

## Taxonomic Status of the East Asian *Pyrola faurieana* (Ericaceae)

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### 東アジア産カラフトイチャクソウの分類

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The east Asian species *Pyrola faurieana* was investigated to clarify its taxonomic distinction from the circumboreal *P. minor*, the Eurasian allotetraploid *P. media* and the North American hybrid *P. asarifolia* × *P. minor*, with which it has been confused, and to evaluate its possible hybrid origin. In its overall morphology, *P. faurieana* is most similar to the hybrid *P. asarifolia* × *P. minor*, but is distinguished by its more floriferous scapes, shorter bracts and higher sepal length/width ratio, its variable production of viable pollen, seemingly normal seeds and distinctive leaf flavonol markers. *Pyrola faurieana* has the same leaf flavonol pattern as *P. media* and is similar to it in pollen and seed morphology, but differs in being diploid, smaller in stature and in having distinctively smaller anthers, generally more flowers, shorter petals and a smaller bract length/width ratio. *P. faurieana* is recognized as a distinct species of hybrid origin with *P. minor* being one of the parents. The second parent is suspected of being the Asian vicariad of *P. asarifolia*, namely, subsp. *incarnata* (DC.) Haber et Takahashi. The first report of chromosome numbers for *P. faurieana* is documented as  $2n=46$ .

### Introduction

Andres (1912) first described *Pyrola faurieana* on the basis of a collection by Faurie made at Korsakof, Sakhalin Is. Its specific status has been questioned, however, and the taxon confused with *P. minor* L. Both *P. faurieana* and *P. minor* were recognized by Hara (1938, 1948) and distinguished on the basis of style, anther, and sepal lengths, and sepal and stigma shapes. Some authors of recent Japanese floras have maintained the distinction of

the two taxa (Kitamura et al. 1978, Yamazaki 1981), but others only recognize *P. faurieana* in Japan (Ohwi 1965, 1983).

*Pyrola faurieana* is also morphologically similar to the North American hybrid *P. asarifolia* × *P. minor* (Haber 1984) and to the Eurasian *P. media* Sw., a presumed amphidiploid ( $2n=92$ ) between the circumboreal *P. minor* and the Eurasian *P. rotundifolia* L. (Hagerup 1941).

A comparative study of *P. faurieana*, *P. media*,

*P. asarifolia* × *P. minor*, and *P. minor* was undertaken to clarify the taxonomic status of *P. faurieana*, especially with regard to its possible hybrid origin. As part of the evaluation of taxonomic status for this taxon, measurements of a number of morphological features were made and analyzed statistically. Pollen stainability and abnormality were examined and seed set determined in *P. faurieana* were compared with the other taxa. Chromosome counts were made to determine ploidy level for *P. faurieana*. Distributional ranges and habitat preferences of the four taxa were also reviewed. The possible relationship of *P. asarifolia* Michaux subsp. *incarnata* (DC.) Haber et Takahashi to *P. faurieana* was also examined.

#### Materials and methods

Specimens from the following herbaria were used for compiling measurement data, distributional information and as sources of leaf material for flavonol pattern analysis: BG, C, CAN, DAO, GB, GH, KANA, KYO, MAK, S, SAPT, TI, TNS, TUS, UPS, Herbarium Ibaraki Univ., Kurashiki Museum of Natural History, and the Faculty of Agriculture of Kyushu University. Abbreviations follow the latest Index Herbariorum; for SAPT, see "News and notes" in *Taxon* 32: 703 (1983).

Statistical data for the means of 11 morphological characters examined in this study were compiled and summarized graphically. A significant difference was inferred in the character means of two taxa being compared when the confidence intervals represented by twice the standard deviation of the mean on either side of the character means did not overlap (Hubbs and Hubbs 1953). Where an overlap was evident, the significance of the sample variances was judged by comparing the calculated F statistics with published values at the .05 level of significance.

A cluster analysis (average linkage) of morphological characters for 77 specimens of *P. faurieana* was performed (with missing data for some specimens) to determine if any geographic differentiation was evident between the more northern Kamchatka specimens (those closest to the range of the morphologically similar *P. asarifolia* × *P. minor*) and those further south, especially on Hokkaido and adjacent islands. As well, data sets for *P. faurieana* and *P. asarifolia* × *P. minor* were combined (108 specimens, total) and analyzed to determine whether any distinctive clustering and separation of specimens could be found. Statistical analyses were performed on a personal computer using commercial software from Systat Inc. (Evanston, IL).

In *Pyrola*, as in the majority of the Ericaceae, the four pollen grains derived from the same pollen mother cell are retained as a pollen tetrad at maturity. Pollen tetrad diameters and concurrent colpi lengths reported in a previous work (Takahashi 1986) for three of the four taxa under study here, excluding *P. asarifolia* × *P. minor*, were evaluated in the context of the present study. Pollen stainability was determined by the toluidine blue-lactophenol method (Radford et al. 1974). Pollen was also compared with the North American and Asian subspecies of *P. asarifolia*.

Overall seed lengths and numbers of testa cells were determined under a light microscope for samples of 20 seeds of *P. faurieana* (6 samples), *P. media* (3) and *P. minor* (10). Seeds were scattered on glass slides and sealed under a cover glass with paraffin.

Chromosome counts were made using rhizome tips and flower buds of *P. faurieana* fixed in acetic-alcohol (3:1) and stored in 70% ethanol. Rhizome tips were treated apart in aceto-carmine, squashed under a cover slip, and heated briefly under a flame, or were softened by heating for one hour

at 37°C in 1 N HCl, then squashed. Young anthers were dissected from flower buds of about 2 mm diameter and teased apart in aceto-carmin to free pollen mother cells. Slides were briefly heated and cells squashed under the cover slip. Chromosomes were counted under oil immersion with the aid of a camera lucida drawing tube. Collections yielding counts are cited in the Appendix.

The two-dimensional paper chromatographic techniques used in determining the leaf flavonol patterns of herbarium specimens were those described by Haber (1983). As in previous studies, only the ultra-violet-quenching compounds (appearing black under U.V.), which serve as consistent and useful markers, were assessed. The similarity in flavonol spot patterns was judged on the basis of the average  $R_f$  values of the compounds as well as their relative positions and concentrations. Spot numbering in the patterns is complementary to that in earlier publications (e.g., Haber and Takahashi 1988). Chromatographed specimens of *P. faurieana*, *P. minor*, *P. media* and *P. asarifolia* × *P. minor* are cited in the Appendix.

The distributional ranges for the four taxa under consideration are based on published data (Haber 1985, Hultén 1930) and on herbarium collections. About 800 and 600 specimens, respectively, were measured for *P. minor* and *P. media* for 11 selected characters (see Table 1). For the geographically restricted *P. faurieana*, 77 specimens were available and only 31 for the sporadically occurring North American hybrid *P. asarifolia* × *P. minor*.

## Results

**Morphological analyses** The statistical data summary, as compiled in Table 1 and graphically portrayed in Figure 1, shows clearly that *P. media* is overall the tallest and most robust of the four taxa compared. It has the tallest scapes, longest

and widest leaves and longest sepals, petals, anthers and style. *Pyrola minor*, in contrast, is significantly the smallest in blade width, bract length and width, sepal length, petal length, anther length and style length.

Of the two taxa with which *P. faurieana* can be most readily confused, *P. media* and *P. asarifolia* × *P. minor*, it is most similar to the latter. The statistical summaries of the character means analyzed (Fig. 1) show no significant differences in the sample means of *P. faurieana* and *P. asarifolia* × *P. minor* in six of the 11 characters (scape height, blade length and width, bract width, sepal length and style length). On the other hand, all eleven character means are significantly different between *P. faurieana* and *P. media*. The means for only two characters (petal length and anther length) are significantly distinct for all four taxa. In absolute measurement values, however, there is a broad range in overlap of most characters so that one must rely on a combination of character measurements as well as other evidence to delimit the taxa. Some qualitative differences in shapes are evident, as in the narrower bracts of *P. media* and *P. minor*, as judged by the length/width ratio (l/w) of 3.1 for these taxa as compared with those of 2.3 and 2.6 respectively for *P. faurieana* and *P. asarifolia* × *P. minor*.

The cluster analysis of *P. faurieana* from Japan, the adjacent islands and Kamchatka resulted in a uniform spread of the Kamchatka specimens (previously treated as *P. media* by Hultén 1930) throughout the various subclusters. No grouping by geographical origin of specimens (i.e., Honshu, Hokkaido, Sakhalin Is., Kurile Islands and Kamchatka) was evident.

The cluster analysis of the combined data sets for *P. faurieana* and the North American hybrid *P. asarifolia* × *P. minor* resulted in a relatively intact separation of the North American hybrid

Table 1. Summary of statistical data for eleven morphological characters in three species and one hybrid of *Pyrola*.

	<i>P. media</i>				<i>P. faurieana</i>				<i>P. minor</i>				<i>P. asarifolia</i> × <i>P. minor</i>			
	N	$\bar{x}$	s	$s_m$	N	$\bar{x}$	s	$s_m$	N	$\bar{x}$	s	$s_m$	N	$\bar{x}$	s	$s_m$
Scape height (cm)	580	22.15	4.28	0.18	74	17.49	3.69	0.43	808	16.18	4.17	0.15	31	16.43	2.89	0.52
Blade length (cm)	583	4.04	0.68	0.03	75	2.93	0.53	0.06	805	3.03	0.76	0.03	31	2.84	0.43	0.08
Blade width (cm)	583	3.59	0.66	0.03	75	2.67	0.46	0.05	805	2.38	0.57	0.02	31	2.62	0.43	0.08
Number of flowers	580	9.55	3.03	0.13	77	10.46	3.19	0.36	808	11.28	3.60	0.13	31	7.03	2.24	0.40
Bract length* (mm)	247	5.50	0.96	0.06	60	4.81	0.80	0.10	323	4.41	0.91	0.05	31	5.74	0.68	0.12
Bract width* (mm)	199	1.79	0.32	0.02	44	2.11	0.44	0.07	293	1.42	0.49	0.03	24	2.21	0.54	0.11
Sepal length (mm)	449	2.34	0.33	0.02	71	2.02	0.26	0.03	744	1.39	0.24	0.01	31	2.00	0.16	0.03
Sepal width (mm)	449	1.68	0.20	0.01	71	1.61	0.18	0.02	744	1.56	0.22	0.01	31	1.90	0.11	0.02
Petal length (mm)	214	6.30	0.62	0.04	57	5.13	0.62	0.08	363	4.32	0.54	0.03	26	5.55	0.49	0.01
Anther length (mm)	472	1.96	0.21	0.01	68	1.64	0.15	0.02	697	1.05	0.11	0.004	31	1.52	0.20	0.04
Style length (mm)	352	4.91	0.79	0.04	66	3.67	0.63	0.08	479	1.49	0.33	0.02	31	3.92	0.67	0.12

Note: Leaf measurements were made on largest leaf, and floral measurements on lowest, most mature flower; N, sample size;  $\bar{x}$ , mean; s, standard deviation;  $s_m$ , standard deviation of the mean; \*bract measurements are those of the inflorescence bracts.

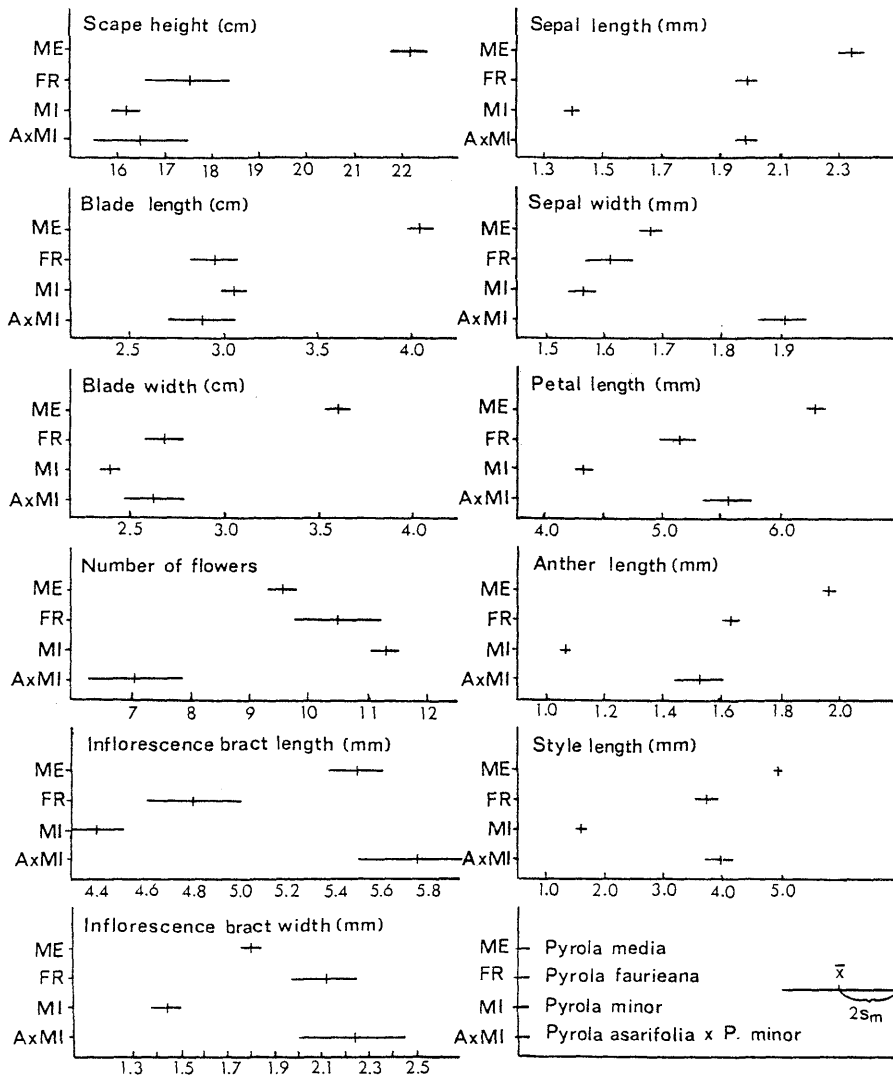


Fig. 1. Graphical comparisons of 11 character means for four *Pyrola* taxa. Horizontal lines represent  $2 \times$  the standard deviation of the mean on either side of the means.

specimens as several interconnected cluster groups. Five out of the 31 hybrid specimens available linked with adjacent *P. faurieana* clusters. Of the 77 *P. faurieana* specimens in the analysis, three were included within the hybrid cluster groupings. Two of these three specimens were from Kamchatka, a geographical region adjacent to the western limit of the range of the North American hybrid in the Aleutian Islands (see Haber 1984).

*Pyrola faurieana* specimens formed several larger interconnected cluster subsets. Out of a total of 108 specimens in the cluster analysis, a total of 8, or about 7% of the combined sample were "incorrectly" aligned with specimens of the other taxon.

Although the similarity between *P. faurieana* and *P. asarifolia*  $\times$  *P. minor* is evident on general inspection of specimens and in the lack of significant differences in the means of six characters, the

cluster analysis indicates that the specimens of the two taxa do exhibit sufficient differences overall that they tend to associate as separate cluster sets. This no doubt reflects the significant differences in the means for number of flowers, bract length, sepal width, petal length and anther length evident in Figure 1.

*Pollen tetrad diameters and stainability* The presence of some genetic irregularity is evident in the holotype of *P. fauriana* and in other representative specimens. Tetrads in the holotype are imperfectly formed and partly shrivelled with many exhibiting a loose tetrahedral arrangement of the four grains. The large tetrads are about  $42\ \mu\text{m}$  in diameter and tend to stain light blue, unlike the deep blue stain characteristic of normal plump tetrads in other species. Large empty and small shrivelled tetrads are also present. Specimens of

this taxon from Japan, Sakhalin Is. and the Kurile Islands have a diameter range of  $36\text{--}46$  ( $57\ \mu\text{m}$  and a mean of  $42\ \mu\text{m}$  (based on values in Table 1 of Takahashi (1986) and additional measurements by Haber). The occasional collection contains up to 10% giant dyads. In the taxon as a whole, most tetrads tend to be somewhat shrivelled and only take on a medium blue stain in lactophenol and aniline blue. About 50% or more of the tetrads in some collections are highly shrivelled and presumed abortive.

Two collections at SAPT from Mt. Makkari-nupuri (Nishida 21 Aug 1906 and Konishi 28 Aug 1922) identified as *P. fauriana* had completely abortive pollen. However, two other collections from the same mountain (13 Aug 1986, Takahashi 6662 and 6664, SAPT) had only the more typically incompletely expanded, somewhat shrivelled

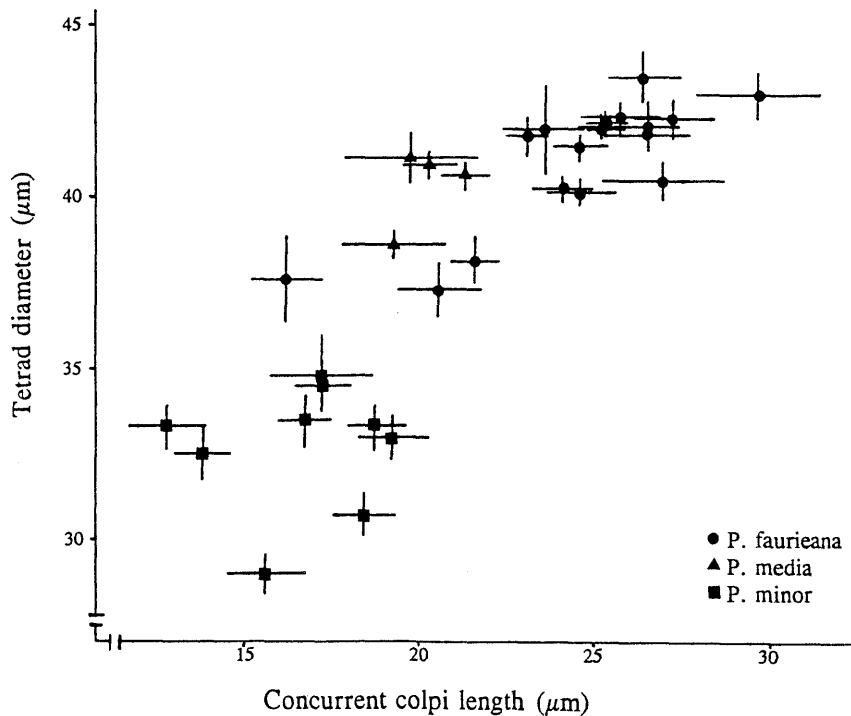


Fig. 2. Bivariate plot of sample means and their confidence limits ( $2 \times$  standard deviation of the mean on either side of the means) for concurrent colpi length and pollen tetrad diameter in three *Pyrola* taxa.

appearance commonly seen in pollen of *P. faurieana*. A somewhat similar set of observations was noted for nearby sites in the Shiretoko Peninsula, Hokkaido. A collection from Mt. Okkapake made by Takahashi and Kushibiki 5164 (SAPT), had highly abortive pollen, yet a second collection by Takahashi & Kushibiki 5157 (CAN), from Futatsu-like several hundred meters away, had mostly well-stained pollen tetrads, but the grains tended to be somewhat collapsed and the tetrads not always clearly tetrahedral in form.

Pollen tetrads in *P. media* range in size from 37–43  $\mu\text{m}$  with a mean of about 41  $\mu\text{m}$ . Data published by Takahashi (1986, Table 1) for this species and additional collections examined for the present study by Haber (citations in Appendix) indicate that pollen stainability, and presumably viability, varies considerably. Most collections of *P. media* have relatively large tetrads, but these generally tend to be shrivelled to various degrees. Estimating the proportion of grains that might be considered to be relatively normal in their appearance and stainability is difficult here, as in *P. faurieana*, because of gradation between tetrads that are somewhat collapsed, but more or less well stained, and those that are progressively more collapsed, empty or weakly stained. Knaben (1944) estimated that pollen viability was reduced to about 23%. A collection such as that made by H. Andres in Germany (Köln, Aug. 1929, CAN) has darkly stained and mainly fully expanded tetrads, yet even here particularly large, 4-celled tetrads, about 45  $\mu\text{m}$  in diameter, are present and in non-tetrahedral formation. In a British collection (Ambleside, 24 Jun. 1869, CAN) in which the tetrads stain dark blue, and are of normal size, most tetrads are highly shrivelled. Age of pollen samples may affect the ability to rehydrate, but the collapsed nature of tetrads, even after rehydration in stain for over a year, is more likely a reflection of the genetic

disorder present in the species. This genetic disorder may also be seen in some specimens of *P. media* that not only have malformed and poorly stained tetrads but also have other floral abnormalities. A collection of *P. media* from the USSR, chromatographed for the present study (Province Orel, 1 Jul. 1906, CAN), is abnormal in having a flowering branch in the lower part of the raceme in addition to having abnormal tetrads that are poorly stained.

*Pyrola minor*, in contrast to the three other taxa, has deeply stained, fully expanded tetrads within 24 hours. These range in size from 27–39  $\mu\text{m}$  with a mean of 33  $\mu\text{m}$ . Tetrads of *P. asarifolia*  $\times$  *P. minor* are highly malformed with collapsed walls and are stained weakly. The larger somewhat collapsed tetrads tend to be 36–38  $\mu\text{m}$  in diameter, also stain weakly and are considered non-viable. Even after five years in stain, the grain contents remain weakly stained, although some of the larger tetrads have grains with expanded walls, a high proportion of malformed tetrads remain.

Pollen tetrad diameters are not significantly different between *P. faurieana* ( $\bar{x} = 42 \mu\text{m}$ ) and *P. media* ( $\bar{x} = 41 \mu\text{m}$ ), and both have larger diameters than those of *P. minor* ( $\bar{x} = 33 \mu\text{m}$ , Fig. 2). *Pyrola faurieana* tetrads are significantly larger than the highly shrivelled and abortive tetrads of the North American hybrid *P. asarifolia*  $\times$  *P. minor*. The highly abortive pollen of the Okkapake collection of *P. faurieana*, (Takahashi and Kushibiki 5164), has a mean diameter of about 39  $\mu\text{m}$ , for the more fully formed tetrads, with a broad range in diameters being present. Although there is a broad overlap in the absolute lengths of concurrent colpi in *P. faurieana* ( $\bar{x} = 25 \mu\text{m}$ ), *P. media* ( $\bar{x} = 20 \mu\text{m}$ ) and *P. minor* ( $\bar{x} = 17 \mu\text{m}$ ), a small but significant statistical difference exists in the means (Fig. 2). Exine sculpturing in *P. faurieana*, *P. media* and *P. minor* is verrucate (Takahashi 1986).

Table 2. Summary of statistical data for two seed characters of three species of *Pyrola*.

Sample	Seed length (mm)			Testa cell number			
		$\bar{x}$	s	$s_m$	$\bar{x}$	s	$s_m$
<i>P. faurieana</i>	1	0.71	0.07	0.03	7.25	0.79	0.35
	2	0.69	0.05	0.02	7.35	0.75	0.34
	3	0.64	0.05	0.02	7.60	0.75	0.34
	4	0.67	0.04	0.02	7.20	0.95	0.42
	5	0.64	0.05	0.02	7.30	1.08	0.48
	6	0.56	0.05	0.02	7.00	0.92	0.41
<i>P. media</i>	1	0.73	0.06	0.03	6.85	1.14	0.51
	2	0.68	0.05	0.02	7.30	1.22	0.55
	3	0.69	0.05	0.02	7.15	1.18	0.53
<i>P. minor</i>	1	0.44	0.05	0.02	7.30	1.30	0.58
	2	0.55	0.05	0.02	7.80	0.89	0.40
	3	0.65	0.05	0.02	9.25	1.33	0.59
	4	0.62	0.04	0.02	8.80	0.95	0.42
	5	0.48	0.03	0.01	7.60	1.10	0.49
	6	0.63	0.05	0.02	8.70	1.53	0.68
	7	0.68	0.04	0.02	8.85	1.35	0.65
	8	0.64	0.06	0.03	8.35	1.09	0.49
	9	0.59	0.05	0.02	9.35	1.09	0.49
	10	0.60	0.05	0.02	8.80	1.11	0.50

*Seed set and size* *Pyrola* seeds are minute, consisting of a small nodule of cells comprising the undifferentiated embryo, centered within an elongate, thin-walled testa. A bivariate graph of testa cell number and seed length of *P. media*, *P. faurieana* and *P. minor*, based on values in Table 2, is given in Fig. 3. There are no sharp distinctions in seed size among the three taxa, although *P. media* and *P. faurieana* tend to have somewhat larger seeds than those of *P. minor*. They also tend to have fewer testa cells per length than *P. minor*. *Pyrola minor*, in contrast, has a broader range in seed length and testa cell numbers, with increased seed length being correlated with increased testa cell number. Capsules of *P. asarifolia* × *P. minor* bear only aborted ovules, a reflection of the highly abortive pollen produced by the hybrid.

*Chromosome counts* Diploid counts of approximately 40 chromosomes were made for *P.*

*faurieana* from 11 metaphase plates in rhizome tips of collections by Takahashi (5249) and Takahashi and Kushibiki (5157). A haploid number of about 23 chromosomes was counted in 12 plates of a collection of the same taxon made by Takahashi and Uematsu 8504 at Hamatonbetsu, 12 Jun. 1988. Perhaps partly because the preserved material was several years old, chromosome separation and staining was not optimal. Chromosome sizes ranged between 2.5–5.0  $\mu\text{m}$  long.

Although chromosome counts were not individually conclusive, they were consistent in magnitude and sufficient in number of counts to indicate that the diploid number is probably  $2n=46$ , the same as has generally been reported in other diploid species of the genus. This is also supported by the haploid counts. One somatic plate was seen that may have had a tetraploid number.



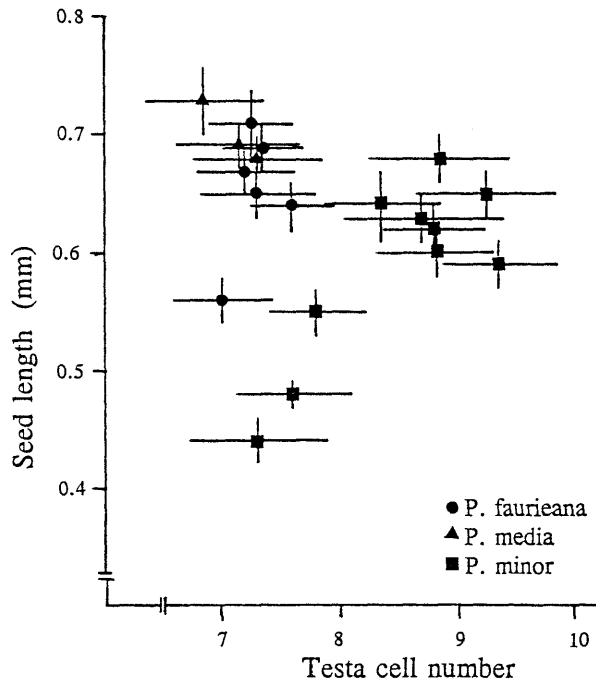


Fig. 3. Bivariate plot of sample means and their confidence limits ( $2 \times$  standard deviation of the mean on either side of the means) for seed testa cell number and seed length in three *Pyrola* taxa.

#### Chromatographic patterns of leaf flavonols

The 2-dimensional chromatographic patterns of leaf flavonols for *P. faurieana* and the three other taxa with which it was compared are given in Fig. 4. Based on the previous work with other species of *Pyrola* (Haber 1983), these UV-quenching flavonols are all glycosides of quercetin (#1–5, 8) and kaempferol (#6).

The flavonol pattern of *Pyrola faurieana* is identical to that of *P. media*. *Pyrola faurieana* differs from the North American hybrid *P. asarifolia*  $\times$  *P. minor* by having a pair of overlapping glycosides (#5 and #8) and in lacking glycoside #1 of the hybrid. The absence of flavonol #5 in *P. asarifolia*  $\times$  *P. minor* is unusual because it is present in both of its parents. A second flavonol (#3), found in *P. asarifolia* (see Haber 1983) is also absent. This hybrid seemingly lacks the full complement of parental flavonols. *Pyrola faurieana* differs from *P. minor* in lacking flavonol

#1 and in having #8.

Collections of *P. faurieana* with pollen that was highly abortive (Konishi, 28 Aug. 1922; Nishida, 21 Aug 1906; Takahashi and Kushibiki 5164, and Yoshimura and Yokoyama 5 Aug 1938) did not differ from the flavonol pattern present in collections with more normal levels of pollen viability. Similarly, the holotype, with its highly collapsed pollen, also did not show any deviation in its flavonol pattern from that of other specimens of this taxon with higher levels of nearly normal pollen.

*Distribution* The worldwide distributions for *P. media*, *P. minor*, *P. faurieana* and *P. asarifolia*  $\times$  *P. minor* are given in Fig. 5. *Pyrola minor* is a widespread circumboreal species, found primarily in mossy coniferous forests but also in mixed woodland sites and deciduous forests in northern Sweden and Japan. It is found over a wide elevational range from near sea level to alpine

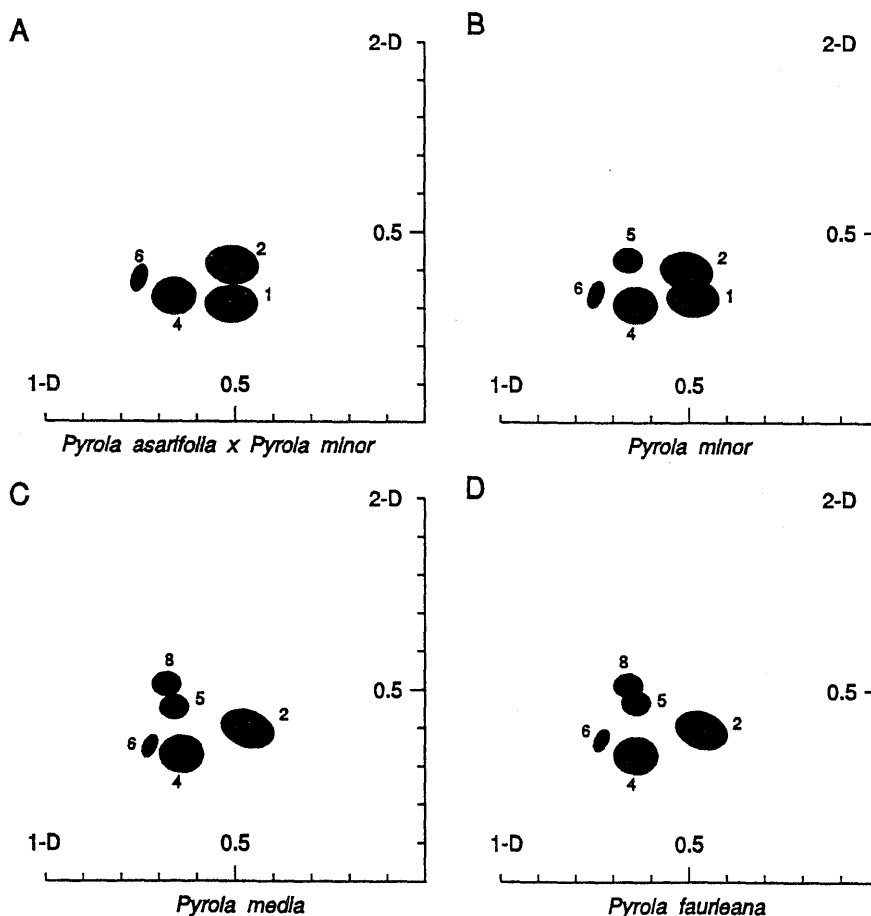


Fig. 4. Two-dimensional chromatographic patterns of UV-quenching leaf flavonols in four *Pyrola* taxa.

meadows. In the more southerly extensions of its range in the Rocky Mountains of Colorado, it reaches elevations of 3600 m and in SE Tibet 4000 m. *Pyrola minor* is rare in northern Japan.

*Pyrola media* is Eurasian with a relatively scattered distribution within its overall broad range. Like *P. minor*, its preferred habitats are mossy coniferous woodlands. It occurs near sea level but is more commonly found in mountainous terrain reaching the upper subalpine meadows. In the Caucasus Mountains, it reaches alpine meadows at about 2800 m. *Pyrola media* extends eastwards in Siberia to about Lake Baikal.

*Pyrola faurleana* has a relatively restricted total

range. It occurs most commonly in Japan (northern Honshu and Hokkaido). However, it is sporadic and considered rare. Northward it is found on Sakhalin Is., where the type was collected, on the Kuriles, southern Kamchatka and Bering Is. It is a plant of higher elevations, occurring in the *Pinus pumila* (Pall.) Regel scrub zone and alpine meadows in northern Japan, associated with such species as *Empetrum nigrum* L. and *Tilingia ajanensis* Regel. Occasionally it is found with *P. minor* and *P. alpina* H. Andres.

Specific site localities for the North American hybrid *P. asarifolia* × *P. minor*, as plotted in Figure 5, have been updated from those first published

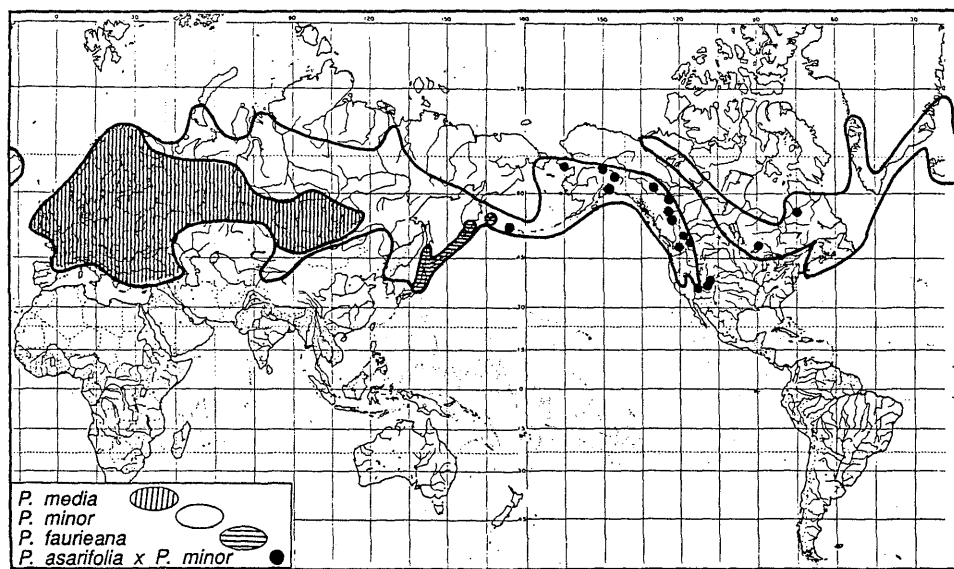


Fig. 5. Worldwide distributions of the four *Pyrola* taxa studied.

by Haber (1984). Three new records are included for Alberta, Colorado and Utah. One record for Colorado plotted by Haber (1984) but not cited in that publication is also cited in the Appendix. This hybrid has been regularly collected with one or both of its parental species.

The distributional ranges of *P. faurieana* and *P. asarifolia* × *P. minor* are virtually contiguous, meeting at the western end of the Aleutian Islands (Attu Is.) and the Commander Islands off the east coast of Kamchatka.

#### Discussion and taxonomic conclusions

Of the four taxa compared in the present study, *P. minor* has the most distinct morphology. It tends to be the smallest of the four, both vegetatively and in its floral features. It is readily differentiated by its small, white to pink-tinged, drooping, actinomorphic flowers that possess a short, straight insert style. Its stigma consists of five radially arched crests that become everted from within the stylar tip as the outer tissue of the tip reflexes on maturation. The stigmatic crests in

other species of *Pyrola*, including those in this study, are short, erect or spreading cylindrical lobes projecting beyond the reflexed stylar tissue that forms a collar below the lobes (see Haber 1984). The short, 1 mm long, anther sacs of *P. minor*, with their truncated ends terminating in large pores the width of the sacs and the relatively slender filaments are also distinctive features of the species. *Pyrola minor* is a diploid species ( $2n=46$ ) with highly fertile, well-stained and developed pollen tetrads.

At the other extreme is *P. media*, a tetraploid ( $2n=92$ ), and in most features, the largest of the four taxa. Its white, occasionally pink-tinged, globular flowers have a slightly exsert, straight to somewhat declinate style. The comparatively large anther sacs, mainly about 2 mm long and with relatively large pores, serve as the most characteristic morphological feature, together with the generally robust size, distinguishing this species from the others under consideration. Its pollen tetrads are substantially larger than those of *P. minor* and vary considerably in their stainability

and degree of collapse of grains.

*Pyrola faurieana* is similar in size and morphology to the North American hybrid *P. asarifolia* × *P. minor*. The two are alike in general habit, their pink-tinged globular flowers and possession of attributes that are associated with hybrids in which *P. minor* is one of the parents. These attributes include, most specifically, styles that are slightly exsert and straight, or nearly so, and anthers that have large pores the full width of the truncated or only slightly elongated ends of the sacs (see illustrations in Haber 1984, 1987). Hybrid specimens with such styles and anthers invariably have high levels of pollen irregularity and poor staining. In sterile hybrids, common abnormalities such as split styles or bifid sepal apices or floral branches in the raceme are also found.

The possibility of a hybrid origin for *P. faurieana* has never been suggested, although Takahashi (1986) had indicated the presence of high levels of incomplete expansion of tetrads in most collections and in some cases up to 10% giant dyad formation. Additional examination of pollen for the present study has confirmed this, and as well, several collections with completely abortive pollen were found.

We conclude that *P. faurieana* is of hybrid origin with *P. minor* being one of the parents. Unlike the completely sterile hybrid *P. asarifolia* × *P. minor*, *P. faurieana* has reduced and variable pollen viability but produces seemingly normal seeds. As past attempts to propagate plants from *Pyrola* seeds have not been successful (Christoph 1921, Lihnell 1942), the viability of *P. faurieana* seeds is difficult to establish.

In view of the morphological similarity of *P. faurieana* to *P. asarifolia* × *P. minor* and the contiguous nature of their ranges, the second parent of *P. faurieana* is suspected of being the Asian vicariad of *P. asarifolia*, namely, subsp.

*incarnata* (DC.) Haber et Takahashi. This subspecies of *P. asarifolia* is found in northern Japan, the Kuriles, central Kamchatka and eastern continental Asia (see Fig. 1, Haber and Takahashi 1988) and overlaps the ranges of both *P. minor* and *P. faurieana*. However, subsp. *incarnata* presently tends to occur in northern Japan only at lower elevations in broad-leaved deciduous forests and open *Larix* forests. Both *P. asarifolia* subsp. *incarnata* and *P. minor* may be found in closer proximity in the Kuriles and Kamchatka. Subspecies *asarifolia* and subsp. *incarnata* differ primarily in the narrower sepals of subsp. *incarnata* and in the leaf flavonol pattern of this subspecies that resembles more closely that of the Eurasian *P. rotundifolia* (Haber and Takahashi 1988). *Pyrola faurieana*, like *P. asarifolia* subsp. *incarnata*, has a sepal width mean that is significantly narrower than that of *P. asarifolia* × *P. minor*.

*Pyrola faurieana* is also similar to *P. media* in general morphology and flavonol pattern. However, this is interpreted to be a reflection of its past origin as yet another hybrid with *P. minor* as one of its parents. The similar size of pollen tetrads in these two taxa argues against their being different ploidal variants of the same taxon. *Pyrola faurieana* is maintained here as a distinct species of hybrid origin with *P. minor* as one of its parents. It is morphologically most similar to *Pyrola asarifolia* × *P. minor*, produces seemingly normal seeds, and has reduced pollen viability.

*Diagnostic key and synoptic comparison of the four taxa studied* Measurement ranges are not absolute minimum/maximum values but represent values for about 70% of specimens as determined by the means +/– the standard deviation.

1 Style insert, straight, about 1.5 mm long, stigma peltate with 5 radially spread ridges; anthers mainly about 1 mm long and plump, ends of

- sacs without tubes, truncate and open at dehiscence; pollen highly fertile, tetrad diameter about  $33\ \mu\text{m}$ ;  $2n=46$  . . . . . *P. minor*
- 1' Style exsert, straight to somewhat declinate, averaging 3–6 mm long, stigma of 5 erect to divergent cylindrical lobes projecting from a reflexed collar, anthers mainly over 1.5 mm long and elongate, sacs constricted at ends into short tubes with conspicuous pores; pollen with variable viability, tetrad diameter over  $36\ \mu\text{m}$  . . . . . 2
- 2 Anthers mainly 1.8–2.2 mm long; petals 5.5–7.0 mm long; inflorescence bracts 1.5–2 mm wide; pollen only about 30% normal, tetrad diameter averaging  $41\ \mu\text{m}$ ; plants mainly 18–26 cm tall;  $2n=92$  . . . . . *P. media*
- 2' Anthers mainly 1.3–1.8 mm long; petals 4.5–6.0 mm long; inflorescence bracts 1.7–2.7 mm wide; pollen viability variable, tetrad diameter variable;  $2n=46$  . . . . . 3
- 3 Sepals mainly 1.8–2.0 mm wide; pollen sterile with tetrads highly malformed, largest tetrads about  $36\text{--}38\ \mu\text{m}$  in diameter;  $2n=46(?)$  . . . . . *P. asarifolia* × *P. minor*
- 3' Sepals mainly 1.4–1.8 mm wide; pollen generally with perhaps 50% nearly normal tetrads, diameter variable,  $36\text{--}46$  ( $56$ )  $\mu\text{m}$ , average about  $42\ \mu\text{m}$ ;  $2n=46$  . . . . . *P. fauriana*

The following is an updated description of *P. fauriana*.

***Pyrola fauriana*** H. Andres, Verhandl. Bot. Ver. Prov. Brandenburg 54: 218–227 (1912) – *Pyrola yezoensis* (in sched.) – *P. minor* L. sensu some Jap. authors. – TYPE: Sakhalin Is., Korsakof, Faurie 611 (holotype: E!)

Perennial, scapose, evergreen herb, clonal from spreading rhizomes. Leaves several, approximate,

forming basal rosette representing 1–several years growth; petioles commonly shorter or subequal to blades, occasionally longer; blades ovate to elliptic, or orbicular, occasionally obovate, 1–4.5 cm long, 1.5–4.5 cm wide; apex rounded or mucronulate; base rounded or shallowly cordate and commonly abruptly decurrent; margins entire to crenulate. Scapes 10–26 cm tall, with several ovate bud scales at base and 1–several scales below raceme. Raceme symmetric, 4–18-flowered; bracts ovate, 3–7 mm long, 1–3 mm wide, commonly longer than pedicels. Flowers, globular, radially symmetric, drooping, white to pink, 6–8 mm across. Sepals elliptic to broadly ovate, 1.5–2.5 mm long, 1.3–2.0 mm wide; apex blunt to subacute; bases generally overlapping; margins entire to erose. Petals 4–7 mm long, 3.3–4.7 mm wide. Stamens included, uniformly positioned around pistil; filaments narrow, 2.5–5.0 mm long. Anthers 1.4–2.0 mm long, creamy white to tan, oblong, without clearly defined tubes; pores relatively large, at ends of the narrowed sacs. Pollen tetrads  $35\text{--}46\ \mu\text{m}$  diameter,  $\bar{x}=42\ \mu\text{m}$ . Style straight to somewhat declinate, barely exserted, 2.0–4.8 mm long; stigma with conspicuous reflexed collar and 5 divergent, cylindrical lobes 0.5 mm long. Capsule pendent, 5-locular, 5–6 mm diameter; dehisced valves connected by fibers. Chromosome number  $2n=46$ . Mainly alpine meadows and sometimes edges of open subalpine deciduous broad-leaved forests of N Honshu, Hokkaido, Kuriles, Sakhalin, Kamchatka and Bering Is.; 10–2000 m elevation.

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#### Appendix of Specimen Citations

*Pyrola asarifolia* × *P. minor* (+ indicates specimen was chromatographed; \*pollen was examined). CANADA. Alberta: \*Poboktan Creek, 26 Jul. 1908, Brown 1351, (CAN); Moraine Lake, Banff National Park, 11 Aug. 1964, Scoggan 16314 (CAN). British Columbia: + \*Sustut L., 23 Jul. 1977, Gillett and Boudreau 17401b (CAN); + Peak L., 2 Aug. 1977, Gillett and Boudreau 17711b (CAN). Northwest Territories: \*Brintnell L., Red Mtn., 7 Aug. 1939, Raup and Soper 9737 (CAN). Yukon: + \*Mt. Sheldon, 13 Aug. 1944, Porsild and Breitung 11092 (CAN). USA. Alaska: Nome, 4–8 Aug. 1945, Scamman 3897 (GH); Attu Is., Massacre Bay, 1 Sep. 1945, Schaack 973 (GH). Colorado: Marshall Pass, 27 Jul. 1896, Shear 5146 (NY); Cottonwood Pass, 14 Aug. 1971, Childers and Pinkava 8952 (ASU). Utah: 24 km E of Cedar City, 12 Jul. 1940, Maguire 19464 (CAN).

*Pyrola media* (+specimens used for chromatographic analyses; \*pollen evaluation) FINLAND. + Jaaski, 9 Jul. 1927, Valle s.n. (DAO); + Nylandia, 26 Jul. 1952, Marklund s.n. (DAO); + Etela-Savo, 6 Jul. 1983, Ulvinen s.n. (CAN). GERMANY. + \*Köln, Aug. 1929, Andres s.n. (CAN). GREAT BRITAIN. \*Ambleside, Lus(?), 24 Jun. 1869 (CAN). SWEDEN. + Sjobottom, 9 Jul. 1964, Porsild 23296 (CAN). USSR. + \*Province Orel, District Brjansk, 1 Jul. 1906, Protopopov, Rudnev and Chitrovo s.n. (CAN).

*Pyrola minor* (all specimens used for chromatographic analyses) CANADA. Alberta: Cypress Hills, 16 Aug. 1947, Breitung 5658 (DAO). British Columbia: 40 mi. W of Anahim Lake, 11 Jun. 1956, Calder, Parmelee and Taylor 17321 (DAO); 10 mi. N. of Bull R., 13 Jul. 1958, Taylor and Ferguson 2730 (DAO). Manitoba: Reindeer L., 10 Aug. 1951, Baldwin 2397 (CAN). Newfoundland: Gander, 7 Jul. 1949, Bassett 434 (DAO). Ontario: Jackfish, 19 Jul. 1937, Hosie, Losee and Bannan 2397 (CAN). Quebec: Corner of the Beach, 15 Jul. 1946, Terrill 4466 (CAN). Saskatchewan: Cypress Hills Park, 22 Jul. 1947, Breitung 4962 (DAO). Yukon: mile 95, Canol Rd., 11 Jul. 1944, Porsild and Breitung 10398 (CAN). FINLAND. Lake Oulunjarvi, 15 Jul. 1969, Alho and Laine s.n. (DAO). FRANCE. Clermont-Ferand, 15 Jul. 1960, Lugagne 3923 (DAO). GERMANY. Wissental, 30 Jun. 1933, Schumacher s.n. (DAO). GREENLAND. Nigerdleg, 8 Jul. 1966, Jorgensen 66–168 (CAN). JAPAN. Rishiri Is., 20 Aug. 1984, Takahashi 5248 (CAN). SCOTLAND. Black Loch, Jun. 1959, Lamond 3062 (DAO). SWEDEN. Angermanland, 28 Jun. 1921, Samuelsson 1265 (CAN); Jukkasjarvi, 22 Aug. 1949, Asplund s.n. (DAO).

*Pyrola faurieana* (citations are provided for all records seen of this taxon because of the common confusion with *P. minor*; + indicates specimen was chromatographed; \*pollen was examined; ! chromosome counts were made).

JAPAN. HOKKAIDO. Abashiri Province: Mt. Io-zan (= Iwo), 18 Jul. 1951, Misumi et al. 41172 (SAPT); Mt. Shiretoko, 900–1050 m, 19 Jul. 1952, Samejima et al. (SAPT). Shari, 15 Aug. 1965, Shiota and Yoshitake (Herb. Ibaraki Univ.), Mt. Kikin, 21 Jul. 1974, Matsuki (MAK); Mt. Shari, 1500 m, 12 Aug. 1983, Takita 1669 (KYO); + \*! Shiretoko Pen., Futatsu-ike, 1300–1400 m, 12 Aug. 1984, Takahashi and Kushibiki 5157 (SAPT, CAN); + \*Shiretoko Pen., Mt. Okkapake, 12 Aug. 1984, Takahashi and Kushibiki 5164 (SAPT). Hidaka Province: Mt. Poroshiri (= Porojiri), 10 Jul. 1929, Tokunaga and Sakamoto (SAPT); + Mt. Tottabetsu, Kar, 9 Sep. 1933, Hoshino (SAPT); Mt. Poroshiri, 1600–1700 m, 26 Jul. 1971, Koyama et al. 3906 (TNS); 14 Aug. 1979, Umezawa (TI), 1800 m, 1 Aug. 1983, Takahashi 4588 (SAPT); Mt. Chiroro, 1710–1848 m, 7 Aug. 1985, Takahashi et al. 5865 (SAPT). Ibaraki Province: + \*Mt. Yotei-zan (= Makkarinupuri), 21 Aug. 1906, Nishida (SAPT), + \*28 Aug. 1922, Konishi (SAPT), 1610 m, 13 Aug. 1986, Takahashi 6662 and 6664 (SAPT). Ishikari Province: + \*Mt. Yubari (= Yuparo, Yupari), 8 Aug. 1912, Yanagisawa (SAPT), 7–9 Aug. 1913, Nishida (SAPT); Mt. Tokachi, Aug. 1915, Koidzumi (TI); Mt. Yubari, Aug. 1916, Koidzumi (TI), 22 Jul. 1933, Hara (TI), Aug. 1938, Honda (TI); + \*Mt. Ishikari, 8 Aug. 1952, Samejima and Misumi (SAPT); Mt. Yubari, 1380 m, 29 Jul. 1987, Takahashi 7576 (SAPT), 1400 m, 7 Aug. 1987, Yamazaki (TI), Uno 16820 and 17231 (Herb. Kurashiki Mus.). Kushiro Province: Mt. Meakan, Aug. 1893, Fujimura (SAPT), Aug. 1897, Kawakami (SAPT), 2 Aug. 1937, Yokoyama 4273 (SAPT); Mt. Mashu, 4 Sep. 1954, Okamoto 1166 (KYO); Teshikaga, Pekere, 13 Jul. 1959, Kimura (TNS); Mt. Oakan, 1250 m, 7 Aug. 1981, Takita 678 (KYO). Soya Province: Rebun Is., 5 Jul. 1920, Tatewaki 19699 (SAPT), 200 m, 28 Jun. 1983, Takahashi 4320 (SAPT), 400–490 m, 18 Aug. 1984, Takahashi 5241 (SAPT); Wakkanai, Noshappu-misaki, 22 Jul. 1956, Hara (TI); Rishiri Is., 800 m, 19 Jul. 1982, Takahashi 2802 (SAPT), + ! 930 m, 20 Aug. 1984, Takahashi 5249 (SAPT); !Hamatonbetsu, Beniya-genseikaen, 12 Jun. 1988, Takahashi and Uematsu 8504 (SAPT). Tokachi Province: Mt. Saoro (= Sahoro), 13 Aug. 1913, Nishida (SAPT); Mt. Satsunaitake, 24 Jul. 1917, Nishida (SAPT). HONSHU. Akita Prefecture: Mt. Eboshi, 16 Jul. 1958, Kikuchi (TNS). Aomori Prefecture: Mt. Sukayu, 27 Aug. 1897, Hiratsuka (SAPT). Iwate Prefecture: Mt. Iwate-san, Aug. 1905, Sakurai (TNS). Miyagi Prefecture: Mt. Katta, 14 Jul. 1936, Hara (TI); Daikokuten, 1500 m, 4 Jul. 1950, Kimura and Sugaya (TUS); Mt. Sugigamine, 1720 m, 24 Jul. 1977, Ueno and Suzuki 20182 (TUS). Yamagata Prefecture: Mt. Azuma-san, Aug. 1927, Yuhki (KYO). USSR. KURILE ISLANDS: Shumushu Is., Bettobi, 2 Aug. 1943, Akiyama (KANA); Paramushir Is., Urafutoyama, 8 Aug. 1920, Kudo (TUS), Ziguro (?), Kozima (KYO); Matsuwa Is., Yamamotowan-Ainuwan, 7 Aug. 1928, Tatewaki and Tokunaga 12160 (SAPT); Shimshir Is. (= Simushir), Broton

- Bay, 13 Aug. 1928, Tatewaki and Tokunaga 11613 (SAPT), Yamagoshizaki, 16 Aug. 1928, Tatewaki and Tokunaga 11797 (SAPT); Etorofu Is., Shibetoro, 30 Jul. 1884, Miyabe (SAPT), 19 Jul. 1906, Miura (SAPT), 21 Jul. 1906, Miura (SAPT), Moyoro-Shibetoro, 5 Aug. 1938, Yoshimura and Yokoyama (SAPT); Kunashiri Is., Mt. Chacha, 26 Jul. 1929, Nagai and Shimamura (SAPT), 1 Aug. 1929, Okada (TNS), Mt. Tomari, 20 Aug. 1936, Tatewaki 25520 (SAPT). SAKHALIN: Kaibato Is., Mt. Dainan, 28 Jul. 1931, Kimoto et al. (SAPT); Precise locality unknown, 4 Aug. 1910 (TI); Shikka (= Sikka-gun): Mt. Asase-yama, 9 Aug. 1935, Sugawara (SAPT); Chirikoro-daiichisiryu, 2 Aug. 1935, Sugawara (SAPT); Mt. Kawashima, 9 Aug. 1936, Yoshimura (SAPT); Horonoberezan, Mimizuku, Nagamatsu (KYO); Hoshi (?), Sugawara (KYO). W. Coast: Anbetsu, 16 Jul. 1927, Ishiyama (SAPT). Motodomari: Mt. Kashipo, 7 Aug. 1928, Hiratsuka (SAPT); Mt. Tosozan, Kume 2597, Uno 21226 (Herb Kurashiki Mus.). Ootomari (= Ohdomari, Korsakoff): Sakaehama, 22 Jul. 1937, Yoshimura and Hara (SAPT), Otogiri (KYO); Ohdomari, 28 Jul. 1936, Hara (S); Takadai, 22 Jul. 1937, Yoshimura and Hara 132 (TNS); 16 Jul. 1907, Miyake (SAPT), 16 Jul. 1907, Miyake (TNS), 12 Jul. 1906, Miyabe and Miyagi (SAPT), 8 Aug. 1923, Sawada (TI), Aug. 1924, Numajiri (TNS), 31 Jul. 1933, Akiyama (KANA), Faurie (KYO), 17 May 1907, Miyake (TNS), 17 May 1907, Miyake (SAPT), 28 Jul. 1936, Hara (S). S. KAMCHATKA: between Petropavlovsk and Avatcha volcano, 6 Aug. 1920 (Hultén 771 (S), 22 Aug. 1920, Hultén 1025 (S); Avatcha volcano, 5 Aug. 1920, Hultén 747a (S); pass between T(?)avan and T(?)hadulka rivers, 1 Aug. 1921, Hultén 2575a (S); Savoiko, 28 Aug. 1928, Eyerdam (S).
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## 要旨

東アジアに分布する *Pyrola faurieana* カラフトイチャクソウの分類学的取扱には、これまで問題があった。特に、周北極要素の *P. minor* エゾイチャクソウ、ユーラシアに広がる異質4倍体の *P. media*、北アメリカに生育する自然雑種 *P. asarifolia* × *minor* との区別が難しかった。外部形態、花粉と種子の微細形態・稔性、染色体数、葉フラボノール成分、地理分布の比較から、*P. faurieana* は2倍体の独立種であることを明らかにした。これら4種類を区別するための検索表をつくり、さらに *P. faurieana* の最新の記載と充分な標本引用をおこなった。これらの形質から総合判断して、*P. faurieana* は片親に *P. minor* をもつ雑種起源の種と推定された。もう一方の片親は、北アメリカに分布する *P. asarifolia* のアジア産姉妹種 *P. asarifolia* subsp. *incarnata* ベニバナイチャクソウである疑いがある。