Porsild spruce in Canada

by Rodney Arthur Savidge¹

ABSTRACT

The natural range of Porsild spruce (*Picea glauca* var. *porsildii* Raup), a white spruce variety distinguished by its smooth bark and resin blisters, has long been considered to be restricted to northwestern North America, but here it is noted that the same phenotype exists in wild stands in Ontario, Quebec, and Atlantic Canada. No record of Porsild spruce trees yet exists in the region between Alberta and western Ontario, or anywhere in the United States other than Alaska. The forestry community is requested to document any encounters with Porsild spruce in unmanaged stands, in order that its full range can be established. History and potential scientific importance of Porsild spruce are given consideration.

Keywords: Acadian Research Forest, bark, Beringia, boreal forest, hybridization, periderm, phellem, *Picea glauca* var. *porsildii* Raup, Pinaceae, post-glacial forest, primeval forest, resin blister

RÉSUMÉ

La distribution naturelle de l'épinette de Porsild (*Picea glauca* var. *porsildii* Raup), une variété d'épinette blanche qui se distingue par son écorce lisse et ses vésicules résinifères, a longtemps été considérée comme étant limitée au nord-ouest de l'Amérique du Nord, mais on a relevé que le même phénotype se retrouve dans des peuplements naturels de l'Ontario, du Québec et des provinces de l'Atlantique. Cependant, aucun relevé d'épinette de Porsild n'a été enregistré dans les régions situées entre l'Alberta et l'ouest de l'Ontario, ainsi qu'aux États-Unis à l'exception de l'Alaska. La communauté forestière est priée de documenter toute observation d'épinette de Porsild retrouvée dans des peuplements non aménagés, de façon à ce que la distribution complète de cette variété puisse être établie. L'historique et l'importance scientifique potentielle de l'épinette de Porsild sont présentés à titre informatif.

Mots clés : Centre de foresterie de l'Atlantique, écorce, Bérिंगie, forêt boréale, hybridation, périderme, suber, *Picea glauca* var. *porsildii* Raup, Pinacées, forêt post-glaciaire, forêt primaire, vésicule résinifère

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Introduction

Porsild spruce (*P. glauca* var. *porsildii* Raup) is a designation for a phenotype of white spruce (*Picea glauca* [Moench] Voss) that can be unequivocally differentiated by the presence of resin blisters on its non-scaly trunk surface (Fig. 1). Porsild spruce has been described as a "geographic variety" to be found only in northwestern North America (Alden and Loopstra 1987).

However, evidence presented below indicates that Porsild spruce trees are also native to southeastern Canada. Research into Porsild spruce is wanting and may help resolve taxonomic issues underlying management of the boreal forest. Knowledge about formation, chemistry and physiology of Porsild spruce bark could also set the stage for innovations in forest health management.

Historical Commentary

According to Raup (1947), the first two specimens of Porsild spruce to be collected came from near Jasper, Alberta, and were deposited with the Arnold Arboretum herbarium in 1922 by J. G. Jack, a Canadian professor of forestry at Harvard University. In making those collections, Jack presumably recognized that the phenotype was unusual. However, the specimens deposited in the Arnold Arboretum by Jack were not annotated until 1939 and, inexplicably, the annotations were made by A.E. Porsild and C. Heimbürger as follows (K. Kanchi, Arnold Arboretum Herbarium, personal communication):

J.G. Jack 2719, "*Picea glauca* var. *typica*;"

J.G. Jack 2807, "*Picea glauca* var. *arctica* (Murr.) new. comb."

P. glauca var. *arctica* was evidently intended as a scientific epithet for Porsild spruce, but no supporting description is known to exist. Consequently, *P. glauca* var. *arctica* remains *nomen nudum*. However, if a published description should be found, one or both of the two herbarium specimens deposited by J. G. Jack is a candidate for a holotype of *P. glauca* var. *arctica*, and that name would probably take precedence over *P. glauca* var. *porsildii*.

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Fig. 1. Examples of Porsild and white spruce. Arrows point to bark blisters. **A)** Old-field Porsild spruce tree in PEI National Park; all other white spruce trees in this old farm field appeared to be scaly barked. **B)** Trunk of the tree shown in A. **C)** Deformed Porsild spruce on the edge of the ocean beach, PEI National Park. **D)** 33-year-old tree (the one behind the person) in northeastern NB; **E)** smooth bark with resin blisters on tree trunk of D. **F–J)** Parts of a large Porsild spruce tree in northeastern NB: F, twig; G, trunk at breast height; H, branch at junction with trunk; I, root collar; J, seed cone (mm scale). **K)** Scaly-barked *P. glauca* × *P. engelmannii* hybrid in ARF. **L)** Smooth blister-barked *P. glauca* × *P. glauca* controlled-pollination phenotype with smooth bark and bark blisters. **M)** Porsild spruce tree within ARF range-wide provenance trial, seed source Riviere Shipshaw, PQ 48.7°N, 71.1°W. **N)** Northwestern NB roadside Porsild spruce tree; note the relatively light-coloured bark surface. **O)** Scaly-barked white spruce (left) and Porsild spruce at Brewer Lake near east gate of Algonquin Provincial Park. **P)** Porsild spruce trunk in Algonquin Provincial Park. **Q, R)** Valley bottom Porsild spruce near Mount Pattison in never-glaciated Yukon Beringia: Q, cone (mm scale); R, trunk. **S)** Trunk of a scaly-barked white spruce growing within one meter of that shown in R. **T–V)** Sub-alpine Porsild spruce in never-glaciated Yukon Beringia: T, an old solitary tree in the tundra; U, bark of tree shown in T (GPS unit length = 14 cm); V, seed cone and needles on tree shown in T.

In 1939, the type specimen described as “*Picea glauca* Voss var. *Porsildii*² var. nov.” was collected as part of an Arnold Arboretum expedition to the Northwest Territories (Raup 1947). The holotype material was obtained from a 12-meter-tall tree standing at 790 m a.s.l. near the west end of Brintnell Lake within the Mackenzie Mountain Range (62.087632°N, 127.58544°W), approximately 36 km northeast of the mining town of Tungsten. That same expedition collected additional herbarium specimens of Porsild spruce at Hay River, NT, and the bark-blistered phenotype was also noted to be present in forest along the Mackenzie River near Fort Simpson, NT (Raup 1947).

In addition to its novel bark features, Raup (1947) suggested that Porsild spruce was distinguished by its spreading crown. Daubenmire (1974) doubted the taxonomic value of Porsild spruce crown form on the basis that tree crowns are subject to competitive modification. Among widely spaced open-grown Yukon subalpine spruce trees growing on never-glaciated terrain, a variety of distinctive crown shapes occur in close proximity (Savidge 2012), and narrow- as well as wide-crowned Porsild spruce trees are found growing on open tundra (e.g., Fig. 1T). Thus, if a link exists between crown form and blistered-bark phenotype, it is not obligatory.

Prior to Raup's 1939 Arnold Arboretum expedition, Mr. A. E. Porsild of the Canadian Museum of Nature had himself undertaken extensive botanical exploration within north-western North America. Porsild's taxonomic assistance was acknowledged by Raup (1947) when he first described Porsild spruce and, in view of Porsild and Heimbürger's 1939 annotation of Prof. J.G. Jack's herbarium specimens, it is puzzling why Porsild did not himself publish a description of the bark-blistered spruce phenotype. Garman (1957) later quoted correspondence from Porsild stating that Porsild spruce “obviously is a true Cordilleran race extending from Banff Park along the Mackenzie Valley to its delta and through interior Yukon and Alaska lowlands west at least to Fairbanks.” The Banff, AB, reference was confirmed by Porsild (1959), who noted “clumps of tall *Picea glauca* var. *Porsildii* growing around a rich calcareous bog” on a valley slope a short distance south of Banff. Johnson and Raup (1964) encountered Porsild spruce in southern Yukon along the Alaska Highway between Haines Junction and Pine Creek, and they reiterated the view that Porsild spruce was “only in Yukon, western

Mackenzie, the northern Rocky Mountains, and the eastern interior of Alaska.” Porsild (1975) thought that Porsild spruce “is probably the common race of white spruce in Yukon, dominant in rich soil in lowland situations.” However, *P. glauca* var. *albertiana* is also very common in Yukon (Cody 2000), and it remains uncertain which variety is the more prevalent. More recently, the mapped range of Porsild spruce was extended eastward to the southern Hudson Bay/James Bay region (Riley and Walshe 1985), and Cody (2000) indicated that Porsild spruce occurs “from Keewatin and northern Saskatchewan westward.”

When the Porsild spruce taxon was created (Raup 1947), the forest genetics community had already relegated *P. glauca* var. *albertiana* S Brown (1907), to the status of probable hybrid (Elwes and Henry 1912). That interpretation was based more on presumption than fact, but Porsild spruce became viewed similarly soon after it was named (see Strong and Hills 2006).

Taking into consideration the geographic barrier posed by the Laurentide ice sheet during the Wisconsin glacial period, eastern white spruce trees were considered to represent the only non-hybridized or “true” *ab initio* line of *P. glauca*. But within infraspecific classification, eastern white spruce was elevated to the status of *P. glauca* var. *glauca*. Thus, whether considered merely as “eastern white spruce” or as the only “pure variety” of *P. glauca*, eastern white spruce became the benchmark against which to compare performance of infrageneric hybrid phenotypes. This thinking was inviolate until the present observation of Porsild spruce in southeastern Canada. Whether they are viewed as scaly-barked and smooth blister-barked *P. glauca*, or as *P. glauca* var. *porsildii* and *P. glauca* var. *glauca*, the co-existence of the two phenotypes in southeastern Canada introduces classification difficulty into the conceptual framework.

Porsild Spruce in Southeastern Canada

The tree icons in Fig. 2 indicate the expanded range of Porsild spruce as was determined using a hand-held geographic positioning unit (WGS-84 coordinates) during recent field trips. All southeastern Canada sites indicated on Fig. 2 are based on having observed at least one white spruce tree that displayed smooth bark with one or more resin blisters within which fluid resin was confirmed to be present.

Porsild spruce trees were readily found on the north shore of Prince Edward Island (Fig. 1A–1C), and they were seen at many locations within New Brunswick (Fig. 1D–1J). In Quebec, specimens proved difficult to find, but one Porsild spruce tree was encountered near Saint-Antonin and many more

²Recommendation 60F.1 of the International Code of Botanical Nomenclature (ICBN – McNeill *et al.* 2006) does not support capitalizing infraspecific epithets; thus, *porsildii* rather than *Porsildii* is correct usage. For common reference, Porsild spruce is acceptable.

Fig. 2. Currently established locations of Porsild spruce in Canada, indicated by tree icons. The location of the Porsild spruce holotype (Raup 1947) is indicated by H.

were found in northern New Brunswick a short distance south of the Quebec border (Fig. 1N).

The largest Porsild spruce yet found stands in northeastern New Brunswick (47.4°N, 65.4°W) on ground several km removed from any plantation forest (Fig. 1F–1J). The NB Department of Natural Resources verified that the site had never been subjected to any intervention other than harvesting of hardwood for firewood. In 2012 that tree had the following measurements: 55 cm DBH, 18 m in height, 90% live crown, basal crown diameter 8 m. No flaky bark was present on the grey bark of the trunk (Fig. 1G), on the branches (Fig. 1H) or on the roots (Fig. 1I). Blisters containing liquid resin were present on both trunk and root collar but were difficult to find, dried up blisters with hardened resin inside being more common. No blisters were seen on the tree's smooth-barked branches (Fig. 1H). The non-scaly root collar bark surface is reddish brown and displays closely spaced horizontal bands (Fig. 1I). Mature seeds cones are approximately 6 cm in length, cylindrical with conical ends. Edges of seed scales frequently display a singular pronounced notch near the center of the scale margin (Fig. 1J). Cones of Yukon Beringia Porsild spruce are of similar shape and size, their scales also having a central notch (Figures 1Q, 1V). Twigs of the large NB Porsild spruce are non-pubescent with pronounced sterigmata and needles egressing almost perpendicularly to twigs (Fig. 1F). Needle length varies, some being as short as one cm whereas others exceed two cm. Porsild spruce in Yukon Beringia displays similar variation in needle length.

In Ontario, Porsild spruce roadside saplings were observed to be common near the eastern (Whitney) gate within Algonquin Provincial Park (Figures 1O, 1P). As illustrated in Fig. 1O, scaly-barked and smooth-barked white spruce can be found standing side by side, just as they do on Prince Edward Island (Fig. 1A), in New Brunswick (Fig. 1D) and in primeval Yukon Beringia (Savidge 2012). Larger Porsild spruce specimens were also found in unmanaged forest in the Huntsville and North Bay regions of Ontario. In Algonquin Park, roadside Porsild spruce trees generally display

wide crowns. However, in forested regions of Atlantic Canada, narrow as well as wide-crowned specimens of Porsild spruce have been noted (Figures 1A, 1D).

As far as is known, the east gate region of Algonquin Provincial Park has never been subjected to any white spruce tree-planting activity and, therefore, Porsild spruce specimens near the east gate of Algonquin Provincial Park can be considered as wild white spruce progeny native to that region (J. Yaraskavitch, Ontario Ministry of Natural Resources, personal communication). Recognizing that considerable shuffling of white spruce provenances has occurred throughout Canada in association with tree improvement/nursery stock production and tree planting, additional evidence was sought to alleviate the concern that Porsild spruce phenotypes in unmanaged forests of southeastern Canada today might have originated from seed derived from plantation trees which

themselves originated outside of southeastern Canada. In this respect, it is noteworthy that northwestern provenances of "white spruce" grown in southeastern Canada within provenance trials have in general failed or at best become overshadowed by other provenances (D. Simpson, Natural Resources Canada, personal communication).

Provenance trials in support of tree improvement programs began when outplanting of improved and exotic trees was still in its infancy, and there is no reason to think that the parents of the seeds used in provenance trials were other than part of Canada's unmanaged natural forest. Within this conceptual framework, the interpretation that Porsild spruce is native to eastern Canada was corroborated by examining ~50-year-old trees within range-wide provenance trials in the Acadian Research Forest (ARF – Canadian Forest Service, Experiments 17A, 17B, 19B) a short distance east of Fredericton, NB, where white spruce progeny from 79 North American provenances were planted (Fowler and Coles 1977). More than 3800 trees were examined, and any provenance displaying Porsild spruce bark was duly noted. Many such trees were encountered (e.g., Fig. 1L). Excepting the Ontario and Quebec locations mentioned above, all Ontario and Quebec Porsild spruce locations indicated in Fig. 2 are based on observation of ARF provenance trial trees, the mother trees of which had pre-recorded geographic coordinates. In view of the many range-wide provenance trials of white spruce still in existence, it can be suggested that considerable information about the natural history of Porsild spruce could be had by investigating those trials in greater detail.

Seaside and evidently salt-tolerant specimens of gnarled and probably quite old Porsild spruce were noted along the southeastern Hudson Bay shoreline by Riley and Walshe (1985), and similarly old and deformed trees were observed near the coast at several locations in the Prince Edward Island National Park (e.g., Fig. 1C). At the other topographical extreme, subalpine Porsild spruce trees occur on mountains within both the Mackenzie Mountain Range and in Yukon Beringia (Raup 1947, Savidge 2012). Examples of Porsild spruce in Yukon Beringia are shown in Figures 1Q, 1R, and

1T–1V. The Porsild spruce phenotype also occurs on rich alluvial soils and near calcareous bogs (Porsild 1959, 1975). It is apparent that Porsild spruce can tolerate a broad range of environmental conditions, and it therefore cannot be considered as a specialized ecotype.

Eastern white spruce became the focus of tree improvement and reforestation beginning many decades ago (Griffith 1940, Wright 1955, Roche *et al.* 1969, Fowler and Morgenstern 1990), and no satisfactory explanation can be offered for why Porsild spruce has been overlooked in eastern North America for so long. In wild unmanaged forest, the smooth-barked tree not uncommonly becomes covered with lichens, and perhaps they have been misinterpreted as scales. Up-close visual observation alone is sufficient for identifying the smooth-barked phenotype, but tactile probing of the surface is sometimes needed in order to locate resin blisters.

Porsild Spruce Bark

The smooth and blistered bark surface of Porsild spruce contrasts with the scaly, flaky bark (e.g., Figures 1K, 1S) that develops on other white spruce varieties (*viz.*, *P. glauca* var. *glauca*, var. *albertiana* and var. *densata*) and other spruce species beginning at a young age (Farjon 1990). The only other spruce species described as having bark blisters is *Picea morrisonicola* Hayata (syn: *P. glehnii* Matsum. & Hayata), a tree of Taiwan (Farjon 1990). Superficially, the smooth blistered bark of Porsild spruce is similar to the bark that is characteristically found on sapling trunks of balsam fir (*Abies balsamea* [L.] Mill.) trees. In both, bark blisters may be more or less abundant, sometimes entirely absent on the smooth bark surface. When Porsild spruce and balsam fir are examined carefully it is apparent that blister size and shape, resin colour and odour, and bark colour are quite different. Bark blister formation and resin chemistry/biochemistry remain to be researched in Porsild spruce.

Conifer resins in general consist of a large number of terpenes and terpenoids co-existing in liquid state as water-insoluble lipids. Formation of resin blisters in *Abies* species involves specialized gene expression and enzyme activity in support of biosynthesis and secretion of the terpenes/terpenoids across cell membranes into free space, where they accumulate in large quantity (Zerbe *et al.* 2012). This aspect of tree biochemistry is highly relevant to insect and disease resistance and also has perceived chemotaxonomic value (Franceschi *et al.* 2005, Phillips *et al.* 2006).

On the trunk surface, resin blisters on Porsild spruce are circular to elliptical, varying in longest diameter from a few mm to >10 mm, and in frequency from abundant to scarce (Fig. 1). This applies to both Yukon and eastern Canadian trees. Young Porsild spruce seedlings and saplings of <4 cm DBH rarely display resin blisters. The older needles and peg-like sterigmata on the trunks give young bark a roughened appearance until epidermis, cortical tissue and sterigmata have fallen away. Some older Porsild spruce trees also display no resin-containing resin blisters, rather only solidified remnants of them on the smooth bark surface.

Spruce species in general display smooth bark during their early years, but with ongoing diameter growth the periderm more or less quickly begins to exfoliate as flaky scales in most species (Farjon 1990). Considering trees in general, smooth bark is believed to persist if the original cylindrical periderm

has the ability to remain uncracked in its superficial position, and for some species it is known that uncracked periderm prevails throughout the life of the tree (Borger 1973). Flaky scales originate from discrete “lenses” of underlying periderm, those lenses being more or less bounded by peridermal cracks. Once peridermal lenses have begun to form, the process is said to continue for the life of the tree (Borger 1973). It is tempting to project the existing meager knowledge about bark development to spruce to explain Porsild spruce bark characteristics, but the research has not been done and the underlying explanation for development of the Porsild spruce phenotype remains uncertain.

Anatomical description of inner periderm of “*Picea Canadensis*” (an earlier epithet for “white spruce”) was provided by Thomson and Sifton (1925), but they did not describe the outer barks of the investigated trees. Chang (1954) made observations on “white spruce” scaly bark, and his micrographs show similar anatomy to that figured by Thomson and Sifton (1925).

From first principles of physiology, the environment in which a tree grows could influence the bark phenotype displayed by spruce trees. Research in this realm remains to be done with white spruce, but eastern white pine (*Pinus strobus* L.) underwent its predictable juvenile–mature transition, from smooth to rough bark, somewhat more rapidly when trunks were exposed to sunlight, as opposed to canopy shading (De Zeeuw 1941). Perhaps the difference in transition time observed by De Zeeuw (1941) was due to temperature, hence growth rate differences. In the case of white spruce, scaly-barked and smooth blister-barked trees of similar diameter have been encountered growing side by side, both in densely shaded stands and in sunlight (Figures 1A, 1D, 1O, 1R, 1S).

Some preliminary evidence indicates that light may influence surface colour of Porsild spruce bark. Subalpine open-grown Porsild spruce trees in Yukon Beringia generally display pale pinkish grey to silver white bark (Fig. 1U) whereas those standing in closed-canopy mountain valley stands have darker grey bark (Fig. 1R). Variation in Porsild spruce bark colour between roadside and closed canopy trees was also noted in New Brunswick, roadside trees generally being light grey and interior forest trees darker grey (cf. Figures 1E and 1N). Farjon (1990) noted that a few other mountain species of spruce, *viz.*, *P. breweriana* S. Watson of Oregon/N. California, *P. brachytyla* (Franch.) Pritzl of India/Burma/China and *P. spinulosa* (Griff.) Henry of Himalayas/Bhutan, also display pinkish grey bark. Much remains to be learned about the regulation of Porsild spruce bark development in terms of physiology, morphogenesis, anatomy and chemistry.

Barks of infrageneric hybrids

The bark phenotype of eastern white spruce trees as researched by forest geneticists was never clearly specified. They most likely had flaky scales, but because scaly-barked white spruce and Porsild spruce co-occur in southeastern Canada and have not been consciously distinguished, which trees were actually used in the many subsequent investigations and publications addressing “white spruce” is uncertain. In this context, all that is known is that eastern white spruce (of uncertain bark phenotype) can hybridize with many other spruce species (Wright 1955; Nienstaedt and Teich 1972; Daubenmire 1974; Fowler 1983, 1987).

The ARF supports a variety of infrageneric spruce hybrids, and more than 1100 of them at 36 years of age were examined in 2012. The examined hybrids had been produced by applying pollen of other spruce species (*P. sitchensis*, *P. pungens*, *P. omorika*, *P. engelmannii*) to developing white spruce cones in 1974 and 1975, followed by seed collection, germination of the seeds in 1976, and transplanting into the field at the ARF in 1978 (Fowler 1983, 1987). Of all bark phenotypes examined, none of the *P. glauca* × *engelmannii* hybrids, nor hybrids resulting from pollination by any other spruce species, displayed a smooth blistered bark like that of Porsild spruce. In fact, barks of many of the ARF hybrids were exceptionally scaly (e.g., Fig. 1K). Fortuitously, *P. glauca* × *P. glauca* crosses were also included in that hybridization experiment, and many (but not all) trees of that non-hybridized line displayed the smooth blistered bark of the Porsild spruce phenotype (e.g., Fig. 1M). More observations such as these are needed and would be possible by examining hybridization trials on other sites. However, as a preliminary conclusion the long-standing assumption about a hybrid origin of Porsild spruce appears not to be supported.

Some Speculation about the Scientific Importance of Porsild Spruce

Presently, almost nothing is known about the physiology, genetics, evolutionary history, or even wood and bark properties of Porsild spruce. Nevertheless, the mere presence of Porsild spruce throughout unmanaged regions of southeastern Canada serves to unsettle if not entirely to undermine much of the existing conceptual basis for post-glacial reinstatement of Canada's forests, and it can be foreseen that the overall systematic treatment of North American spruce species could be affected. This is so because *P. glauca* var. *porsildii* Raup has long been assumed—though in the absence of any solid scientific evidence—to have originated within western Canada as a natural *P. glauca* × *engelmannii* hybrid (Little 1953, Wright 1955, LaRoi and Dugle 1968, Roche *et al.* 1969, Morgenstern 1996, Strong and Hills 2006).

Assuming that *P. engelmannii* had always been restricted to western North America and that the Laurentide ice sheet stood for thousands of years as a major geographic barrier between eastern and western Canada, Strong and Hills (2006) made the reasonable further assumption that *P. glauca* × *engelmannii* hybridization never occurred east of longitude 95°W (i.e., near the boundary separating southern Manitoba and Ontario) and, therefore, that morphological features of seed cone scales of eastern white spruce trees represented “pure” *P. glauca* var. *glauca*. As an outcome of their extensively detailed investigation, Strong and Hills (2006) suggested that Porsild spruce should be reclassified as *P. albertiana* ssp. *albertiana* var. *porsildii* (Raup) Strong & Hills. However, the presence of Porsild spruce in forests east of 95°W contradicts the treatment by Strong and Hills (2006), and there clearly is need to revisit the origins and taxonomic treatments of all white spruce varieties if, in fact, that is all that they are.

The confusion attending infraspecific treatment of *Picea glauca* has long polarized the research community, some being inclined to solve the difficulty simply by ignoring varietal taxa (Little 1953, Wright 1955, Nienstaedt and Teich 1972, Bongarten and Hanover 1982). Others have accepted the extra taxonomic complexity introduced by varieties but

would wish it to be better founded (Strong and Hills 2006). In the latter respect, a number of forest scientists have questioned whether *P. engelmannii* should continue to be treated as a species. Garman (1957) considered that “White spruce and Engelmann spruce are two branches of a common stock which was divided by a glacial epoch and brought together again by migration in Recent time.” Taylor (1959) thought that *P. engelmannii* was no more than a subspecies derived from *P. glauca*, and Roche *et al.* (1969) noted “no major discrete morphological, physiological or chemotaxonomic differences between them.” Khalil (1986) described *P. engelmannii* as a *P. glauca* × *sitchensis* hybrid.

North American spruce classification is presently an entangled web rather than an ordered structure. As expressed by Ran *et al.* (2006) concerning the genus *Picea*, “infrageneric classification of the genus remains quite controversial.”

The crucial question at the heart of worldwide *Picea* systematics concerns recognition of the *ab initio* North American spruce phenotype. One plausible scenario for an *ab initio* ancestral spruce tree from which the various presently recognized spruce species may have descended can be formulated from the following considerations. Stockey and Wiebe (2008) described *Picea*-like fossil needles in Early Cretaceous sediments on Vancouver Island, evidence that a tree somewhat similar to today's spruce tree had begun evolving in North America more than 100 million years ago. LePage (2001) described 45 million-year-old spruce fossils on Axel Heiberg Island, evidence that the *Picea* genus was in existence then. After analysis of chloroplast DNA data, Ran *et al.* (2006) proposed that the present world distribution of spruce could be explained in terms of two distinct dispersals of spruce germplasm from northern North America to Asia, via a land bridge that emerges across the Bering Strait as sea level drops during glacial periods.

Porsild spruce trees stand today in Alaska and on remote subalpine landscape in Yukon primeval Beringia (Figures 1Q, 1R, 1T–1V) not far from the Bering Strait. Because that realm of northwestern North America has never been glaciated, it is possible that the ancestors of today's Porsild spruce continually populated the same location over many millions of years. However, palynological studies in subalpine Yukon Beringia to test the latter hypothesis remain to be done. If fossil spruce pollen should be found in the never-glaciated valley bottoms of the mountainous uplands and can be dated to demonstrate ongoing persistence of the trees throughout the distant past, it would become appropriate to ask if trees of primeval Yukon Beringia were the genetic link between the ancient spruce trees that stood in Canada's far north 45 million years ago and the spruce species distributed throughout the world today. The fact that few if any genetic barriers exist to prevent “white spruce” crossing with either European or Siberian species appears to agree with this idea (Wright 1955). Such a scenario, of course, is entirely hypothetical at present, because great gaps in spruce research remain to be addressed.

It also remains to be determined whether Porsild spruce of northwestern North America and Porsild spruce of southeastern Canada are equivalent. Bark of southeastern Canada Porsild spruce appears very similar in every respect to Porsild spruce of never-glaciated valley bottoms within primeval Yukon Beringia (cf. Figures 1E, 1R). On the other hand, as shown in Fig. 1U, Porsild spruce trees in alpine tundra of

Yukon Beringia display barks that are silver white to pinkish grey, strikingly different in colour from those in the valley bottoms.

Canada's two geographic populations of Porsild spruce can be assigned to the identical taxon within ICBN guidelines, but additional research data are needed to decide whether such treatment is truly warranted. Formation of bark blisters and resin accumulation undoubtedly involve many aspects of gene expression (Zerbe *et al.* 2012), but until more information is available it remains possible that scaly-barked and smooth-barked varieties of supposedly "pure" *P. glauca* are merely divergent genetic polymorphs of an evolving species. Or, as suggested above, it may be that the *ab initio* phenotype of *P. glauca* was smooth-barked, and that subsequent evolution into a species such as *P. pungens* or *P. mariana* conferred capability for scaly bark formation. Long ago, the genus *Picea* likely arose through hybridisation of other genera. Continuing investigation can be recommended as a way to decide if the ARF observations are generally relevant.

The probable existence of infrageneric hybrids together with plausible existence of distinct phenotypes from infraspecific crosses within *Picea* elevates classification complexity by at least an order of magnitude. There can be little doubt that a DNA approach such as that reported by Ran *et al.* (2006) will ultimately decide the matter, but molecular genetics investigations into white spruce done already have only begun to set the stage for achieving improved taxonomic resolution (e.g., Tulsieram *et al.* 1992, Sigurgeirsson and Szmidt 1993, Smith and Klein 1994, Gosselin *et al.* 2002, Gupta *et al.* 2005, Nkongolo *et al.* 2005, Rajora *et al.* 2005, Pelgas *et al.* 2006). Individuals within natural "white spruce" populations can present strikingly diverse phenotypes, and during sampling in support of DNA research decisions must be made regarding whether to "force" the diversity of phenotypes into the category "white spruce" or to split them into subgroups based on phenotypic differences. It is conceivable that the forcing done to date has worked against genuine progress in terms of resolving the *ab initio* spruce tree. Difficulty in making lineage sense from DNA data is exacerbated by the fact that primer pairs used with "white spruce" also prime transcription in other spruce species and other genera within Pinaceae (e.g., Hodgetts *et al.* 2001). Sorting of "white spruce" phenotypes into subgroups based on physiological, morphological, anatomical and biochemical differences is certain to facilitate interpretation of DNA data. In terms of managing Canada's forests wisely, both now and for future generations, the pragmatic abilities to sample wild stands with taxonomic resolution and to communicate without ambiguity about our trees should be overriding considerations.

As is apparent in Fig. 2, Porsild spruce remains to be found in Saskatchewan, Manitoba and western Ontario. Perhaps that void will be filled once Porsild spruce phenotypes begin to be sought. However, if that region should prove to be genuinely lacking or even notably deficient in Porsild spruce, that difference could be interpreted in relation to geographic barrier effects of the Wisconsinan glacial period (Löve 1959). Such a finding would raise the possibility that Porsild spruce populations in southeastern and northwestern Canada are remnants of a primeval spruce forest that spanned all of Canada prior to the last ice age and then became distantly separated due to the extended persistence of the Laurentide

Ice Sheet followed by glacial Lake Agassiz. Field foresters can answer this question in short order, and it would be helpful to the future of Canadian forestry if any Porsild spruce encounter in unmanaged forest is documented by geographic coordinates.

Summary

Porsild spruce is present and widely distributed in southeastern as well as northwestern Canada and, consequently, the assumption that Porsild spruce is a *Picea glauca* × *engelmannii* hybrid is in question. Porsild spruce displays unequivocally diagnostic bark features and is a major and, presumably, very ancient component within the refugium of never-glaciated Yukon Beringia. As such, Porsild spruce offers exceptional opportunity to improve taxonomic definition and identify species ancestries and infrageneric relationships within *Picea* of North America.

Porsild spruce has been overlooked in forestry research and a great deal remains to be discovered about it. Field foresters can make valuable contributions to Canadian forest science by noting any presence of Porsild spruce in unmanaged forests, particularly in the region spanning from eastern Alberta to western Ontario. Scientific forest management is effective only insofar as forest phenomena are clearly resolved and defined, and with ongoing research the discovery of Porsild spruce in southeastern Canada has the potential to change Canadian forestry for the better.

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