The foliage and cone of *Pinus strobiformis* subsp. *strobiformis* taken near El Salto, Durango. This species is one of a group of white pines that grow at high altitudes in Mexico and south western United States

The high altitude white pines of Mexico and the adjacent SW USA

(*Pinus* L. subgenus *Strobus* Lemmon, Pinaceae)

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Abstract: The newly described white pine from northeast Mexico *Pinus stylesii* Frankis ex Businský is compared with other related pines, including *P. flexilis* James, *P. reflexa* (Engelm.) Engelm., *P. strobiformis* Engelm., *P. veitchii* Roezl, and *P. ayacahuite* Ehrenberg ex Sclechtendal. The new combination *Pinus strobiformis* subsp. *veitchii* (Roezl) Frankis is made, transferring this taxon from *P. ayacahuite* under which it has traditionally been treated as *P. ayacahuite* var. *veitchii* (Roezl) Shaw.

The white pines in *Pinus* L. subgenus *Strobus* Lemmon in Mexico and the south-western United States have been discussed on a number of occasions with differing and often somewhat confused interpretations (Shaw, 1909; Martínez, 1945, 1948; Loock, 1950, 1977; Andresen & Steinhoff, 1971; Steinhoff & Andresen, 1971; Rushforth, 1987; Perry, 1991; Carvajal & McVaugh 1992; Kral, 1993; Farjon & Styles, 1997). Farjon & Styles (1997: 215) pointed out that white pine cone morphology on Cerro Potosí and surrounding mountains in north-eastern Mexico was unusual, and concluded that further research was required in this area.

A range of specimens has been examined from this area and surrounding areas in the USA and Mexico. Six taxa were identifiable over the larger area, and are treated here as five species and one subspecies, all substantially allopatric and all readily discernible on cone morphology. One additional taxon of limited range was also observed and concluded to be a natural hybrid involving two of the other taxa. The single taxon occurring in north-eastern Mexico was found to lack a valid name. This was described on my behalf by Businský (2008), who (in preparing his monograph on *Pinus*) was unable to await this long-delayed publication. A discussion of the related taxa follows.

Pinus flexilis E.James, Account Exped. Pittsburgh 2: 27, 35, 1823.

This taxon, the first described in the group, is upheld as currently circumscribed (e.g. Kral, 1993). It is distinguished by its small cones 7-13cm long, scales with the apophysis crescent moon-shaped below, fairly small seeds 7-10mm long with no more than a very short vestigial wing, and short, entire needles.

Pinus reflexa (Engelm.) Engelm., Bot. Gaz. 7: 4, 1882.

≡ *Pinus flexilis* var. *reflexa* Engelm., in Wheeler, Rept. U. S. Geog. Surv. W.

Pinus stylesii.
Tree. Cerro Potosí,
Nuevo León.

100th Merid. 6: 258, 1878.

∫ *Pinus flexilis* subsp. *reflexa* (Engelm.) E. Murray, Kalmia 12: 23, 1982.

= *Pinus flexilis* var. *macrocarpa* Engelm., in Wheeler, Rept. U. S. Geog. Surv. W. 100th Merid. 6: 258, 1878.

= *Pinus flexilis* var. *serrulata* Engelm., in Wheeler, Rept. U. S. Geog. Surv. W. 100th Merid. 6: 258, 1878.

= *Pinus* × *novaemexicana* Landry, Phytologia 65: 479, 1989.

The white pine of Arizona and New Mexico was first described under three different varietal names in *P. flexilis* (Engelmann, 1878) though he later (Engelmann, 1882) raised his var. *reflexa* to the rank of species. It has subsequently been regarded as either as Engelmann first published it (e.g.

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Pinus stylesii. Cerro Potosí, Nuevo León

photograph © Jeff Bisbee

Pinus strobiformis subsp. *veitchii*. Foliage and cone. East side of Popocatepetl, Puebla.

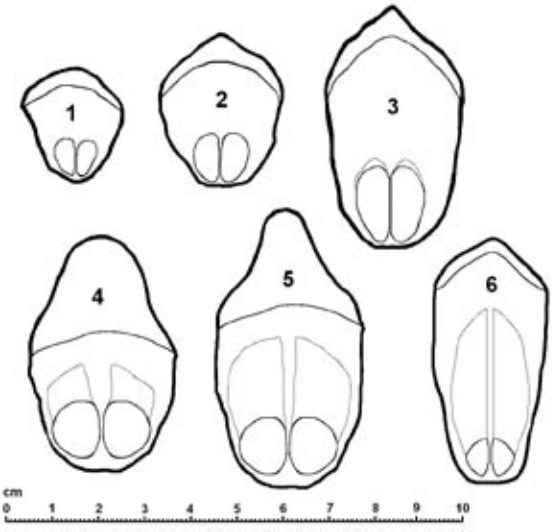
Douglass, 1958; Farjon & Styles, 1997), or more often cited as *P. strobiformis* (e.g. Sudworth, 1897; Critchfield & Little, 1966; Andresen & Steinhoff, 1971; Kral, 1993). It differs from *P. strobiformis* from Chihuahua southward in several aspects of cone and foliage morphology, in which it shows varying degrees of similarity to *P. flexilis*. These include usually partly serrulate needles, very rarely entire or fully serrulate, with the serration mainly in the apical half of the leaf and entire in the basal half; shorter mean cone length, unstriated smooth glossy buff-yellow scales with less prolonged apophyses, basal scales not or less revolute, and smaller (primarily narrower) seeds. The cones are variable in these characters, both from tree to tree and population to population, and specimens can be found closely resembling either of these species. This suggests that this regional population may originate in hybrid introgression between them. This situation could have arisen as a result of regional extinction during one or more periods of unfavourable climate in relatively recent geological history (possibly drought at interglacial maxima), followed by re-colonisation from both north and south when favourable conditions returned.

Pinus stylesii Frankis ex Businský, Acta Pruhoniciana 88: 6, 2008.
A tree to 15-25 (-30?)m tall. Needles five per fascicle, 6-12 cm long, glossy green with glaucous stomatal bands on the inner faces, margins fully serrulate, sheath deciduous. Cones 14-25cm long, 8-11cm broad when open

(exceptionally smaller, 10cm long, when stunted in severe exposure at highest altitudes or damaged by insect infestation), scales straight or reflexed (but never recurved), moderately thickened, striated, orange-buff, apex acute, not greatly prolonged; basal scales numerous and congested, reflexed but not recurved. The seeds are very large, 14-17 × 8-11mm, the longest seed of any American white pine, with a rudimentary wing 0.5-2 (-4)mm long.

This species is confined to the northern Sierra Madre Oriental of NE Mexico, at altitudes of 2300m to 3600m, often on limestone soils. It is named in honour of the late Dr Brian T. Styles (1934-1993), in recognition of his major contribution to the taxonomy of Mexican pines. None of the material examined from the Sierra Madre Occidental or from the USA shows the characters of this taxon, and it is not considered to occur in these regions.

Martínez (1945, 1948) and Loock (1950) identified this tree as *P. reflexa* (Engelm.) Engelm.; they and Perry (1991) also identified stunted, high altitude specimens of it as *P. flexilis* James. *P. stylesii* differs from both of these in the



Cone scales, showing apophysis extension at apex, seed (dark grey) and seed wing (light grey). All specimens in author's collection.

1. *Pinus flexilis.* Pikes Peak, Colorado. D K Bailey s.n.
2. *Pinus reflexa*. Santa Catalina Mts., Arizona. F G Hawksworth s.n.
3. *Pinus stylesii*. Mesa de las Tablas, Coahuila. M P Frankis 117.
4. *Pinus strobiformis* subsp. *strobiformis*. Guachochi, San Juanito, Chihuahua. Hjerting & Ødum 890266.
5. *Pinus strobiformis* subsp. *veitchii*. Texcaltitlán, Mexico State. N D G James s.n.
6. *Pinus ayacahuite*. Cultivated, Bodnant, Wales. M P Frankis s.n.. Matches specimens from Hidalgo.

broader cones and longer seeds, and in consistently serrated needles (entire in *P. flexilis*, weakly serrulate in *P. reflexa*) with stomata confined to the inner faces.

Critchfield & Little (1966), Perry (1991) and Farjon & Styles (1997) identified this tree as *P. strobiformis* Engelm., from which it differs in the straight (not recurved or revolute) and slightly thinner cone scales, shorter apophysis prolongation with an acute (not rounded) apex, and relatively longer, less rounded seeds.

Specimens examined: **México: Nuevo León:** *E. L. Little, Jr. 18984*, Cerro Potosí km.16, 2950m (9700'), 30 March 1963, tree 18m tall and 30cm diameter, in *Pinus* / *Abies* / *Pseudotsuga* forest on limestone. *E. L. Little, Jr.* 18989, Cerro Potosí, km.16, 2950m (9700'), 30 March 1963 (K, US); *C. H. Mueller & M. T. Mueller* 1244, Cerro Potosí, 26 July 1934 (F); *J. W. Stead & B. T. Styles* 630 & 631, Cerro Potosí, 2900m, 13 March 1980 (FHO); *J. W. Stead & B. T. Styles* 634, 635 & 636, Cerro Potosí, 3420m, 13 March 1980 (FHO); *D. K. Bailey* s.n., Cerro Potosí, 3100m, 5 November 1975 (FPF); *K. D. Rushforth* 415A, 465, Cerro Potosí, 3000m, 25-28 October 1984 (E), *K. D. Rushforth* 557, Zaragosa, Cañada las Tinajas, 2600m, 1 November 1984 (E); *M. P. Frankis* 166, Zaragosa, Cañada las Tinajas, 2560m, 15 November 1991 (E). **Coahuila:** *D. K. Bailey* s.n., Cuatro Cienegas, Sierra de la Madera, 2440m, 12 January 1975 (FPF); *M. P. Frankis* 117, Mesa de las Tablas, 2800m, 10 November 1991 (E, FHO); *Wynd & Mueller* 630, Sierra el Carmen, Sentenela Canyon, 9 July 1936 (E, K).

Published photographs of specimens identifiable as *P. stylesii*: **Nuevo León:** Cerro Potosí, Martínez (1948): 105, cited as *P. flexilis*. Cerro Potosí, Perry (1991): 46, cited as *P. flexilis*. **Coahuila:** Sierra de San Marcos, Martínez (1948): 109, cited as *P. reflexa*. **Locality not given:** Loock (1977): 111 t.4.2, 116 t.5, cited as *P. reflexa*; Perry (1991): 47-right, cited as *P. strobiformis* Engelm.

Pinus strobiformis Engelm., in Wislizenus, Mem. Tour North Mexico 102, 1848.
Pinus strobiformis subsp. ***strobiformis***.

∫ *Pinus ayacahuite* var. *brachyptera* Shaw, [Pines Mexico] Publ. Arnold Arbor. 1: 11, 1909.
∫ *Pinus ayacahuite* subsp. *strobiformis* (Engelm.) E. Murray, Kalmia 13: 21, 1983.
= *Pinus strobiformis* var. *carvajalii* Silba, Phytologia 68: 61, 1990.
= *Pinus ayacahuite* var. *novogaliciana* Carvajal, in Carvajal & McVaugh, Flora Novogaliciana 17: 48, 1992.

Pinus strobiformis subsp. ***veitchii*** (Roezl) Frankis, **comb. nov.**
Basionym: *Pinus veitchii* Roezl, Cat. Graines Conif. Mexic. 32, 1857.

∫ *Pinus ayacahuite* var. *veitchii* (Roezl) Shaw, [Pines Mexico] Publ. Arnold Arbor. 1: 10, 1909.

= *Pinus bonapartea* Roezl ex Gordon, Gard. Chron. ser. 3, 1858: 358, 1858. Further synonymy in Farjon & Styles (1997).

Pinus strobiformis is characterised by large cones (15-) 20-40 (-60)cm long with thick, inflexible woody scales with a strongly prolonged apophysis, heavily striated and usually matt (occasionally shiny as in *P. flexilis*), yellowish or reddish brown; the basal scales are revolute and fewer in number than in *P. stylesii*.

Seed morphology is constant throughout the range, broad ovoid 10-13 × 9-10mm, freckled dark on paler grey-brown, but with a wing of variable length, 0.5-5mm in the north of the range increasing southwards to 12-18mm in subsp. *veitchii*; the wing tends to be very broad (unless also very short), relatively thick, inflexible and brittle, and usually striated dark on paler brown. From *P. stylesii* it is also told by the thicker and usually broader scales, not congested and invariably revolute at the base, and the shorter and relatively broader seeds; from *P. flexilis*, by the larger cones, broader, more rounded seed, usually longer winged, and the heavily striated, less bright and glossy, and more elongated scales (but see also *P. reflexa*, above). From *P. ayacahuite* it differs in the considerably larger seed with a short, broad inflexible wing and thick, broad, inflexible scales.

The treatment of either subspecies of *P. strobiformis* as varieties under *P. ayacahuite* (Shaw, 1909; Carvajal & McVaugh, 1992) leads to a substantial (five- to ten-fold) difference in seed weight and conspicuously different wing shape combined in a single species, a degree of variation not recognised in any other conifer species. This marked difference in seed morphology is best regarded as a specific discriminant despite the similarity in foliage.

The treatment proposed by Perry (1991) and followed by García Arévalo & González Elizondo (1998) of *P. strobiformis* and *P. ayacahuite* var. *brachyptera* as different taxa is not valid. Shaw's 1909 name is a nomenclatural synonym based on the same type, as he cited Engelmann's name and type specimen in his description (Carvajal & McVaugh, 1992). Should two taxa exist in the Sierra Madre Occidental as proposed by Perry, that for which they used Shaw's name would require a new name. However, no evidence could be found for more than one white pine taxon in this range, and that interpretation is rejected here.

The typical subspecies *strobiformis* occurs in the central to northern part of the species' range, from Chihuahua and Sonora south to Jalisco. The holotype specimen, *Wislizenus* 231 (MO!; Carvajal & McVaugh, 1992; Farjon & Styles 1997), is from Cosiquirachi, Chihuahua. The specimen *Wislizenus* 155 (MO!) from the same locality has also been cited as the type (Andresen & Steinhoff, 1971), but is a seedling, not described in the protologue, and can only be considered additional original material with no type status.

In many specimens, the tips of the fertile cone scale tips are recurved along

the full length of the cone, not just at the base, curling to 90-180° (-270°), but in some, only the infertile basal scales are recurved, with the fertile scales nearly straight. This variation occurs across the range of the type subspecies and is considered here to be of no taxonomic significance.

Populations from Jalisco were described (Carvajal, 1986, in Spanish only) as *P. novogaliciana* Carvajal *nom. nud*. This oversight was noted by Silba (1990), who validated it with a new name and type as *P. strobiformis* var. *carvajalii* Silba, but including Carvajal's holotype as a paratype. The oversight was also later corrected by Carvajal in Carvajal & McVaugh (1992, presumably unaware of Silba 1990) as *P. ayacahuite* var. *novogaliciana* Carvajal within the very broad concept of *P. ayacahuite* used in that flora. I concur with Farjon & Styles (1997) that these trees fall within the range of variation of typical *P. strobiformis*.

Pinus strobiformis subsp. *veitchii* has long been treated as a variety of *P. ayacahuite* (Shaw, 1909; Carvajal & McVaugh, 1992; Farjon & Styles, 1997), but is much closer to *P. strobiformis* in cone and seed morphology. Recently however, Businský (2008) treated it as a species *P. veitchii*. It shares the broad, thick cone scales and large seed. The only reliable distinction from subsp. *strobiformis* is the size of the seedwing, consistently longer in subsp. *veitchii*, 12-18mm long, thus longer than the seed. The scales are similar in their variation in degree of curvature, though spreading S-shaped scales are more frequent than in subsp. *strobiformis*. The needles also tend to be slightly longer but with much overlap (Farjon & Styles, 1997).

Pinus ayacahuite Ehrenberg ex Schlechtendal, Linnaea 12: 492, 1838.
This species as circumscribed here is confined to south and east-central Mexico, in humid areas relatively close to the Caribbean and Pacific monsoons: in Vera Cruz, the eastern parts of Puebla, Hidalgo and Tlaxcala, Guerrero, Oaxaca, Chiapas, and in Guatemala, Honduras and El Salvador. It can be identified by its long, slender, lightweight cones with thin flexible scales, and small seeds with a long slender wing. In these it is similar to *P. monticola* Douglas ex D. Don in Lambert, but larger, the cones (16-) 20-40 (-45)cm long, the seeds 8-10 × 5-6mm with a long, slender 25-30 × 10mm wing. These characters very readily distinguish it from the other taxa discussed above.

In parts of Tlaxcala and Puebla, *P. ayacahuite* meets and hybridizes with *P. strobiformis* subsp. *veitchii* (Perry, 1991); this natural hybrid (e.g. *Hunt* 799, México: Tlaxcala, 15km from Tlaxco on Zacatlan road, 19°49'N 98°05'W 2690m, K; *Farjon & Mejía* 326, same locality, E, K, FHO) is intermediate between the parents, with a moderately large seed with a long and moderately broad wing, and moderately thickened scales. It is variable; of the two specimens cited, the former is closer to *P. strobiformis* subsp. *veitchii* and latter closer to *P. ayacahuite*. The extent of the zone of hybridization is not known, but is evidently narrow, as specimens have been noted only from Tlaxcala and Puebla (Perry, 1991). Plants from Vera Cruz (e.g. *Nee* 23165, *Nee & Taylor* 27054

& 29084, *Taylor & Narave* 371, *Calzada* 5732 & 5931; F) 50km E/NE of the above hybrid site are normal *P. ayacahuite*, while typical *P. strobiformis* subsp. *veitchii* occurs on Volcan Popocatepetl (Roezl, 1857), 60km W/SW. In common with most natural pine hybrids, no name has ever been given to this hybrid, and as it is scarce and confined to a relatively small area, it is not proposed to name it here.

TABLE OF CHARACTERS

TAXON	*flexilis*	*reflexa*	*strobiformis* subsp. *strobiformis*	*strobiformis* subsp. *veitchii*	*stylesii*	*ayacahuite*
Cone length *(cm)*	7-13	10-23	20-50	20-50	14-25	16-45
Open cone width *(cm)*	5-7	6-9	7.5-11	9-13	8-11	7-11
Dry cone weight *(g)*	15-70	30-75	75-250	200-480	60-160	20-160
Scale width *(mm)*	20-30	23-33	25-35	25-38	25-35	20-30
Scale thickness *(mm)*	4-6	4-6	4-5	4-6	3-5	2-3
Sterile basal scales	20-30	20-35	10-25	15-25	30-60	20-30
Apophysis prolongation *(mm)*	4-10	6-18	15-25	15-22	7-14	5-10
Seed length *(mm)*	7-10	8-12	10-13	10-13	14-17	8-10
Seed width *(mm)*	6-8	7-9	9-10	9-10	8-11	5-6
Seedwing length *(mm)*	<0.5	<0.5-5	0.5-12	12-18	0.5-4	25-30
Leaf length *(cm)*	3-7	5-10	8-20	10-20	6-13	10-20
LEAF SERRATIONS *(per cm)*						
Basal half of leaf	0	0-1	8-12	8-12	8-12	8-12
Apical half of leaf	0	2-7	8-12	8-12	8-12	8-12
Stomatal lines (inner)	2-3	3-5	4-5	4-5	4-5	4-5
Stomatal lines (outer)	1-3	0-2	0	0	0	0

NOTE: *all cone dimensions refer to fully mature open cones, free of insect or fungal damage.*

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