes on upper part of trunk and major branches. Leaves:

glaucous green.”, also available as a photograph at the herbarium Z & ZT website).

There are two problems associated with the former neotype: First, the collection time was too early to evaluate the orientation of the conelets, which best studied from August, first year, to March next year. Secondly, when the locality region (correctly, it should read “2 km NW of Pontresina”) was studied again by R. B. in 2005 and 2007, it became clear that hybrid pines are very rare in the area and only one tree of apparent hybrid origin was found corresponding to the description of the site. It belongs to the parental combination of *P. sylvestris* × *P. uncinata* subsp. *uncinata* and, in all likelihood, is identical with the former neotype tree. The other possible parent from the group of *P. mugo*, i. e., *P. mugo* s. str., does not occur in the area and closest occurrences of it were found about 3 km to the NW across the main Inn valley above Samedan, at and above 2000 m a.s.l.

In order to interpret the new lectotype, we select an epitype from the above tree at the stage of development allowing safe identification of its hybrid status:

Pinus* × *rhaetica BRÜGGER, Jahresber. Naturforsch. Ges. Graubünden's, ser. nov., 29: 173 (1886). – **Lectotype**, designated here: [icon in] H. CHRIST, Flora, Regensburg, 47: Plate I, Fig. VII (1864), upper part of the figure: a branchlet with a newly developed closed cone and a subterminal female cone (our Fig. 3). [The plate is often loosely attached to the volume of the journal, in some libraries bound, often at the end of the volume.] – **Epitype**, designated here: Switzerland, Graubünden, ca. 2 km NW of Pontresina, E of St. Moritz, about 120 m SW of a road junction St. Moritz – Samedan – Pontresina near Punt Muragl, alt. 1735 m, 46°30'39.2"N, 9°52'39.0"E (GPS: WGS-84); 19 September 2007, R. BUSINSKÝ 65105, tree with 87 cm trunk circumfer., 10.5 m h., ca. 60–70 years, branched from base, morphologically somewhat closer to *P. sylvestris* (epitype: PR; isoepitypes: BM, G, P, PRA). See also Fig. 4. – Taxonomic interpretation: *Pinus uncinata* RAMOND ex DC. subsp. *uncinata* × *P. sylvestris* L. In view of the fact that there is another nothosubspecies within this nothospecies, the epitype belongs to *P.* × *rhaetica* nothosubsp. *rhaetica*.

5.6. *Pinus uncinata* subsp. *uncinata* × *P. sylvestris*: Distribution and Populations Examined

The occurrence of hybrids between *Pinus uncinata* subsp. *uncinata* and *P. sylvestris* is known from almost all areas of geographic distribution of the former taxon, i. e., from its southwesternmost isolated site in E Spain (Penarroja massif in Teruel Province) through the Pyrenees, W and C Alps to N Alps (Oberbayern/Tirol border) and also from the Vosges Mts. (isolated peatbog population near Beillard). However, in most of these regions only rare individual hybrids are found in places of contact or vicinity

of populations of the parental species. Only in the W Alps frequent occurrences of hybrids and even larger hybrid swarms were revealed. In longer valley systems we find a common altitudinal distribution of both pines: in lower altitudes of ca. 1000–1500 m a. s. l. \pm pure stands of *P. sylvestris*, between ca. 1500 and 1700 m hybrid swarms are found, and above 1700 m (up to usually 2100–2300 m) pure stands of *P. uncinata* subsp. *uncinata* occur.

List of localities investigated:

- Spain, Teruel Prov., Sierra de Gudar, Penarroja massif, alt. 1950 m, hybrids rather frequent (May 1993)
- France, Pyrénées Atlantiques Dept., Puerto de Somport, near frontier of Spain, alt. 1630 m, hybrids sporadic (May 1993)
- Spain, Lleida Prov., Pirineu Occidental Mts., Upper valley of Noguera Ribagorçana S of Vielha tunnel, alt. 1500 m, hybrids sporadic (May 2006)
- Italy, Piemonte, between Cesana Torinese and Col de Montgenevre, alt. 1500–1600 m, hybrids rather frequent (Sept. 1992)
- France, Hautes Alpes Dept., Parc National Régional du Queyras, along the road S below Col de l'Izoard, around alt. 1900 m hybrids rather frequent (Sept. 2004)
- France, Hautes Alpes Dept., above Guillestre towards Col de Vars, alt. 1550–1700 m, a hybrid swarm (Sept. 1992)
- France, Alpes de Haute Provence Dept., valley between Jausiers and Col de la Bonette, alt. 1500–1700 m, a hybrid swarm (Sept. 1992, Oct. 2004, May 2006)
- France, Vosges Mts. and Dept., Gérardmer, Morte Femme peatbog Natur. Res. near C. Beillard, alt. 610–615 m, hybrids rather sporadic (May 2006)
- Switzerland, Graubünden, Rätische Alpen, mouth of upper Albula valley above Filisur 17 km SW of Davos, alt. 1100–1500 m, hybrids sporadic (Oct. 2005)
- Switzerland, Graubünden, about 120 m SW of a road junction St. Moritz – Samedan – Pontresina near Punt Muragl, ca. 2 km NW of Pontresina, alt. 1735 m, one hybrid individual (Sept. 2007)
- Austria, Tirol, Reutte, Mt. Zwieselberg, S-SE slopes above N shore of Plansee lake, alt. 980–1100 m, limestone screes (neotype locality of *Pinus rotundata* LINK), hybrids rather frequent (Sept. 2002)
- Austria, Tirol, foot of NE slopes W opposite Nassereith NE of Imst, alt. >850 m, hybrids sporadic (Sept. 2005)
- Germany, Oberbayern, near frontier of Austria, Isar valley S of Mittenwald, alt. 930 m, a small hybrid swarm (Sept. 1994)

6. Hybrids Between *Pinus uncinata* subsp. *uliginosa* and *P. sylvestris*

According to our present concept (see also BUSINSKÝ, 2008, 2009), *Pinus uncinata* subsp. *uliginosa* (bog pine) is distributed mainly in the territory of the Czech Republic, with localities in the adjacent regions of the neighbouring countries not more than 30 km from the Czech border (SW Poland, Sachsen, Oberfranken, Oberpfalz and Oberösterreich). The occurrence of



Fig. 4. *Pinus x rhaetica*, epitype tree from the vicinity of Pontresina east of St. Moritz in Graubünden, Switzerland.

this taxon depends on peatbog biotopes (for the altitudinal range, see Table 1), where it often grows in the vicinity of natural and/or planted populations of *P. sylvestris*. Both pines commonly hybridize with one another, more frequently at lower altitudes where hybrid swarms usually occur.

The only name taxonomically interpretable as a hybrid of the *Pinus uncinata* subsp. *uliginosa* × *P. sylvestris* parentage was published by BECK 1888 at the rank of a species as “*Pinus digenea (sylvestris* × *uliginosa)*”. Original syntype material of *P. × digenea* BECK corresponding to the protologue is deposited in PRC. It consists of several specimens with the following label: “Waldtorfmoor bei Kösslersdorf (Böhmen) nächst Litschau; 29.6.1887”. Original determination is “*Pinus digenea (uliginosa* × *silvestris)*”. The place of collection is in accordance with the first sentence of the protologue: “Schliesslich erwähne ich noch einer hybriden Föhre, die auf den Torfmooren von Kösslersdorf an der böhmischen Grenze, zerstreut auch im Sophienwalde bei Erdweis und im schwarzen Moos bei Brand von mir beobachtet wurde.” The first locality, “Torfmoore bei Kösslersdorf” is a peatbog, which is called “Široké blato” today and situated on the Czech side of the border frontier E of Suchdol nad Lužnicí. A large hybrid swarm of pines in question still exists there. The “Schwarzes Moos” is found 4 km southwards on the Austrian side but a small remnant of a hybrid population of these pines is recently found near the W margin of the peatbog on the Czech territory. The last site, “im Sophienwalde bei Erdweis” is called “Žofinka” today and is situated 5 km from the Austrian border W of Nová Ves nad Lužnicí, also with a hybrid swarm. The first sentence of the description given in the protologue: “Aufrechter Baum mit bräunlichgrauer Rinde an den älteren Aesten”, and especially the following character “einjährige Zapfen ... auf gekrümmten Stielen nickend” clearly prove a hybrid influence of *P. sylvestris*. (For the illustration of the important conelet character, see also Fig. 5.)

The correct name for this hybrid, when we accept the bog pine at the subspecific rank is *Pinus* × *rhaetica* BRÜGGER nothosubsp. *digenea* (BECK) K. RICHT. 1890.

The lectotype specimen shows most of the diagnostic characters closer to *P. sylvestris* (fully reflexed female cones, shape of apophyses, almost square epidermis cells, long distance between vascular bundles, see Tab. 2), whereas the hybrid influence of *P. uncinata* subsp. *uliginosa* is not easy to observe (it can be recognized chiefly in the character of sclerenchymatic cells in the vicinity of vascular bundles). For this reason, in order to interpret the lectotype, we select an epitype from the representative hybrid tree found at the same locality.

Pinus × *digenea* BECK, Ann. K. K. Naturhist. Hofmus. 3: 77 (1888). – Lectotype, selected by CHRISTENSEN 1985: Niederösterreich, Waldtorfmoor bei Kösslersdorf (Böhmen) nächst Litschau, 29.6.1887, G. R. BECK VON

Table 2. – Basic leaf anatomy of the type specimens examined

	epidermis cells in cross section	number of resin ducts	distance between v.b., as a multiple of v.b. width	*sclerenchymatic cells along and between v.b.
<i>Pinus × rhaetica</i> epitype [UN × SY]	almost square	D 4–6, V 1–3, max. 8 together	0.8–1.2	state 3
<i>Pinus × celakovskiorum</i> lectotype [MU × <SY]	square	D 8–11, V 3–4, max. 15 together	1.5–1.8	state 4
<i>Pinus × celakovskiorum</i> epitype	radially oblong	D (6)7–9, V (0)1–2(3), max. 11 together	0.8–1.3	state 4
<i>Pinus × digenea</i> lectotype [UL × <SY]	almost square	D 6–8, V 1–4, max. 11 together	1.7–2.4	state (1)2–3
<i>Pinus × digenea</i> epitype	shortly radially oblong	D 8–11, V 1–2(3), max. 13 together	0.9–1.3	state 4
<i>Pinus × ascendens</i> type [MU × UN]	radially oblong	D 2–4, V 0–1	0.7–1.0	state 4–5
<i>Pinus × ascendens</i> nothosubsp. <i>skalickyi</i> type [MU × UL]	radially oblong	D 4–5, V 1	0.6–1.7	state 1–2
<i>Pinus uncinata</i> var. <i>ancestralis</i> type	radially oblong	D 1–3, V 0–1	(0.3–)0.8–1.4	state 2–3

Abbreviations used: v.b. = vascular bundles, SY = *Pinus sylvestris*, UN = *P. uncinata* subsp. *uncinata*, UL = *P. uncinata* subsp. *uliginosa*, MU = *P. mugo*, D = resin ducts along the dorsal side of the needle, V = resin ducts along the ventral side of the needle.

* See the character states used in Table 1 and Fig. 2.

MANNAGETTA s.n., PRC, No. 451408. – **Epitype**, designated here: Czech Republic, S Bohemia (near frontier of Austria), Jindřichův Hradec District, Chlum u Třeboně, abandoned village Nová Ves u Klikova (former Kösslersdorf), Široké Blato peatbog Natur. Res., N part, peatbog pine wood, together with *Pinus sylvestris*, alt. 500 m, 48°54'52.0"N, 14°59'13.0"E (WGS-84), [tree: 115 cm trunk circumfer., 20.5 m high, middle aged], 5.11.2009, as *Pinus × rhaetica* BRÜGGER nothosubsp. *digenea* (BECK) K. RICHT.; R. BUSINSKÝ CS 09/5–03 (epitype: PRC; isoepitypes: PR, PRA, BM, G, P).

List of localities investigated:

Germany, Bayern, Oberfranken, Fichtelgebirge Mts., Fichtelberg, Fichtelsee Moor Natur. Res., alt. 745–770 m, several hybrid individuals at margins of the peatbog (Oct. 2007)

- Germany, Bayern, Oberfranken, Fichtelgebirge Mts., peatbog N of Eger source, W of Weißenstadt, alt. 650 m, remnant of a bog pine population with majority of hybrid individuals (Oct. 2005)
- Germany, Bayern, Oberfranken, Peatbog Natur. Res. 4.5 km SE of Selb, 1 km from frontier of W Bohemia near Libá (Cheb Distr.), alt. 575 m, remnant of a bog pine population with several hybrid individuals (Oct. 2007)
- Czech Republic, W Bohemia, Cheb Distr., Hájek, Soos Natur. Res., alt. 435 m, a hybrid swarm (June 1983)
- Czech Republic, W Bohemia, Sokolov Distr., V rašelinách peatbog Natur. Res. 3.5 km NW of Oloví, alt. 665–675 m, a hybrid swarm at margins of the peatbog (Jan. 2002, Nov. 2005)
- Czech Republic, W Bohemia, Tachov Distr., Lesná, Farské bažiny peatbog Natur. Res., alt. 730 m, several hybrid individuals (July and Aug. 1991, Sept. 2002)
- Czech Republic, W Bohemia, Tachov Distr., Lesná, Podkovák peatbog Natur. Res., alt. 705 m, a hybrid swarm (Aug. 1991, Apr. 1993)
- Poland, Lower Silesia (Dolny Ślask), Bory Dolnoślaskie region, moorlands N of Wegliniec railway station, alt. 195 m, scattered hybrid individuals (Apr. 2003)
- Czech Republic, S Bohemia, Prachatice Distr., Šumava Mts., Lenora, Velká Niva peatbog, alt. 746–760 m, hybrids rather frequent (Mar. 1991)
- Czech Republic, S Bohemia, Prachatice Distr., Šumava Mts., Volary, Malý and Mrtvý Luh peatbogs, alt. 733–743 m, several hybrid individuals (Aug. and Sept. 1985, May and July 1986)
- Czech Republic, S Bohemia, Český Krumlov Distr., Bobovec peatbog Natur. Res. SW of Světlík, alt. 775 m, a hybrid swarm (Sept. 2006)
- Czech Republic, S Bohemia, Tábor Distr., Borkovice, Borkovická blata peatbog Natur. Res., alt. 423–425 m, hybrids frequent (Jan. 2002, May 2003, May, Sept., Oct. 2007, May, June, Sept. 2008)
- Czech Republic, S Bohemia, Červené Blato peatbog Natur. Res. SW of Suchdol nad Lužnicí, alt. 470–475 m, a hybrid swarm at margins of the peatbog (Apr. 1986, Aug. 1995, Sept. 2001)
- Czech Republic, S Bohemia, Jindřichův Hradec Distr., Dvory nad Lužnicí, Žofínka peatbog Natur. Res., alt. 470–475 m, a hybrid swarm (Sept. 2001)
- Czech Republic, S Bohemia, Jindřichův Hradec Distr., Losí blato u Mirochova peatbog Natur. Res. E of Mirochov, alt. 470–478 m, hybrids frequent (Oct. 2001, July 2003)
- Czech Republic, S Bohemia, Jindřichův Hradec Distr., Chlum u Třeboně, Široké blato peatbog Natur. Res., alt. 490–500 m, hybrids frequent at margins of the peatbog (Oct. 2001, May 2002, June 2007)
- Czech Republic, S Bohemia, Jindřichův Hradec Distr., western margin of Schwarzes Moos peatbog 3 km E of Rapšach, along frontier of Austria, alt. 505 m, several hybrid individuals (June 2007)
- Czech Republic, Moravia, Žďár nad Sázavou Distr., Dářko peatbog Natur. Res., Velké Dářko pond, alt. 620 m, hybrids scattered at margins of the peatbog (Dec. 2001, May 2002, Apr. 2003)



Fig. 5. *Pinus × rhaetica* nothosubsp. *digenea*, intermediate position of female cones in a tree from the Majdalena vicinity in the district of Jindřichův Hradec, S Bohemia.

7. Notes on the Hybridization Between *Pinus mugo* s. str. and *P. sylvestris*

7.1. Variation Observed in the Non-hybrid Populations of *Pinus mugo* s. str.

One of the key characters of *P. mugo* in this complex is cone actinomorphy. In the Alps, the Carpathians and in the Balkans, and also in the northernmost sites in the Krkonoše Mts. (the Giant Mts.), this feature is quite stable, not showing any geographic trend. The only exception to this rule was found in a few Italian populations: the Maiella Mts. in Abruzzo, Monte Nero in the Appennino Ligure, and in the vicinity of Bormio in Lombardy. An old introgressive influence of *P. uncinata* might have been responsible for frequent zygomorphic cones in these marginal populations (MINGHETTI 1997, BORATYŇSKA & al. 2005). On the other hand, another population considered as introgressive (with an influence of *P. uncinata*) by MINGHETTI 1997 and MINGHETTI & NARDI 1999 in the vicinity of Monte Baldo east of Lago di Garda, proved to be very close to average populations of *P. mugo*. As the latter population is a source of the lectotype of this name, there is no need for conserving another type for this name (cf. BRUMMITT 2001).

As regards the shrubby habit of *P. mugo*, there are also exceptional individuals, scattered in some extrazonal peatbog populations. They are almost erect to suberect, with many stems. Many of them are plants growing at sites surrounded by higher trees at lower altitudes. Their cone morphology does not point to any influence of hybridization. The type population of *P. uncinata* var. *pseudopumilio* WILLK., later often treated as a hybrid between *P. mugo* and *P. uncinata* subsp. *uliginosa* (*P. mugo* × “*P. rotundata*”), from the vicinity of Boží Dar (Gottesgab) in the Krušné hory Mts. (the Erzgebirge) is an example of this non-hybrid aberrant habit (BUSINSKÝ & KIRSCHNER 2006). Very rarely the non-hybrid *P. mugo* may develop even an erect monocormic habit, usually seen in very sporadic individuals in populations (BUSINSKÝ 1998).

List of localities investigated:

Pinus mugo with suberect shrubby habit:
(all in the Czech Republic)

W Bohemia, Karlovy Vary Distr., Krušné hory Mts., Boží Dar, Božídarské rašelinistiě peatbog Natur. Res., alt. 1000–1030 m (Sept. 1995, Nov. 2005)

W Bohemia, Chomutov Distr., Krušné hory Mts., Klínovec massif, peatbog between Mt. Macecha and Meluzina, alt. 1040 m (Apr. 1993)

N Bohemia, Chomutov Distr., Krušné hory Mts., Červené blato peatbog 2 km SE of Kovářská, alt. 895 m (Aug. 2005)

N Bohemia, Chomutov Distr., Krušné hory Mts., peatbogs W to N of Hora Sv. Šebestiána, alt. 830–870 m (June 1985, June 1986, May and June 1987, Aug. 2005)



Fig. 6. *Pinus × ascendens*, type tree from the vicinity of Wolfgang Pass between Davos and Klosters in Graubünden, Switzerland.

- N Bohemia, Chomutov Distr., Krušné hory Mts., Jindřichova Ves, Novodomské rašeliniště peatbog Natur. Res., alt. 810–828 m (June 1985, Sept. 1995, Aug. 2005)
- S Bohemia, Prachatice Distr., Šumava Mts., Borová Lada, Chalupská slať peatbog Natur. Res., alt. 905–915 m (May 1992, Sept. 1995, Oct. 2005)
- S Bohemia, Prachatice Distr., Šumava Mts., peatbogs in vicinity of Knížecí Pláně, alt. 970–995 m (Oct. 2005)
- S Bohemia, Prachatice Distr., Šumava Mts., peatbog 1 km E of Žďárecká hora between Strážný and Knížecí Pláně, alt. 907 m (Sept. 1990, Oct. 2005)
- S Bohemia, Český Krumlov Distr., Šumava Mts., Loučovice, Rašeliniště Kapličky peatbog Natur. Res., alt. 903 m (Sept. 2007)

Pinus mugo with erect monocormic habit without hybrid characters:

- Czech Republic, S Bohemia, Klatovy Distr., Šumava Mts., Modrava, peatbog 2.2 km W of Modrava crossroads in the Mlynářská & Rybářská slať peatbog complex, alt. 1040 m, several monocormic individuals in shrubby pine growth (Sept. 2006)
- Poland, Izerskie Góry Mts., along frontier of N Bohemia, ca. 0.3 km SE of Gorzysztow hut in the Torfowisko Doliny Izery peatbog Natur. Res. SE of Izera/Jizera source, alt. 840 m, a group of monocormic individuals at a margin of shrubby pine growth, WGS-84: 50°51'12"N, 15°21'57"E (May 2003)
- Slovakia, NW part of Nízké Tatry Mts., Salatín massif, Mt. Malý Salatín (1444 m), NNE top ridge, alt. ca. 1450 m, rocky limestone ridge at a spruce timber line and lower limit of *Pinus mugo* local occurrence, one monocormic tree-like individual: 100 cm trunk circumfer., 6 m h. (top dead), more than 100 years old, specimen: R. BUSINSKÝ CS 87/7-01 (20 June 1987, Sept. 1990)

7.2. Frequency of Hybridization Between *Pinus mugo* and *P. sylvestris*

In contrast to the frequent and complex hybridization between *Pinus sylvestris* and *P. uncinata* s. lat., the parental combination of *P. mugo* s. str. and *P. sylvestris* is strikingly rare and geographically restricted. This difference between the behaviour of *P. mugo* and *P. uncinata* is one of the indicators of their separate specific status. Although *P. mugo* and *P. sylvestris* are frequently sympatric and their populations are not rarely in contact, the hybrid individuals are rare or absent throughout large areas (in particular, a striking absence of the hybrid is known from the large territory of the Balkans and Dinarids). Hybrid swarms, a result of frequent hybridization and introgression between the two species, are known only from a few peatbog sites at the W and NW foothills (640–830 m a.s.l.) of the Tatra Mts.: Zuberec, N Slovakia, Suchá Hora, N Slovakia, S and SW of Nowy Targ, S Poland, and at the E foot (750 m a.s.l.) of Mt. Pilsko near Oravská Polhora, N Slovakia (STASZKIEWICZ & TYSZKIEWICZ 1969, BOBOWICZ 1990a, BUSINSKÝ 1998, KORMUTAK & al. 2008, 2009).

7.3. Nomenclature of the Hybrid

The hybrid combination was mentioned several times in the literature, and ASCHERSON & GRAEBNER 1897 introduced a binomial for it (as "*P. sil-*

vestris × *pumilio*): *P. × celakovskiorum* ASCH. & GRAEBN., Syn. Mitteleur. Fl. 1: 230 (1897). The authors of the binomial refer to two specimens, each also mentioned in the literature, i.e. [South Bohemia] “Im südlichem Böhmerwalde Seeau im Kessel unter dem Plöckensteiner See nur ein Baum (L. ČELAKOVSKÝ fil. ! vgl. L. ČELAKOVSKÝ Sitzb. Böhm. G. Wiss. 1893 X. 6., and [Austria, S. of Innsbruck] Tirol: Trins R. v. WETTSTEIN ! Sitzb. Akad. Wiss. Wien XCVI. 324 und br.)”.

For the sake of completeness, we have to mention that, in spite of repeated literature records, the name *P. × celakovskiorum* originally did not refer to a hybrid between taxa at the species rank. It most probably was meant as a binomial for the *P. sylvestris* subsp. *sylvestris* × *P. montana* subsp. *pumilio* combination which ought to have been accorded the rank of nothosubspecies (ICBN, Art. H.5.1, H.5.2, McNEILL & al. 2006). However, although the name was incorrect at the time of publication, it becomes correct when used for a hybrid between two species; it cannot be considered as illegitimate (Art. 52.3. Note 3) although two older binomials were quoted by ASCHERSON & GRAEBNER 1897 for the same combination of parental species.

The two specimens mentioned in the text (and marked with !, which indicates that P. ASCHERSON might have seen the specimens) have to be treated as syntypes. CHRISTENSEN 1987 selected a lectotype, the specimen collected by L. F. ČELAKOVSKÝ (fil.) at Plešné jezero (Lake, Plöckensteiner See) in 1892. Exactly one hundred years after the ČELAKOVSKÝ's collection, two relatively young individuals of this hybrid were found by R. BUSINSKÝ at the same locality, among boulders of the moraine below the lake, at 1070 m a. s. l.

The lectotype specimen is substantially closer to *P. sylvestris* (shape and colour of apophyses, square epidermis cells, high number of resin ducts, long distance between vascular bundles, see Tab. 2), whereas the hybrid influence of *P. mugo* is hardly discernible. Because female cones are absent in the lectotype specimen, the most important diagnostic character is not available. In order to safely interpret the lectotype, we select an epitype from a newly found, more intermediate individual at the same locality.

Pinus × celakovskiorum ASCH. & GRAEBN., Syn. Mitteleur. Fl. 1: 230 (1897). – Lectotype (selected by CHRISTENSEN 1987): Böhmenwald, “in der Seeau” unter dem Plöckensteiner See, ein einziger, bei 16 m. hoher Baum unter den Eltern, Aug. 1892, L. ČELAKOVSKÝ jun. s.n., PRC, No. 451409 (not PR as mistakenly stated by CHRISTENSEN 1987). – **Epitype**, designated here: Czech Republic, S Bohemia (near frontier of Austria), Šumava Mts., Prachatice District, Nová Pec, NE slopes of Mt. Plechý (1378 m), boulder moraine called “Kamenné moře” on E side of Plešné Jezero lake, margin of *Pinus mugo* growths with scattered *P. sylvestris* along forest of *Picea abies*,

alt. 1060 m, 48°46'36.2"N, 13°52'21.8"E (WGS-84), [slender tree with one prostrate, 7 m long trunk, 43 cm in circumfer., and one main S-shaped branch], 12.11.2009; R. BUSINSKÝ CS 09/ 6-05 (epitype: PRC; isoepitypes: PR, PRA, BM, G).

List of localities investigated:

- Czech Republic, W Bohemia, Chomutov Distr., Krušné hory Mts., Klínovec massif, peatbog between Mt. Macecha and Meluzina, alt. 1040 m, one hybrid individual (Apr. 1993)
- Czech Republic, S Bohemia, Prachatice Distr., Šumava Mts., Borová Lada, Chalupská slať peatbog Natur. Res., alt. 905 m, several hybrid individuals along E margin of the peatbog (May 1992, Sept. 1995, Oct. 2005)
- Czech Republic, S Bohemia, Prachatice Distr., Šumava Mts., Boulder moraine E of Plešné Jezero lake, NE slopes of Mt. Plechý, alt. 1070 m, two hybrid individuals (May 1992)
- Poland, Klodzko, Góry Stolowe Mts., near frontier of E Bohemia, Sandstone rocks of Bledne Skaly Natur. Res., alt. 850 m, several hybrid individuals (May 2003)
- Slovakia, Malá Fatra Mts., Mt. Sokolie, N slopes above Terchová, alt. 1000–1100 m, several hybrid individuals (Oct. 1989)
- Slovakia, Slovenské (Oravské) Beskydy Mts., Oravská Polhora, Tisovnica peatbog Natur. Res., alt. 745 m, a hybrid swarm (Oct. 1989)
- Slovakia, Dolný Kubín Distr., Oravská kotlina basin, near frontier of Poland, peatbogs N of Suchá Hora, alt. 750 m, several hybrid individuals (May 1985)
- Slovakia, Západné Tatry Mts., NW foot, Zuberec, Medzi Borami peatbog, alt. 840 m, a hybrid swarm (May 1985, May 1988)
- Italy, Trentino – Alto Adige, Dolomiti Mts., west slopes of Kreuzkofel massif above Abtei (Badia) in Gader valley, alt. 1750 m, several hybrid individuals (Oct. 2007)
- Italy, Trentino – Alto Adige, Dolomiti Mts., upper part of Valle di Cassiano at SW foot of Cunturines massif, alt. 1650 m, one hybrid individual (Oct. 2007)

8. Hybridization Between *Pinus mugo* s. str. and *P. uncinata* subsp. *uncinata*

The name *Pinus rotundata* LINK was referred either to what is called *P. uncinata* subsp. *uliginosa* in the present paper, or to a hybrid between *P. sylvestris* and *P. mugo* (cf. STASZKIEWICZ & TYSZKIEWICZ 1972), or more frequently to hybrid or hybridogenous forms between *P. mugo* and *P. uncinata*. The latter conception was introduced by CHRISTENSEN 1987 who used the epithet at the rank of a nothosubspecies. A detailed study of the variation of *P. uncinata* and the neotype locality of *P. rotundata* (BUSINSKÝ & KIRSCHNER 1996) showed that the name *P. rotundata* LINK refers to *P. uncinata*, much closer to subsp. *uncinata* than to subsp. *uliginosa*, so that the name may be best treated as a synonym of the type subspecies. An inevitable conclusion inferred from this fact is that there is no binomial referable to the parent combination of *P. mugo* TURRA, s. str. and *P. uncinata* RAMOND ex DC. A new binomial is therefore introduced here:

Pinus* × *ascendens* BUSINSKÝ, *nothospec. nova**Parents:** *Pinus mugo* TURRA × *P. uncinata* RAMOND ex DC.

Note: The new name refers to all hybrid forms with the above parentage but the diagnosis below primarily refers to nothosubsp. *ascendens*, as another nothosubspecies is included in *P. × ascendens* below.

Diagnosis: Arbor hybridae originis a parentibus dictis notis sequentibus distinguitur: arbor humilis truncis pluribus (saepissime 3–4) erectis, basi saepe ascendentibus, a *Pinus mugo* differt strobilis zygomorphis apophysibus plus minusve pyramidalibus.

A low tree with several (usually 3–4) erect trunks, often with an ascending base, main branches often bow-like, elongated-ascending, ovulate strobili always erect in the first year, seed cones zygomorphic, with ± pyramidal apophyses.

Type: Switzerland, Canton Graubünden, Wolfgang Pass region between Davos & Klosters, E slope of overgrown screes NW above the pass; growth of prostrate shrubs of *Pinus mugo* together with sparse hybrid individuals near forest stand of *Pinus uncinata*, siliceous ground; alt. 1745 m, 46°50'11"N, 9°50'46"E (GPS: WGS-84), erect shrubby tree 5 m high with four main (& one slender) trunks from the ground with 52, 50, 50 cm trunk circumfer. at 1.3 m h. and 75 cm t. c. at 0.7 m h., the last bifurcated at 0.8 m h., 22.10.2005; R. BUSINSKÝ 61102 (holotype: PR; isotypes: PRA, BM, G, P). – See also Fig. 6.

List of localities investigated:

- Switzerland, Graubünden, Wolfgang Pass region between Davos and Klosters, alt. 1700–1800 m, several hybrid individuals (Oct. 2005)
- Switzerland, Graubünden, Ober-Engadin, Val Susauna, alt. 1880 m, a small hybrid swarm (Sept. 1992)
- Switzerland, Graubünden, west side of Ofenpass (Pass dal Fuorn) towards Ova dal Fuorn E of Zernez, alt. 2100–2200 m, several hybrid individuals (Sept. 2005)
- Italy, Lombardia, Ortles Alps, Valle del Braulio along the road from Bormio to Passo di Stelvio, alt. 1600–1900 m, an introgressive subpopulation between both parent recent occurrence (Sept. 1994, Sept. 2005)
- Italy, Lombardia, Ortles Alps, Bernina Mts., E branch of Val Malenco, vicinity of Campo Moro, alt. 2000 m, several hybrid individuals (Sept. 2005)
- Germany, S Bayern, North foot of Mt. Grasköpfl in the Isar valley between Vorderriß and W corner of Sylvensteinsee, alt. 760 m, several hybrid individuals of *Pinus mugo* × *P. uncinata* var. *ancestralis* (Sept. 2005)

Pinus mugo s. str. × *P. uncinata* s. str. – introgressive populations without recent occurrence of both parents in the vicinity

- Germany, Baden-Württemberg, Nord-Schwarzwald, Hohlohsee peatbog Natur. Res. NE above Forbach, alt. 980 m (Sept. 2004)

- Germany, Baden-Württemberg, Nord-Schwarzwald, Wildseemoor Natur. Res. SW of Bad Wildbad, alt. 900–910 m (Sept. 2004)
- France, Haut-Rhin Dept., Vosges Mts., around E corner of Lac Blanc above Colmar, alt. 1060–1110 m (Sept. 2004)
- France, Haut-Rhin Dept., Vosges Mts., above E corner of Lac Noir above Colmar, alt. 970 m (Sept. 2004)
- Italy, Emilia-Romagna, Piacenza and Parma Prov. boundary, Appennino Ligure Mts., Maggiorasca massif, Monte Nero (1754 m), alt. 1500–1750 m (Oct./Nov. 2006)

9. Hybridization Between *Pinus mugo* s. str. and *P. uncinata* subsp. *uliginosa*

Hybridization between *P. mugo* and *P. uncinata* takes place also farther to the northeast, on peatbog sites in the regions where the latter parent is represented by the subsp. *uliginosa*. Individuals or hybrid swarms phenotypically corresponding to this hybrid combination were found in areas of contact between the parental taxa (BUSINSKÝ 2008). The hybrid was most frequently found in S Bohemia (the Šumava Mts., Böhmerwald) and in NW Bohemia (the Krušné hory Mts., Erzgebirge); its occurrence is probable also in the Saxonian part of the Erzgebirge in Germany because intermediates between the two taxa are reported from there (GOLDE 2000).

Pinus* × *ascendens* nothosubsp. *skalickyi* BUSINSKÝ, nothosubsp. *nova

Parents: *Pinus mugo* TURRA × *P. uncinata* subsp. *uliginosa* (NEUMANN) BUSINSKÝ

Diagnosis: A subspecies typica differt apophysibus humile pyramidalibus usque obtusis et praesentia in sphagnetis.

From the type subspecies it differs by low pyramidal to obtuse apophyses and by its occurrence on peatbogs.

Type: Czech Republic, S Bohemia, Šumava Mts., Prachatice District, Nová Pec, NE foot of Mt. Plechý (1378 m), woodland peatbog Jezerní Luh Natur. Res., peatbog with mixed stands of shrubby mountain pine and monocormic bog pine, together with *Pinus sylvestris* & *Picea abies* along margins, alt. 910 m, 48°47'21.9"N, 13°52'20.0"E (WGS-84), [erect shrubby tree 7 m high, with two main trunks (60 & 56 cm circumfer.), one slender trunk and four basal bow-like ascending branches (max. 34 cm circumfer.)], 12.11.2009; R. BUSINSKÝ CS 09/6-06 (holotype: PR; isotypes: PRA, PRC, BM, G, P).

Paratype: Czech Republic, S Bohemia, Šumava Mts., Prachatice District, Strážny, Splavské Rašelinište peatbog Natur. Res., peatbog with growths of shrubby mountain pine, with scattered monocormic bog pines and intermediary hybrid forms, alt. 810 m, 48°53'51.1"N, 13°44'02.3"E (WGS-84), [erect shrubby tree 8 m h., with three trunks: 60, 54 & 52 cm

circumfer.], 11.11.2009; R. BUSINSKÝ CS 09/6-02 (paratype: PR; isoparatypes: PRA, PRC, G).

Eponymy: After Vladimír SKALICKÝ, the author of the account of the *Pinus mugo* complex and its hybrids in the Flora of the Czech Republic (SKALICKÝ 1988).

This hybrid combination is generally more difficult to discern. The main reason is that plants with the intermediate general habit of the hybrid can be confused with marginal forms of *P. mugo* with suberect growth and several to many stems. It is therefore necessary to evaluate both the population situation at the locality and the geographic context. Below, separate lists of localities are given for populations where both parental taxa are present and old introgressive populations with recent occurrence of only one of the parents in the area.

List of localities investigated:

- Czech Republic, W Bohemia, Sokolov Distr., Krušné hory Mts., Haar peatbog Natur. Res. 3 km SW of Přebuz, alt. 820 m, a hybrid swarm (Nov. 2005)
- Czech Republic, W Bohemia, Chomutov Distr., Krušné hory Mts., peatbog 1.5 km E of Kovářská, alt. 870 m, several hybrid individuals (Aug. & Nov. 2005)
- Czech Republic, S Bohemia, Prachatice Distr., Šumava Mts., Strážný, Splavské rašeliniště peatbog Natur. Res., alt. 805–817 m, a hybrid swarm (Mar. 1991, May 1992)
- Czech Republic, S Bohemia, Prachatice Distr., Šumava Mts., Nová Pec, Jezerní Luh peatbog Natur. Res. at NE foot of Mt. Plechý (1378 m), alt. 910 m, a hybrid swarm (Nov. 2009)
- Czech Republic, S Bohemia, near frontier of Austria, Český Krumlov Distr., Šumava Mts., Multerbergské rašeliniště peatbog Natur. Res. SW of Přední Výtoň, alt. 790 m, a hybrid swarm (Oct. 2005)

Pinus mugo s. str. × *P. uncinata* subsp. *uliginosa* – introgressive populations with recent occurrence of only one of the parents in the area

- Czech Republic, W Bohemia, Cheb Distr., Slavkovský les Mts., Kladská, Kladské rašeliny – Lysiny peatbog Natur. Res., alt. 925–950 m, a population 2 km distant from an occurrence of *Pinus uncinata* subsp. *uliginosa* (Apr. 1993)
- Czech Republic, S Bohemia, Český Krumlov Distr., Novohradské hory Mts., Pohří na Šumavě, Pohorské rašeliniště peatbog Natur. Res., alt. 895 m, a small population 3 km distant from an occurrence of *Pinus mugo* s. str. (Aug. 1999, May 2007)
- Austria, Niederösterreich, Weitra-Region, Freiwald (Waldviertel) Mts., Grosse Heide peatbog Natur. Res., Karlstift, alt. 880 m, a population 4 km distant from an occurrence of *Pinus mugo* s. str. (June 2007)
- Poland, Góry Bystrzyckie Mts., Duszniki Zdroj – Zieleniec, Czarne Bagno and Topielisko peatbogs, Torfowisko pod Zieleniecem Natur. Res., alt. 750–765 m, a population 11 km distant from an occurrence of *Pinus uncinata* subsp. *uliginosa* (Apr. 1997, May 2002)

10. A Nomenclatural and Taxonomic Survey of Hybrids with
Pinus mugo, *P. uncinata* and *P. sylvestris* as Parents

Pinus × *celakovskiorum* ASCH. & GRAEBN., Syn. Mitteleurop. Fl. 1: 230 (1897).

Lectotype (fide CHRISTENSEN 1987): L. ČELAKOVSKÝ jun. s.n./Aug. 1892, PRC, No. 451409.

Epitype: R. BUSINSKÝ CS 09/ 6-05 (epitype: PRC; isoepitypes: PR, PRA, BM, G).

= *Pinus mugo* TURRA s. str. × *P. sylvestris* L.

Pinus × *rhaetica* BRÜGGER (nothosubsp. *rhaetica*), Jahresber. Naturf. Ges. Graubünden's, ser. 2, 29: 173 (1886).

Orig. material unknown; Neotype (fide CHRISTENSEN 1987): CHRISTENSEN CH2-5a (neotype: Z); superseded by an element of the original material:

Lectotype: [icon in] H. CHRIST, Flora, Regensburg, 47: Plate I, Fig. VII (1864). – Epitype: R. BUSINSKÝ 65105, (epitype: PR; isoepitypes: BM, G, P, PRA).

= *Pinus uncinata* RAMOND ex DC. subsp. *uncinata* × *P. sylvestris* L.

Pinus × *rhaetica* nothosubsp. *digenea* (BECK) K. RICHT., Pl. Europ. 1: 3 (1890).

Basionym: *Pinus* × *digenea* BECK, Ann. K. K. Naturhist. Hofmus. 3: 77 (1888).

Lectotype (fide CHRISTENSEN 1987): G. R. BECK VON MANNAGETTA s.n. / 29.6.1887 (lectotype: PRC, no. 451408).

Epitype: R. BUSINSKÝ CS 09/ 5-03 (epitype: PRC; isoepitypes: PR, PRA, BM, G, P).

= *Pinus uncinata* subsp. *uliginosa* (NEUMANN) BUSINSKÝ × *P. sylvestris* L.

Pinus × *ascendens* BUSINSKÝ (nothosubsp. *ascendens*) in BUSINSKÝ & KIRSCHNER, Phytion (Horn, Austria) 50 (1): 51 (2010).

Type: R. BUSINSKÝ 61102 (holotype: PR; isotypes: PRA, BM, G, P).

= *Pinus mugo* TURRA s. str. × *P. uncinata* RAMOND ex DC. subsp. *uncinata*

Pinus × *ascendens* nothosubsp. *skalickyi* BUSINSKÝ in BUSINSKÝ & KIRSCHNER, Phytion (Horn, Austria) 50 (1): 52 (2010).

Type: R. BUSINSKÝ CS 09/6-06 (holotype: PR; isotypes: PRA, PRC, BM, G, P).

= *Pinus mugo* TURRA s. str. × *P. uncinata* subsp. *uliginosa* (NEUMANN) BUSINSKÝ

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