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A Study of the *Pinus mugo* Complex

(Variability and Diagnostic Value of Characters in Some Bohemian Populations)

Studie o komplexu *Pinus mugo*
(Variabilita a diagnostická hodnota znaků v několika populacích z Čech)

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Abstract — In six local population samples of the taxa *rotundata*, *pseudopumilio* and *pumilio*, a biometrical analysis has been carried out on the following characters: number of trunks, direction and curving of trunks or main branches, symmetry of cones, height of apophysis. The paper discusses introgressive hybridization as a cause of the variability and transgression of characters. The results of the analysis show that for taxonomic diagnosis a group of characters rather than single characters should be used, though habit is of major importance. The taxa *rotundata* and *pumilio* differ significantly in the six characters, so that they can be placed in different species. The taxon *pseudopumilio* is a component of the species *P. mugo* Turra s. s. The central umbo is not typical for taxon *mugus*. The taxa *rotundata* and *pseudopumilio* have the nature of hybrids between *P. uncinata* and *P. mugo*.

Mountain pine is a variable and taxonomically difficult species. On the whole, it occupies an extensive but disjointed area, covering the European mountain regions (the Pyrenees, the Alps, the Carpathians). In central Europe it reaches the middle regions, and sometimes even the basins (south Bohemia, Austria).

The ecological requirements of the species are diverse, but they fulfil at least one of these two conditions: A) mountain climate — here it grows on the most varied soil (limestone, acid rocks, peat); B) peat-bogs; here it is found in various climatic conditions from the basins to the mountains.

The morfological variability concerns the habit (mono- and polycormic, erect or decumbent), as well as the shape of the cones (size, symmetry, shape of apophysis). This diversity is further emphasised by the relative isolation of some parts of the area (Svoboda 1953).

Many taxa have been described, of which the majority have the rank of forma or not even that (Hartig in Willkomm 1861, Niezabitowski 1909 and others). Taxonomically significant are those which are based on a number of characters and which can be classed at least as varieties. These are (Willkomm 1887, Novák 1953):

rostrata Ant. — arborescent, cones large, zygomorphic, height of apophysis equal to, or greater than the width;

rotundata Link. — arborescent, cones zygomorphic; height of apophysis less than the width; umbo eccentric;

pseudopumilio Willk. — shrubby; cones small, zygomorphic; umbo eccentric;

pumilio Haenke — shrubby; cones actinomorphic; umbo eccentric;

mugus Scop. (*typica* Dom.) — shrubby; cones actinomorphic, umbo central.

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The individual taxa are not usually defined in all characters, which makes identification more difficult. These taxa form a continuous series; the higher taxa *uncinata* RAM. and *mugo* TURRA have either a species value, or *uncinata* is regarded as a subspecies from *P. mugo*.

The extent of this series can be schematically indicated as follows:

uncinata				*mugo*
rostrata	*rotundata*	*pseudopumilio*	*pumilo*	*mugus* (*typica*)

With various authors, the extent of the taxa *uncinata* and *mugo* varies considerably. WILLKOMM (1861) combined the first three as *uncinata*, the fourth and fifth are separate. DOMIN (1935) and NOVÁK (1953) maintain that subsp. *uncinata* has the same scope, while *pumilio* and *mugus* (*typica*) are combined as subsp. *mugus*. GAUSSEN (1960) distinguishes taxa *uncinata* (to which he adds var. *rotundata*), *mugus* and *pumilio*; he does not consider *pseudopumilio* at all. ROTHMALER (1963) likewise does not specifically mention them, but he includes these formas in the taxon *rotundata*, which he connects with *pumilio* and *mugus* as *P. mugo* TURRA; *P uncinata* RAM. he divides into a separate species. GAUSSEN, HEYWOOD and CHATER (1962) distinguish *P. mugo* TURRA (*P. mugus* SCOP., incl. *P. pumilio* HÄNKE as a variety) and *P. uncinata* MILL. As a variety of the latter they include *P. rotundata* LINK. also with shrubby forms, but they do not mention it in central Europe. SVOBODA (1953) has quite a different approach. He distinguishes only climatypes within a single species. This concept is criticized by other authors (HOLUB et MORAVEC 1954).

This divergence of opinion springs from the variability, slight reliability and varied evaluation of individual characters. External morphology remains the basis of taxonomical classification, as neither the anatomical structure nor the number of chromosomes provide sufficient distinguishing characters (NOVÁK 1953).

Of the modern taxonomical methods, biometrical analysis of the populations can prove very useful. It facilitates a more objective assessment of individual characters and their diagnostic value. To make such a biometrical analysis is the aim of the present paper.

Material and Methods

Local population samples were chosen so as to be sufficiently representative. That is why taxa *rotundata*, *pseudopumilio* and *pumilio* were selected in six localities in various altitudes. Their brief characteristics are given and abbreviated names are used throughout the paper.

1. Barbora (*rotundata* type): forest range of Barbora near Třeboň (south Bohemia), 430 m above sea level, deep peat, drained and forested as early as the first half of the last century. Mixed forest (*Pinus silvestris*, *Picea excelsa*); also scattered *P. digenea* BECK (*P. silvestris* × *P. rotundata*).

2. Volary (*pseudopumilio* type): peat-bog „Mrtvý luh" near Volary (Šumava mountains), 750 m above sea level; central part of peat-bog with deep peat; pure stand. On the margin of the peat-bog are fragments of arboraceous stand (*rotundata* type), which were not included in the research.

3. Šebestián (*pseudopumilio* type): two small peat-bogs „Polské" and „Pod Novoveským vrchem" in the neighbourhood of the town Hora sv. Šebestiána in Krušné hory (mountains), 850 m above sea level; pure stand, in parts mixed with *Picea excelsa*. Part of the bog covered by spruce forest or destroyed; research carried out on the whole area of the stand.

4. Boží Dar (*pseudopumilio* type): peat-bog in close vicinity of the town Boží Dar in Krušné hory, 1020 m above sea level; mainly pure stand, part of the bog is destroyed. In the surroundings a few individuals of *P. silvestris*. Research carried out on the whole area of the stand.

5. Kvilda (type related to *pumilio*): peat-bog „Jezerní slať" near Horská Kvilda (Šumava mountains), 1060 m above sea level, pure stand on peat-bog of varying depth, sporadically also on mineral soil. Research carried out on the whole area of the stand.

6. Pančice (*pumilio* type): peat-bog on the Pančická louka (Pančice-meadow) in Krkonoše mountains, 1250 m above sea level, pure stand with a slight mixture of *Picea excelsa*; shallow peat or mineral soil. Research carried out on the whole area of the stand.

In each locality the habit characters of one hundred fertile specimens were recorded on the spot, and from each a sample of cones was taken. The aim was a complex classification of various

Tab. 1: Number of trunks (frutescence) — A

Tab. 1: Počet kmenů (keřovitost) — A

	A	a		0	1	2	
Barbora (*P. rotundata*)	—	100		—	—	100	
Šebestián (*P. pseudopumilio*)	85	15		57	28	15	
Boží dar (*P. pseudopumilio*)	97	3		83	14	3	
Volary (*P. pseudopumilio*)	97	3	$\chi^2 = 4.07$	93	4	3	$\chi^2 = 6.74$
Kvilda (*P.* cf. *pumilio*)	99	1	$P > 0.30$	98	1	1	$P > 0.10$
Pančice (*P. pumilio*)	100	—		99	1	—	

character groups (habit, symmetry of cones, shape of apophysis). Therefore, a number of characters were recorded on each plant and for the next step the most suitable were chosen. The majority of them could only be assessed qualitatively, with the aid of various scales.

From the values obtained, the frequencies, mean, variance etc. were calculated. The statistical concordance, or homogeneity was assessed with the aid of the t-test or chi square (Weber 1964, Myslivec 1957), at the significance level 0.05. Probability less than 0.5, but greater than 0.01 is mentioned separately.

All the qualitative characters of the cones were practically identical on the same individual, also in cones of various ages. Indications to the contrary, mentioned in the literature (Novák 1953, Svoboda 1953) are obviously to be ascribed to various deformations of the cones, which sometimes are very slight and are only evident when comparing extensive material. On the other hand, length of cone showed a greater variation on the same individual; whilst the difference between samples were not very great.

Tab. 2: Direction (B) and curving of main branches (C)

Tab. 2: Směr (B) a zakřivení hlavních větví (C)

	B: 0	1	2	3	4		C: 0	1	2	
Barbora (*P. rotundata*)	100	—	—	—	—		100	—	—	
Volary (*P. pseudopumilio*)	65	24	8	3	—		47	35	18	
Šebestián (*P. pseudopumilio*)	5	47	36	10	2		18	30	52	
Boží dar (*P. pseudopumilio*)	7	35	48	10	—	$\chi^2 = 1.61$	6	12	82	$\chi^2 = 4.80$
Kvilda (*P.* cf. *pumilio*)	2	46	44	8	—	$P > 0.30$	3	24	74	$P > 0.20$
Pančice (*P. pumilio*)	1	13	45	39	2		5	14	81	

Tab. 3: Shape of crown (BC)

Tab. 3: Tvar koruny (BC)

	0	1	2	3	4	5	6	
Volary (*P. pseudopumilio*)	33	40	14	4	7	2	—	
Šebestián (*P. pseudopumilio*)	1	11	29	24	23	9	3	
Boží dar (*P. pseudopumilio*)	2	6	12	22	46	12	—	$\chi^2 = 3.60$
Kvilda (*P.* cf. *pumilio*)	—	4	17	33	37	9	—	$P \doteq 0.30$
Pančice (*P. pumilio*)	—	1	10	12	33	42	2	

Results

1. Habit

A. Frutescence (number of trunks) — tab. 1. This character is assessed on the one hand alternately (polycormic — A, monocormic — a), on the other hand by three grades (0 — clearly polycormic, 1 — transitional type; plant with one trunk, but at the basis there are traces of former branches, 2 — clearly monocormic). The difference between the *rotundata* type and the others is very marked.

B) The predominant direction of the trunks or main branches — tab. 2 (0 — vertical, 1 — between and 45°, 2 — roughly 45°, 3 — between 45° and horizontal, 4 — roughly horizontal).

C) Shape (curving) of the trunks or main branches — tab. 2 (0 — straight, 1 — hooked at basis, 3 — bow-shaped or otherwise fully curved).

Both these characters are interrelated and determine the habit of the tree or shrub. Distribution of frequencies changes according to elevation and seems therefore ecologically conditioned and does not show the relationship of individual populations. For this the most suitable is the relation of both characters. It is evident from tab. 2 that they change in the same way in the populations 2—6.

BC) The shape of the crown — the sum of B and C values (0—6) — tab. 3. Statistical concordance of B and C characters is found only between the populations of Boží Dar and Kvilda, which have approximately the same elevation. The dependence on ecological factors (elevation) is very marked (fig. 1).

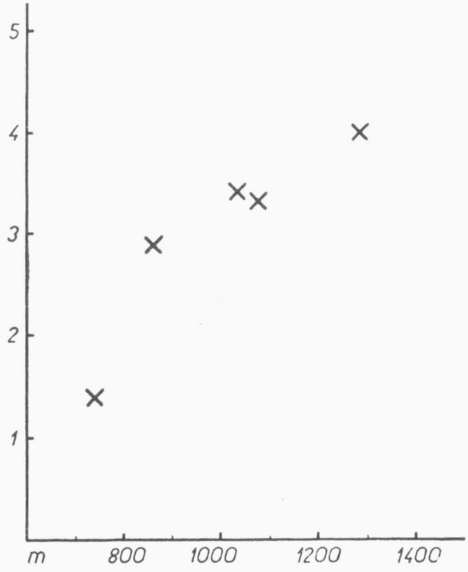

Fig. 1. — Effect of elevation on the shape of crown (x — altitude, y — BC)
Obr. 1. — Vztah tvaru koruny k nadm. výšce (x — nadm. výška, y — BC)

2. Symmetry of cones

D) Position of stalk of cone (eccentricity) — tab. 4 (0 — clearly eccentric, 1 — transitional type, 2 — clearly actinomorphic). The *pseudopumilio* type in this case differs from the *rotundata* type and from the *pumilio* type, but it is hardly homogeneous.

E) Symmetry of apophyses on the basis of the cone — tab. 4 (0 — apophyses different at the same distance from the stalk, 1 — transitional type, 2 — equally shaped in the same distance from the stalk).

F) Symmetry of apophyses on the sides of the cone — tab. 4 (0 — clearly different, 1 — transitional type, 2 — equally shaped).

With the characters of E and F we find a statistical concordance (in the latter case at the 0.01 level only) between the populations of Volary, Šebestián and Boží Dar, i.e. in the *pseudopumilio* type. The Kvilda population differs from all others.

DEF) The total symmetry of the cones — the sum of D, E, F values (0—6), tab. 5. The different distribution of frequencies is conspicuous in the *rotundata* type in comparison with the others. The *pseudopumilio* type populations are again statistically homogeneous. If we join Kvilda to them, the homogeneity sinks very markedly ($P \doteq 0.01$).

If we assess the total symmetry by three grades only, the difference increases. Volary, Šebestián and Boží Dar are highly homogeneous ($P > 0.70$), whereas Kvilda sifnificantly differs from this populations.

3. Apophyses

G) Relative height of apophysis (ratio between height and with) — tab. 6 (0 — height : width ratio very small, apophysis flat, 1 — height: width ratio less than $^1/_2$, 2 — roughly $^1/_2$, 3 — greater than $^1/_2$, 4 — roughly 1). Populations of the *pseudopumilio* type form a gradual transition between the extreme types, they are however closer to the *pumilio* type.

H) Placing of the umbo — tab. 7 (0 — below centre, 1 — central, 2 — above centre). In all populations apophyses with centric umbo prevail. Distribution of frequencies in the *pseudo-*

Tab. 4: Symmetry of cones: placing of the stalk (D), apophyses on the base (E) and on the sides of cone (F)

Tab. 4: Souměrnost šišek: poloha stopky (D), apofysy na bazi (E) a na bocích šišky (F)

	D: 0	1	2		E: 0	1	2		F: 0	1	2	
Barbora (*P. rotundata*)	8	30	62		10	20	70		12	31	57	
Šebestián (*P. pseudopumilio*)	32	61	7	$\chi^2 =$	44	42	14	$\chi^2 =$	52	30	18	$\chi^2 =$
Boží Dar (*P. pseudopumilio*)	55	38	7	$= 16.8$	40	44	16	$= 5.29$ $P >$	58	36	6	$= 10.26$ $P >$
Volary (*P. pseudopumilio*)	35	55	10	$P =$	53	30	17	> 0.10	44	37	19	> 0.025
Kvilda (*P. cf. pumilio*)	44	52	4	$= 0.01$	74	23	3		76	24	—	
Pančice (*P. pumilio*)	96	3	1		97	3	—		89	11	—	

pumilio type is not homogeneous. Šebestián coincides with the *rotundata* type, Volary has an even greater number of apophyses with eccentrical umbo than the *rotundata* type; it forms with both preceding types a homogeneous population. Boží Dar and Kvilda are a separate group which, however, is closer to the *pumilio* type.

4. Quantitative characters

Size (length) of the cones — tab. 8. Here, the data form a continuous series; the sequence of population is different from the other characters. Significant concordance is only found between the samples of Kvilda and Volary.

The number of scales in the cone was measured only in *rotundata* and *pumilio* types, between which no statistically significant difference was noted.

5. Relations between characters

Evident correlations between characters or group of characters exist in two cases. Firstly between the direction and the curving of the branches (B and C), i.e. the habit plasticity) in the *pseudopumilio* and *pumilio* types. Secondly that between the total symmetry (DEF) of the cones and the height of the apophyses (G) in the *pseudopumilio* and *rotundata* types. These phenomena will be investigated more in detail.

Mutually quite independent are pairs of characters, one of which is vegetative and one reproductive, e.g. A—DEF, BC—DEF and others. Similarly the size of the cones is not correlated with the symmetry and the height of the apophyses. This is evident from fact that these characters are the same in cones of the same individual, whereas the size of the cones changes generally on a larger scale.

Tab. 5: Total symmetry of cones (DEF)

Tab. 5: Celková souměrnost šišek (DEF)

	0	1	2	3	4	5	6		0	1	2	
Barbora (*P. rotundata*)	3	6	7	6	14	18	46		9	27	64	
Šebestián (*P. pseudopum.*)	25	20	13	19	10	10	3	$\chi^2 = 11.13$	45	42	13	$\chi^2 = 1.40$
Boží Dar (*P. pseudopumil.*)	35	13	19	16	7	7	3	$P > 0.30$	48	42	10	$P > 0.70$
Volary (*P. pseudopumil.*)	33	12	9	20	11	10	5		45	40	15	
Kvilda (*P. cf. pumilio*)	40	31	12	11	5	1	—		71	28	1	
Pančice (*P. pumilio*)	86	12	—	1	1	—	—		98	2	—	

6. Hybrid index

This was formed on the basis of five characters, as shown in tab. 9. The *pumilio* type forms a statistically homogeneous population. The local population Kvilda appears a transition between *pseudopumilio* and *pumilio* type (fig. 2).

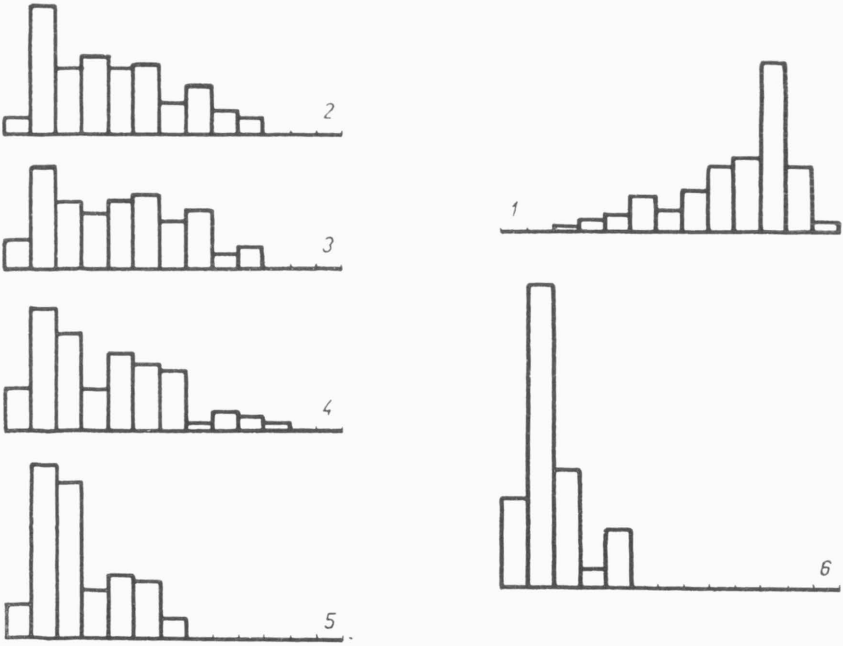

Fig. 2. — Hybrid index: index values and their frequencies; 1 — Barbora, 2 — Volary, 3 — Šebestián, 4 — Boží Dar, 5 — Kvilda, 6 — Pančice.
Obr. 2. — Index hybridnosti: hodnoty indexu a jejich četnosti; 1 — Barbora, 2 — Volary, 3 — Šebestián, 4 — Boží Dar, 5 — Kvilda, 6 — Pančice.

Reasons for variability

The polymorphic forms of the *Pinus mugo* complex are mainly concentrated in the central parts of the area. To the West and to the East the variability declines. This can be explained basically by two reasons:

1. Introgressive hybridization of two differentiated species. 2. Clinal pattern

Tab. 6: Relative height of apophysis (G)

Tab. 6: Relativní výška apofysy (G)

	0	1	2	3	4	
Barbora (*P. rotundata*)	2	14	67	14	3	
Volary (*P. pseudopumilio*)	5	61	28	6	—	$\chi^2 = 12.8$
Šebestián (*P. pseudopumilio*)	15	57	22	6	—	$P \doteq 0.05$
Boží Dar (*P. pseudopumilio*)	19	43	30	7	1	
Kvilda (*P. cf. pumilio*)	13	63	24	—	—	$\chi^2 = 4.64$
Pančice (*P. pumilio*)	19	68	13	—	—	$P \doteq 0.10$

Tab. 7: Placing of umbo (H)

Tab. 7: Poloha pupku (H)

	0	1	2	
Barbora (*P. rotundata*)	26	67	7	$\chi^2 = 8.47$
Volary (*P. pseudopumilio*)	39	59	2	$P > 0.05$
Šebestián (*P. pseudopumilio*)	28	70	2	
Boží Dar (*P. pseudopumilio*)	5	85	10	$\chi^2 = 4.44$
Kvilda (*P.* cf. *pumilio*)	7	75	18	$P > 0.02$
Pančice (*P. pumilio*)	1	92	7	

of a polymorphic species. The first opinion is mentioned for instance by LÜDI (1929), more recently also by GAUSSEN, HEYWOOD and CHATER in „Flora Europaea" (1964). The second opinion stems from the interpretations of other authors (NOVÁK, 1953, SVOBODA 1953), although it is not directly mentioned.

The results of observations and biometrical studies support the first opinion mainly for the following reasons:

1. In natural populations under study besides fully fertile individuals there are often found individuals with a small number of cones or entirely sterile, which show the lessened vitality of some lines. This is easy to observe because the cones last many years.

2. The transitional types have the nature of a relic and their habitat likewise supports the theory of hybridization. These habitats are peat-bogs of the glacial and postglacial ages. It is possible that just at this time, the hybrid swarms arose, because great changes connected with the glacial age might have removed the barriers between the two species. Peat-bogs, as a new formed habitat, became for these hybrids a suitable niche.

Transgression of characters

In populations of the *pseudopumilio* type, characters of *P. mugo* prevail, but they are not represented to the same extent; they are as if differently resistant towards the penetration of alternative characters of *P. rotundata* (*P. uncinata* respectively). Very constant is the number of trunks (frutescence), and the relation between the shape and the curving of the branches (i.e. the habit

Tab. 8: Length of cones (mm)

Tab. 8: Délka šišek (mm)

	$\bar{x}$	s^2	n	d	
Barbora (*P. rotundata*)	34.41	40.27	400		
Boží Dar (*P. pseudopumilio*)	32.53	42.61	300	1.88	$P < 0.01$
Šebestián (*P. pseudopumilio*)	31.29	25.05	385	1.24	$P < 0.01$
Volary (*P. pseudopumilio*)	28.28	31.54	375	3.01	$P < 0.01$
Kvilda (*P.* cf. *pumilio*)	28.17	30.21	322	0.11	$P > 0.50$
Pančice (*P. pumilio*)	26.20	21.42	193	1.67	$P < 0.01$

Tab. 9: Hybrid index

Tab. 9: Index hybridnosti

	mugo	rotundata
Number of trunks (frutescence) — A	0	2
Total symmetry of cones — DEF	0	6
Relative height of umbo — G	0	4
	0	12

plasticity) also. The latter is, of course, noticeable in the whole population. In these vegetative characters of the *pseudopumilio* type, we find a coincidence with the *pumilio* type.

In reproductive characters, on the other hand, there is a remarkable difference between the *pumilio* and the *pseudopumilio* types. Above all, this is true of the total symmetry of the cones. In this character the *pseudopumilio* type is differentiated from the neighbouring ones, but in the pattern of distribution it is nearer to the *pumilio* type. The height of the apophysis again connects the *pseudopumilio* type into one whole but apart from that there exists a vague relationship of this whole with the local population sample of Kvilda ($P \doteq 0.01$) as well as between the samples of Barbora and Volary ($P \doteq 0.01$). Here then, the *P. rotundata* characters penetrate in other taxa evidently.

Relatively most constant are those characters which have a certain relation to the ecological factors, i.e. the vegetative characters (the number of trunks, the shape of the crown). Less constant are the reproductive characters which have an indirect or no relation to the environment (the total symmetry of the cones). And finally, the most penetrating are those characters which have no visible relation with the environment (the height of the apophysis).

We can say in the *P. mugo* complex the transgression is deeper in the reproductive characters than in the vegetative ones (fig. 3). At the same time, the opinions of past monographers, who for taxonomical evaluation preferred the reproductive characters for their supposed greater stability (Willkom 1861 et 1887), appear in a new light.

Diagnostic value of characters

Habit. Characters connected with habit have a varying taxonomical significance. Frutescence (number of trunks) is of prime importance. *Pinus*

Tab. 10: Hybrid index values (in fig. 2)

Tab. 10: Hodnoty hybridního indexu (na obr. 2)

Barbora (*P. rotundata*)			1	2	3	7	4	8	13	14	33	13	2	
Volary (*P. pseudopumilio*)	3	24	12	14	12	13	6	9	4	3				$\chi^2 = 18.35$
Šebestián (*P. psedopumilio*)	5	19	12	10	13	14	9	11	3	4				$P > 0.30$
Boží Dar (*P. pseudopumilio*)	8	23	18	7	14	12	11	1	3	2	1			
Kvilda (*P.* cf. *pumilio*)	6	33	30	9	7	11	4							$\chi^2 = 10.8$
Pančice (*P. pumilio*)	17	57	22	3	1									$0.05 > P > 0.02$

mugo s.s. is polycormic, *P. rotundata* monocormic. As yet this character has not been given proper weight by many authors.

The habit plasticity, which is decided by the direction and curving of the trunk and of the main branches, behaves differently in different species. In *P. rotundata* this character is constant and is exempt from environmental influences, whereas in *P. mugo* the habit adapts plastically to the climatic conditions (height of snowfall, wind exposition). In the severe climate of higher elevations the decumbent forms are more abundant, while in the lower elevations the erect forms prevail, but relation between the two partial characters remains constant (tab. 2).

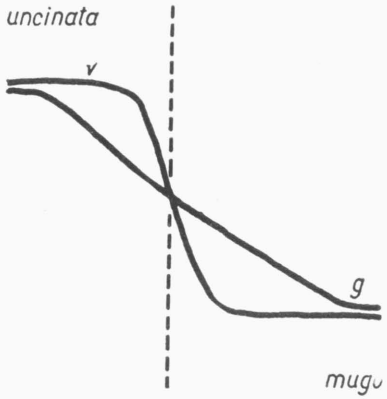

Fig. 3. — Transgression of characters in *Pinus uncinata* and *P. mugo*; v — vegetative characters, g — reproductive characters

Obr. 3. — Transgrese znaků u *Pinus uncinata* a *P. mugo*; v — vegetativní, g — generativní znaky

The effect of the elevation on the crown shape is evident from the diagram (fig. 1). The f. *prostrata* and f. *frutescens* described by TUBEUF (SVOBODA 1953) are probably mere ecomorphoses. Their eventual hereditary fixation could be established only by cultivation.

The behaviour of some hybrids, amongst others, is connected with this plasticity. Monocormic forms (characters of *P. rotundata*) with growth plasticity (character of *P. mugo*) have at higher elevations a typical habit. They are low trees with strongly slanted and twisted trunks and they can be clearly distinguished from both parental types. On the other hand at lower elevations they are erect and blend phenotypically with *P. rotundata*.

The symmetry of cones is often considered as the most important distinguishing character, but it has become evident that this has been grossly overestimated. A typical *P. mugo* has all cones nearly exclusively actinomorphic, but the *P. rotundata* cones are not uniformly zygomorphic; they have a considerable number of central forms and cones clearly actinomorphic are to be found. The cones alone therefore are not sufficient for a safe determination. This is even more conspicuous with the *pseudopumilio* type population, where roughly half the cones are indistinctly zygomorphic or actinomorphic.

The shape of apophyses is the least reliable distinguishing character. The curving of the top and bottom field of the apophysis is immensely variable and changes gradually from the base of the cone to the top, in zygomorphic cones even on the circumference of the cone. That is why only a certain part of the cone is taken into consideration, usually the bottom third, averted from the branch, where the apophyses are best developed. However, even this is not sufficiently exact, and recent papers mostly do not take this character into consideration any more. In the populations under study, this character was studied, but its statistical evaluation proved to be almost impossible.

Less variable are the height of the apophyses and the position of the umbo. In the height of the apophyses there is a significant difference between the two species (tab. 6), but the variation curves overlap to a great extent (fig. 4).

The position of the umbo (central or below the middle) is indicated as the distinguishing character between the taxa *mugus* and *pumilio*. The results given in tab. 7 show that even in taxa *rotundata* and *pumilio*, the central umbo is predominant. The number of eccentric apophyses is very small and there is very little difference among the individual populations. From this character then, the two taxa cannot be distinguished.

The size of cones has a variation curve similar to the height of the apophyse (fig. 4). Even in this case the diagnostic value is limited; more so, because the size of the cones of the same tree varies considerably.

In all populations some relations are constant, so that we can also regard them as characters of some taxa. The relation between the shape and curving of the branches (the habit plasticity) is characteristic for taxa *pseudopumilio* and *pumilio*; the relation between the total symmetry of the cones and the height of the apophyses for the taxa *rotundata* and *pseudopumilio*.

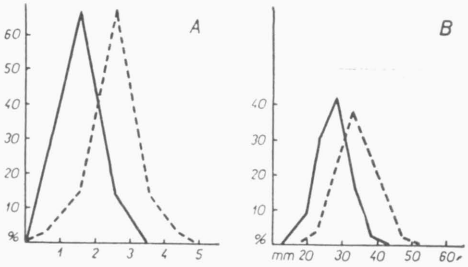

Fig. 4. — Distribution of apophysis height (A), distribution of cone length (B); ———— *Pinus mugo*, — — — — *P. rotundata*
Obr. 4. — Rozdělení výšek apofysy (A) a délek šišek (B); ———— *Pinus mugo*, — — — — *P. rotundata*

If we summarize what has been mentioned, we see that the diagnostic characters are only the following: the number of trunks (frutescence), the total symmetry of the cones and the height of the apophyses. A further group are the statistical characters applicable only to whole populations: the habit and the relation between the total symmetry of the cone and the height of the apophysis.

The internal classification of the *Pinus mugo* complex

The results obtained in the study of local population samples permit certain conclusions to be drawn about the taxonomical classification of the *P. mugo* complex. Of course, for a final solution of this question, a study of the whole range of this complex is necessary.

In all characters studied there appeared a prominent difference between the *rotundata* and the *pumilio* types, which justifies a division of the *P. mugo*-complex into two species — *P. rotundata* Link. and *P. mugo* Turra. The first of these is provisional, until the relation to *P. uncinata* Ram. is established. *P. rotundata* is probably a part of the species *P. uncinata* Ram.

The forms presented in this paper as the *pseudopumilio* type are, as it has been mentioned before, most probably of hybrid origin. They grow in a mixture with typical specimens of *P. mugo* which prevail in all the studied localities except at Barbora. The forms close to *P. rotundata* are rare and appear mostly in places where *P. rotundata* grows either on the same site (Volary) or at least in the same region (Šebestián).

For this reason, I do not consider it correct to classify the taxon *pseudopumilio* with *P. rotundata* (Rothmaler 1963) or even with *P. uncinata* (Domin 1935, Janchen et Neumayer 1942, Janchen 1959). From what has been

shown here it is evident that this taxon is a component of the species *P. mugo* Turra s.s. A further study will show whether it is a relatively segregated hybridogenous type or merely a hybrid swarm.

When comparing the hybrid index for the *rotundata* type we notice that it is as it were a mirror image of the *pseudopumilio* type. From this it is possible to conclude that not even *P. rotundata* is a good species but probably a product of hybridization between *P. mugo* and *P. uncinata*, where the characters of the latter are prevalent. Here, too, a further study is necessary.

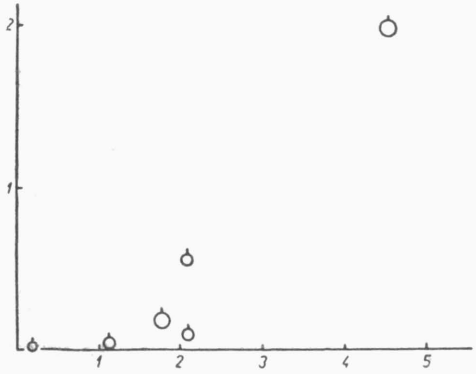

Fig. 5 — Scatter diagram for six populations investigated in the study; x — total symmetry of cones (DEF), y — frutescence (A), the size of ring represents the mean size of the cones, the length of the line indicates the mean relative height of apophysis
Obr. 5. — Souhrnný diagram šesti studovaných populací; x — celková souměrnost šišek, y — keřovitost; různá velikost kroužků znázorňuje průměrnou velikost šišek, délka úsečky průměrnou výšku apofysy

If we evaluate the two taxa as separate, they could correctly be named as follows:
Pinus mugo Turra subsp. *pseudopumilio* (Willkomm) comb. nova basionym: *P. uncinata* Ramd. c) *pseudopumilio* Willkomm Jahrbuch d. König. sächs. Akad. f. Forst- u. Landwirte zu Tharandt 40 (= 7 ser. n.) : 166—257, 1861. *Pinus uncinata* Ram. subsp. *rotundata* (Link) Janchen et Neumayer 1942.

The taxa *pumilio* and *mugus* are probably synonyms, but it is still necessary to verify the diagnostic value of the height of the apophyses. It is not impossible that they differ in this character.

Conclusions

The results stemming from an analysis of the variability of characters may be summarized as follows:

1. The taxa *pumilio* and *rotundata* differ significantly in the following characters: the number of trunks, the symmetry of cones, the relation between the symmetry of the cones and the height of the apophysis, and the habit plasticity. This justified their division into two species.

2. The taxon *pseudopumilio* is a component of the species *P. mugo* s.s. to which it is nearer in many characters than to the species *P. uncinata*.

3. The results of observation and statistical analysis support the idea of a hybrid origin of the *pseudopumilio* and *rotundata* taxa.

Tab. 11: Mean values of characters (in fig. 1 and 5)

Tab. 11: Průměrné hodnoty znaků (na obr. 1 a 5)

	A	BC	DEF	G	L
Barbora	2		4.6	2	34.41
Volary	0.1	1.2	2.1	1.4	28.28
Šebestián	0.6	1.9	2.1	1.2	31.29
Boží Dar	0.2	2.3	1.8	1.3	32.53
Kvilda	0	2.3	1.1	1.1	28.17
Pančice	0	3.0	0.2	0.9	26.50

4. The curving of the main branches in *P. mugo* s.s. causing decumbent, ascendent or erect forms, depends on the habitat and has no taxonomical significance.

5. In the taxon *pumilio* (Krkonoše) an overwhelming majority of central apophyses has been found, which strengthens the doubt about differences between the taxa *pumilio* and *mugus*.

Acknowledgments

The author wishes to thank Professor D. H. Valentine from the University of Durham who has been kind enough to provide some special literature and revise the English text and to Docent J. Hájek from the Faculty of Mathematics of Charles University who reviewed the application of the statistical methods.

Souhrn

Jednotlivé populace borovice horské (*Pinus mugo* s. l.) jsou navzájem isolovány a v některých znacích se liší. Ke studiu bylo vybráno šest lokálních populací taxonů *rotundata*, *pseudopumilio* a *pumilio* a v nich byla sledována frekvence těchto znaků: kormie (počet kmenů, keřovitost), habitus (směr a zakřivení hlavních větví), souměrnost šišek, relativní výška apofysy. Na základě získaných hodnot byla pak provedena biometrická analysa.

Z výsledků vyplývá, že diagnostickou hodnotu má pouze celá skupina znaků, při čemž prvořadý význam má počet kmenů (kormie). Taxony *rotundata* a *pumilio* se průkazně liší v šesti znacích, takže je správné řadit je ke dvěma různým druhům. Taxon *pseudopumilio* je součástí druhu *P. mugo* Turra s. s.; centrální poloha pupku není význačná pro taxon *mugus* (*typica*); taxony *rotundata* a *pseudopumilio* mají charakter hybridů mezi *Pinus uncinata* a *P. mugo*. Transgrese znaků je mnohem pronikavější u znaků generativních a slabá u znaků vegetativních.

Nejpravděpodobnější příčinou variability a transgrese znaků je introgresivní hybridisace. Pro tento názor svědčí výskyt neplodných exemplářů v populacích, rozdělení jednotlivých znaků v areálu a dále rozšíření a stanoviště přechodných forem.

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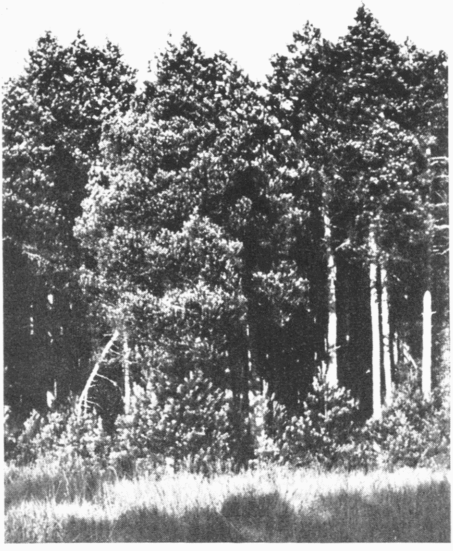
Explanation of the plates — Vysvětlivky k tabulím

Tab. XXI: Above: on the left *Pinus rotundata* on a peat-bog near Borkovice (South Bohemia), on the right transitional type on the edge of a peat-bog near Načetín (Krušné hory mountains). Below: *Pinus* cf. *pumilio* on peat-bog Tříjezerní slať near Modrava (Šumava mountains). Photo Dr. V. Vydra.

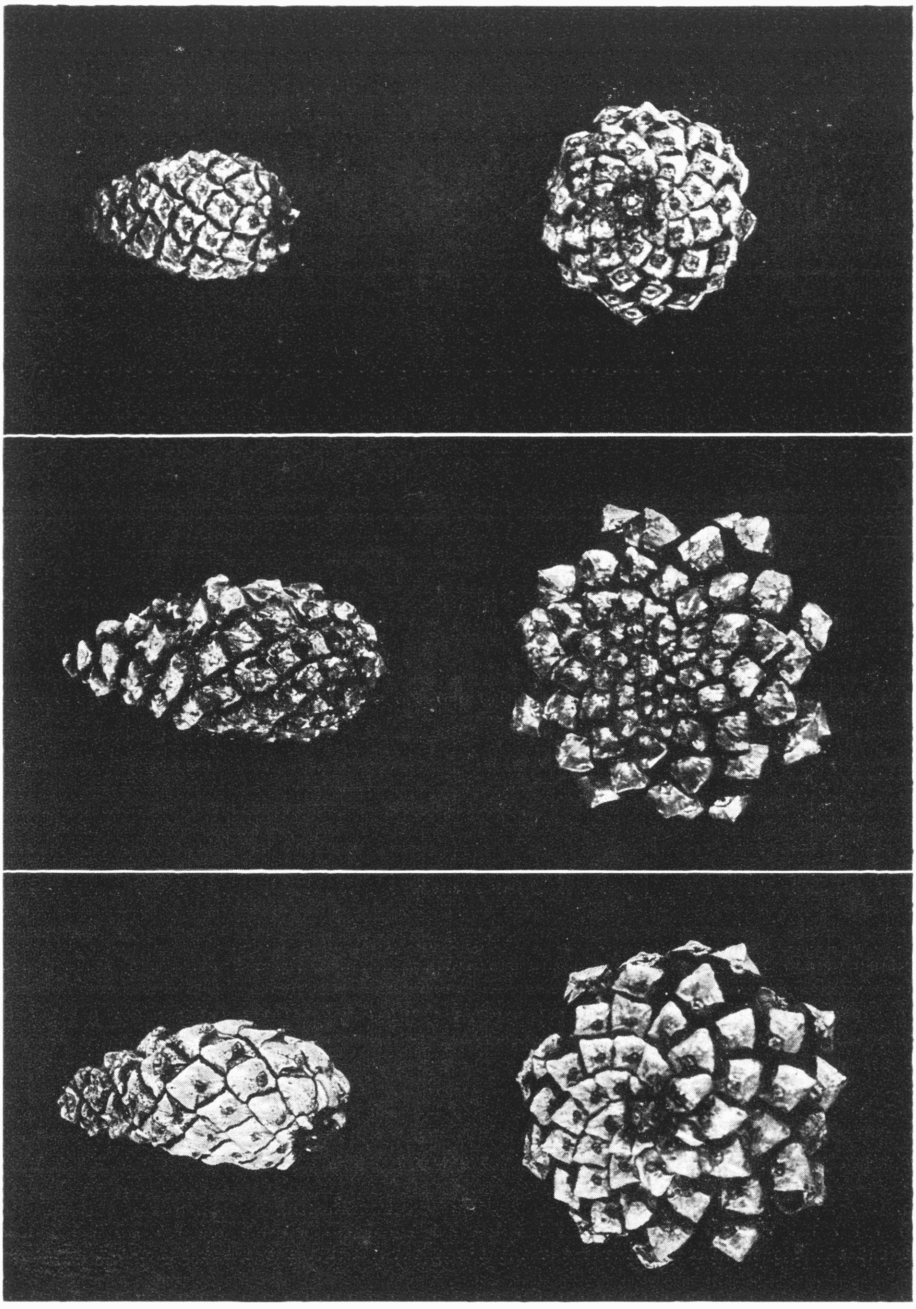
Tab. XXI: Nahoře vlevo: *Pinus rotundata* na borkovických blatech, nahoře vpravo přechodný typ z okraje Načetínského rašeliniště (Krušné hory); dole *Pinus* cf. *pumilio* z Tříjezerní slati na Šumavě. Foto Dr. V. Vydra.

Tab. XXII: Symmetry of cones: above — actinomorphic, in the middle — transitional type, below — zygomorphic. Photo T. Sýkora.

Tab. XXII: Souměrnost šišek: nahoře — pravidelné, uprostřed — přechodná forma, dole — souměrné. Foto T. Sýkora.



B. Holubičková: A study of the Pinus mugo complex



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