

A revision of the Asian *Pinus* subsection *Strobus*1(Pinaceae)

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ROMAN BUSINSKÝ

A revision of the Asian *Pinus* subsection *Strobus*¹ (*Pinaceae*)

Abstract

Businský, R.: A revision of the Asian *Pinus* subsection *Strobus* (*Pinaceae*). – Willdenowia 34: 209–257. – ISSN 0511-9618; © 2004 BGBM Berlin-Dahlem.

The Asian taxa of *Pinus* subsect. *Strobus* are revised, based on available type and other authentic material as well as on extensive field studies, including populations at the type localities. *P. fenzeliana* is neotypified and transferred to *P.* subsect. *Flexiles*. Statistical evaluation of ample material revealed that the original description of *P. kwangtungensis* is based on heterogeneous material, including a population from Hainan Island, which is here distinguished and described as the new species *P. orthophylla*. The continental *P. kwangtungensis* s. str., which is morphologically very close to *P. wangii*, is recognized as a subspecies of the latter, besides subsp. *varifolia*. An isolated population in N Vietnam, near the Laotian border, hitherto also considered to belong to *P. kwangtungensis*, is described as the new species *P. eremitana*. The Japanese *P. parviflora*, with two subspecies, is found to be closely related to *P. wangii* and *P. eremitana*. The imperfectly known Taiwanese *P. uyematsui*, mostly included in the other Taiwanese endemic *P. morrisonicola*, is maintained as a separate species similar to the Vietnamese *P. dalatensis*, and a hybrid between the two Taiwanese species is described as the nothospecies *P. xhayatana*. The E Himalayan *P. bhutanica* is recognized as a subspecies of *P. wallichiana*. A key to all members of *P.* subsect. *Strobus*, comprising nine Eurasian and six American species, and a revised classification of the Eurasian species in two series and three subseries, one series and two subseries here described as new, are provided.

1. Introduction

The aim of the present study is to clarify the taxonomy of the Asian soft pines of *Pinus* subg. *Strobus* sect. *Quinquefoliae* subsect. *Strobus* Loudon, based on the investigation of the populations in the field as well as of herbarium specimens. In addition, the geographic distribution and very incompletely known ecology (Richardson 1998) of the taxa involved has been investigated. Special emphasis is laid on the taxonomy of the difficult and, in the view of the present author, hitherto incompletely known ‘*Pinus wangii* aggregate’, which according to the present study comprises *P. wangii* (with three subspecies, including *P. kwangtungensis*), and two new species that were hitherto not distinguished from *P. wangii* s. lat.

¹ The author has been made aware by Prof. W. Greuter of the Editorial Council of “Willdenowia”, that the widely used form “*Strobi*” for the epithet in the name of the subsection and of lower ranks is incorrect, since this epithet is formed from that of *Pinus strobus* L., which is a noun.

2. Material and methods

Material and field work. – Natural populations of all Asian species and subspecies of *Pinus* subsect. *Strobus* were studied by the author during the following expeditions: Vietnam 1986, Japan & Taiwan 1991, Sichuan, Yunnan & Tibet 1992, S China & Vietnam 1993/1994, N Pakistan 1994, China 1995, Tibet & Yunnan 1996, Vietnam 1997, Japan 1997, China 1998, Yunnan & Tibet 1999 and E India 2004. This includes the following taxa and regions, with the year of the field investigation (= locality or region of origin of the type specimen):

Pinus dalatensis Ferré var. *dalatensis* – # Dalat vicinity, S Vietnam, 1986;

– var. *bidoupensis* Businský – # Bi Doup Mts, S Vietnam, 1994;

– subsp. *procera* Businský – # Ngoc Linh Mts, central Vietnam, 1997.

Pinus eremitana Businský, sp. nova – # Pa Co vicinity, border of Ha Son Binh & Son La Prov., Vietnam, 1994.

Pinus morrisonicola Hayata – # Taichung Co., Taiwan, 1991.

Pinus orthophylla Businský, sp. nova – # Wuzhi Shan Mts, Hainan Island, China, 1993.

Pinus parviflora Siebold & Zucc. subsp. *parviflora* – Takakuma Mts (Kagoshima Prefecture), S Kyushu, Japan, 1991; Ishizuchi Mts (Ehime & Kochi Prefecture), central Shikoku, Japan, 1997;

– subsp. *pentaphylla* (Mayr) Businský – Hida Mts (Nagano & Toyama Prefect.), central Honshu, Japan, 1997; Hidaka Mts, S Hokkaido, Japan, 1997.

Pinus uyematsui Hayata (& *P. ×hayatana* Businský, nothosp. nova) – # Yushan Mts region, N border of Kaohsiung & Taitung Co., Taiwan, 1991.

Pinus wallichiana A. B. Jacks. subsp. *wallichiana* – Nanga Parbat region, Pakistan, 1994; Murree Hills above Islamabad, Pakistan, 1994;

– subsp. *bhutanica* (Grierson & al.) Businský – Valleys between Dongjug and Tangmai in E Xizang (Tibet), China, 1992 & 1996; Tawang, Dirang and Rupa vicinity, W Kameng distr., Arunachal Pradesh, India, 2004.

Pinus wangii Hu & W. C. Cheng subsp. *wangii* – # Taipingjie and Tiechang vicinity, Yunnan 1996, China; Xiajinchang vicinity, Yunnan, China, 1999;

– subsp. *kwangtungensis* (Chun ex Tsiang) Businský – # Lechang Co., Guangdong, China, 1994; Rucheng Co., Hunan, China, 1994;

– subsp. *varifolia* (Nan Li & Y. C. Zhong) Businský – # Tiandeng vicinity, Guangxi, China, 1998.

Sampling during these field investigations was standardized for better comparison of individuals and populations regarding biometrical (quantitative) and morphological (qualitative) characters: samples were taken of representative trees and always from the middle or top of the tree crown.

Older herbarium specimens were not included in the biometrical analyses, in view of their insufficient representation, the deficiency of adequate material (especially cones and seeds) and incomplete collecting data. This material, however, was consulted for qualitative morphological comparison and in the final evaluation.

A list of all material examined is given in an electronic supplement to this paper at <http://www.bgbm.org/bgbm/library/publikat/willd34/businsky.pdf>.

Representative specimens have been and are being sent to a number of institutional herbaria including such in the countries of origin. Other specimens and their duplicates are deposited in the herbarium of the RILOG (Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Průhonice, Czech Republic).

Field explorations and observations, study of populations, collecting of samples and logistic organisation during all expeditions, except for the one in 2004, were done by the author together with his wife, Ludmila Businská, horticulturist at the Institute of Experimental Botany, Academy of Sciences of the Czech Republic, Prague. For this reason, references to these field activities are given in the text below in plural.

Character measurement and evaluation. – The morphological characters evaluated are summarised in Table 1. The morphological comparison of the taxa of the difficult '*Pinus wangii* aggregate' and the allied *P. parviflora* was statistically evaluated. Six quantitative characters (three for

Table 1. Morphological characters determined and evaluated (* = characters selected for statistical evaluation; ▲ = quantitative characters, ► = qualitative characters).

Tree		Cone [continued]	
▲	height	►	general shape of cone
▲	maximum crown diameter	►	thickness, shape & surface of apophyses
▲	trunk circumference at 1.3 m (= t.c.)	►	morphology of apophysis apex & distal edges
►	general habit	►	*morphology of umbo
►	branching system		
Leaves		Shoots	
▲	*length	►	presence & character of indumentum
▲	*width	▲	quality (gloss, pruinosity & colour of surface)
▲	number of stomatal lines ventrally	►	*morphology of umbo
▲	*angle of curvature		
►	apex morphology		
►	serration of edges	Seeds (see Fig. 1)	
►	pruinosity ventrally	▲	seed length including wing
►	position of resin ducts	▲	*corpus length % of seed length
		▲	length of corpus
		▲	width of corpus
Conelets (ovulate strobiles after the first growing season)		▲	length/width of corpus
▲	length	▲	length of the elongated thickening of the wing (= e.t.w.)
►	shape of exposed part of scales	▲	e.t.w. /corpus length ratio
		▲	*length of wing (from corpus apex including e.t.w.)
Cones		▲	width of wing
▲	length of peduncle	▲	length/width of wing
▲	length of cones	►	morphology of corpus border
▲	number of scales	►	shape of e.t.w.
▲	length/width of the four largest scales	►	position of e.t.w. apex
▲	*average length/width ratio of the four largest scales		

leaves, two for seeds and one for cones) and one qualitative character (morphology of umbo) were selected for statistical evaluation (see Table 1). The following conventions were applied:

- *Leaf length and width* were measured from fresh or moistened samples (because during drying, mature needles lose 7-20 % of width and 5 % of length);
- *Leaf curvature* was measured as the inward angle between the base and apex of a needle (differences in curvature between fresh and dry needles were not ascertained);
- *Seed wing length* was measured from the distal end of the seed corpus, i.e. without the seed border, but including the elongated thickening of the border;
- *Corpus length percentage of seed length*, i.e. corpus length/total seed length × 100 (= n/s × 100);
- *Ratio of cone scale length/width* was calculated for the four largest scales of each measured cone (two longest and two widest ones bearing fully developed seeds); scale length was measured along the ventral side from the basal wood strand;

- *Umbo morphology* was evaluated on a five point relative scale, referring to the transition between umbo and apophysis and the relative degree of the depression of the umbo:
 - (1) umbo situated at the level of the apophysis surface
 - (2) umbo abuts the apophysis surface showing an indistinct depression
 - (3) umbo moderately depressed in the apophysis
 - (4) umbo conspicuously depressed in the apophysis
 - (5) umbo extremely depressed.

Statistical evaluation. – Comparative analyses of biometrical data were carried out using the programme SOLO (BMDP). The level of probability used was $p = 0.05$. The normality of distribution of individual characters was tested. Nested ANOVA and Duncan's test were applied to the original data in cases where an evaluated character displayed normality of distribution. Where normality was rejected, averages per sampled tree were analysed by the nonparametric Kruskal-Wallis & Conover's test (Siegel 1956). Averages per sampled tree were also analysed by Canonical Variates Analysis using the programme CANOCO-CCA with Hill's scaling (Braak & Šmilauer 1998). The data tables of the statistical evaluation are given in the electronic supplement to this paper, see <http://www.bgbm.org/bgbm/library/publikat/willd34/businsky.pdf>.

Taxonomic concept. – Two infraspecific ranks are accepted in this study: subspecies and variety. Taxa at the subspecific level should, in addition to apparent morphological differences, have a relatively homogeneous geographic range, and should be mostly allopatric when compared with other subspecies of the same species. Taxa at the rank of variety are understood as populations of different morphotypes sharing all major morphological characters with the other populations of the species. They do not occupy a definite geographic range and their status may be a result of different ecological conditions (sometimes occurring polytopically, e.g., in high mountains); there may be more or less gradual transitions towards the common morphotype.

A detailed study of the natural populations of the taxa under revision was experienced as essential to delimit the taxa adequately and to correctly understand and evaluate their variation. During the population study, attempts were made to track the most common morphotypes, the average variation and the extremes. The most common morphotypes, particularly those from the region of the type locality, are called 'typical' and considered as the most useful for characterizing the taxon. The extremes of the variation of a taxon were compared with the variation of closely related taxa. Extents of variation are used as one of the criteria of taxa delimitation. The variation ranges of taxa often overlap in many groups of *Pinus*, at least in a low proportion of individuals. In cases where the variation in closely related taxa overlaps to a small extent, the specific status is retained.

3. Special morphology of seed wings

In certain groups of *Pinus*, in *P. subg. Strobus* in particular, analysis of the seed morphology hitherto neglects some important diacritic characters. These primarily pertain (a) to the extent of development of seed wings and (b) to the secondary suppression of their functionality as shown by the difference in their relative length and width and their firmness and manner of attachment to the seed corpus. The membranous seed surface that extends to the wings provides several other valuable diagnostic characters, particularly the variable shape of the base where the wing attaches to the seed corpus. These characters are found in seeds with primarily effective adnate wings typical of *P. subsect. Strobus*. Two seed types can be morphologically distinguished, probably representing two phases in the evolution of adaptations to diverse habitats. Morphotype A is supposedly ancestral, morphotype B derived. In their most typical form they can be circumscribed as follows:

Morphotype A is characterized by small seeds with relatively long and narrow wings – Fig. 1A.

The border of the wing base around the seed corpus is conspicuously elongated above the distal end of the corpus to form a thickened narrowly triangular ridge usually with an acute apex, stiff-

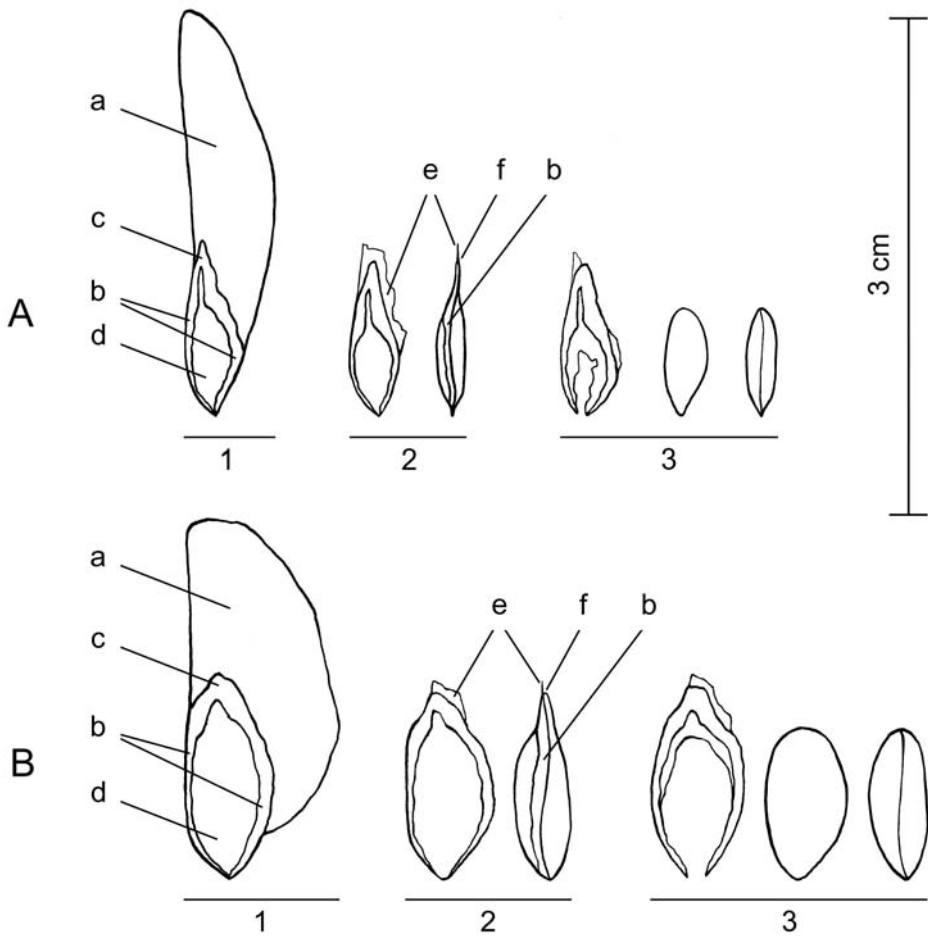


Fig. 1. Two seed types found in *Pinus* subsect. *Strobis* – A: small-seeded morphotype as represented by *P. orthophylla*; B: large-seeded morphotype as represented by *P. eremitana* – 1: entire seed (dorsal side); 2: seed with wing blade broken off (dorsal & lateral exterior view); 3: empty wing base and removed seed (dorsal & lateral view); a: membranous wing blade, b: thickened seed border of the wing base, c: elongated thickening, d: seed corpus, e: remnants of the wing blade broken off, f: joint of the wing blade and the thickening.

ening the base of the membranous wing blade. The proportion of the wing thickening compared with the corpus length is, on average, 0.2-0.5. The transition between the corpus border and the membranous wing blade often forms an irregularly and distinctly undulating line, and the elongated thickening passes over into the membranous part. The attachment of the membranous blade is relatively firm. The apex of the thickening usually is adjacent to the interior wing margin. *Pinus orthophylla*, *P. dalatensis* or *P. uyematsui* are typical examples of this supposedly ancestral morphotype.

Morphotype B is characterized by large, robust seeds with relatively short and broad wings – Fig. 1B.

The border of the wing base around the seed corpus is only slightly elongated above the distal end of the corpus to form a short broadly triangular thickening usually with an obtuse apex. The pro-

Table 2. Evaluation of characters that have values displaying normality of distribution. Nested ANOVA: averages and ‘F-values / probability level p’ (TAXON and TREE as a main and nested factor, respectively). When followed by the same letter, averages within a column are not significantly different (p = 0.05).

Taxon/Character	leaf length	leaf width	leaf curvature	seed wing length
‘wangii’	44.905 b	1.233 ab	93.029 a	13.487 a
‘kwangtungensis’	43.626 bc	1.314 a	74.525 b	11.298 a
‘varifolia’	41.863 bcd	1.227 b	84.083 ab	5.690 bc
‘eremitana’	36.938 cd	0.984 d	37.277 cd	8.068 b
‘parviflora’	36.263 d	1.070 c	34.672 cd	4.963 c
‘pentaphylla’	41.638 bcd	0.982 d	42.275 c	12.146 a
‘orthophylla’	69.494 a	1.080 c	25.139 d	14.030 a
F TAXON / p	27.13 / 0.0001	26.86 / 0.0001	40.91 / 0.0001	24.23 / 0.0001
F TREE / p	15.76 / 0.0001	10.59 / 0.0001	7.03 / 0.0001	81.94 / 0.0001

Table 3. Evaluation of characters where normality of distribution was rejected. Nonparametric test: medians and ‘Chi-quadrat-values / probability level p’ (TAXON as a factor). When followed by the same letter, medians within a column are not significantly different (p = 0.05). For the only qualitative character (‘umbo’), values of individuals based on a five-point relative scale (ordered numerically according to collection numbers) are given in parentheses.

Taxon/Character	corpus % of seed length	cone scale l. / w. ratio	umbo (five-point relative scale)
‘wangii’	42.00 bc	1.36 ab	2 bc (3323222)
‘kwangtungensis’	47.95 b	1.21 bc	2 c (2222211)
‘varifolia’	62.15 ab	1.19 abcd	2 abc
‘eremitana’	53.35 b	1.09 c	4 a (5445343345)
‘parviflora’	67.50 a	0.98 d	3 ab (53453332344)
‘pentaphylla’	43.45 bc	1.14 c	2 c (23222212222131122)
‘orthophylla’	36.40 c	1.50 a	4 ab (452443)
Chi-q / p	36.09 / 0.001	35.12 / 0.001	39.61 / 0.001

portion of the wing thickening compared with the corpus length is, on average, 0.1-0.2(-0.25). The transition between the corpus border and the membranous wing blade is abrupt, being a smooth or moderately undulating line, and the border (particularly in the vicinity of the obtuse apex) does not pass over into the membranous blade but forms an elevated mound that often exceeds the line between corpus border and wing blade. The wing often easily breaks along that line. The apex of the thickening is usually remote from the interior wing margin. *Pinus eremitana*, *P. wangii* s. lat. and *P. morrisonicola* are typical examples. This supposedly derived seed type is assumed to represent an evolutionary tendency towards a secondary increase in seed volume, wing loss and non-anemochorous dissemination mode. In some populations (e.g. in southern stands of *P. parviflora* subsp. *parviflora*) or individuals with this seed type (e.g. in the population of *P. eremitana*), the wings are short and vestigial. This secondarily ineffective form of wings can occur in various stages of the individual development and represents an exception in *P.* subsect. *Strobus* otherwise characterized by effective seed wings.

Note. – When only an open cone but no seeds are available, an indirect method based on examining the seed imprints in the ventral side of cone scales can easily be used to identify the general character of the seeds and thus ascribe the sample to one of the above morphotypes. Some additional characters, above all the shape and length of the wing base thickening, can also be observed. This method can be used even when only a separated but complete and well-developed seed scale is available.

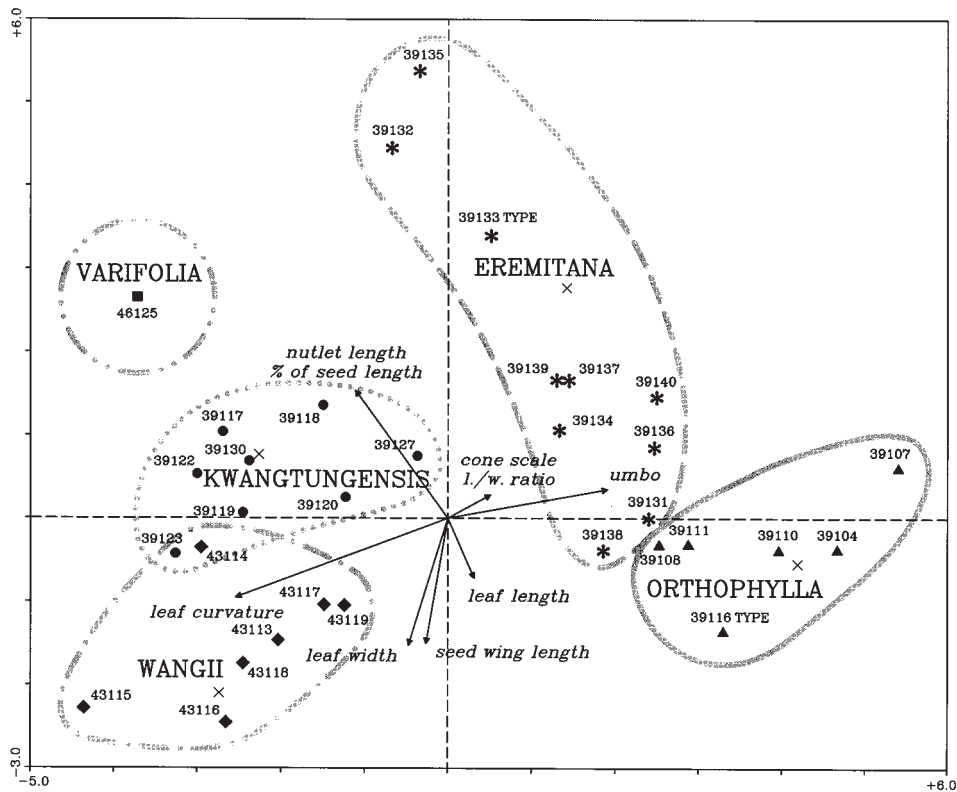


Fig. 2. Ordination diagram A – based on a CVA of seven selected characters measured on samples of the two new species *P. eremitana* (10 trees) and *P. orthophylla* (6 trees), and the three subspecies of *Pinus wangii*, i.e., subsp. *wangii* (7 trees), subsp. *kwangtungensis* (8 trees), and subsp. *varifolia* (1 tree). – All samples were collected in regions of the origin of the type specimens (for sample numbers see electronic supplement ‘Herbarium material collected’).

4. Statistical comparison of the taxa of the ‘*Pinus wangii* aggregate’ and *P. parviflora*

The statistical evaluation based on six quantitative (Table A of Appendix II, electronic supplement) and one qualitative character (Tables 2-3) shows the following results.

Among the four characters of which normality of distribution was confirmed the lowest variance was found for the character ‘leaf width’ ($v = 9-14\%$), while the character ‘leaf curvature’ exhibited the highest variance ($v = 35-78\%$); the average values for these two characters are significantly lower in *Pinus eremitana* and *P. orthophylla*, which are described as new species in the systematic part, and both subspecies of *P. parviflora* than in the three subspecies of *P. wangii* (subsp. *wangii*, subsp. *kwangtungensis* and subsp. *varifolia*).

Among the subspecies of *Pinus wangii*, significant differences were found for the character ‘leaf width’ between subsp. *kwangtungensis* and subsp. *varifolia*, for ‘leaf curvature’ between the former and subsp. *wangii*, and for ‘seed wing length’ between subsp. *varifolia* and both other subspecies. Among all three subspecies, however, the non-significant difference for the character ‘cone scale l./w. ratio’, which normally correlates with seed shape characters, suggests that the values for ‘seed wing length’ in the only available individual of subsp. *varifolia* are perhaps rather atypical.

Canonical Variates Analysis. – The ordination diagram A (Fig. 2), arranged according to the first two axes, explains 40.1 % of the variance comprised in the taxa data. The Monte Carlo permutation test, based on the first canonical eigenvalue, showed the F-ratio = 6.98. The resulting p-value is 0.005, indicating that the first canonical axis is statistically significant at the 1 % level. The characters that best correlated with the first axis are ‘leaf curvature’ ($r = -0.91$) and ‘umbo’ ($r = 0.68$). Also the Monte Carlo test, based on the sum of all canonical eigenvalues, showed that the relation between the taxa and the characters measured is significant ($p = 0.01$).

Results. – Considering taxa delimitation, the analysis reveals that both new species *Pinus eremitana* and *P. orthophylla* are not only very different from one another, but also from all three subspecies of *P. wangii*. The spatial distribution of samples of *P. wangii* subsp. *wangii* and subsp. *kwangtungensis* shows only a narrow overlap.

The ordination diagram B (Fig. 3), arranged according to the first two axes, explains 36.4 % of the variance comprised in the taxa data. The Monte Carlo permutation test, based on the first canonical eigenvalue, showed the F-ratio = 10.3. The resulting p-value is 0.005, indicating that the first canonical axis is statistically significant at the 1 % level. The characters that best correlated with the first axis are ‘corpus % of seed length’ ($r = -0.78$) and ‘seed wing length’ ($r = 0.79$). Also the Monte Carlo test, based on the sum of all canonical eigenvalues, showed that the relation between the taxa and the characters measured is highly significant ($p = 0.005$).

Results. – *Pinus eremitana* is considerably different from all three subspecies of *P. wangii*, but the extensive spatial distribution of its samples overlaps with that of *P. parviflora*, especially with its subsp. *pentaphylla*. Both subspecies of *P. parviflora*, however, are very different from one another, whilst the spatial distribution of samples of *P. wangii* subsp. *wangii* and subsp. *kwangtungensis* notably overlap (by a single sample 39123).

5. Systematic treatment

5.1. Identity and typification of *Pinus* (subject. *Flexiles*) *fenzeliana*

The name *Pinus fenzeliana* was published by Handel-Mazzetti (1931) on the basis of material collected by H. Fenzel on the Hainan Island, China, in the Limu Ling range at an altitude of 1000 m and deposited at W. In 1945, after the end of World War II, portions of the collections at W, including the original material from Fenzel, seem to have been lost in a conflagration. Even with the kind support of various curators, attempts to locate authentic material have failed. The name has been interpreted therefore in various ways for a long time. Most authors referred to it as a taxon belonging to *P.* subject. *Strobos*. Wu (1956) was the first to reduce it to a variety of the Japanese *P. parviflora*, and to simultaneously synonymize *P. kwangtungensis* Chun ex Tsiang with it. European and American authors followed Wu in considering *P. fenzeliana* and *P. kwangtungensis* conspecific (Critchfield & Little 1966, Mirov 1967, Farjon 1984, 1998, Richardson 1998) or at least closely related (Gausson 1960, Mirov 1961). However, on the basis of additional collections, both taxa were treated as two different species again by Kwei & Lee (1963), Cheng & al. (1975), Law & al. (1978), Sykes (1991: 361) and Fu & al. (1999).

Pinus fenzeliana has been reported not only from Chinese territory but also from Vietnam (Critchfield & Little 1966, Farjon 1998, Fu & al. 1999), but actually referring to the northernmost population of *P. dalatensis* (see Businský 1999a). *P. fenzeliana* was also identified with *P.* (subject. *Flexiles*) (Shaw) *P. Landryi armandii* Franch., repeatedly reported from Hainan Island (Merrill & Chun 1940, Critchfield & Little 1966, Mirov 1967, Farjon 1984, 1998, Fu & al. 1999) on the basis of determinations in the 1930s.

In order to interpret the name correctly, the author and his wife visited Hainan in 1993 to study the population of which the type material was collected. A population of a single *Pinus* species on the E slope of the mountain Ying Ge Ling (1815 or 1822 m), the highest massif of the Limu Ling (= Hungmoleng) range, at an altitude of c. 1000 m, is most likely the one of which Fenzel collected the type, if the local situation is considered. Our samples from several trees from here and the neighbouring massif Wuzhi Shan, as well as material from the herbaria PE and

KUN, proved to be in full agreement with the protologue of *Pinus fenzeliana*. In 1998, the author studied and collected the same species on the mainland, in the Daming Shan Mts, Guangxi.

Pinus fenzeliana, represented by the mentioned populations and examined samples, is a separate, distinct species that does not belong to *P.* subsect. *Strobus* but to *P.* subsect. *Flexiles*. The species is allied to, but conspicuously different from, *P. armandii* and *P. dabeshanensis* W. C. Cheng & Y. W. Law. This conclusion is in conformity with Law & al. (1978) and Fu & al. (1999). However, the treatment of *P. dabeshanensis* as a variety of *P. fenzeliana* by Fu & al. (1999) is not accepted here, above all on the basis of own studies of *P. dabeshanensis* at the type locality in the Dabie Shan Mts near the border between Anhui and Hubei.

To prevent further misinterpretation of the name, a neotype is designated below. The problems surrounding this name were probably caused by the fact that Handel-Mazzetti based his description on the only available, imperfectly developed seeds [“semina (paucā abortiva quae remanebant) 4 mm longa”] and on probably shaded, lower, slender branchlets with leaves shorter than on average.

Pinus fenzeliana Hand.-Mazz. in Oesterr. Bot. Z. 80: 337. 1931. – Holotype: Hainan, in silvis montium Hungmoleng et Ngitse-leng dispersa inter arbores sempervirentes, in utroque semel tantum inventa, 1000 m, 10.-11.1929, *Fenzel* 55 (W, lost, probably destroyed; no material found in WU, either). – Neotype (designated here): China, Hainan Island, central part, Ying Ge Ling massif (1822 m), E-NE slopes above road pass NE of elev. point 1822 m, below lateral N ridge on a beginning steep stony ENE declivity, together with bamboo, 1040 m, 19°04'20"N, 109°32'30"E, tree: 270 cm trunk circ., 20 m h., 20 m diam., branched from 5 m, very old, 22.12.1993, *Businský* 39103 (W; isoneotypes: B, G, BM, MO, P, PE, PR).

lc. – Cheng & al. 1975: pl. 30, fig. 1-8 (reprinted in Law & al. 1978: pl. 52, fig. 1-8, and in Fl. China Illustr. 4, 2001: fig. 24/1-8); *Businský* 1999b: 53 (five different cones; the closed cone at top left after *R. Businský* 39103).

Pinus fenzeliana is characterized by robust seeds with a rudimentary, always ineffective wing. The wing is frangible, usually has a lacerate distal margin and sometimes is reduced to a slightly elongated, distal membranous seed corpus border. The cone scales are relatively thick in the apophysis. These two attributes clearly show that *P. fenzeliana* is a member of *P.* subsect. *Flexiles*. The erecto-patent posture of ripe cones is regarded as a remarkable diagnostic (probably ancestral) character of *P. fenzeliana*, not found in other members of this subsection. The umbrella-like crown of old trees is exceptional in the group in question. The cone apophyses in most trees from the Hainan populations (less distinctly in the continental populations) have the distal keel with umbo conspicuously shifted towards the apophysis centre; the extreme forms may resemble soft pines with a dorsal umbo. The latter character is shared by *P. fenzeliana* and *P. dabeshanensis*, and is rarely found in *P. armandii*. *P. fenzeliana* primarily differs from *P. armandii* in having distinctly shorter, up to 12 cm but most frequently less than 9 cm long cones, seeds with a wing and a thinner seed-coat.

5.2. *Pinus wangii* s. lat.

Pinus wangii Hu & W. C. Cheng in Bull. Fan Mem. Inst. Biol. ser. 2, 1, 2: 191. 15 May 1948. – Holotype: China, “Yunnan, Shi-Chou, Fa-Tou, Ku-Chu-Chun, alt. 1400 m, on open ridge of limestone hills; height 10 m, d.b.h. 50 cm; wood good for making cask and barrels locally; Dec./Jan. 1940” C. W. Wang 85830; original field label: “Yunnan, Wang & Liu 85830, 1939-40.” (KUN! [correct coll. date probably is 17.12.1939, according to isotypes in PE and number sequence of further specimens]; isotypes: PE! [four specimens dated 17.12.1939 or 2.1.1940]).

Pinus wangii as accepted in the present paper, comprises three subspecies: subsp. *wangii*, subsp. *kwangtungensis* and subsp. *varifolia*. The main differences are summarized in Table 4.

lc. – Fig. 4.

Description. – Low trees, usually 8-20 m high, with short, unbranched basal part of trunk up to 100 cm in diameter, irregularly ramifying or straight inside a broad crown, rounded or flat on the top; branches often horizontal with relatively dense secondary branching. Foliage bright, greyish or silver green, persisting for two years. First-year shoots densely or sparsely pubescent, or entirely glabrous, with the surface pale to dark brown, dull or glossy, sometimes pruinose when young. *Leaves* in fascicles of (2)3-5, in general conspicuously crescently curved up to 80°-140°(180°), (15-)30-60(-80) mm long and (0.85-)0.95-1.5(-1.75) mm wide [a width of 0.8 mm only exceptionally in subsp. *varifolia* in extremely weak di- and trimerous fascicles], ± abruptly terminated in an obtuse to acute apex, densely or remotely and then often irregularly, acutely serrate on all edges except for the attenuate base (sometimes entire up to the quarter of the length, or rarely higher), with (13-)18-40(-50) teeth per centimetre in the middle part, dark green and usually grooved on the dorsal side, indistinctly greyish green to conspicuously white pruinose and with (3)4-9(-12) stomatal lines on each ventral side. Resin ducts two, marginal, submarginal or median, located dorsally, and usually an additional median duct situated symmetrically or asymmetrically near the ventral edge (rarely replaced by marginal duct with an asymmetric position). Hypodermis of one cell layer, occasionally with cells in a second layer on the dorsal side, mostly near the groove; cell walls ± thickened. *Conelets* subterminal or pseudolateral, solitary, in 2-4-merous whorls, erect on relatively slender peduncles or sometimes nodding on curved peduncles; ovoid to oblong-ovoid or ellipsoidal, (8-)10-18(-20) mm long. Exposed part of conelet scales flat or distally thickened, with slightly to distinctly deflected distal edge, rounded-cuneate to nearly rounded in outline, with a weakly acute or almost indiscernible apex. *Cones* pendulous on medium thick or slender, (5-)6-20(-25) mm long peduncles; oblong-ovoid, narrowly ovoid or narrowly ellipsoidal when closed, with relatively broad, abruptly obtuse apex, (3-)4-10(-11) cm long and (3-)3.5-6.5 cm wide when fully open; after seed dispersal cones sometimes early deciduous, or more often, not firmly, persisting for one or a few years. *Scales* (30-)35-65(-75), the largest (16-)18-30(-34) mm long and (14-)16-24(-26) mm wide with a length/width ratio of (0.8-)0.95-1.65(-1.85); basal sterile scales inflexed or deflected, sometimes slightly recurved towards the peduncle. *Apophyses* usually very thick and firm, with smooth or longitudinally finely grooved surface, cinnamon brown and glossy on freshly ripened cones, with a nearly straight longitudinal dorsal line or convex in the proximal part; distally (obtusely) cuneate to rounded in outline, with the apex and distal edges inclined towards the cone axis or straight, apophyses in seed scales in the basal half of the cone with distal edges often ± deflected. *Umbo* transverse and flat, 5-8(-9) mm wide in seed scales, even with the apophysis surface or only indistinctly depressed into a concavity at the end of the scale; distal edge sharp, in outline ± weakly acute or rounded, often elevated upwards. *Seeds* including the relatively short and broad wing 12-28.5 mm long, corpus 7.8-12.8 mm long, representing (on average) 39-65 % of the seed length; corpus border of the wing base scarcely elongated or elongated into a broad, 0.5-3.5 mm long thickening, attached to the seed corpus; average thickening/corpus length ratio 0.1-0.25; obtuse apex of the thickening often remote from the interior margin of the wing; transition between the thickened corpus border and the membranous blade of the wing straight or irregularly undulate and, on the ventral side of the seed, the thickening often not passing over into the blade but forming a protruding mound; the blade frangible along the corpus border. *Wing* 4-18 mm long and 5.5-11.2 mm wide, with an average length/width ratio of 0.8-1.8; with finely dispersed, dense, dark pigmentation or inconspicuously striped longitudinally.

5.2.1. *Pinus wangii* subsp. *wangii*

Taxonomic history. – The taxon was discovered at the turn of 1939 and 1940 at three localities on karst hills in two neighbouring regions, Xichou Co. and Malipo Co. in SE Yunnan, not far from the Vietnamese border. In the protologue it is described in detail, compared with the Japanese *Pinus parviflora* and considered to be related to it (Hu & Cheng 1948). The description, however, is based only on collections that consist of material with unusual small cones and seeds, from a

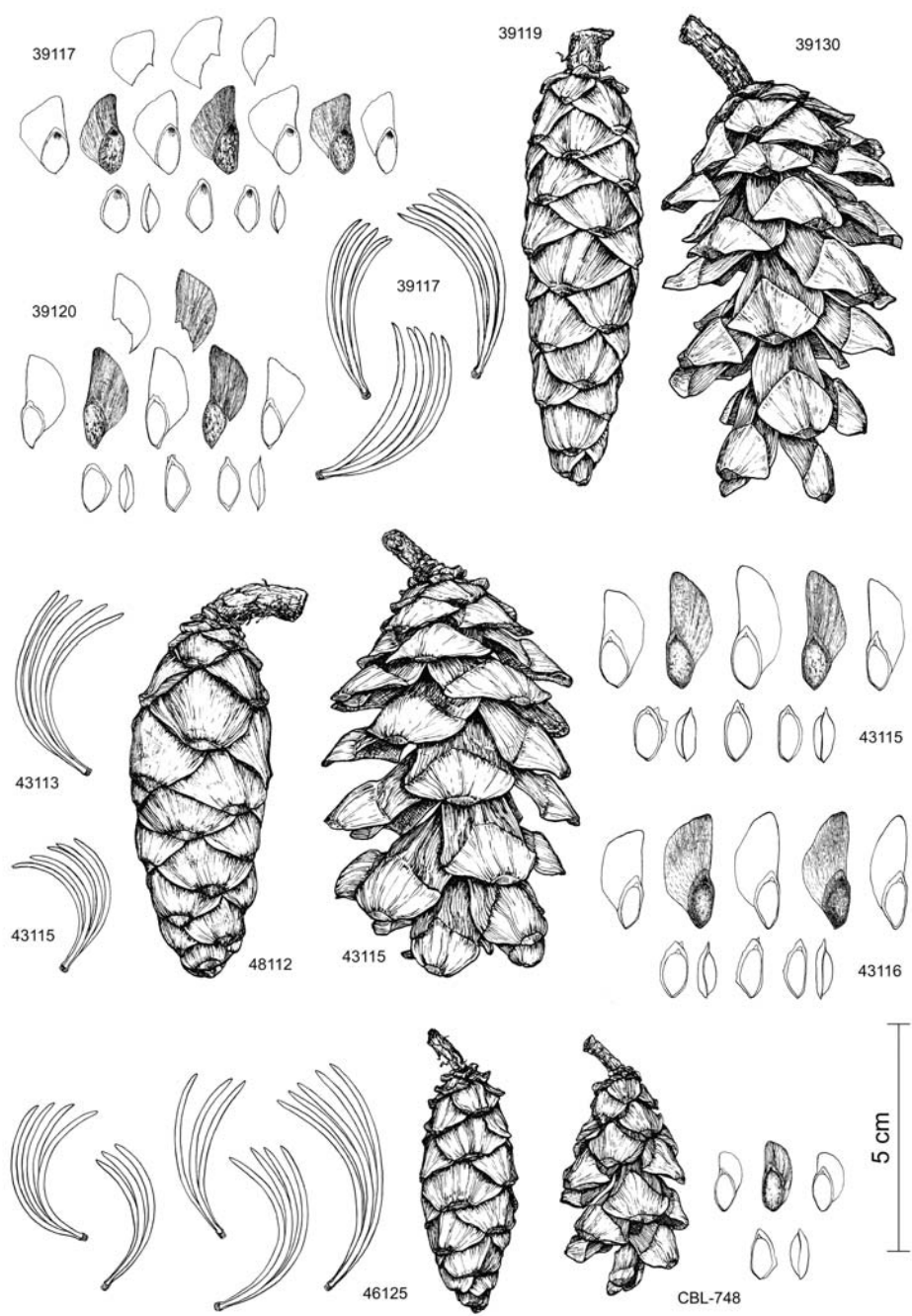


Fig. 4. *Pinus wangii* s. lat. – cones, seeds and leaves; top: subsp. *kwangtungensis*, middle: subsp. *wangii*, bottom: subsp. *varifolia*. – All to the same scale; drawn by L. Businská after specimens collected by the author in regions of the type localities, and after Averyanov & Phan Ke Loc, CBL-748.
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tree growing under extreme conditions after deforestation, “on open ridge of limestone hills”. Four other specimens, collected by K. M. Feng between September and December 1947, were not considered. Ranges of values for the quantitative characters were slightly widened later by Law & al. (1978) and repeated without change by Fu & al. (1999).

Wu (1956) mentions *Pinus wangii* in a note referring to *P. parviflora* var. *fenzeliana* (Hand.-Mazz.) C. L. Wu: “*Pinus wangii* Hu & W. C. Cheng perhaps is similar (related) to our taxon, and it is possible that it forms forests in the mountains of southern China” [in Chinese]. Using only one character “[leaf] parenchyma with sclerenchyma” in his identification key, Gaussen (1960) distinguishes *P. wangii* from related species and compares its central resin ducts with the marginal resin ducts of the separately treated *P. kwangtungensis* and *P. parviflora* (see below). Ferré (1960) treated *P. wangii* in more detail: “It differs from all the other [Eurasian five-leaved pines] by the presence of mesophyll cells with strongly sclerified folds ... In numerous characters, particularly in the epidermis characters, it is allied to the group of *P. parviflora*. However, the central resin ducts suggests a relationship with the group of *P. armandii*, whilst the short seed with a long wing rather reminds the group of *P. excelsa*. It is quite possible that our species remained close to the common predecessor of the cluster, a certain ancestral point of diversification of our three groups.” Mirov (1967) mentions *P. wangii* only in passing, Farjon (1984), Critchfield (1986) and Wang & Szmidt (1993) do not list it at all.

Geographic distribution and ecology – According to the data available, *Pinus wangii* subsp. *wangii* has a very small distribution range (with maximum distance of about 32 km between localities) in Xichou Co. and Malipo Co., both in the Wenshan Prefecture (Fig. 5). The range is close to the border with Vietnam (2 and 12 km distant for the closest localities), and it is possible that the taxon can also be found on Vietnamese territory, as already suggested by Hu & Cheng (1948). At present, only two small, but not yet fully explored areas are known to harbour it.

The main distribution area is located in the mountains SE of Xiajinchang (a small town at 23°10'55"N, 104°48'06"E, 12 km NE of Malipo). This area includes two occurrences.

In the one closer to the town (2.5–3.5 km) the individuals are dispersed on three karst hills between 1700 and 1800 m high and some rocky elevations in their vicinity. The middle hill is situated S of (just above) a minor road from Xiajinchang to Babu, between km 29 and 30; its summit is at 23°10'15"N, 104°49'46"E. The stand was discovered in January 1940 and was referred to as the village then called ‘Hwang-gin-yin’ (or with a similar transliteration), which is in a valley (at about 1400 m) c. 1.3 km NE of the mentioned summit. The first gathering from this locality (C. W. Wang 86308) is reported from an altitude of 1100 m, two later collections dated 1947 from 1300–2000 m (with a note ‘common’). Considering the surrounding landscape, the original altitudinal range of this pine could hardly exceed the limits of 1400 and 1900 m. Today, the locality represents the richest known population of *Pinus wangii* subsp. *wangii*, comprising about 50 individuals of mostly younger age, often not yet fertile, dwarf trees. Nowadays, the vegetation on these hills, particularly in the upper parts of the slopes where this pine grows, is seriously disturbed by long-term tree felling, but still to a lesser extent than in the broader vicinity.

In 1999, we revealed another locality 6 km SE of Xiajinchang, about 2–3 km from the Vietnamese border. Using a telescope, we observed an occurrence of several well-developed old trees between 1600 and 1800 m on a ridge descending towards SE, at 23°08'25"N, 104°50'30"E. The locality and its closer vicinity is characterized by well-preserved primary forest stands, thanks to its remoteness from the settlements in the agricultural landscape. This unexplored locality is hardly accessible because of the surrounding wild, varied karst covered with dense tropical vegetation.

The second distribution area of *Pinus wangii* subsp. *wangii*, located at the NW margin of Malipo Co. and approximately centred in the vicinity of Taipingjie village (23°24'30"N, 104°59'E), extends SE to the vicinity of the Tiechang village (23°22'30"N, 105°02'20"E) and westwards probably to Xichou Co. At an altitude of 1500–1600 m only one small group and scattered isolated trees on a few conical hills were found in the fragments of the primary forest (near Taipingjie) or on otherwise totally deforested sites (near Tiechang). These occurrences were dis-

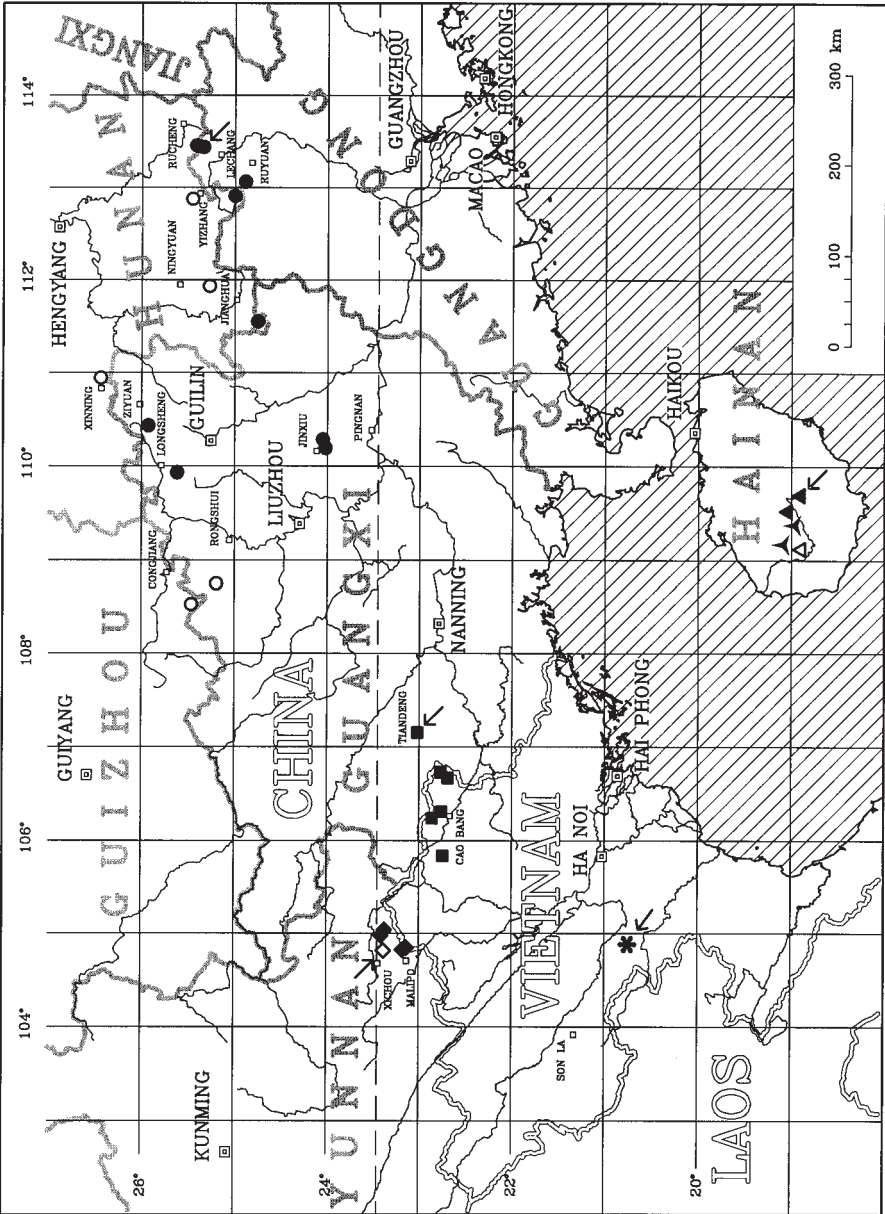


Fig. 5. Distribution of *Pinus wangii* subsp. *wangii* (◆ present & ◇ extinct occurrence), *P. wangii* subsp. *kwangtungensis* (● confirmed & ○ roughly located occurrence), *P. wangii* subsp. *eremitana* (■ confirmed, △ possible), *P. orthophylla* (▲ confirmed by the author, △ possible), ⚡ type localities.

covered by us only in July 1996. The stand reported from this region in 1947 (at Tungting), as well as the classical locality near Fadou village (13 km SE of Xichou) have both vanished, in the latter locality at least since 1964. A more extensive, at least 25 km long band with scattered stands probably existed in this region between 23°20'N and 23°27'N.

The occurrence of *Pinus wangii* subsp. *wangii* is confined to steep rocky limestone hills, today at an altitude of 1500–1800 m but, according to data on old herbarium specimens and the field characteristics, the maximum altitudinal range was between 1400 and 1900 m (Law & al. 1978 give “500–1800 m,” a printing error repeated by Fu & al. 1999). The pine occurs in small stands or as individual trees usually scattered on the tops and ridges of steep hills or on exposed places on the upper parts of slopes. Karst covers only a part of Xichou and Malipo Counties and forms one large system and several smaller complexes there. The majority has been totally deforested. The rocky limestone hills harbouring this pine are, or were, in the upper parts of slopes and summit areas covered with species-rich and relatively dense stands of primary woodlands with lower broad-leaved, predominantly evergreen trees and scattered conifers. At the locality near Xiajinchang and Taipingjie and rarely also near Tiechang we found *Tsuga chinensis* (Franch.) E. Pritz. var. *chinesis*; at the former two sites we found also *Podocarpus wangii* C. C. Chang and only near Xiajinchang we observed *Taxus chinensis* (Pilg.) Rehder and *Amentotaxus yunnanensis* H. L. Li.

Notes. – (1) Recent findings of *Pinus wangii* in Xichou Co. (Song & al. 1995) have not been supplemented with any accurate localisation but samples for chemical analyses of oleoresins were collected from several 5–8 m high trees, with a DBH of 18–44 cm.

(2) The record of *Pinus wangii* from Binh Tri Thien Province, central Vietnam (Hiep & Vidal 1996), refers to *P. dalatensis* subsp. *procera* (Businský 1999a). Farjon (1998) listed *P. wangii* from ‘Mai Chou’ in Vietnam; the population there, however, is described below as a new species, *P. eremitana*.

(3) Richardson (1998: 20, 24) reported *P. wangii* “from limestone hills of Yunnan just north of Burma”, erroneously for “just north of Vietnam”.

5.2.2. *Pinus wangii* subsp. *kwangtungensis*

Pinus wangii subsp. *kwangtungensis* (Chun ex Tsiang) Businský in Acta Pruhon. 68: 11. 1999 ≡ *Pinus kwangtungensis* Chun ex Tsiang in Sunyatsenia 7: 113–114. 11.1948 ≡ *Pinus wangii* var. *kwangtungensis* (Chun ex Tsiang) Silba in Phytologia 68: 64. 1990. – Type: Kwangtung, Loh-Chang [Lechang], in scrub, tree 13 m, 17.6.1929, C. L. Tso 21130 (n.v.; depository of the type not given in the protologue, not found at PE).

Taxonomic history. – Between 1929 and 1944, Chinese collectors gathered a number of samples of a new soft pine with effective seed wings at several localities in S China. The oldest specimen from the mainland was selected as the nomenclatural type of *Pinus kwangtungensis* (the name first used in an unpublished manuscript of N. K. Chun, see Tsiang 1948). The protologue includes not only specimens from the mainland provinces of Guangdong (formerly Kwangtung), Guangxi (formerly Kwangsi) and Hunan, but also from Hainan Island. Tsiang (1948) compared the new species primarily with *P. fenzeliana* Hand.-Mazz. and *P. morrisonicola* Hayata. For the further history of its alliance or identification with *P. fenzeliana* and *P. parviflora* see under 5.1.

The indumentum of shoots and branchlets is reported to be the most conspicuous diagnostic character distinguishing *Pinus kwangtungensis* from *P. wangii*. Shoots of the former were described as glabrous or, only rarely, sparsely pubescent, shoots of the latter as densely pubescent (Gaussen 1960, Law & al. 1978, Fu & al. 1999). Another important distinguishing character considered in the literature is the position of the dorsal resin ducts in leaves (Gaussen 1960, Kwei & Lee 1963, Law & al. 1978). In *P. kwangtungensis* the resin ducts were described as marginal, in the other taxon as median.

A chemical analysis of turpentine oleoresins (Song & al. 1995) revealed significant differences in the content of alpha-pinene and myrcene for *P. wangii* subsp. *wangii* and subsp.

kwangtungensis. The former does not differ from most of the other analysed soft pines in the content of the two terpenes, whereas *P. wangii* subsp. *kwangtungensis* appears to be anomalous because of an exceptionally low content of alpha-pinene (1.0 %, compared to 19.1 % in *P. wangii* subsp. *wangii*, or 4.4 % to 39.4 % in the other 21 pine taxa analysed) and an extraordinarily high myrcene content (16.1 %, compared to 0.2 % in *P. wangii* subsp. *wangii*, or 0.2 % to 1.0 % in all the other taxa). While alpha-pinene (bicyclic terpene) is the most widespread terpene in pines, found in a high percentage in the oleoresin of most species of *Pinus*, myrcene (beta-myrcene, olefinic open chain terpene) is a marginal component, reported to occur in only a few species of *Pinus* in low quantities of 1-5(-8) % (Mirov 1961, 1967: 496, 515). The data for *P. wangii* subsp. *kwangtungensis* thus need corroboration.

Geographic distribution and ecology. – The Hainan Island populations referred to thus far as *Pinus kwangtungensis* are here separated as a new species described below. *P. wangii* subsp. *kwangtungensis* is therefore understood here in a new, narrower concept, and to occur only in mainland S China.

The distribution range of *Pinus wangii* subsp. *kwangtungensis* is disjunct within a relatively large territory. It is limited to higher mountain massifs between 23°50' to 26°30'N and 108°00' to 113°30'E. The maximum distance between eastern and western localities is about 550 km. The occurrence of the taxon is limited to four particular areas, three of them in the main northern distribution zone near 25-26°N: (1) The largest area is the eastern one, in mountain massifs of the Nan Ling system along the border between the Guangdong and Hunan Provinces, with a possible extension into Guangxi in the region of the Mengzhu Ling Mts (W of the point where the three province borders meet). In this largest area, is the classical, easternmost site in Lechang Co., and an occurrence in the neighbouring Ruyuan Co. (both in Guangdong Prov.). In Hunan the taxon occurs in Rucheng, Yizhang and Jianghua Counties, and allegedly also in Ningyuan Co. (Law & al. 1978: 233; voucher not found). (2) In the second area to the W (the northernmost of the whole distribution range of *P. wangii* s. l.), it occurs in the N corner of Guangxi in Ziyuan Co. (documented from the N side of the Miao'er Shan massif, 2142 m) and in Longsheng Co. This occurrence extends northwards into Xinning Co. in Hunan. (3) The third, westernmost area is situated in the boundary mountain range of the Jiuwan Dashan system, where the taxon is documented from Guangxi (Rongshui Co.) and extends into the Guizhou Province (Law & al. 1978: 233; voucher not found), where it probably occurs in Congjiang Co. (4) The fourth area is more to the S, around 24°N, in the Dayao Shan Mts (1979 m) SE of Liuzhou City, as documented by specimens from Jinxiu Co. and Pingnan Co., both in the E part of Guangxi.

The subspecies is confined to rocky mountain slopes and ridges on acid eruptive rocks or metamorphic substrates, where it usually forms large, sometimes almost pure stands (Tsiang 1948: 112; own observations). Sykes (1991) reports *P. kwangtungensis* from limestone in Guangxi (without geographic details) but this report refers more likely to *P. wangii* subsp. *variifolia*. *P. wangii* subsp. *kwangtungensis* is reported to occur at 700-1600 m (Law & al. 1978: 233; this report does not include the Hainan populations and thus corresponds to the concept in the present paper).

The Lechang Co. population of *P. wangii* subsp. *kwangtungensis* was found at an altitude between 900 and 1200 m on the SE slopes of a granitic, rocky gorge at 25°21'N, 113°27'E (E of Jiufeng town). The vegetation of these steep rocky slopes is formed by mixed forest of broad-leaved trees (to a considerable proportion evergreen) predominating on relatively less rocky places, while the conifers are mostly found on exposed rocky habitats. The subspecies is primarily accompanied by a hard pine, *P. massoniana* Lamb., more rarely by *Nothotsuga longibracteata* (W. C. Cheng) C. N. Page, *Fokienia hodginsii* (Dunn) A. Henry & H. H. Thomas and by *Podocarpus macrophyllus* (Thunb.) D. Don. The more extensive Rucheng Co. population, found on the N rocky slopes of the boundary range, was studied at its upper altitudinal limit near 1500 m, where it is accompanied by another hard pine, *P. hwangshanensis* W. Y. Hsia (Businský 2003). The upper parts of these boundary mountains (max. elevation 1726 m) are almost completely deforested, but at middle altitudes the forests along both sides of the province border has mostly been preserved.

Note. – Critchfield & Little (1966: 8, map 14) gave the distribution of *Pinus wangii* subsp. *kwangtungensis* under the name *P. fenzeliana* Hand.-Mazz. (see above). All “isolated occurrences” shown in this publication on the Chinese mainland (i.e., in “Kwangtung, Hunan and Kwangsi”) belong to *P. wangii* subsp. *kwangtungensis*, except for the westernmost point (at S side of the Xun Jiang River), which belongs to true *P. fenzeliana* (the point represents its occurrence in the Daming Shan Mts).

5.2.3. *Pinus wangii* subsp. *varifolia*

Pinus wangii subsp. *varifolia* (Nan Li & Y. C. Zhong) Businský in Acta Pruhon. 68: 11. 1999 = *Pinus kwangtungensis* var. *varifolia* Nan Li & Y. C. Zhong in Novon 7: 262. 1997. – Holotype: China, SW Guangxi, “Longing Xian, Tiandeng Xian, summits of limestone mountains, ca. 540 m”, Y. C. Zhong 80834 (PE; isotype: GXF).

Description. – Low trees, at maturity with broadly rounded crown and irregularly ramifying trunk. First-year shoots slender, conspicuously glossy, dark castaneous brown, entirely glabrous from the very beginning. Leaves in fascicles of (2)3-5, (20-)30-50(-60) mm long, (0.8-)0.95-1.45(-1.65) mm wide, with (15-)20-35(-40) teeth per centimetre in the middle part, indistinctly greyish green on the ventral sides, on each with (3)4-7(8) stomatal lines, resin ducts median (two of them located dorsally and usually one near the ventral edge). Conelets 8-12 mm long. Cones small, only 3-6 cm long, on slender, (5-)6-8(-10) mm long peduncles. Seeds about 10 mm long with wings usually shorter.

Taxonomic history. – In the mid 1990s, a population of this taxon was discovered in N Vietnam, in the Cao Bang Province, not far from the border of the Chinese province of Guangxi, and identified as *P. kwangtungensis* (Prof. Phan Ke Loc, Univ. of Science, Hanoi, pers. comm., Jan. 1997). The same taxon was described as *P. kwangtungensis* var. *varifolia* from Chinese territory, from Tiandeng Co., Guangxi, based on the single, undated specimen Y. C. Zhong 80834.

Geographic distribution and ecology. – *Pinus wangii* subsp. *varifolia* occurs within a narrow band of some 140 km extending from W to E between 22°40' and 23°05'N (Fig. 5). The largest discontinuity, probably caused by the deforestation of the limestone areas in Chinese territory, is about 55 km between the NE-most locality at Tiandeng and the closest known site in the E corner of the Cao Bang Province. The other two gaps between the three regions of confirmed occurrences in Vietnam represent distances of about 40 km. The westernmost site of the taxon is at the W margin of a large karstic area covering a considerable proportion of the territory of the Cao Bang Province.

The distance between the ranges of *P. wangii* subsp. *varifolia* and subsp. *wangii* is more than 100 km, and between the former and subsp. *kwangtungensis* about 300 km.

With the exception of *P. amamiana* Koidzumi from S Japan, the sites of *P. wangii* subsp. *varifolia* have the lowest average altitude among the Eurasian soft pines. The altitude is lower in the NE part of the range (slightly above 500 m), and the highest known sites are in the W part (about 1400 m).

The known Vietnamese sites are located in three regions of the Cao Bang Province: (1) in its E corner in the district of Ha Lang (two localities less than 10 km from the Chinese border) at an altitude of about 800 m, (2) in the district of Tra Linh about 3 km from the Chinese border at about 1000 m, and (3) about 45 km W of the town of Cao Bang in the district of Nguyen Binh at an altitude of about 1400 m. All populations are found near ridges and summits of rocky limestone hills in karstic regions. The ecological amplitude is therefore similar to that of *P. wangii* subsp. *wangii*.

In August 1998, we examined an extensive territory of limestone hills within a 10-25 km radius around Longming, a small town near a road crossing about 16 km SW of Tiandeng. The landscape is characterized by a very varied hilly karst, formed by numerous steep rocky conical

hills with relative elevation of about 50–300 m. These limestone hills, formerly covered by dense broad-leaved forest, are now almost entirely deforested or covered with scattered remnants of shrubby vegetation permanently suffering from cutting. The only species of conifers is *Pinus massoniana* Lamb., which rarely reaches the karstic hills from the neighbouring non-limestone hills, where it locally forms rich stands.

A similar karstic hilly area is on the outskirts of Tiandeng, where the deforestation dates back to an earlier time. The town itself is located (the centre at 23°05' N, 107°08' E) on an open plateau at an altitude of less than 400 m, surrounded by groups of karstic hills with relative elevation of about 150 m. During our field exploration of the type locality in Tiandeng Co., only a single, isolated tree of *P. wangii* subsp. *varifolia* was found, just above the SE outskirts of the town of Tiandeng. It has survived some 30 m below a rounded summit at the upper edge of an about 100 m high perpendicular cliff of the marginal group of hills; the cliff has a NW exposure facing the town. The surrounding vegetation is formed only by sparse remnants of shrubbery. Pine seedlings, or saplings were not found. The tree seemed healthy and of well-developed habit, with its crooked trunk irregularly ramifying from the base. Its circumference was 250 cm (1.3 m above the basal branch), the crown broadly rounded, about 18 m in diameter and approximately of the same height. The main branches were erecto-patent, with lateral branchlets nearly horizontal. Considering the character of branching, the length of annual growth, and the ecological conditions at the locality, it is possible to estimate its age to be over 300 years. In its habit and in most other characters it is very similar to individuals of *P. wangii* subsp. *wangii*. Compared to trees of subsp. *kwangtungensis*, differences, particularly in habit and in the colour of the ventral sides of the leaves, which are inconspicuously greyish in this single tree, are more distinct. However, the tree near Tiandeng exhibits a unique character, not found even in the other members of *P. sect. Quinquifoliae*: its leaves are in fascicles of three, four or five, with uneven frequency. Fascicles of three or four prevail in branchlets of lower branches (although even these lower branches bear a great number of first year ovulate cones) while in the upper part of the crown, normal fascicles of five predominate. It seems again safe to assume that it is this tree near Tiandeng from which the original material of *P. wangii* subsp. *varifolia* was collected. The sample examined from the Vietnamese locality in the Ha Lang district also has a variable number of leaves per fascicle. Presumably, this character is the result of a mutation to be found in at least the E part of the distribution range of this taxon (but likely to occur in all of its populations).

Note. – The name ‘Longing’, as given in the protologue, is certainly an error for Longming, and the use of the term ‘Xian’ (county) is incorrect in this case, because this town is situated in Tiandeng Co. In Fu & al. (1999) the same town is mistakenly interpreted as “Longlin Gezu Zizhixian in SW Guangxi”, situated in Guangxi about 260 km NW of Tiandeng.

5.2.4. Summary of the differences between the subspecies of *Pinus wangii*

Variation and distribution of the three characters most commonly used in the literature to distinguish subsp. *wangii* from subsp. *kwangtungensis* are analysed (see also Table 4). The variation of the third subspecies, the recently described subsp. *varifolia*, could not be studied in the same way because of the lack of appropriate material.

Surface of shoots. – The surface of shoots is pubescent in all trees of *Pinus wangii* subsp. *wangii* studied by the author and the indumentum fully persists a second and often a third year. The density and length of the unevenly distributed trichomes show inconspicuous individual variation. Similar to other species of *P. sect. Quinquifoliae* with pubescent shoots, the thicker, fertile terminal shoots are more glabrous, while the slender lateral shoots are more densely and more persistently hairy. At first, the shoots are also pruinose, which is apparent in living material as late as in the summer months, and still, though less distinct in dry material. All the revised older herbarium specimens had an identical indumentum, with the exception of the pruinosity, which was rarely preserved as faint remnants.

Table 4. Comparison of the main differences between the three accepted subspecies of *Pinus wangii* s. lat.

Character \ Subspecies	<i>wangii</i>	<i>varifolia</i>	<i>kwangtungensis</i>
Shoots	always pubescent	entirely glabrous, conspicuously glossy	glabrous, glabrescent or pubescent
Number of leaves per fascicle	constantly 5	usually (2)3-5	constantly 5
Ventral sides of leaves	usually greyish white pruinose	indistinctly greyish green	conspicuously white pruinose
Number of stomatal lines on each ventral side	(3-)5-9(-12)	(3)4-7(8)	(4-)6-8(-11)
Dorsal resin ducts of leaves	median	median	mostly marginal, rarely median
Length of cones	(3.5-)4.5-8.5(-10) cm	3-6 cm	(5-)7-10(-11) cm
Habitat	1400-1900 m; karstic limestone rocks	500-1400 m; karstic limestone rocks	700-1600 m; eruptive or metamorphic rocks

In the populations of *Pinus wangii* subsp. *kwangtungensis* studied in Lechang and Rucheng countries, most individuals possessed glabrous shoots, mostly with remnants of pruinosity (in January). However, several individuals were found to have unevenly pubescent shoots, with trichomes usually concentrated below short-shoot insertions (e.g., *Businský 39122*). In all older specimens at PE (only a selection is cited in electronic supplement) from Lechang Co. and the neighbouring Ruyuan Co. only glabrous shoots were observed, while partly densely hairy shoots were found in each a specimen from the neighbouring Yizhang Co. (*C. J. Qi 1099*) and from Jianghua Co., S Hunan (*B. G. Li 05269*). Four specimens were examined from the centre of the main northern distribution area; one (*Z. Z. Chen 51818*) has uneven short pubescent shoots, the others (*S. C. Luo 018*, ‘*Canton*’ *01094*, *J. S. Ying 0002*) have shoots with dense hairs as in subsp. *wangii*. From the W distribution area in the Jiuwan Dashan Mts three specimens were studied, all from Guangxi; one (*S. Q. Chen 15370*) has glabrous shoots, the others (*S. Q. Chen 15447 & 15502*) shoots with unevenly and sparsely distributed pubescence. No material was available from the southern area in the Dayao Shan Mts, SE of Liuzhou City.

The shoot indumentum in *Pinus wangii* subsp. *kwangtungensis* thus shows a wide range of variation. It seems likely that there is a noticeable clinal variation, with an increasing frequency and density of the indumentum from E to W, towards the distribution range of subsp. *wangii*, in which the indumentum is relatively constant. In the eastern populations of subsp. *kwangtungensis*, from which the taxon was described, individuals with glabrous shoots decisively predominate. A co-occurrence of plants with completely glabrous shoots and those with pubescent shoots is not exceptional among soft pines, but also found in, e.g., *P. dalatensis* and *P. krempfii* Lecomte (both in the Bi Doup mountain region NE of Dalat, Vietnam) as well as in the newly described *P. eremitana*.

Leaf anatomy. – The leaves of *Pinus wangii* subsp. *wangii* studied, have, in accordance with published data (Gaussen 1960, Kwei & Lee 1963, Law & al. 1978), mostly dorsal resin ducts in median position, and sometimes a duct closer to the hypodermis or in a submarginal position. The resin duct near the ventral edge is always present and has a median, usually symmetric position. Leaves of several trees of subsp. *kwangtungensis* from the classical locality in Lechang Co. and from the neighbouring Rucheng Co. have partly a marginal (or submarginal) and partly a median position of the dorsal resin ducts, but the (sub)marginal position prevails (an intermediate submarginal position is found quite frequently). The ventral resin duct is developed in some leaves only, and usually has a median but often asymmetric position (in some trees, a marginal asymmetric position is found). However, in some individuals, leaves with dorsal resin ducts in a purely marginal position occur to a lesser extent (e.g., *Businský 39120*), and occasionally leaves with all resin ducts in a purely median position are found (in *Businský 39122* they even predomi-

nate), which is a situation known from subsp. *wangii*. Thus, the position of dorsal resin ducts is not diagnostic for subsp. *wangii* and subsp. *kwangtungensis*. An imperfect fixation of this character is also reported in *P. armandii* Franch. (Grierson & al. 1980: 304).

The presence of sclerenchymatic cells in the mesophyll of *Pinus wangii* subsp. *wangii* differs from individual to individual, and may be ecologically determined. The taxonomic value of this character is therefore problematic (Sato 1995 a, b). In our samples of subsp. *wangii*, sclerenchymatic cells were observed with various frequency in leaves of different trees. In *Businský 43117* & *43119*, e.g., sclerenchymatic cells were found in a less developed form, or were altogether lacking. No distinctly developed sclerenchymatic cells were found in the mesophyll of our samples of subsp. *kwangtungensis*.

In contrast to the stated differences in the number of stomatal lines on the ventral side of leaves (Silba 1990), this number is almost identical in all our samples of both taxa (see Table 4).

Seed size. – Ferré's (1960: 4) interpretation of seed characters of *Pinus wangii* subsp. *wangii* was based on the protologue, where the seed size (excluding the wing) is reported to be 8×5 mm, and the wing size to be 15×7 mm. While this seed size represents the bottom length limit, the wing is extraordinary long and narrow (with a length/width ratio of 2.14). The highest wing length/width ratio measured by the present author is 2.067 in a single seed of *Businský 43117*, where the wing size (15.3×7.4 mm) is similar to that given in the protologue, whereas the seed corpus is the largest observed (12.8×6.1 mm). Similar small seeds as in the type material were found in *Businský 43119*, with a corpus of 8.0×5.2 mm and a wing of 14.8×7.2 mm, which, however, represents extreme values untypical even for the individual tree, because it comes from the cone apex. These discrepancies are obviously due to the fact that the original material encompasses a low number of seeds of not very representative, small cones.

5.2.5. Comparison of *Pinus wangii* s. lat. with other Asian species of *P.* subsect. *Strobus*

Pinus uyematsui, *P. dalatensis* and *P. wallichiana* s. lat. – These species share a number of characters and are here considered to be closely related. This relatively homogeneous group differs from *Pinus wangii* s. lat., primarily in having small seeds with relatively long, narrow wings, and, as a rule, conspicuously larger cones with thinner scales. In addition, they possess longer, narrower and straight leaves.

Pinus morrisonicola – According to the biometric evaluation, *Pinus wangii* subsp. *wangii* and the Taiwanese *P. morrisonicola* have almost identical or very similar average values in all of the ten measured quantitative seed characters. However, in subsp. *kwangtungensis* the values are lower in most characters (the biggest difference is in the wing length/width ratio), and in subsp. *variifolia* the values are still lower (its seeds are distinctly smaller and have relatively shorter wings).

In addition, there are distinct differences in leaf characters of *P. morrisonicola*: they are straight, longer, narrower (on average 65 mm long and less than 1 mm wide), with a small number of stomatal lines on the ventral sides, gradually narrowing towards an acute apex. The most conspicuous differences are found in the cone morphology: cones of *P. morrisonicola* are, in fact, unique among Asian representatives of *P.* sect. *Quinquefoliae* (see Chapter 5.6. & 5.10.), and a little longer on average and relatively broader. Also the general habit of the Taiwanese species is different, and the trees reach larger dimensions.

Pinus parviflora s. lat. – *P. parviflora* resembles *P. wangii* in several characters and is undoubtedly closely related. It differs in the following characters: the cones are usually ovoid or oblong-ovoid, subsessile or on short, 2-6(-8) mm long peduncles, very firmly persistent, usually in whorls of 3-6(8); the cone scales (on a longitudinal section in the scale axis) usually have distinctly convex apophyses in the distal or central part. The leaves are somewhat less curved and narrower, with only (2-)4-11(-15) teeth per centimetre in the middle part and (2)3-7(-9) stomatal lines on each ventral side. Mature trees are usually 15-30 m high, with often narrow crown tapering on the top.

Notes. 1. – The character “apophyses more wrinkled, when ripe” given by Farjon (1984) as diagnostic for *Pinus kwangtungensis* was not observed in both populations studied in January 1994 when fully ripe cones were open. Material collected at various phases of ripening from a fertile grafted sapling cultivated in the Arboretum of the Research Institute of Ornamental Gardening, Průhonice, Czech Republic (whose mother plant originated from the Institute of Forest Genetics, Placerville, California, USA; cf. Mirov 1967: 274; see Weger CA95/27) over several years revealed that the wrinkled apophyses develop as a consequence of early collecting of incompletely ripe cones, or of imperfect ripening under aberrant climatic conditions (at least in some years) in culture. This conclusion is supported by a drawing of an untypically open and shaped cone (Farjon 1984: 96).

2. – In contrast to the statement in the protologue of *Pinus wangii* (Hu & Cheng 1948) “shorter seed with a longer wing” [compared to *P. parviflora*], the wing length is suitable only for distinguishing *P. wangii* subsp. *wangii* from *P. parviflora* subsp. *parviflora*, as wings of the latter are more or less rudimentary (but both taxa have a very similar seed corpus size), whereas subsp. *pentaphylla* has seeds and wings of almost the same proportions as those of *P. wangii* s. lat.

5.3. *Pinus orthophylla*, a new soft pine from the Hainan Island

In late December 1993, we explored the two highest mountain ranges on Hainan Island, not only to elucidate the then still uncertain taxonomic status of *Pinus fenzeliana* (see above), but also to study those island pine populations that had hitherto been referred to as *P. kwangtungensis* (Tsiang 1948, Law & al. 1978, Fu & al. 1999). The latter, very dissimilar to but growing together with the former, was found at middle altitudes of the Mt Wuzhi Shan. Examination of a number of trees from various altitudes soon brought to light that the local pine substantially differs from *P. kwangtungensis* as originally described from Lechang Co. in N Guangdong Prov., visited by us in early 1994. After a detailed examination of older herbarium specimens of both taxa from Hainan and from several regions on the mainland, and, in particular, after a detailed comparison and morphometric analysis, it became clear that the population on Hainan Island represents a distinct, new species.

Pinus orthophylla Businský, sp. nova – Fig. 6

Holotype: China, Hainan island, central part, Wuzhi Shan Mts, NW ridge of the main massif (1867 m), in dense mixed forest on stony ridge above bottom limit of species occurrence, together with *Pinus fenzeliana*, 1100 m, 18°54'40"N, 109°41'20"E, tree: 220 cm t.c., 17 m h., old, 28.12.1993; Businský 39116 (PR; isotypes: B, G, K, MO, P, PE).

A simili *Pinus wangii* subsp. *kwangtungensis*, quacum confunditur, notis sequentibus perspicue differt. *Folia* recta vel solum apice parum curvata, (40-)55-80(-90) mm longa et (0.83-)0.95-1.25(-1.35) mm lata, in lateribus ventralibus cano-pruinosa (non distincte alba), sensim acutata, in angulis remote acute serrulata, praeter basim usque 1/4(-1/2) longitudinis integerrimam vel dentibus singularibus interdum praeditam. *Strobili* apice comparate angusto sensim attenuato; squamae strobilorum maxime (14-)17-21(-24) mm latae, cum proportione saepissima longitudinis ad latitudinem 1.32 usque 1.65; apophyses in parte strobili basali (1/4-1/3 longitudinis) marginibus distalibus plerumque insigniter recurvatis; umbo conspicue abrupte impressus in depressionem ad finem squamae truncatus. *Semina* parva alis longis et angustis; corpora 5.7-8.7(-10) × 2.6-4.7 mm magna (i.e. mediocriter 29-40 % longitudinis totius seminis); limbus in basi alae argutus, rugosus, conspicue elongatus in gracilem incrassationem, 2.7-4.1 mm longam (incrassatio in proportione 0.4 usque 0.5 ad longitudinem corporis); ala 11.2-19.2 mm longa (incrassatione inclusa), tantum 4.5-8.7 mm lata, cum proportione longitudinis ad latitudinem 1.7 usque 2.9.

Description. – Low trees, usually not exceeding a height of 20 m, of broad habit, generally with short, often crooked trunk up to 100 cm in diameter. Branches of mature trees irregularly forked, usually horizontal, with relatively dense secondary branching. Foliage greyish green, persisting

Table 5. Main differences between *Pinus orthophylla* and the closely related *P. wangii* subsp. *kwangtungensis* (* range of individual average values only; # average value).

Diagnostic characters	<i>Pinus orthophylla</i>	<i>Pinus wangii</i> subsp. <i>kwangtungensis</i>
Leaves		
shape	± straight; gradually narrowing towards an acute apex	usually conspicuously crescently curved; usually abruptly narrowing towards an obtuse apex
margin	in basal 1/4-1/2 often entire	serrate except for the attenuate base
colour	greyish glaucous ventrally	conspicuously whitish ventrally
length	(40-)55-80(-90) mm	(25-)35-50(-70) mm
width	(0.83-)0.95-1.25(-1.35) mm	(0.95-)1.25-1.45(-1.75) mm
number of teeth per middle cm	(10-)12-28(-34)	(18-)22-40(-50)
Length/width ratio of the largest cone scale	(1.13-)1.25-1.8(-1.94); # 1.44	(0.81-)1.1-1.3(-1.55); # 1.18
Umbo	conspicuously abruptly depressed into a concavity	even with the apophysis surface
Seed corpus		
length %* of seed length	29.5-39.9(-45.7)	(38.9-)45.5-51.8
length	(5.7-)6.2-8.7(-10.2) mm	(7.9-)8.8-11(-11.5) mm
width	(2.6-)2.7-4.3(-4.7) mm	(4.1-)4.7-6.3(-7.1) mm
Length of thickening of wing	(2.7-)3-3.8(-4.1) mm	(0.5-)0.8-2(-2.3) mm
Length/width ratio* of wing	1.65-2.83	0.98-1.64

for two years. First-year *shoots* glabrous, pruinose when young, later dark brown, slightly glossy. *Leaves* relatively stiff and erect, straight or slightly curved at the end, (40-)55-80(-90) mm long and (0.83-)0.95-1.25(-1.35) mm wide, in the terminal part gradually narrowing towards an acute apex, irregularly, acutely serrate on all edges except for the base or basal 1/4 (sometimes edges almost entire up to the middle), with (10-)12-28(-34) teeth per centimetre in the middle part, dark green dorsally, greyish glaucous (but not conspicuously white pruinose) and with (3-)5-8(-10) stomatal lines on each ventral side. Resin ducts 2-3, two marginal on the dorsal side, and usually a third one near the ventral edge, either a marginal one situated laterally or a median one situated symmetrically opposite the edge. Hypodermis of one cell layer, occasionally with some cells in a second and, rarely, single cells in a third layer on the dorsal side; cell walls somewhat thickened. *Conelets* subterminal, solitary or in pairs, (10-)13-17(-20) mm long, ovoid to ob-long-ellipsoidal, erect on slender, approximately equally long or longer peduncles. Exposed part of the conelet scales flat, with only slightly deflected distal edge (more deflected in basal scales), rounded-cuneate in outline, with the apex abruptly narrowed to a short, acute, fragile tip or without discernible apex. *Cones* pendulous on relatively slender, 8-20(-25) mm long peduncles (often with resin vesicles in the phloem tissue), narrowly ovoid or narrowly ellipsoidal when closed, attenuate towards the apex, (4-)6-10(-12) cm long and 4.5-6.5 cm wide when fully open; after seed dispersal early deciduous, or at least not firmly persisting into the next year. *Scales* 40-65, the largest (19-)26-30(-32) mm long and (14-)17-21(-24) mm wide, with a length/width ratio of (1.13-)1.25-1.8(-1.94); basal sterile scales around the peduncle insertion inflexed or deflected, occasionally recurved towards the peduncle. *Apophyses* thick, firm and smooth, cinnamon brown and glossy on freshly ripened cones, often slightly pruinose, with a straight to slightly convex longitudinal dorsal line (sometimes with traces of a low keel); distally obtusely cuneate to rounded in outline, with distal edges of seed scales in the basal 1/4-1/3 of the cone usually distinctly turned outwards to recurved. *Umbo* transverse and flat, 4-7 mm wide in seed scales, con-

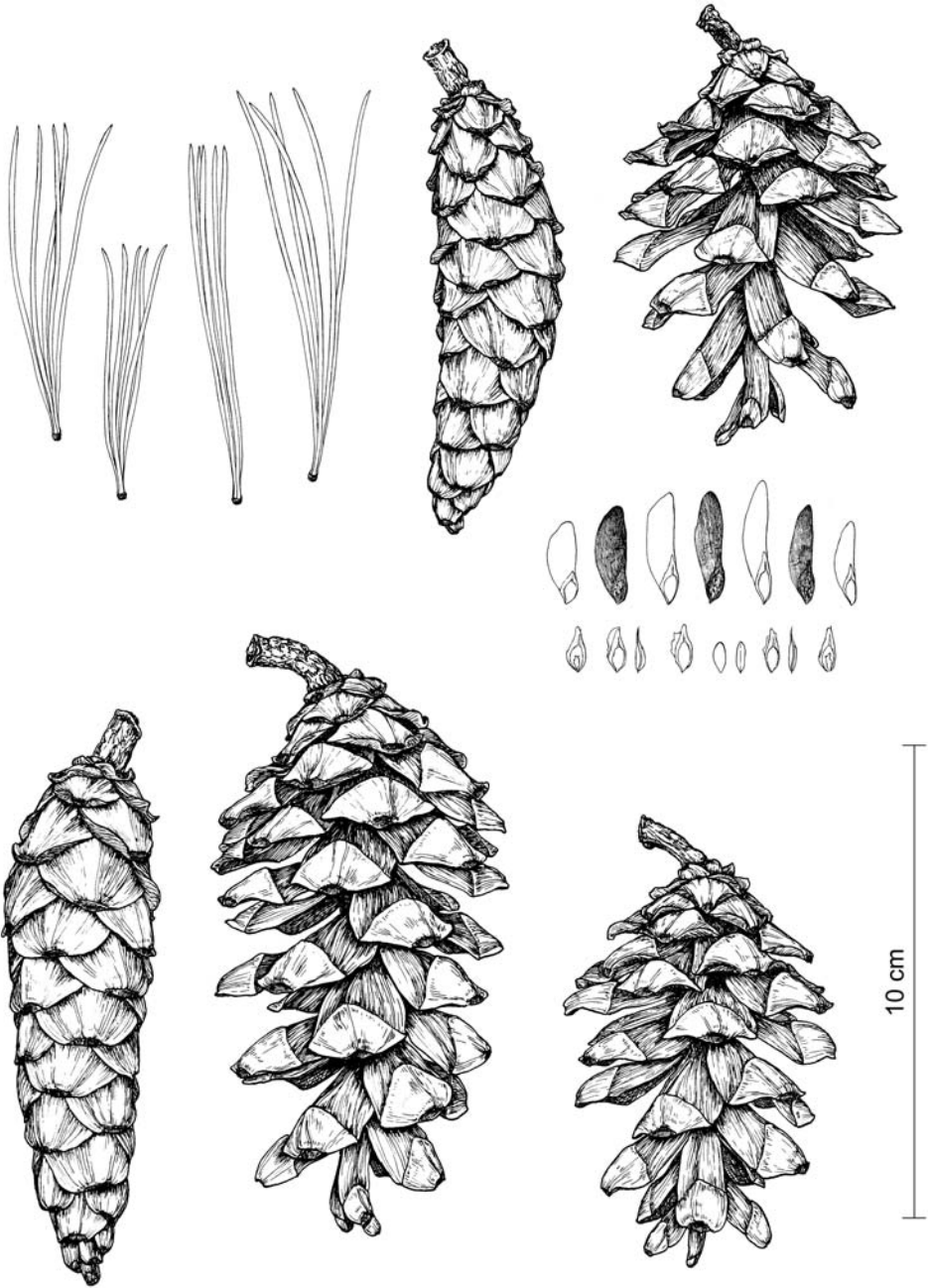


Fig. 6. *Pinus orthophylla* – leaves, two cones above and seeds after the type; two cones bottom left & middle after *Businský 39111*, the cone bottom right after *Businský 39110*, all from the type locality. – All to the same scale; drawn by L. Businská.

spicuously and abruptly depressed into a concavity at the truncate end of the scale; the distal edge sharp, often elevated upwards or recurved, in outline truncate to weakly acute. *Seeds* including the relatively long and narrow wing 17–27 mm long; seed corpus 5.7–8.7(–10) mm long and 2.6–4.7 mm wide, representing 29–40(–46) % of the seed length; corpus border of the wing base distinct, rugose and conspicuously elongated into a rib-like, slender, 2.7–4.1 mm long thickening attached to the corpus; average thickening/corpus length ratio 0.4–0.5; the acute apex of the thickening very close to the interior margin of the wing; transition between the thickened corpus border and the membranous wing blade distinctly irregularly undulate and, even on the ventral side of the seed, thickening gradually connected to the blade. *Wing* 11.2–19.2 mm long and 4.5–8.7 mm wide, with an average length/width ratio of 1.7–2.9; with finely dispersed, dense, dark pigmentation.

Taxonomic history. – *Pinus orthophylla* was discovered already in 1920 by N. K. Chun, in the Wuzhi Shan Mts on Hainan Island, and was the first record of a representative of *Pinus* subsect. *Strobus* in S China (Tsiang 1948). The first samples (McClure 9393) were collected at the same locality two years later and identified by E. D. Merrill as *P. morrisonicola* Hayata. Since Tsiang (1948) in the protologue of *P. kwangtungensis* also included specimens from that Hainan Island population, it has usually been identified as *P. fenzeliana* or *P. kwangtungensis*, most recently so by Fu & al. (1999). The differences between the new species and *P. wangii* subsp. *kwangtungensis* are summarised in Table 5.

The study of specimens at PE corroborated that all the Hainan collections identified as *Pinus kwangtungensis* belong to *P. orthophylla*. None of them are suitable for typification. Thus, I selected an own collection of the most completely developed individual of nine sampled trees representing the whole altitudinal range of *P. orthophylla* in the Wuzhi Shan Mts, where this pine was discovered for the first time.

Geographic distribution and ecology – *Pinus orthophylla* is confined to the highest mountains of Hainan Island (Fig. 5). Tsiang (1948) gives a list of eight specimens from Hainan (under *P. kwangtungensis*) indicating two localities. The first is “Five Finger Mt” = Wuzhi Shan. McClure 9393 from 1922 was reported from an altitude of 1600 m, Tang 402 from 1936 is without altitude record, while Tso & Chun 44092 and 44197, both from 1932, are reported to come from an “alt. 300 m”, probably meaning 1300 m. “Ting An” given on three specimens (Wang 35273, 35542, 35629), not to be confused with the town Ding’an in the lowlands in the N of the island, probably refers to Yinggen (= Qiongzong), a town located in the NE foothills of the Wuzhi Shan Mts.

The second locality, “Loh-Tung” (= Ledong = Baoyou), after Lau 27270 in sched. from 1936, is a town in the SW of the island. The only mountain of adequate altitude there is Mihou Ling (= Hou Hsien Ling; 1654 m, alternatively 1670 or 1676 m, at 18°54'N, 109°08'E), which forms the W part of the Limu Ling Mts. McClure 719, collected in 1929 (PE!) at “Hung Mo Tung, summit of Hung Mo, above Fan Ta” refers to the Mt Ying Ge Ling (1815 or 1822 m, at 19°02'N, 109°32'30"E, S above Fan Ta village), the highest peak of the Limu Ling range and the second highest of the island (the name ‘Hung Mo Tung’ probably corresponds to Limu Ling).

The above data represent all known stands safely referable to *Pinus orthophylla*. An extensive population was studied by us in detail for several days in the first locality, in the Wuzhi Shan Mts in December 1993. The Wuzhi Shan culminates in a mountain of the same name, at 18°54'N, 109°42'E, with two separate summits, the NE one is indicated by the elevation point 1867 m (alternatively 1879 or 1892 m). The Wuzhi Shan Mts are an isolated massif divided SE-wards by a c. 10 km wide belt of foothills and the low valley of the Changhua Jiang river from the extensive Limu Ling Mts. The Wuzhi Shan massif occupies an area of about 10 × 10 km and shelters a intact dense primary mountain forests in a landscape that is otherwise almost totally deforested. The surrounding hilly country occasionally reaches and rarely exceeds an altitude of 1000 m. The relief of the Wuzhi Shan is very varied, with steep rocky slopes formed by eruptive rocks. *P. orthophylla* inhabits rocky ridges and other open rocky places, above all on the N side, but without any particular expo-

sure preference between 1000 and 1870 m up to the summits. It usually forms mixed stands with broad-leaved evergreen trees. At lower altitudes (up to 1250–1300 m) it is often associated with *P. fenzeliana* or with *Dacrydium pectinatum* de Laub. Sometimes it forms almost pure stands in favourable rocky sites.

Since *Pinus orthophylla* can easily be recognised from the distance by the very conspicuous, horizontally arranged, dense branches with greyish foliage, we could, by means of a strong telescope, observe a great number of old trees in the second locality, on the NE slopes of Ying Ge Ling in an intact primary forest, from c. 1200 m up to the summit. Scattered trees probably can be found there even at lower altitudes on rocky ridges as well, but there *P. fenzeliana* dominates. *P. orthophylla* may also be expected in the Limu Ling range between Ying Ge Ling in the central part of the range and Mihou Ling in the W, around the highest summits of the connecting ridge, particularly on the mountain called Eji Ling (= O-Chi Ling; 1588 or 1586 m, at 18°58'N, 109°24'E), and perhaps on the one called He Ling (1575 m, at 19°05'N, 109°10'E) in the NW part of the range.

Generally, *Pinus orthophylla* is a species of rocky sites above 1000 m around 19°N in the tropical mountain forests that gradually change along the altitudinal gradient into subtropical vegetation dominated by mostly low evergreen trees and shrubs.

As regards the conservation status of *P. orthophylla*, a positive fact is that the Wuzhi Shan is a nature reserve and tree felling prohibited. However this isolated refugium may be vulnerable during dry winters to fires escaping from the surrounding agricultural land. The primary forest of the highest massifs of the Limu Ling range is also relatively intact, in spite of some tree felling (mainly large trees of *Dacrydium pectinatum*).

Evolutionary considerations. – During the Tertiary migration to the south, the gradual evolution of E Asian pines was enhanced by their occurrence in generally scattered populations within mixed forests (Mirov 1967: 68–69, 116–118, 569–575). Under the pressure of competition, they were displaced to commonly less favourable exposed rocky sites, where they succeeded, owing to their drought tolerance and preference for sunny sites. Among the soft pines, those species with small seeds and relatively long, narrow, adnate wings (with an elongated rib-like thickening protecting the wing against breaking off), corresponding to the relatively narrow and thin cone scales (a combination of characters typical for *P. orthophylla*), supposedly represent ancestral forms. These were well-adapted to anemochorous dispersal and a nutrient-rich soil, in which a small megagametophyte would have sufficed for the establishing of seedlings. As an adaptation to less nutrient rich soils in rocky habitats, small-seeded soft pines subsequently evolved larger seeds with larger megagametophyte and a less effective wing, obviously to the detriment of anemochory and in favour of enabling their rolling down the precipice into rock crevices, or of their attractiveness for potential dispersal by birds or rodents. Southern populations of the Japanese *P. parviflora* seem to be good examples for this. The secondarily reduced, fragile wings with lacerate margins are adhered to the cone scales, while the heavy seeds are easily released by the widely opening cones with sparse scales.

The hypothesis of this evolutionary trend seems to some extent be supported by the range of morphological variation found in *Pinus orthophylla* along an altitudinal gradient in the Wuzhi Shan massif. With increasing altitude, and, consequently, with gradually less favourable conditions and steeper, rocky and exposed sites, an increase in the size and relative width of the seeds and wings is apparent. The largest seeds with broadest wings are from a dwarf tree on an exposed cliff of the highest summit (*Businský 39106*) and from a low tree on a sheer cliff at c. 1800 m (*Businský 39108*). Both samples, however, retain the distinctly elongated thickened wing base typical of this species.

While *Pinus orthophylla* is here considered to be a relic species closely resembling the hypothetical ancestral type, *P. wangii*, *P. parviflora* and *P. eremitana* clearly illustrate various stages of a more advanced evolutionary development within a probably monophyletic group, from which *P. morrisonicola* is excluded on evidences presented further below.

5.4. *Pinus eremitana*, a new soft pine from N Vietnam

At the end of January 1994, Dr Nguyen Tien Hiep, Dept. of Botany, Institute of Ecology and Biological Resources, Hanoi, directed the author's attention to the fact that at the beginning of the 1980s, a soft pine species was discovered in the vicinity of Pa Co village near Mai Chau (SW of Hanoi), which was referred to as *Pinus kwangtungensis* Tsiang (Loc 1984). The only available herbarium material in several herbaria in Hanoi, especially in HNU and HN consisted of four samples (each on a few herbarium sheets) collected in 1981, 1982 and 1991, which were not of a quality allowing unequivocal determination. However, distinct variation in the indumentum of young shoots (pubescent in one and glabrous in another sample), i.e., in the major diagnostic character used for the discrimination of *P. wangii* and *P. kwangtungensis* at that time, prompted us to search for this species in the field.

At the turn of January and February 1994, we found a scarce population on the summits and ridges of the local karst hills near the village Pa Co. The pine population was studied in detail for three days and samples were collected from ten selected representative trees of various size and age on two hills. During the field study it became apparent that this pine differs from *Pinus wangii* subsp. *kwangtungensis* (which was studied by us at the type locality only three weeks earlier). Subsequent biometrical and statistical evaluation corroborated that this pine represents a highly variable but distinctly morphologically delimited new species.

Pinus eremitana Businský, sp. nova – Fig. 7

Holotype: Vietnam, Son La Prov., E border near Ha Son Binh Prov., the karstic hills approx. 1.5–2 km W of Pa Co village NW of Mai Chau, below the top of the 'Eastern hill', rocky top ridge of limestone hill with dense low woods, W exposure, about 1480 m, 20°45'N, 104°53'E; tree: 115 cm t.c., 9 m h., 1.2.1994, *Businský 39133* (PR; isotypes: B, G, HN, K, MO, P).

A simili *Pinus wangii* (etiam a subspecie eius orientali, subsp. *kwangtungensis*, quacum confunditur) notis sequentibus perspicue differt. Foliatio ramorum clare viridis vel summe parum glaucescens, anno uno vel annis duobus persistens. Ramuli novelli glabri vel in individuis nonnullis inaequaliter pubescentes, solum ramuli tenues infra bases brachyblastorum densius pubescentes. Folia comparate mollia, recta vel tantum inconspicue arcuato-curvata (raro in ramis fructiferis crassis individuorum nonnullorum arcuata), solum (0.72-)0.85-1.15(-1.28) mm lata, in latere dorsali dilute viridia et plerumque manifeste canaliculata, in lateribus ventralibus cano-viridia (non distincte alba), stomatum seriebus (3-)5-6(-8) praedita, sensim acutata, in angulis parte superiore remote (interdum interrupte) acute serrulata, in parte basali (saepius 1/4-1/2 rarius supra 1/2 longitudinis) integerrima vel dentibus singularibus interdum praedita. Strobili ovoidei usque oblongo-ovoidei, apice plerumque rotundato; saepe pseudolateraliter dispositi, usque per 5-6 in verticillis; apophyses valde validae et durae, plerumque superficie subtiliter longitudinaliter sulcatae, biformes – i.e. in parte strobili quarta basali planae cum marginibus distalibus recurvatis, apophyses in parte strobili subapicali plerumque manifeste convexae, ad finem truncatae et inflexae; squamae basales steriles plerumque recurvatae; umbo plerumque insigniter et abrupte impressus in depressionem ad finem squamae truncatus.

Description. – Low trees, usually not exceeding a height of 15 m (rarely c. 20 m high), trunk generally straight, up to 100 cm in diameter, crown often broader than the tree's height. Branches of mature trees usually horizontal, with relatively dense secondary branching. Foliage bright green or, at most, slightly greyish green, persisting for only one or two years. First-year shoots pale brown to greyish brown, glabrous or, in some individuals, unevenly pubescent with highest density of hairs chiefly on slender branchlets below the short-shoot insertions. Leaves relatively soft but erect, straight or only indistinctly curved (rarely curved on stout fertile branchlets of some trees), (20-)30-45(-65) mm long and (0.72-)0.85-1.15(-1.28) mm wide, in the terminal part gradually narrowing towards an acute apex, irregularly, acutely serrate (serration sometimes interrupted) on all distal edges, entire or almost entire in the basal part or up to the middle or, rarely, even above the middle, with (0-)8-25(-30) teeth per cm in the middle part; pale green and usually

Table 6. Differences between *Pinus eremitana* and closely related species (# average value).

Diagnostic characters	<i>Pinus eremitana</i>	<i>Pinus wangii</i> s.lat.	<i>Pinus parviflora</i>
Height of mature trees	8-15(-20) m	8-20 m	15-30 m
Leaves			
shape	straight or moderately curved (# 37°); gradually narrowing towards an acute apex	in general conspicuously crescently curved (# 84°); usually abruptly narrowing towards an obtuse apex	in general moderately curved (# 39°); gradually narrowing towards an acute apex
margin	in basal 1/4-1/2 often entire	usually serrate except for the attenuate base	in basal 1/4-1/2 often entire
width [mm]	(0.72-)0.93-1.05(-1.3); # 0.98	(0.85-)0.95-1.5(-1.75); # 1.27	(0.7-)0.75-1.3(-1.45); # 1.02
number of teeth per middle cm	(0-)8-25(-30)	(13-)18-40(-50)	(2-)4-11(-15)
position of resin ducts	median	median to marginal	marginal
Number of cones per node	usually in whorls of 5-6	single or in whorls of 2-3(4)	usually in whorls of 3-6(8)
Cone persistence	deciduous or weakly persistent	deciduous or weakly persistent	very firmly persistent
Length of cone peduncle	5-15(-22) mm	6-20(-25) mm	2-5(-7) mm
Shape of apophysis	usually conspicuously convex in scales of the apical third of the cone	usually not convex (or convex proximally only)	usually conspicuously convex distally or in the central part
Umbo	conspicuously abruptly depressed	even with the apophysis surface or moderately depressed	variable between both extremes
Posture of basal sterile scales	recurved or reflexed	inflexed, deflected or slightly recurved	inflexed or deflected

distinctly grooved dorsally (particularly when dry), with a greyish hue due to a fine pruinosity and with (3-)5-6(-8) stomatal lines on each ventral side. Resin ducts 2-3, two median located dorsally (rarely one of them submarginal or marginal) and usually an additional median duct near the ventral edge. Hypodermis of one cell layer, occasionally with a few cells in a second layer on the dorsal side; cell walls somewhat thickened. *Conelets* often pseudolateral and usually in 5-6-merous whorls, erect on relatively slender peduncles or nodding on curved peduncles; ovoid to oblong-ovoid or ellipsoidal, (10-)12-16(-18) mm long. Exposed part of the conelet scales distally thickened, with ± deflected distal edge, broadly cuneate to nearly rounded in outline, with a weakly acute or almost indiscernible apex. *Cones* pendulous on 5-15(-22) mm long, medium thick peduncles (often with conspicuous resin vesicles in the phloem tissue), ovoid to oblong-ovoid with usually rounded apex when closed, (4-)5-7(-9) cm long and (4-)4.5-6.5 cm wide when fully open; after seed dispersal usually early deciduous, rarely persisting for a few years. *Scales* (35-)45-60(-65), the largest (17-)20-25(-32) mm long and (17-)19-23(-25) mm wide, with a length/width ratio of (0.79-)0.95-1.35(-1.60); basal sterile scales around the peduncle insertion recurved or reflexed. *Apophyses* very thick and firm, often with a finely longitudinally grooved surface, cinnamon brown on freshly ripened cones; dimorphic: those of seed scales of the basal quarter of the cone flat, distally obtusely cuneate in outline, with their distal edges usually recurved, and those of scales of the apical third of the cone distinctly convex, distally rounded, with distal edges straight; the apex of all seed scales truncate and inclined towards the cone axis. *Umbo* transverse and flat, 4-6(-7) mm wide in seed scales, in general conspicuously and abruptly depressed into a concavity at the truncate end of the scale, and therefore concavely bent; the distal edge sharp, in outline ± weakly acute (sometimes with shallow sinuses on both sides), often

slightly elevated upwards. *Seeds* including the relatively short and broad wing 11-27 mm long; seed corpus 6.7-12.7 mm long and 3.5-6.2 mm wide, representing (41-)55-60(-62) % of the seed length; corpus border of the wing base scarcely or only shortly elongated into a broad and only 0.7-2.4 mm long thickening attached to the corpus; average thickening/corpus length ratio 0.13-0.2; the obtuse apex of the thickening often remote from the interior margin of the wing; transition between the thickened corpus border and the membranous blade of the wing straight or irregularly undulate and, on the ventral side of the seed, the thickening not gradually connected to the blade but forming a protruding mound; the blade being frangible along the corpus border. *Wing* usually very oblique, 3.5-16.2 mm long and 5.2-9.5 mm wide, with an average length/width ratio of 0.8-2; often darkly striped longitudinally.

Taxonomic history. – *Pinus eremitana* is cited by Hiep & Vidal (1996) under *P. kwangtungensis*, and the species is morphologically in fact close to *P. wangii* s. lat. The two subspecies of *P. wangii* geographically nearest to *P. eremitana*, subsp. *wangii* and subsp. *varifolia*, both similarly narrow endemics, also occur in karstic regions and grow under very similar conditions. *P. eremitana*, however, is a species with a generally well-defined character set and the majority of its individuals can easily be distinguished from the subspecies of *P. wangii*. Nevertheless, in spite of the limited size, the hitherto only known population of *P. eremitana* exhibits a conspicuously wide range of morphological variation. A comparable extensive variation is, however, also found in *P. dalatensis*, e.g. in the small population of var. *bidoupensis* (Businský 1999a).

Geographic distribution and ecology. – *Pinus eremitana* is a species known from a single locality in the vicinity of the Pa Co village in the border region of the provinces Ha Son Binh and Son La in N Vietnam about 100 km SSW of Hanoi and less than 30 km from the Laotian border (Fig. 5). Its isolated occurrence is about 270 km distant from the nearest locality of *P. wangii* subsp. *wangii* in Malipo Co., Yunnan, China, and about 240 km from the nearest known locality of *P. wangii* subsp. *varifolia* in the Cao Bang Province, Vietnam.

According to the 1:100 000 map (Anonymus 1953) the village of Pa Co is located at 20°45'30"N, 104°54'10"E. During the exploration of the karstic hills in its vicinity we found trees of *Pinus eremitana* in higher frequency only around ridges and summits at altitudes between 1450 and 1500 m, above all in a group of rocky hills about 1.5-3 km WSW to W and also on one hill about 1 km NW of the village. The area of *P. eremitana* might even continue in the direction to the hills farther W (around the point 1536 m) or NW (around a massif called Phu Phũng, 1424 m). Its altitudinal range was estimated to be (1250-)1350-1500 m, and I consider the range of 900-1500 m given by Hiep & Vidal (1996) as rather unlikely.

The trees of *Pinus eremitana* are a very conspicuous element among the local vegetation, because of their general habit and their inhabitants of exposed sites around summits and connecting ridges of the local conical karstic hills. These hills are densely covered by very sharp, often several metre high and very intricately eroded rocks of hard limestones. The varied relief harbours a dense, diverse vegetation of woody plants, palms and herbs decreasing in size towards the summits, where low broad-leaved trees and shrubs predominate. Apart from the very summits and crests, pine trees can also be found in the upper parts of mostly N to W facing steep slopes, where they represent the most robust elements of the vegetation. *P. eremitana* is not the only gymnosperm there; also present are *Taxus chinensis* (Pilg.) Rehder (the only known occurrence in Vietnam, see Hiep & Vidal 1996), *Amentotaxus argotaenia* (Hance) Pilg., *Podocarpus neriifolius* D. Don and *P. pilgeri* Foxw.

In view of its very restricted occurrence *Pinus eremitana* appears to be an extremely endangered species. We estimated the size of the population to 100-150 adult trees. Young individuals can sporadically be met, but regeneration is poor with seedlings only rarely occurring. In this region, primary vegetation survives only as a mosaic on the almost inaccessible conical karstic hills, while the hollows, valleys and less rocky bases of hills are entirely deforested, although only partly being exploited for farming. It is said that the local people cut down the pine trees, which was confirmed on a barely accessible rocky ridge 2 km W of the village of Pa Co, where we found two

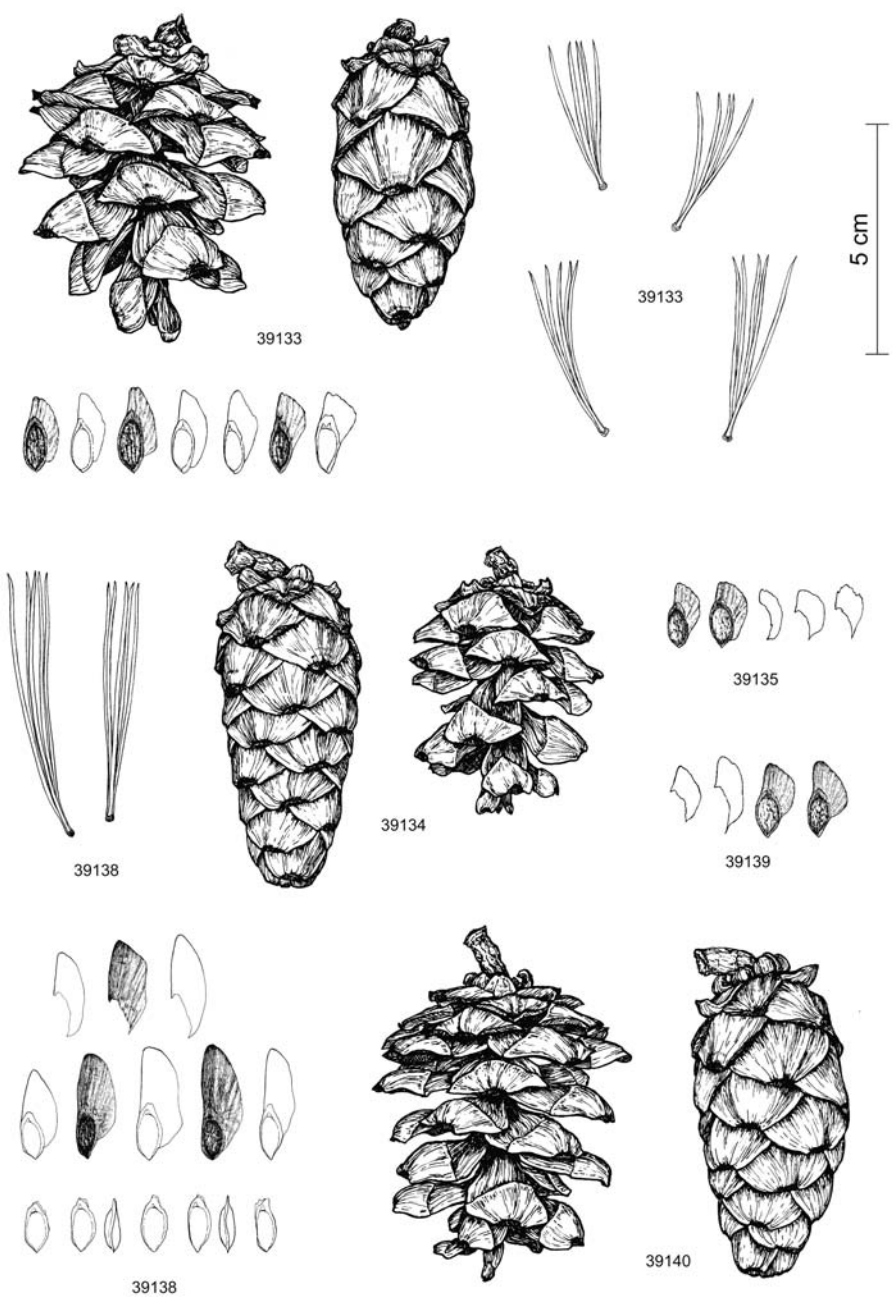


Fig. 7. *Pinus eremitana* – variation of cones, seeds and leaves after specimens collected by the author in the population of the type locality (including the type, *Businský 39133*). – All to the same scale; drawn by L. Businská.

large pine trees felled several years ago with no signs whatsoever of having served any purpose. Effective protection of the relict population of *P. eremitana*, including the unique primary vegetation that, moreover, has not yet been satisfactorily explored, is thus urgently required.

Notes. – *Pinus eremitana* seems to be a relatively derived species with an advanced seed morphology already less adapted to anemochorous dispersal. However, the supposed advanced characters of large seeds with secondarily reduced, ineffective wings, frangible along the border of the seed corpus, are still quite variable among individuals of *P. eremitana*. A similar combination of characters, viz. ineffective wings together with a specific cone morphology (typically developed in *Businský* 39132, 39134, 39135), was also found in populations of the Japanese *P. parviflora* subsp. *parviflora* (e.g., *Businský* 32103) from the SW-most locality of the species in the Takakuma Mts, Kagoshima Prefecture, Kyushu, or in the Ishizuchi-san Mts, central Shikoku (*Businský* 45155, 45161). Apart from seed morphology, *P. eremitana* and *P. parviflora* share similar leaf characters. The most conspicuous characters distinguishing both are tree habit (including the height of mature trees) and the seed cones, which are sessile and persistent in the Japanese species, with appressed basal sterile scales and evenly convex seed scales. For a summary of the differences between both species and also *P. wangii*, see Table 6.

5.5. *Pinus parviflora* s. lat.

Pinus parviflora Siebold & Zucc., Fl. Jap. 2: 27, t. 115. 1842. – Lectotype (designated by Farjon 1993: 138): ‘*Pinus cembra*’, Japan, *P. F. von Siebold* (L 901.138-394).

= *Pinus himekomatsu* Miyabe & Kudô, Icon. Essent. Forest Trees Hokkaido 1: 29. 1921.

The protologue of Siebold & Zuccarini is somewhat confusing, regarding both morphological description and geographic range of the species. No herbarium material is mentioned; the description is supplemented by an illustration with analytical drawings, which seem to represent more than one taxon. The seeds are illustrated as distinctly wingless, which is not the case in the pine in question. Hence, Miyabe & Kudô (1921) supposed that the name *Pinus parviflora* represents “a mixed species, consisting probably of three species”, and that was why they replaced Siebold & Zuccarini’s name by the new name *P. himekomatsu* but without designating a type. The confusion was resolved recently by Farjon (1993: 138), who designated a lectotype of the name *P. parviflora*.

Detailed descriptions of the species, based on material from most of its geographic range, were provided by Wilson (1916: 23) and Yamazaki (1995). Only a few minor comments are given here (see also quantitative characters in Table B of the electronic supplement).

Shoot indumentum – According to Wilson (1916) “the shoots are more or less densely covered with a short pubescence or are quite glabrous, or the stout shoots are glabrous and the weaker ones pubescent”. Also Yamazaki (1995) states: “shoots puberulent sometimes glabrous”. We did not find, among many dozens of trees investigated in detail in the field, any with all first-year shoots entirely glabrous. Usually are the thicker shoots (fertile or terminal ones in branches of secondary orders) very sparsely pubescent to completely glabrous and slender side shoots densely or sparsely pubescent, with frequently uneven distribution of trichomes (higher density below the short-shoot insertions). The indumentum persists during the second year, and often even during the third year. No difference was found between the two subspecies in the shoot indumentum.

Leaf length – Wilson (1916) reports it to range “from 3 to 8 (usually from 4 to 6) cm”. We did not find any tree with leaves longer than ca. 6 cm; the same upper limit is given by Yamazaki (1995) and Sato (2001). It might be possible that the longer leaves reported by Wilson originated from trees in cultivation (which are mentioned several times, Wilson 1916: 22-25).

Mayr (1890) described *Pinus pentaphylla* from the Japanese islands as closely related to *P. parviflora* and supposed its distribution north of 38°N. A detailed study and comparison of both taxa were first carried out by Wilson (1916), who concluded that both are conspecific. Miyabe &

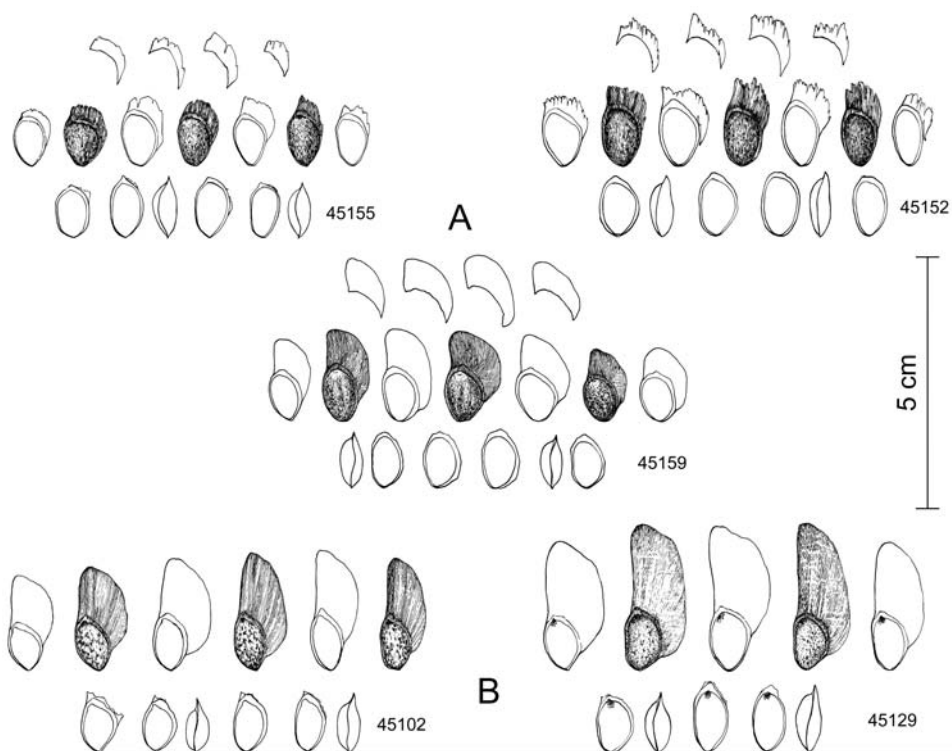


Fig. 8. *Pinus parviflora* s. lat. – variation of seeds. A: subsp. *parviflora*, after specimens collected by the author from three individuals in the Ishizuchi-san mountain region, Shikoku (*Businský* 45159 represents an infrequent morphotype with entire wings); B: subsp. *pentaphylla*, after *Businský* 45102 from the Hidaka Mts, Hokkaido, and after *Businský* 45129 from the Hida Mts, Nagano Pref., Honshu. – All to the same scale; drawn by L. Businská.

Kudô (1921), however, kept the two species apart, and so did, e.g., Gaussen (1964) and Mirov (1967). Authors of Japanese floras accepted only a single species, *P. parviflora*, with the variety *pentaphylla* confined to the northern part of its geographic range (Ohwi 1965, Yamazaki 1995). Sato (2001) examined 17 leaf characters of *P. parviflora* s. lat. from 43 populations ranging from Hokkaido to Kyushu (more than ten trees in each population were sampled but only one leaf fascicle of a tree was examined). The study revealed “no significant correlation between any character and habitat latitude”.

We studied populations of *Pinus parviflora* s. lat. on all four main Japanese islands representing the whole range of the species’ natural distribution (Critchfield & Little 1966: map 13). Drawings of the cones have been published recently (*Businský* 1999b: 42–45). The differences found (see Table 7), suffice to treat the two taxa as different subspecies due to a geographic pattern of the differences between the two taxa (see Yamazaki 1995). Whereas subsp. *parviflora* has, in essence, ineffective, rudimentary, frangible wings with mostly lacerate distal margin, subsp. *pentaphylla* possesses effective wings, which are longer than the seed corpus and have an entire margin (see Fig. 8).

Pinus parviflora subsp. *pentaphylla*

Pinus parviflora subsp. *pentaphylla* (Mayr) *Businský* in *Acta Pruhon.* 68: 12. 1999 \equiv *Pinus pentaphylla* Mayr, *Monogr. Abietin. Japan.* Reich.: 78, t. 6, f. 20. 1890 \equiv *Pinus parviflora* var. *pentaphylla* (Mayr) A. Henry in *Elwes & Henry, Trees Great Britain Ireland* 5: 1033. 1910 [\equiv *Pinus parviflora* (Mayr) A. Henry in *Elwes & Henry, Trees Great Britain Ireland* 5: 1033. 1910]

Table 7. Comparison of both subspecies of *Pinus parviflora* according to the author’s field study and collections (* range of individual average values only; # average values; ! main diagnostic characters). For methods of measurement and statistical evaluation see Chapters 2. and 4.

Character \ Subspecies	<i>parviflora</i>	<i>pentaphylla</i>
Leaf length [mm]	(20-)25-50(-55)	(25-)30-55(-60)
Leaf width [mm]	(0.75-)0.85-1.3(-1.45)	(0.7-)0.75-1.25(-1.3)
Length of cones [cm]	(4-)5-8(-9)	(5-)6-10(-12)
Cone scale l./w. ratio	*0.88-1.12; #0.99	*1.01-1.31; #1.17
! Umbo [five-point relative scale]	2-5	1-3
! Seed length in total [mm]	(10.6-)11.5-18(-19)	(16-)18-28
Seed corpus length [mm]	(7.4-)8.5-12.5	(6.7-)8-11(-12)
! Corpus % of seed length	50.9-83.5; #67.1	32.7-53.8; #43.8
! Seed wing length [mm]	2.0-9.1; #4.96	7.7-18.9; #12.15

subsp. *pentaphylla* (Mayr) Novák in Klika & al., Jehliěnaté [Conifers]: 166. 1953, nom. inval.] – Type not designated (Farjon 1993).

Note. – Yamazaki (1995) diagnoses var. *pentaphylla* through “wings of seed 10-12 mm long, ca. 8 mm wide, longer or as long as seed; seminiferous scales more or less appressed until after maturity”. The latter character is described conversely as “seminiferous scales loosely overlapping at maturity” in var. *parviflora*. However, no difference has been found between the two taxa in how tightly appressed (or to what extent) are the distal edges of the apophyses. The apex and the distal edges of the apophyses in *P. parviflora* always point inwards, towards the cone axis. This position is supported by an often conspicuously convex apophysis shape, which is a character already mentioned by Shaw (1914) as diagnostic for *P. parviflora*. The degree of the convexity of the apophyses is very variable in this species and ranges from slightly to extremely convex (with the scale apex closer to the scale base than the top of the abrupt convexity). All the forms of convexity, however, are encountered within populations, approximately with a comparable frequency in both subspecies. Extremely convex apophyses were commonly found in both the northernmost and the southernmost population.

Geographic distribution and ecology – *Pinus parviflora* subsp. *pentaphylla* is confined to the central and northern part of Honshu, Sado(ga)-shima Island, and to S Hokkaido including the Okushi-to (Okushiri) Island, while subsp. *parviflora* occurs on Kyushu, Tsushima-to Island, Shikoku, and in the SW part of Honshu. The isolated occurrence of the species on the Korean island Ullung-do (Utsurio-to) probably refers to subsp. *parviflora*. *P. parviflora* subsp. *pentaphylla* is reported to occur at altitudes of 60-800 m in Hokkaido and of 300-2500 m in Honshu, subsp. *parviflora* at 200-1800 m (Yamazaki 1995). Subsp. *parviflora*, however, grows in Shikoku up to the very summit of the rocky ridge dominating the highest mountain on the island, Ishizuchi-san (1982 m). Wilson (1916) reported the occurrence of the species in the massif of “Tsubakura-dake (Shinano Province, Hondo) between 1300 and 2600 m”. In September 1997, we visited the Tsubakuro-dake (2763 m, 36°24'10"N, 137°43'E), in the NE branch of the Hida Range (the North Japan Alps), nowadays in the Nagano Prefecture, Honshu. There and in the neighbouring mountains, where the forest stands do not exceed 2500 m, subsp. *pentaphylla* does not reach the timber line and is confined below 2300 m. We observed the lowest site of subsp. *pentaphylla* in the Hidaka Range in Hokkaido, with old trees descending below 100 m, at the SE extremity of the main ridge, steeply falling to the E coast at 42°06'N.

5.6. *Pinus morrisonicola*

Pinus morrisonicola Hayata in Gard. Chron., ser. 3, 43: 194. 28.3.1908 ≡ *Pinus formosana* Hayata in J. Linn. Soc., Bot. 38: 297, t. 22. 3.6.1908 [& in J. Coll. Sci. Imp. Univ. Tokyo 25(19): 217, t. 9.

23.7.1908] \equiv *Pinus parviflora* var. *morrisonicola* (Hayata) C. L. Wu in Acta Phytotax. Sin. 5, 3: 141. 1956. – Holotype: Formosa, Shohakulin, 21.1.1898, *C. Owatari* (TI!).

Tall *trees* attaining a height of 30–35 m, rather densely, irregularly branched in the crown with age, and fully developed often with conspicuously robust basal skeletal branches. Trunk of old trees covered with a thin, densely scaly bark (scales small, arranged longitudinally). Foliage dense, persisting for two years. First-year *shoots*, the slender lateral ones in particular, at first irregularly, sparsely to densely pubescent, with relatively long hairs (below short-shoot bases in particular), usually soon glabrescent, cinnamon brown, glossy, at least the thicker main shoots sometimes conspicuously pruinose when young. *Leaves* erect, straight, relatively stiff, (40–)55–75(–95) mm long and (0.75–)0.85–1.05(–1.2) mm wide, tapering towards an acute apex, remotely to almost densely and often irregularly serrate on all edges except for the basal part, with (23–)30–50(–55) teeth per centimetre in the middle part, deep green on the dorsal side, distinctly greyish white pruinose and with (3)4–6(8) stomatal lines on each ventral side. Resin ducts two, marginal, on the dorsal side, and usually an additional marginal duct laterally near the ventral edge. Hypodermis of one cell layer (occasionally with a few cells in a second layer), cell walls somewhat thickened. *Conelets* often pseudolateral (particularly on terminal branchlets), solitary or more often in up to 6(–10)-merous whorls, erect on peduncles usually shorter than the conelet; broadly ovoid to almost cylindrical, (11–)15–22 mm long. Exposed part of the conelet scales distinctly transversely and sharply carinate, projected to a broad, recurved protuberance abruptly sunken to the convex dorsal side of the scale and terminated in an acute tip that forms a decurrent, relatively obtuse, gradually disappearing keel on the ventral side, perpendicular to the main transverse keel. *Cones* patent, on relatively thick, (3–)5–15(–30) mm long peduncles; narrowly ovoid or ellipsoidal when closed, 7.5–13 cm long and 5.5–7.5 cm wide when fully open, very resinous; after seed dispersal usually easily deciduous. *Scales* (50–)60–80, the largest (25–)27–31(–34) mm long and (22–)23–25(–26) mm wide with a length/width ratio of (1.04–)1.1–1.3(–1.46). *Apophyses* thick but fragile, relatively weakly lignified, thickest at the base, usually smooth, almost without any longitudinal dorsal keel, pale brown and glossy on freshly ripened cones, sometimes also pruinose, slightly wrinkled when dry; distally obtusely cuneate to rounded in outline, with the apex and distal edges distinctly elevated and \pm recurved, apophyses therefore deflected from the neighbouring inner scales in the closed cone. Ventral surface of apophysis broad, conspicuously widened towards the scale apex. *Umbo* usually as a transverse depression or the top of the apophysis apex, 4–9 mm wide in seed scales bilaterally steeply sloped from the transverse keel and with rhomboidal dorsal and narrow ventral side, with \pm recurved, up to 1 mm long prickle; main dorsal side with an arcuate concavity along the broad base of the prickle. *Seeds* including the relatively broad wing (15–)19–27(–28.5) mm long; seed corpus 7.7–12.8 \times 3.8–6.8 mm, usually with dull striae on ventral side representing (on average) 38–48 % of the seed length; corpus border of the wing base very distinct, shortly elongated into a broad, 1.1–2.8 mm long, swollen thickening firmly attached to the corpus; average thickening/corpus length ratio 0.14–0.22. *Wing* 6.5–18 mm long and 5.7–10.2 mm wide (the widest part usually next to the distal corpus end), with an average length/width ratio of 1.3–1.8; usually with a finely dispersed, dense pigmentation; wing apex very close to the margin of the ventral surface of the apophysis.

Taxonomic history. – The original material (holotype) only consists of a branchlet with one single, malformed cone. At first, Hayata identified this specimen collected by Owatari as *Pinus parviflora*. Later, upon obtaining well-developed cones collected by G. Nakahara at Yagatayama (near) Taichu (= Taichung, W Taiwan) in February 1907, he corrected the original identification and recognised it as a new species, named on the label *P. formosana*, and he attached one of the new cones to Owatari's specimen. By a curious coincidence, the description of the new species was published in almost the same form under two different names in two different journals in the same year, with *P. morrisonicola* having priority over *P. formosana* (see Hayata 1908b: 297, 1908c: 217). Despite the obvious differences in cone and other characters, most authors subsequently synonymized *P. morrisonicola* with the Japanese *P. parviflora* (Shaw 1914, Dallimore &

Jackson 1923) or relegated it to a variety of the latter (Wu 1956). Only Wilson (1916: 24), when studying the variability of *P. parviflora* concluded: "I have seen the type of Hayata's plant and it is certainly a distinct species". Since the 1960s, *P. morrisonicola* is unanimously accepted as a separate species, included in the Flora of Taiwan (Li 1975).

Notes. – In November 1991, we investigated the variability of a large population of *Pinus morrisonicola* in the vicinity of Kukuan village (within an altitudinal belt between 600 and 900 m) in the valley of Tachia river, Taichung Co. Drawings of cones, collected from this population, have been published recently (Businský 1999b: 46-47). The results of this study confirm that *P. morrisonicola* is not only justified as a separate species but that it is also the most distinct taxon in the group of Asian pines of *P.* subsect. *Strobos* having large seeds with broad, effective, although relatively short wings (also comprising *P. parviflora*, *P. wangii* and *P. eremitana*).

Several descriptions of *Pinus morrisonicola* published in the literature, however, are apparently based on material also of *P. uyematsui* (Li 1963: 49, 1975: 523, Law & al. 1978: 229), since the latter is not recognized as a separate species by these authors; the description by Cheng (1930: 11) is in addition based on material from other species occurring outside Taiwan.

Several of the characters (of the morphology of conelet scales and umbo, consistency of cone scales) given in the description above, although quite typical of the species and important for evolutionary considerations, were not considered before.

Klaus (1980) when classifying the genus *Pinus* using umbo morphology did not list *P. morrisonicola* probably because he did not have the opportunity to study it. In accordance with his classification, this species could represent a new morphotype of terminal umbo characterized as the "tectoid" umbo with a prickle (mucro).

Geographical distribution and ecology. – *Pinus morrisonicola* is endemic to Taiwan. The oldest published information about its occurrence is "mountainous districts of the Taichu prefecture, at an altitude of 1500 m" from G. Nakahara (Hayata 1908b). Cheng (1930: 11) reported *P. morrisonicola* also from the Guangdong Province on the mainland and from the Hainan Island, obviously merging it with *P. wangii* subsp. *kwangtungensis* and *P. orthophylla*. The detailed distribution map by Liu (1966) and the altitudinal range of 300-2300 m given by Li (1963) includes also *P. uyematsui*, there considered as conspecific; the same holds true for Li (1975) and Law & al. (1978). According to our field observations, *P. morrisonicola* chiefly occurs at lower altitudes, whereas above 2000 m, at least S of the highest massif of the island, Mt Yushan, *P. uyematsui* predominates.

5.7. *Pinus uyematsui* and its hybrid with *P. morrisonicola*

Pinus uyematsui Hayata, Icon. Pl. Formos. 3: 192, t. 35. 1913. – Holotype: Taiwan, Arisan, 1.10.1912?, *Uyematsu* (TI!).

Tall trees attaining a height of 35 m, with relatively sparse, horizontally spreading branches that form an irregularly ellipsoidal, tall crown beginning in the lower part of the straight trunk. Foliage dense, persisting usually for two years. First-year shoots, the slender lateral ones in particular, sparsely or densely pubescent, with relatively long hairs, or, if only sparsely pubescent (below short-shoot bases in particular) then soon glabrescent, cinnamon brown, glossy, often pruinose when young. Leaves erect, straight, rather stiff, (40-)60-85(-100) mm long and (0.7-)0.8-1(-1.15) mm wide, tapering towards an acute apex, remotely and often irregularly, acutely serrate on all edges except for the basal part, with (16-)20-30(-38) teeth per centimetre in the middle part, deep green on the dorsal side, distinctly greyish white pruinose and with (3)4-7(10) stomatal lines on each ventral side. Resin ducts two marginal, on the dorsal side, and usually an additional marginal duct laterally near the ventral edge. Hypodermis of one cell layer (occasionally with a few cells in a second layer), cell walls somewhat thickened. Conelets subterminal or pseudolateral, solitary, in pairs or in 3(4)-merous whorls, erect on approximately equally long peduncles; 12-26 mm long. Exposed part of the conelet scales distally thickened, transversely sharply carinate, and,

when fully developed, with a broad, obtuse and usually recurved apical protuberance sunken to the dorsal side of the scale and rounded-convex on the ventral side. *Cones* pendulous, on relatively thick, 8–20 mm long peduncles; narrowly ovoid or cylindrical when closed, attenuate towards the apex and sometimes crescent-shaped, 8–18 cm long and (5.5–)6–10 cm wide when fully open, very resinous; after seed dispersal \pm persisting, though not firmly, for a few years. *Scales* (50)60–90(–105), the largest 30–48 mm long and 18–26 mm wide with a length/width ratio of (1.39–)1.55–2.25(–2.41); basal sterile scales around the peduncle insertion deflected or slightly recurved. *Apophyses* with thin distal part, gradually \pm thickened towards the base, smooth, usually with only an indistinct longitudinal dorsal keel, pale brown and \pm glossy on freshly ripened cones, sometimes also pruinose; distally obtusely cuneate to rounded in outline, with distal edges straight, or turned outwards, or slightly recurved, and with the apex obtuse or somewhat truncate, slightly inclined towards the cone axis, or straight, or shortly recurved. Ventral surface of apophysis narrow, with margins parallel, almost appressed to the neighbouring scales (except for the short recurved apex of the most prominent scales in some individuals). *Umbo* transverse, 3–6 mm wide in seed scales, sometimes flat or slightly bilateral, even with the apophysis surface or usually only indistinctly depressed into a concavity at the end of the scale; the distal edge of the umbo sharp, in outline obtuse or weakly acute, elevated upwards or with the recurved apex. *Seeds* including the relatively long and narrow wing (22–)24–34(–38) mm long; seed corpus 6.8–8.4 \times 3.3–4.5 mm, representing (on average) 24–29 % of the seed length; corpus border of the wing base very distinct, rugose and conspicuously elongated into a usually slender, 2.1–4.4 mm long thickening firmly attached to the corpus; average thickening/corpus length ratio 0.38–0.45. *Wing* 15–30 mm long and 5.8–9.6 mm wide, with an average length/width ratio of 2.6–3.1; often with dense, dark longitudinal stripes; wing apex relatively distant from the margin of the ventral surface of the apophysis.

Taxonomic history. – The undated holotype of the name *Pinus uyematsui* was collected, probably in 1912 (according to the herbarium TI), by Uyematsu at medium altitudes (at 7000' according to Hayata 1913) on Mt Alishan (formerly Arisan) within the central mountain range of Taiwan, not far from Mt Yushan (3952 m; formerly known as Mt Morrison), the highest massif of the island. The original description is relatively detailed, correspondingly illustrated and evidently based on the single specimen that has been the only herbarium material of *P. uyematsui* available until very recently. Considering this and the difficult accessibility of the island's mountainous interior, it is not surprising that Taiwanese floras (Li 1963, 1975) and most subsequent works (Liu 1966, Law & al. 1978, Fu & al. 1999) treated *P. uyematsui* as conspecific with *P. morrisonicola*. Only very few authors (particularly Gaussen 1960) conceded specific status to *P. uyematsui*, Dallimore & Jackson (1954) and Ferré (1960) only briefly mentioned it. Mature cones and seeds are in fact imperative to reliably distinguish *P. uyematsui* from *P. morrisonicola*.

Notes. – *Pinus uyematsui* was found by us at the end of 1991 along the Southern Cross-Island Highway (then just under construction), leading across the central mountain range S of Mt Yushan. This population, occurring between 2000 and 2400 m, is divided by the here 2950 to 3650 m high central ridge of the island into two subpopulations on the western and the eastern slopes, respectively. Samples of branchlets, cones and seeds were collected from six adult representative trees from both sides of the divide, and photographic documentation of tree habits completed the investigation. The range of variation, especially of the cones, is so extensive that it was suspected that more than one species is involved. The six sampled trees were compared with samples of four typical individuals of *P. morrisonicola* from the locality near the village of Kukuan (Taichung Co.). Seeds of all ten trees were available. Evaluation of this material, including the types, revealed that *Businský* 32160, 32168 & 32169, from both sides of the divide near Mt Yushan, clearly represent *P. uyematsui* (for drawings of cones from the three corresponding trees see *Businský* 1999b: 38–39). The trees sampled as *Businský* 32161 & 32162 from the W slopes and *Businský* 32170 from the E slopes, in contrast, are morphologically more or less intermediate between both species and strongly indicate an introgressive hybridization of the *P. uyematsui* population with *P. morrisonicola*. The existence of hybrids in populations of *P. uyematsui* decreases the possibility to clearly identify this species in the absence of adequate material. To draw

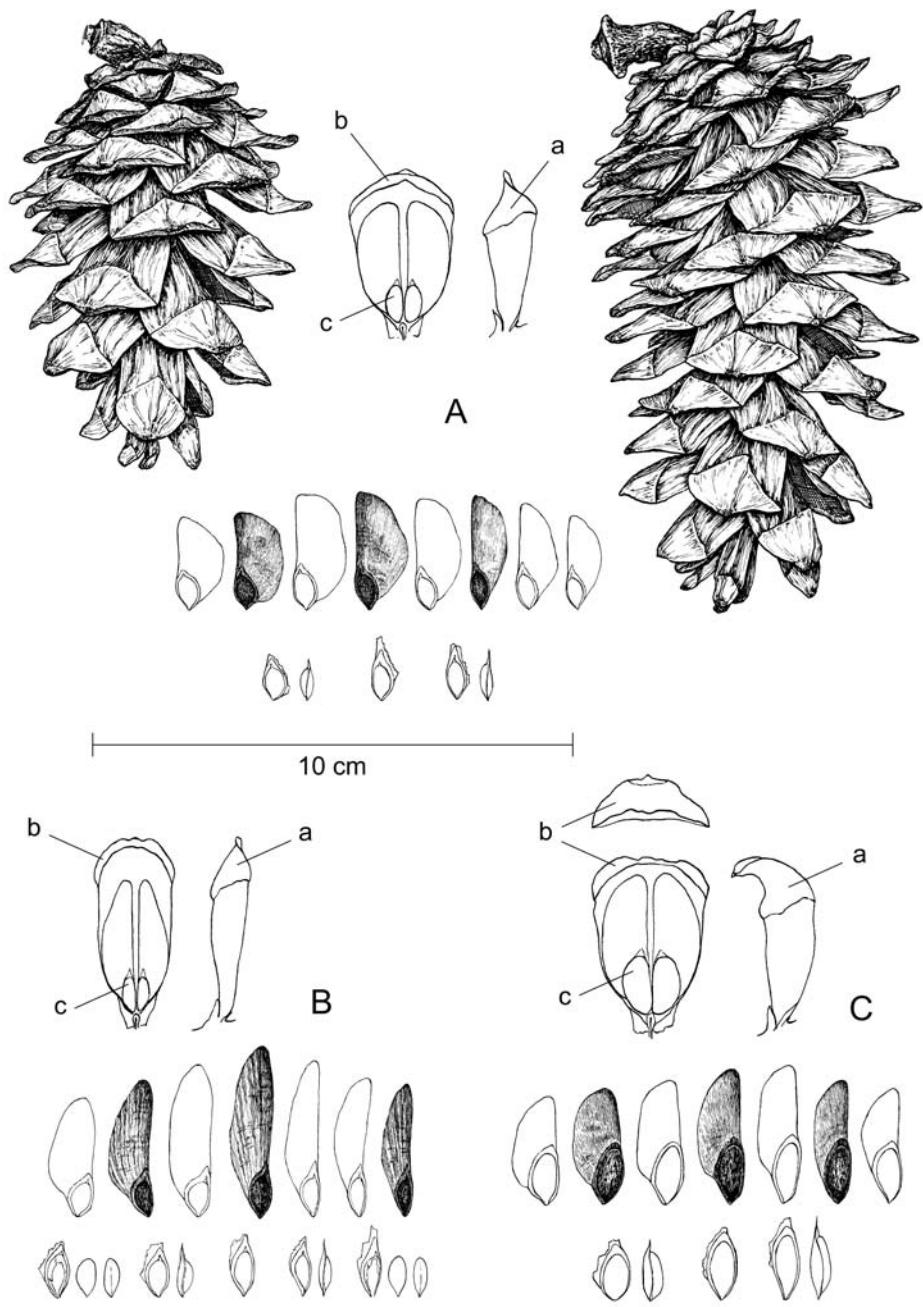


Fig. 9. A: *Pinus xhayatana* (= *P. uyematsui* × *P. morrisonicola*) – cones, ventral and lateral side of a cone-scale, seeds (after the type); B: *P. uyematsui* – ventral and lateral side of a cone-scale (after Businský 32168), seeds (after Businský 32169); C: *P. morrisonicola* – ventral, front and lateral side of a cone-scale (after Businský 32134), seeds (after Businský 32129); a: apophysis; b: ventral surface of the apophysis; c: print of seeds with wings. – All to the same scale; drawn by L. Businská.
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attention to the hybridization between both species and to assist safe identification, the hybrid is formally described as a nothospecies. The following description is based on *Businský 32170* from the E slopes, which represents the most intermediate material and serves as the nomenclatural type; further non-quantitative data are added from *Businský 32161* & *32162*, which represents individuals morphologically closer to *P. uyematsui*.

***Pinus* × *hayatana* Businský, **nothosp. nova** – Fig. 9A**
(= *Pinus uyematsui* Hayata × *P. morrisonicola* Hayata)

Holotype: Taiwan, Taitung Co., NW corner, near Southern Cross-Island Highway on S headland of the peak about 3600 m high, on a rock of S exposure in dense mixed forest on SW slope, 2060 m, 23°15'N, ×120°59'30"E; tree: 290 cm t.c., 28 m h., old, 16.12.1991, *Businský 32170* (PR; isotypes: B, G, K, MO, P, PE, TAI).

Arbor hybridae originis a parentibus dictis notis sequentibus distinguitur. A *Pinus uyematsui* differt squamis strobilorum relative brevioribus et latoribus (i.e. squamae maximae 28-32 × 24-28 mm magnae cum proportione longitudinis ad latitudinem mediocriter 1.22) cum limbo distale interno relative lato, ad apicem insigniter dilatato; seminibus alis inclusis 20-25.5 mm longis, alis relative latis, 12.7-17.5 × 7.2-11.2 mm magnis (cum proportione longitudinis ad latitudinem mediocriter 1.7), basi alae incrassata 1.3-3.2 mm longa (in proportione mediocriter 0.32 ad longitudinem corporis), formae variabilis, sed non insigniter gracili. A *Pinus morrisonicola* differt strobilis 50-105 squamis compositis, apophysibus tenuibus cum parte distale apice incluso recta vel tantum modice sursum curvata, umbone plano cum apice indistincto, obtuso et plerumque tantum modice surgente; corporibus seminum relative parvis, tantum 6.5-8.3 × 3.4-4.4 mm magnis, basi alae seminum incrassata 1.3-3.2 mm longa.

A hybrid morphologically intermediate between its parents, which are two closely related species differing chiefly in the characters of their reproductive organs.

Trees attaining a height of about 30 m. First-year *shoots* markedly densely pubescent in general (the thicker terminal branchlets less densely pubescent), becoming glabrescent during the second or the third year; at first partly pruinose on the glossy surface. *Leaves* (43-)55-80(-90) mm long and (0.7-)0.75-0.95(-1.03) mm wide, edges acutely serrate except for the entire or sparsely serrate basal part, with (17-)22-28(-36) teeth per centimetre in the middle part. *Cones* on 5-20 mm long peduncles, 7.5-13 cm long and up to 7 cm wide when fully open. *Scales* 50-105, the largest 28-32 mm long and 24-28 mm wide with an average length/width ratio of 1.22. *Apophyses* relatively thin, with distal edges and the apex straight or moderately curved upwards; the ventral surface (i.e., borders on the interior side of the scale along its distal edges) rather broad, markedly widened towards the scale apex, almost appressed to (not distinctly deflected from) the neighbouring scales. *Umbo* transverse, flat, with an inconspicuous, usually slightly elevated obtuse apex. *Seeds* including the relatively long and broad wing 20-26 mm long; seed corpus 6.5-8.3 × 3.4-4.4 mm, representing, on average, 32 % of the seed length; corpus border of the wing base elongated into a 1.3-3.2 mm long thickening of variable shape, average thickening/corpus length ratio 0.32. *Wing* 12.7-17.5 mm long and 7.2-11.2 mm wide, with an average length/width ratio of 1.7; wing apex almost reaching the margin of the ventral part of the apophysis.

5.8. *Pinus dalatensis* s. lat.

Pinus dalatensis Ferré in Bull. Soc. Hist. Nat. Toulouse 95: 178, fig. 3. 1960 [& in Trav. Lab. Forest Toulouse, 1(6), Art. 4: 8, fig. 3. 1960] ≡ *Pinus wallichiana* var. *dalatensis* (Ferré) Silba in Phytologia Mem. 7: 59. 1984. – Type: Sud Vietnam, Trai-Mat, 6 km de Dalat, 12.1957, *H. Gaussen* (TLF).

Pinus dalatensis in the broad sense accepted here comprises also var. *bidoupensis* and subsp. *procera*. For a detailed revision see Businský (1999a), and for drawings of cones and seeds see Businský (1999b: 34-37).

Trees attaining a height of 30-40 m, with a usually tall, unbranched, straight trunk up to about 2.5 m in diameter and with a conspicuously spreading and horizontally branched, umbrella-like crown up to about 30 m wide when old; bark greyish brown, fissured into small irregular plates. First-year *shoots* densely or sparsely (unevenly) pubescent, or entirely glabrous, pale brown, often with a rusty tinge, glossy, sometimes pruinose when young. *Leaves* slender and relatively soft, erect and straight, (30-)50-110(-140) mm long and (0.5-)0.6-1.1(-1.25) mm wide, in their terminal part gradually narrowing towards an acute apex, with sparse (often irregular) to almost dense, acute serration on all edges except for up to the basal 1/5 (rarely up to 1/3), light green on the dorsal side, slightly glaucous pruinose and with (3-)4-6(-8) stomatal lines on each ventral side. Resin ducts mostly two marginal on the dorsal side, and usually an additional duct near the ventral edge, either a marginal one situated laterally or a median one situated symmetrically. Hypodermis of one cell layer (occasionally with some cells in a second layer on the dorsal side). *Conelets* subterminal, solitary in 2-3-merous whorls, erect or semi-erect on slender to thick, approximately equally long peduncles; ovoid to oblong-ellipsoidal, (12-)15-25(-30) mm long. Exposed part of the conelet scales flat to distally thickened, with deflected or recurved distal edge, usually rounded-cuneate in outline, gradually changing to an indistinctly obtuse or acute apex. *Cones* pendulous on relatively thick, (8-)15-30(-45) mm long peduncles (often with resin vesicles in the phloem tissue), narrowly ellipsoidal or cylindrical with a length/width ratio of 2.5-6 when closed, somewhat attenuate towards the apex and sometimes crescent-shaped, (5.5-) 7-20(-23) cm long and (5)6-9 cm wide when fully open; after seed dispersal usually persisting, not firmly though, for a few years. *Scales* (35-)50-100(-120), the largest (27-)33-44(-48) mm long and (15-)19- 27(-31) mm wide with a length/width ratio of (1.22-)1.4-2.1(-2.26); basal sterile scales around the peduncle insertion appressed, deflected or sometimes recurved. *Apophyses* thin to relatively thick and firm, often with a longitudinally, finely grooved surface, glossy or dull pale brown in freshly ripened cones, sometimes also pruinose, with a straight to slightly convex longitudinal dorsal line, often with a distinct keel; distally obtusely cuneate to rounded in outline, with distal edges straight to recurved and the apex slightly inclined towards the cone axis, or straight, or rarely recurved. *Umbo* transverse, 4-10 mm wide in seed scales, flat, in general abruptly depressed into a concavity at the truncate end of the scale, therefore concavely bent; distal edge sharp, in outline truncate to weakly acute, often elevated upwards, or with the recurved apex. *Seeds* including the relatively long and narrow wing (19-)22-37(-39) mm long; seed corpus 6.7-10.5 × 3.3-5 mm, representing (on average) 23-36 % of the seed length; corpus border of the wing base distinct, rugose and elongated into a thickening of variable shape, but often slender, 0.9-5.5 mm long, firmly attached to the corpus; average thickening/corpus length ratio 0.13-0.46. *Wing* (11.5-)15-27(-29) mm long and 5.3-11 mm wide, with an average length/width ratio of 2.2-3.2; often with dark longitudinal stripes, or with a dominant, finely dispersed, dense pigmentation.

Taxonomic history. – Although the oldest dated specimen of this species cited by Ferré (1960) is from 1941 (*Poilane* 32581), we now know that the species was collected already in 1918 (Businský 1999a). The single specimen, *Chevalier* 38353, with the fragment of a first-year branchlet and a cone that soon became lost, is the oldest evidence for the presence of *Pinus* sect. *Quinquefoliae* in Indo-China. Over the past some 80 years, the specimen was referred to with five different specific names, and even Ferré (1960) provisionally named it “Pin du Moyen Annam”, considering it distinct from *P. dalatensis*. After completing detailed historical, geographic and taxonomic studies, the identity of this specimen was firmly established; the corresponding population of the “Pin du Moyen Annam”, explored in 1997 in the mountain region of Ngoc Linh (in central Vietnam at 15°N), was described as a new, northern subspecies, *P. dalatensis* subsp. *procera* Businský (1999a). A recent name to be synonymized with this subspecies is *P. fenzeliana* var. *annamiensis* Silba (2000), based on *Chevalier* 38353. Prior to the rediscovery and identification of the “Pin du Moyen Annam” in 1997, an unexpected variation of *P. dalatensis* was found at the beginning of 1994 in the Chu Yang Sinh massif and near the Bi Doup massif, both in the southern part of the species’ distribution range. The taxon with entirely glabrous shoots and relatively

thick and firm apophyses was described as var. *bidoupensis* Businský (1999a). According to updated knowledge, *P. dalatensis* is confined to two mountain regions in central Vietnam and to another, more extensive mountain area in S Vietnam (see Businský 1999a: fig. 4). Its likely occurrence also in Laos has not yet been confirmed.

Relationships. – Without giving any reason Silba (1984) relegated *Pinus dalatensis* to a variety of *P. wallichiana*. Despite that the largest cones of subsp. *procera* may be similar to those of *P. wallichiana*, *P. dalatensis* is very distinct from that species. In contrast, *P. dalatensis* is most similar to the Taiwanese *P. uyematsui*. In view of the overlapping ranges of extensive variation in morphological characters, the correct determination of these two taxa solely based on material in herbaria (apart from its origin) is rather problematic. The most conspicuous diagnostic character separating *P. dalatensis* and *P. uyematsui* is the habit of mature trees. In the Vietnamese species, the stem is tall, branchless, with a broad, umbrella-like crown, while that of the Taiwanese species is of an irregularly ellipsoid shape, branched from a lower part of the stem. Gaussen (1960) took the number of cone scales as the main character distinguishing *P. uyematsui* from *P. dalatensis*, reporting more than 60 scales in the former species (in accordance with the present study) and 30-50 in the latter. However, our much more extensive material of *P. dalatensis* (see Businský 1999a) has cones with (35-)50-100(-120) scales. Similarly, the differences briefly mentioned by Ferré (1960) to distinguish between *P. uyematsui* and *P. dalatensis*, and/or the Balkanic *P. peuce* Griseb., reflect the, at that time, incomplete knowledge of the two Asian taxa.

5.9. *Pinus wallichiana* s. lat.

Pinus wallichiana A. B. Jacks. in Bull. Misc. Inform. Kew 1938: 85. 1938 ≡ *Pinus excelsa* Wall. ex D. Don in Lambert, Descr. Pinus, ed. 2, 1: 40, t. 26. 1828, nom. illeg. (non Lam. 1778). – Lectotype (selected here): [icon] Lambert, Descr. Pinus, ed. 2, 1: t. 26. 1828.

= *Pinus nepalensis* Chambray, Traité Arbr. Resin. Conif. 342. 1845, nom. illeg. (non J. Forbes, 1839).

= *Pinus griffithii* M'Clelland in Griffith, Notul. Pl. Asiat. 4: 17. 1854 [& Icon. Pl. Asiat. 4: t. 365. 1854], nom. illeg. (non Parl. 1868).

Pinus wallichiana in the broad sense accepted here comprises also *P. bhutanica* as a subspecies.

Trees attaining a height of 40-50 m, with relatively sparse, ± horizontally spreading branches that form an irregularly pyramidal, oblong pyramidal or later subcylindrical, tall crown beginning from the lower part of the straight trunk; bark fissured into small longitudinal plates. First-year *shoots* entirely glabrous, glabrescent or sparsely to densely pubescent, light greyish or brownish green, glossy, often conspicuously whitish pruinose when young. *Leaves* slender and soft, usually drooping or conspicuously pendulous from the base, (60-)100-250(-320) mm (in young individuals up to 400 mm) long and (0.7-)0.8-1.2(-1.3) mm wide, in their terminal part gradually narrowing towards an acute apex, remotely and often irregularly serrate on all edges except for the basal part, with (13-)15-35(-45) teeth per centimetre in the middle part, light to dark green on the dorsal side, glaucous to white pruinose and with 3-6(-8) stomatal lines on each ventral side. Resin ducts mostly two marginal or submarginal on the dorsal side, and usually an additional duct near the ventral edge, either a median one situated symmetrically or 1(-2) (sub)marginal one(s) situated laterally. Hypodermis usually of one cell layer. *Conelets* subterminal or sometimes pseudolateral, solitary or in 2-4(-7)-merous whorls, erect or semi-erect on straight, slender, usually longer peduncles, oblong-ellipsoidal to cylindrical, (15-)20- 30(-40) mm long. Exposed part of the conelet scales flat, with only slightly deflected distal edge, rounded-cuneate in outline, with an obtuse or weakly acute apex. *Cones* pendulous on relatively slender, (15-)30-50(-90) mm long peduncles (sometimes with resin vesicles in the phloem tissue), cylindrical with a length/width ratio of 3.5-7 when closed, sometimes crescent-shaped, (11-)15-25(-30) cm long and (5)6-9.5 cm wide when fully open; after seed dispersal usually not firmly

persisting in the next year. *Scales* (65-)80-140(-180), the largest (26-)35-48(-52) mm long and (18-)20-30(-33) mm wide with a length/width ratio of (1.13-)1.3-1.9(-2.22); basal sterile scales around the peduncle insertion appressed or deflected (rarely a few of them indistinctly recurved). *Apophyses* relatively thin, usually conspicuously convex, often with a longitudinally, finely grooved surface, dull tawny in freshly ripened cones, sometimes also pruinose, often with a blunt or almost sharp longitudinal keel; distally rounded in outline, with the apex and distal edges \pm inclined towards the cone axis. *Umbo* transversely rhomboidal to almost triangular, 4-8 mm wide in seed scales, flat or obtusely carinate to convex, even with the apophysis surface and usually protruding from the front outline of the scale; distal edge sharp, in outline obtuse or weakly acute, often with \pm attenuate apex. *Seeds* including the relatively long and narrow wing (21-)27-40(-45) mm long; seed corpus (6.2-)7-9.5 \times 3.4-6 mm, representing (on average) 21-33 % of the seed length; corpus border of the wing base distinct, rugose, scarcely or distinctly elongated into a thickening of variable shape, 0.7-5(-8) mm long, firmly attached to the corpus; average thickening/corpus length ratio 0.12-0.54. *Wing* (14-)20-30(-35) mm long and 6-11 mm wide, with an average length/width ratio of 2-3.3; often with dark longitudinal stripes, or with a dominant, finely dispersed, dense pigmentation.

5.9.1. *Pinus wallichiana* subsp. *wallichiana*

Pinus wallichiana subsp. *wallichiana* was studied by the author in N Pakistan, to document the extent of its variation along most of its altitudinal distribution. According to Mirov (1967), the species in this largest part of its range (here defined as subsp. *wallichiana*) can be found most commonly between 1800 and 3000 m, but the lowest known occurrence is reported to be at 1200 m from the Murree Hills above Rawalpindi (Islamabad), N Pakistan. In November 1994, two populations were investigated here, one growing close to stands of *P. roxburghii* Sarg. at around 2000 m, N of Murree, the other associated with *Cedrus deodara* (Roxb.) G. Don, between 2000 and 2400 m in the Ayubia National Park. *P. wallichiana* can be found as low as c. 1700 m on the SW slopes of the hills, between Murree and Islamabad; on lower sites, the natural vegetation is usually entirely destroyed, with the sole exception of some frequently pruned trees of *P. roxburghii* commonly descending to about 1000 m, or, individually, even as low as 800 m. In the Murree Hills, *P. wallichiana* has pendulous leaves usually 12-21 cm long and 0.75-1 mm wide. The upper distribution limit of *P. wallichiana* was studied in the region of the Nanga Parbat massif (8126 m). At the foot of the front moraine of the Bazhin Glacier flowing down the SE flank towards the Rupal Valley, a sparse outpost subpopulation of *P. wallichiana* reaches the altitude of 3400 m. Below the N flank of the Nanga Parbat, along the Raikot Glacier, especially on the left side of the valley, *P. wallichiana* locally forms pure, dense stands up to an altitude of c. 3500 m. Near pastures called 'Fairy Meadows', on an old lateral glacial moraine with forest vegetation between 3250 and 3450 m, *P. wallichiana* was found to have almost straight, relatively short leaves usually 7-12 cm long and 0.95-1.25 mm wide and in some individuals even as short as (5-)6-9(-10) cm. The trees at this locality thus conspicuously resemble a sister species from the Balkans, *P. peuce* Griseb. Also the cones of this high altitude population were short and very similar to those of the Balkan species.

5.9.2. *Pinus wallichiana* subsp. *bhutanica*

Pinus wallichiana subsp. *bhutanica* (Grierson & al.) Businský in Acta Pruhon. 68: 10. 1999 = *Pinus bhutanica* Grierson & al. in Notes Roy. Bot. Gard. Edinburgh 38: 299. 1980. – Holotype: Bhutan, 4 km N of Tschilingor, N of Samdrup Jongkhar, 27°04'N, 91°25'E, 2400 m, 26.6.1979, Grierson & Long 2282 (K; isotypes: A, BM, DD, K!, TI, THIM).

In 1992 and 1996, we studied a large population of a pine identified as *Pinus griffithii* McClelland by Critchfield & Little (1966) and Law & al. (1978) in the valleys of the Yigong Zangbo and the lower Lang Ho Rivers (with their confluence located at 30°02'N, 95°01'E), along the Ti-

bet-Sichuan Highway between Dongjug and Tangmai villages in E Xizang (Tibet). The most conspicuous features of this otherwise morphologically quite uniform population were the very long leaves (14–28 cm), pendulous from the base, and the densely pubescent branchlets. Samples collected from this population were compared with the isotype of *P. bhutanica* at K, which they perfectly match. In 2004, the author studied many trees of this pine of various age in three regions in W Arunachal Pradesh, India, close to the border with Bhutan. These populations exhibit a wide range of variation in shoot indumentum (from glabrous to densely pubescent, most frequently shortly, irregularly pubescent) and in posture and length of the leaves. Both the Tibetan and the Arunachal populations were also compared with populations of *P. wallichiana* s.str. from two regions of N Pakistan and with collections from N India (Jammu, Uttaranchal). These comparisons confirmed the relatively distinct differences in vegetative characters between the two taxa but failed to disclose any differences in the characters of cones and seeds. In view of this, and considering the variation of E Himalayan populations and the general geographic distribution of the two taxa, the Bhutanese pine is here treated as an eastern subspecies of the Himalayan *P. wallichiana*.

Pinus wallichiana subsp. *bhutanica* is distributed in the E Himalayas (Bhutan and W Arunachal Pradesh, E India) and in high mountain ranges of E Xizang, N Myanmar and NW Yunnan (see Critchfield & Little 1966: map 12, eastern occurrences under *P. griffithii*). In Bhutan, there is a certain zone of sympatric occurrence of both subspecies, but the main boundary between them is at about 91°E (Grierson & al. 1980). Further to the NE, in E Xizang (along the Tibet-Sichuan Highway, near the great bent of the Yarlung Tsangpo / Brahmaputra River), more morphologically homogenous populations of subsp. *bhutanica* have been found. Fu & al. (1999), in contrast, state that *P. bhutanica* occurs in SE Xizang and *P. wallichiana* in S Xizang and NW Yunnan. The specimens preserved at KUN from the easternmost part of the geographic range of *P. wallichiana* s. lat. in NW Yunnan (Gongshan Co.), however, were found to match subsp. *bhutanica*. Similarly, two specimens from NW Yunnan were stated by Grierson & al. (1980: 306) to “approach *P. bhutanica* very closely” (with the exception of the non-pubescent shoots, a character sometimes not constant in soft pines – see 5.2.4. Surface of shoots). Therefore it is more likely that subsp. *wallichiana* occurs in China only along the border with Nepal (see Critchfield & Little 1966).

Recently, Silba (2000) described a new variety, *Pinus bhutanica* var. *ludlowii*, based on *Ludlow, Sherriff & Taylor 6421* (A, BM) from an altitude of 3300 m near Tsona in S Xizang not far from the NE border of Bhutan, only about 100 km away from the type locality of *P. bhutanica*, but a paratype from NW Yunnan is also included. The stated characters are rather vague and important ones, such as shoot indumentum and leaf posture, are not given, so that its status and affinity are difficult to judge.

The population of *Pinus wallichiana* subsp. *bhutanica* along the Tibet-Sichuan Highway occurs in deep river valleys in rich, pure groups or as scattered trees on steep rocky slopes of eruptive rocks, mainly between 2100 and 2600 m. The Bhutanese pine prefers slopes and steep ridges of NW to NE exposure. The habitats are overgrown with dense mixed forest often dominated by conifers; associated with the Bhutanese pine are *Cupressus gigantea* W. C. Cheng & L. K. Fu, *P. yunnanensis* Franch., *P. armandii* Franch. and *Tsuga dumosa* (D. Don) Eichler in various proportions. In W Arunachal Pradesh populations of the Bhutanese pine occur on middle to steep slopes of valleys at 1200–3000 m (most commonly at 1600–2800 m) without clear preference to some exposure but preferably in rather rocky habitats. At lower to middle altitudes it is usually associated with deciduous broad-leaved trees, mostly oaks, E of Dirang also with *P. roxburghii*; at upper altitudes with *T. dumosa*.

5.10. Supraspecific classification and conspectus of the Eurasian taxa of *Pinus* subsection *Strobus*

The Eurasian species of *Pinus* section *Quinquefoliae* subsection *Strobus* Loudon are classified into two series, one of them new, and into three new subseries. The North and Central American species form the third series (*P. ser. Strobus*) of this subsection.

***Pinus* series *Dalatenses* Businský, ser. nova**

Strobili anguste ovoidei usque cylindrici, (4-)6-20(-23) cm longi, maturitate se aperientes, squamis (35-)50-100(-120), apophyses plus minusve validae umbone terminali depresso. Corpora seminum relative parva (6-10 mm longa), oblonge elliptica, alae relative longae (11-30 mm) adnatae, limbus in basi alae conspicue elongatus in longam gracilem incrassationem. Folia (3-)5-11(-14) cm longa, semper quina vaginis deciduis, fasciculo vasorum simplici praedita. Species Asiae orientalis.

Cones narrowly ovoid to cylindrical, (4-)6-20(-23) cm long, with (35-)50-100(-120) scales; apophyses \pm thickened with umbo often depressed. *Seed* corpus relatively small (6-10 mm long), generally oblong ellipsoidal (usually at least 1.9 times longer than wide), the wing relatively long (11-30 mm), the corpus border often conspicuously elongated into a long and slender thickening. *Leaves* (3-)5-11(-14) cm long.

Type. – *Pinus dalatensis* Ferré

Species included

Pinus dalatensis Ferré

subsp. *dalatensis*

var. *dalatensis* – S Vietnam: Dalat environs, Chu Yang Sinh massif

var. *bidoupensis* Businský – S Vietnam: high mountains N-NE of Dalat

subsp. *procera* Businský – C Vietnam: Ngoc Linh Mts., mountains SW of Hue, mountains along the Laotian border?; Laos?

Pinus orthophylla Businský – central range of the Hainan Island

Pinus uyematsui Hayata – central range of Taiwan around the highest massif Mt. Yushan

***Pinus* series *Chylae* P. Landry in Bull. Soc. Bot. France 124: 471. 1977.**

Type. – *Pinus wallichiana* A. B. Jacks.

Pinus* subseries *Chylae

Strobili cylindrici usque longe cylindrici, 8-25(-30) cm longi, maturitate se aperientes, squamis (40-)50-140(-180), apophyses plerumque conspicue convexae sed relative tenues margine distali generaliter orbiculato, umbo terminalis, non depressus, saepe exsertus, squamae basales steriles non recurvatae. Corpora seminum relative parva (6-10 mm longa), late elliptica, alae relative longae (11-35 mm), adnatae, limbus in basi alae vix elongatus vel elongatus in brevem latam incrassationem. Folia (6-)10-25(-32) cm longa, semper quina vaginis deciduis, fasciculo vasorum simplici praedita. Species euroasiaticae.

Cones cylindrical or long cylindrical, 8-25(-30) cm long, with (40-)50-140(-180) scales, apophyses usually conspicuously convex but relatively thin, with generally rounded distal edge and the apex tending inwards, umbo not depressed, often protruding from the front outline of the scale, the basal sterile scales not recurved. *Seed* corpus relatively small (6-10 mm long), generally broad ellipsoidal (usually at most 1.9 times longer than wide), the wing relatively long (11-35 mm), the corpus border scarcely elongated or elongated into a usually short and broad thickening. *Leaves* (6-)10-25(-32) cm long.

Species included

Pinus wallichiana A. B. Jacks.

subsp. *wallichiana* – Central and W Himalayas and W adjacent regions (69°-92°E)

subsp. *bhutanica* (Grierson & al.) Businský – E Himalayas and E adjacent regions (Bhutan, E India, E Xizang, N Myanmar, NW Yunnan; 89°30'-100°E)

Pinus peuce Griseb. – SE Europe: Balkans

Note. – Klaus (1980) characterized the umbo of both *Pinus wallichiana* and *P. peuce* different from those of other species as “laevigat pyramidat erect” terminal umbo.

***Pinus* subseries *Wangianae* Businský, subser. nova**

Syn.: *Pinus* subg. *Strobilus* sect. *Strobilus* subsect. *Strobilus* [“*Strobi*”] ser. *Cosmopolitae* P. Landry in Bull. Soc. Bot. France 124: 472. 1977, p. p. [type: *Pinus parviflora* Siebold & Zucc.].

Arbores plerumque ad 20 vel 25 m altae; strobili ovoidei usque anguste elliptici (3.5-)5-10 (-11) cm longi, maturitate se aperientes, squamis (30-)40-65(-75), apophyses validae, umbo terminalis. Corpora seminum relative magna (7-13 mm longa), alae relative breves (3-17 mm longae) et latae, sed principaliter efficaces et adnatae (interdum secundarie reductae et facile frangentes). Folia (2-)3-6(-8) cm longa, semper quina vaginis deciduis, fasciculo vasorum simplici praedita. Species Asiae orientalis.

Low trees, usually not exceeding a height of 20 or 25 m. *Cones* ovoid to narrowly ellipsoidal, (3.5-)5-10(-11) cm long, with (30-)40-65(-75) scales, apophyses thick. *Seed* corpus relatively large (7-13 mm long), the wing relatively short (3-17 mm long) and broad, effective and adnate to the corpus or, in some individuals, secondarily reduced and frangible. *Leaves* (2-)3-6(-8) cm long.

Type. – *Pinus wangii* Hu & W. C. Cheng

Species included

Pinus eremitana Businský – N Vietnam (mountains between Ha Son Binh Prov. & Son La Prov. not far from the Laotian border)

Pinus wangii Hu & W. C. Cheng

subsp. *wangii* – S China: SE Yunnan (Xichou Co. & Malipo Co.)

subsp. *kwangtungensis* (Chun ex Tsiang) Businský – S China: N Guangdong, S Hunan, NE Guangxi and the Guizhou boundary

subsp. *varifolia* (Nan Li & Y. C. Zhong) Businský – S China: SW Guangxi (Tiandeng); NE Vietnam (Cao Bang Prov.)

Pinus parviflora Siebold & Zucc.

subsp. *parviflora* – Japan: S & W Honshu, Shikoku, Kyushu, Tsushima-to Isl.; S Korea: Ullung-do Isl.

subsp. *pentaphylla* (Mayr) Businský – Japan: C to N Honshu, Sado-shima Isl., S Hokkaido (including Okushi-to Isl.)

***Pinus* subseries *Formosanae* Businský, subser. nova**

Syn.: *Pinus* subg. *Strobilus* sect. *Strobilus* subsect. *Strobilus* [“*Strobi*”] ser. *Extremisorientaliae* P. Landry in Bull. Soc. Bot. France 124: 472. 1977, p. p. [type: *Pinus morrisonicola* Hayata].

Arbores ad 30-35 m altae; strobili maturitate se aperientes, squamae validae, sed fragiles et tantum parum lignosae, apex manifeste declinatus usque reflexus, umbo terminalis, 4-9 mm latus, bilateraliter ardue declivis, in mucronem praevalenter recurvatum, usque circa 1 mm altum procurrentem. Semina et alae in summa 14-30 mm longa, corpora relative magna (7.5-13 mm longa), alae latae (5.5-11 mm), perfecte efficaces, adnatae. Folia semper quina, vaginis deciduis, fasciculo vasorum simplici praedita. Species Asiae orientalis (Taiwan).

Tall trees up to 30-35 m. *Cone-scales* thick, fragile and weakly lignified, with the apex conspicuously turned outwards or often whole distal part reflexed; umbo 4-9 mm wide, bilaterally sloped towards the dorsal and ventral side of the scale, ending with a prickle about 1 mm high and generally pointing backwards [exception in *P.* subsect. *Strobilus*]. *Seeds* including wing 14-30 mm long, the corpus relatively large (7.5-13 mm long), wing broad (5.5-11 mm wide). *Leaves* (4-)5.5-8(-10) cm long.

Type and only species. – *Pinus morrisonicola* Hayata – central range of Taiwan.

Notes. – *Pinus* ser. *Dalatenses*, present in Vietnam, on Hainan and on Taiwan, is assumed to be closest to the ancestor of the Eurasian species of *P.* subsect. *Strobilus* (and also of *P.* sect. *Quinquefoliae*). Its three species are supposedly very closely related to (or themselves are) progeni-

tors of the other, derived species, formally constituting *P. ser. Chylae*. According to the morphology, geography and extensive range of variation of these three species, *P. dalatensis* seems to be the closest to the supposed progenitor of all Eurasian taxa of *P. sect. Quinquifoliae*. The supposedly derived species of *P. ser. Chylae* are on the basis of their morphology and assumed relationships here classified into three parallel subseries. From *P. ser. Dalatenses*, *P. orthophylla* probably is the one closest to the progenitor of *P. subser. Wangianae*. This subseries is distributed from N Vietnam to S Hokkaido with the number and extent of populations increasing towards the NE. The Taiwanese *P. morrisonicola*, the only species constituting *P. subser. Formosanae*, seems to be derived from a small-seeded pine most closely allied to *P. uyematsui*.

Most of the Asian species of *Pinus* subsect. *Strobis* have a very restricted, never overlapping geographic distribution within the Southeast-Asian subregion of the Paleotropics, with *P. wangii* subsp. *kwangtungensis* reaching as far north as about 26.5°N. Populations of these taxa usually occur as relicts on isolated mountain ranges or massifs. Only two Asian species of this group have a more extensive geographic range without larger discontinuities – the Himalayan *P. wallichiana* and the Japanese *P. parviflora*, both between 25°N and 43°N. The same N limit is reached by the only European species of this subsection, *P. peuce*, which is restricted to two rather small areas in the Balkans, near 42°N.

5.11. Notes on the American species of *Pinus* subsect. *Strobis*

The American species of *Pinus* subsect. *Strobis* exhibit evident character similarities, presumably resulting from parallel evolution, to the Asian species. The systematic concept of the American taxa supported here is based on the hypothesis that there are three parallel evolutionary lineages differing from one another in seed and cone morphology. These lineages are represented by the following species pairs: 1. *Pinus veitchii* Roehl (= *P. loudoniana* Gordon) and *P. lambertiana* Douglas; 2. *P. ayacahuite* Ehrenb. ex Schltdl. s. str. and *P. monticola* Douglas ex D. Don; 3. *P. chiapensis* (Martínez) Andresen and *P. strobis* L. Each pair includes one, supposedly ancestral species in central to S Mexico (or present also further south in Central America) and another, morphologically similar, supposedly derived, vicariant species in the USA and Canada (or also reaching NW Mexico).

In contrast to this new concept, *Pinus veitchii* has hitherto usually been classified as a variety of *P. ayacahuite* (Farjon & Styles 1997) due to the frequently occurring morphological transitions between both. This variation is interpreted here, however, as a result of introgressive hybridization of the two species, similarly as in *P. morrisonicola* and *P. uyematsui* in Asia. The present author studied such a putative hybrid population N of Tlaxco near the border between Tlaxcala and Puebla, Mexico, in March 1999. The range of variation in cone and seed morphology present includes morphotypes of *P. ayacahuite* s. str., intermediate ones, and such approaching *P. veitchii*. Although Farjon & Styles (1997: 204) determined a specimen from this same population as *P. ayacahuite* var. *veitchii*, no morphotypes were found here to fully correspond with the plants in the type locality of *P. veitchii* between Volcán Popocatepetl and Iztaccihuatl. Martínez (1948: 119) referred the population near Tlaxco to *P. ayacahuite* s. str.

Shaw (1909) included another taxon, *Pinus strobiformis* Engelm., in *P. ayacahuite* under the name *P. ayacahuite* var. *brachyptera* Shaw. However, this taxon is now generally accepted as a separate species (Little 1979, Farjon & Styles 1997) that belongs to *P. subsect. Flexiles*.

Pinus chiapensis and *P. strobis* show certain morphological resemblance to each other (Farjon & Styles 1997: 218), which has often been used as a reason to relegate the former as an infraspecific taxon of the latter, despite a distance of about 2000 km between the geographic ranges of the two taxa. Although most of their quantitative characters show considerable overlap, it is possible to well distinguish them by the generally different cone phyllotaxis, the position of basal sterile cone scales, the length of cone peduncles, and some leaf characters, e.g., by the density of the serration (Andresen 1966). Moreover, the composition of their turpentine is significantly different (Perry 1991) and the recent DNA data indicate that *P. chiapensis* may even represent a separate evolutionary lineage (Liston & al. 1999).

5.12. Key to the species of *Pinus* subsect. *Strobus*

Determining single specimens of *Pinus* subsect. *Strobus* using a key can be difficult in some cases. Firstly, the range of variation within species or local populations often is very extensive, and various characters substantially differ in their stability in different taxa. For instance, both extremes of the branchlet indumentum, i.e., glabrous vs. densely pubescent, may be found in a single population, quite frequently in *P. eremitana*, or in western localities of *P. wangii* subsp. *kwangtungensis*, but the same character is more or less stable in other taxa, e.g., *P. wangii* subsp. *wangii*, *P. dalatensis* subsp. *procera*, and most populations of *P. wallichiana* subsp. *bhutanica*. Secondly, Eurasian and North American representatives alike, considerably overlap in ranges of variation in quantitative characters, which are sometimes even combined with a noticeable similarity in qualitative characters. These overlaps of variability are even frequent in species with very distant geographic ranges and can be misleading in identification, particularly when only limited herbarium material is available. A significant example is the pair *P. dalatensis* (Vietnam) and *P. uyematsui* (Taiwan). If their significantly different habit is disregarded, then discriminating them may be difficult. Considering their notorious rarity in herbaria, it is probably only the distance of their geographic ranges that have so far prevented them from having been treated as merely conspecific.

- 1. Seeds large (corpus, 7-18 mm long), with a relatively short and broad wing; cones with thick, stout apophyses (but sometimes fragile) 2
 - Seeds small (corpus 5-10 mm long), with a relatively long and narrow wing; cones often with relatively thin, flexible scales (if apophyses thickened, then umbo usually depressed) 7
- 2. Cones cylindrical, robust, more than (20-)25 cm long [two species of North America] 3
 - Cones ovoid to narrowly ellipsoidal, less than 15 cm long 4
- 3. Apophyses usually smooth, with rounded or obtusely cuneate distal edge, at most with only slightly elongated apex; leaves 7-10(-14) cm long, usually more than 1.5 mm wide, with stomata on all sides *P. lambertiana*
 - Apophyses usually longitudinally grooved, with apex conspicuously elongated distally; leaves 11-20 cm long, less than 1.5 mm wide, with stomata only on the ventral sides *P. veitchii*
- 4. Cone scales (and apophyses) fragile and weakly lignified, with the apex conspicuously turned outwards or reflexed, umbo bilaterally sloped towards the dorsal and ventral side of the scale, with a prickle c. 1 mm high and generally pointing backwards; leaves (4-)5.5-8(-10) cm long, straight *P. morrisonicola*
 - Cone scales (and apophyses) stout, well lignified, with the apex straight or tending inwards (contiguous to adjacent scales in closed cones), umbo flat, with the distal edge weakly acute or rounded in outline, always without prickle; leaves mostly less than 6 cm long, often curved 5
- 5. Cones sessile or on very short, straight peduncles, patent, usually persisting very firmly for many years; leaf edges mostly with 4-11 teeth per centimetre in the middle part; mature trees usually 15-30 m high, crown often narrow, tapering towards the top *P. parviflora*
 - Cones usually pendulous, on long or short, usually curved peduncles, early deciduous or persisting for a few years; leaf edges mostly with 8-40 teeth per centimetre in the middle part; mature trees usually 8-20 m high, crown broad with rounded or flat top 6
- 6. Leaves, on average, wider than 1 mm, conspicuously crescently curved, often distinctly whitish pruinose on the ventral sides (if not pruinose, then often in fascicles of less than 5, see *P. wangii* subsp. *varifolia*), mostly with 4-10 stomatal lines, edges mostly with 18-40 teeth per centimetre in the middle part; umbo even with the apophysis surface or indistinctly depressed *P. wangii*
 - Leaves, on average, about 1 mm wide or narrower, straight or usually indistinctly curved, greyish green on the ventral sides, mostly with 4-7 stomatal lines, edges mostly with 8-25 teeth per centimetre in the middle part; apophyses with umbo conspicuously abruptly depressed *P. eremitana*

- 7. Apophyses usually conspicuously convex, with rounded distal edge and the apex tending inwards, umbo even with the apophysis surface and often protruding from the front outline of the scale 8
 - Apophyses not conspicuously convex, with cuneate or rounded distal edge and the apex recurved, deflected, or straight, sometimes truncate and then umbo depressed 9
- 8. Leaves usually drooping to conspicuously pendent, (6-)10-25(-32) cm long; cones mostly more than 15 cm long *P. wallichiana*
 - Leaves straight, (6-)7-10(-12) cm long; cones mostly less than 15 cm long *P. peuce*
- 9. Leaves (8-)10-17(-20) cm long; cones 20-45 cm long, apophyses conspicuously elongated with apex deflected or recurved [species of S Mexico & Central America]
 - P. ayacahuite* s. str.
- Leaves (4-)5-10(-14) cm long; cones at most 20(-25) cm long 10
- 10. Cones on conspicuously slender, relatively long (15-45 mm) peduncles, the basal sterile scales not recurved; leaves flexible, very slender, less than 1 mm wide [species of S Mexico & Guatemala] *P. chiapensis*
 - Cones on stout or rather slender, short or medium-long peduncles 11
- 11. Basal sterile cone scales usually recurved towards the peduncle, seed scales including apophyses relatively thin, umbo even with the apophysis surface [two species of North America] 12
 - Basal sterile cone scales mostly not recurved, seed scales more or less thickened, apophyses with umbo often depressed 13
- 12. Leaves flexible, slender, 6-14 cm long; cones conspicuously narrowly cylindrical, with a low phyllotaxis of 3/5 *P. strobus*
 - Leaves stiff, thick, (4-)5-10 cm long; cones cylindrical or conic cylindrical, usually with a higher phyllotaxis of 5/8 *P. monticola*
- 13. Cones (4-)6-10(-12) cm long, 4.5-6.5 cm wide when fully open, with apophyses thick, firm and smooth; first-year shoots glabrous; mature trees low, usually not exceeding 20 m in height, with short, often crooked trunk *P. orthophylla*
 - Cones (6-)8-20(-23) cm long, (5-)6-10 cm wide when fully open, with apophyses thin or thick, often grooved or rugose; first-year shoots often pubescent; mature trees high, usually exceeding 20 m in height, with tall, straight trunk 14
- 14. Apophyses usually with a distinct longitudinal dorsal keel and usually with a truncate apex, umbo often conspicuously abruptly depressed; mature trees with broad, umbrella-like crown in the upper part of the unbranched trunk *P. daltensis*
 - Apophyses usually with only an indistinct longitudinal dorsal keel and usually with an obtuse apex, umbo even with the apophysis surface or indistinctly depressed; mature trees with irregularly ellipsoidal, tall crown beginning from the lower part of the trunk *P. uyematsui*

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