Genus *Primula* L. in Hokkaido, northern Japan

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Primula is the largest genus in the Primulaceae, including seven subgenera, 37 sections, and about 500 species (Fenderson, 1986 ; Table 1), and represented in temperate to arctic regions of the Northern Hemisphere and southern part of South America.

Fourteen *Primula* species are native to Japan. Among them nine species grow naturally in Hokkaido, the northernmost main island of Japan (Table 2). These nine *Primula* species of Hokkaido were divided into the following four geographical distribution groups (Tatewaki, 1955): 1) endemic- *P. hidakana, P. takedana, P. sorachiana, P. yuparensis*; 2) Japanese- *P. japonica, P. jesoana*; 3) eastern Asiatic Pacific- *P. modesta, P. sieboldii*; 4) northern Pacific- *P. cuneifolia.* They are distributed into all five Japanese sections of *Primula*, so even in Hokkaido we can

Table 1. Infrageneric system of *Primula* (According to Fenderson, 1986). Sections in boldface include Japanese species. Numbers of species are indicated in parentheses. In the sections which include Japanese species, (Japanese species number/total species number) is indicated.

Primula [460]	
Subgen. *Sphondylia* [6]	Subgen. *Craibia* [55]
Sect. *Sphondylia* (6)Hi-cAs-Af	Sect. *Chartacea* (4)Hi-seAs
Subgen. *Auriculastrum* [32]	Sect. *Davidii* (13)Ch
Sect. *Auricula* (21)Eu	Sect. *Petiolares* (38)Hi-Ch
Sect. ***Cuneifolia*** (2/3)Jp-NAm	Subgen. *Aleuritia* [277]
Sect. *Parryi* (8)NAm	Sect. ***Prolifera*** (1/25)Hi-seAs-Ch
Subgen. *Primula* [6]	Sect. *Sikkimensis* (11)Hi-seAs-Ch
Sect. *Primula* (3)Eu-wAs	Sect. *Troglodyta* (1)cAs
Sect. *Megaseifolia* (2)wAs	Sect. *Crystallophlomis* (53)cAs-Ch
Sect. *Julia* (1)wAs	Sect. *Cordifoliae* (9)Hi-Ch
Subgen. *Auganthus* [78]	Sect. *Amethystina* (8)Hi-Ch
Sect. *Auganthus* (2)Ch	Sect. *Fedtschenkoana* (1)cAs
Sect. *Monocarpicae* (11)eAs	Sect. ***Oreophlomis*** (1/11)cAs-Jp
Sect. ***Cortusoides*** (3/26)cAs-Jp	Sect. ***Aleuritia*** (3/60)NH,SAm
Sect. *Malvacea* (5)Ch	Sect. *Armerina* (12)NH
Sect. *Pycnoloba* (1)Ch	Sect. *Souliei* (7)Ch
Sect. *Obconicolisteri* (17)Hi-Ch	Sect. *Minutissimae* (26)Hi-Ch
Sect. ***Reinii*** (4/4)Jp	Sect. *Dryadifolia* (5)Ch
Sect. *Pinnatae* (5)Ch	Sect. *Denticulata* (7)cAs-Ch
Sect. *Bullatae* (7)Ch	Sect. *Capitatae* (2)Hi-Ch
Subgen. *Carollinella* [6]	Sect. *Muscarioides* (17)Hi-Ch
Sect. *Carolinella* (6)Ch-seAs	Sect. *Soldanelloides* (22)Hi-Ch

Abbreviations: Af-Africa, As-Asia, Ch-China, Eu-Europe, Hi-Himalaya, Jp-Japan, NH-Northern Hemisphere, NAm-North America, SAm-South America

Table 2. Japanese *Primula* species. Species in boldface indicate the taxa native to Hokkaido. (System is according to Yamazaki, 1993)

Genus *Primula*
  Subgen. I. *Auganthus*
    Sect. 1. *Cortusoides*
      Subsect. *Cortusoides*
        1) ***Primula sieboldii*** E. Morren (2n=24)
      Subsect. *Geranioides*
        2) *Primula kisoana* Miq. (2n=24)
        3) ***Primula jesoana*** Miq. (2n=24)
          var. ***jesoana***
          var. ***pubescens*** (Takeda) Takeda et Hara ex Hara
      Subsect. *Reinii*
        4) *Primula reinii* Fr. et Sav. (2n=24)
          var. *reinii*
          var. *kitadakensis* (Hara) Ohwi
          var. *rhodotricha* (Nakai et F. Maekawa) Ohwi
        5) *Primula tosaensis* Yatabe (2n=24)
          var. *tosaensis*
          var. *brachycarpa* (Hara) Ohwi
    Sect. 2. *Hidakanae*
        6) ***Primula hidakana*** Miyabe et Kudo ex Tatewaki
        7) ***Primula takedana*** Tatewaki (2n=24)
  Subgen. II. *Aleuritia*
    Sect. 3. *Prolifera*
        8) ***Primula japonica*** A. Gray (2n=22, 44)
    Sect. 4. *Aleuritia*
        9) ***Primula modesta*** Bisset et Moore (2n=18)
          var. *modesta*
          var. ***fauriei*** (Fr.) Takeda
          var. ***samanimontana*** (Tatewaki) Nakai
          var. ***matsumurae*** (Petitm.) Takeda
        10) ***Primula sorachiana*** Miyabe et Tatewaki (2n=18)
        11) ***Primula yuparensis*** Takeda (2n=36)
        12) *Primula macrocarpa* Maxim. (2n=36)
  Subgen. III. *Auriculastrum*
    Sect. 5. *Cuneifolia*
        13) ***Primula cuneifolia*** Ledeb. (2n=22)
          var. ***cuneifolia***
          var. *heterodonta* (Fr.) Makino
          var. *hakusanensis* (Fr.) Makino
        14) *Primula nipponica* Yatabe (2n=22)

recognize a sufficient diversity of Japanese primulas.

Taxonomic studies on native *Primula* species of Hokkaido have not been published since old taxonomic treatmens (Tatewaki and Sakamoto, 1927; Tatewaki, 1955). The subsequent taxonomic

treatment of Hokkaido *Primula* is generally based on the newest treatment by Yamazaki (1993) for Japanese *Primula* and some data on type specimen are referred to Fenderson (1986). We are grateful to Sadamoto Watanabe for the critical discussion on the taxonomic position of *P. sorachiana* and *P. hidakana* var. *kamuiana*; and to Yoichi Tateishi for his suggestions on the typification. Helpful information on growing primulas in Hokkaido gardens is indebted to Gozo Yamagata and Eiji Kushibiki, gardeners of our Botanic Garden.

KEY TO *PRIMULA* SPECIES NATIVE TO HOKKAIDO

A. Leaves revolute in bud, chartaceous or membranaceous, teeth generally along entire margin.
  B. Leaves distinctly petiolate, blade and petiole distinct; not farinose; rhizomes covered by scales.
    C. Leaves ovate or oblong-ovate, longer than width, capsules broadly ovoid, much shorter than persistent calyx .... 1. *P. sieboldii*
    C. Leaves orbicular, as long as width, capsules broadly oblong to cylindric, as long as to longer than persistent calyx.
      D. Rhizomes short-creeping, densely covered with soft membranaceous withered scales .... 2. *P. jesoana*
      D. Rhizomes creeping, stout and ligneous, covered with brownish somewhat hard chartaceous persistent scales.
        E. Flowers rose-purple, 1(-2) ; petioles glabrous or with sparse pale brownish pilose hairs .... 3. *P. hidakana*
        E. Flowers white, (1-)2-3 ; petioles with dense brownish (when dry) long pilose hairs .... 4. *P. takedana*
  B. Leaves obscurely petiolate, blade gradually or more or less abruptly narrowed to base, generally hyaline yellowish or white farinose (except in *P. japonica*) ; rhizomes covered with many withered petioles.
    C. Scapes stout, 30-80 cm tall ; not farinose ; inflorescence generally 2-5-tiered .... 5. *P. japonica*
    C. Scapes slender, 2-15 cm tall ; generally farinose ; inflorescence usually in an umbel.
      D. Pedicels usually more than 1.5 cm long, 1/2 to 1/3 as long as the scape, corolla-lobes widely notched, capsules about 5 mm long, nearly as long as persistent calyx .... 6. *P. sorachiana*
      D. Pedicels usually less than 1.5 cm long, 1/3 to 1/10 as long as the scape, corolla-lobes narrowly notched, capsules 5-8 mm long, slightly longer or up to 1.5 times as long as persistent calyx.
        E. Leaves prominently yellow farinose below, obscurely denticulate on margin; bracts not or slightly saccate at base; flowers usually 2-15, heterostylous, corolla-tube 5-7 mm, 1-1.5 times as long as calyx; 2n=18 .... 7. *P. modesta*
        E. Leaves white or not prominently farinose beneath, distinctly denticulate on margin; bracts saccate at base; flowers usually 2-3, homostylous, corolla-tube 10-12 mm long, about twice as long as calyx; 2n=36 .... 8. *P. yuparensis*

A. Leaves involute in bud, rather fleshy, teeth on upper margin .... 9. *P. cuneifolia*

1. **Primula sieboldii** E. Morren in Belg. Hort. 23: 97, t. 6 (1873). —Type: cult. from seeds of *von Siebold* s. n., 1862 (LG? holo.), fide Fenderson (1986). [Plate 1]

Japanese name: Sakuraso, No-sakuraso. サクラソウ，ノサクラソウ

This is the most popular *Primula* species in Japan because it generally grows on readily accessible lowland areas. There have been over 1,000 cultivar names since the Edo era, and even now 200-250 cultivars are usually recognized (Oogaki, 1979). "Sakuraso" in Japanese means a "cherry herb". In order to distinguish the cultivars from wild plants, we use especially the Japanese name "Nihon-sakuraso" for the cultivars and "No-sakuraso" for wild plants. Now, this species is one of the endangered wild species in Japan due to the urbanization in lowland areas, and central southern Hokkaido is the northern limit of its geographical distribution. Conservation biological studies have been conducted in Honshu populations (Washitani et al., 1991; Takahashi et al., 1992).

Inoue (1977) noted that this species is closely to *P. cortusoides* L. native to the Altai Mountains to western Siberia.

Description. White pubescent perennial herbs with creeping rhizomes, covered with membranaceous scales. Leaves 4-8, radical, membranaceous, ovate to ovate-elliptic, 4-12 cm long, 3-9 cm wide, obtuse, truncate or shallowly cordate at base, shallowly incised and irregularly toothed, more or less wrinkled on the upper surface, spreadingly pilose on nerves, petioles 4-18 cm long, white pubescent, 1-4 times as long as blades. Scapes, 10-25 cm tall, white pubescent especially near base, 3-6-flowered in an umbel. Bracts narrowly lanceolate, 3-10 mm long, punctate hairy. Pedicels 0.5-4 cm long, punctate hairy. Calyx 6-10 mm long, punctate hairy, deeply 5-lobed; lobes narrowly lanceolate, 3-6 mm long. Corolla salverform, rose-purple; tube about 10 mm long, deeply 5-lobed; lobes obcordate, about 10 mm long, notched. Capsule broadly ovoid, about 4 mm long, much shorter than persistent calyx. Flowers late April to early June. 2n=24. CS. Hokkaido (Iburi- and Hidaka-sicho; moderately moist lowland *Quercus dentata* and *Q. crispula* forests), Honshu and Kyushyu (sunny moderately moist meadows; lowlands to 1000 m); E. Siberia, Korea and Manchuria.

2. **Primula jesoana** Miq. in Ann. Mus. Bot. Lugd.-Bat. 3: 119 (1867). —Type: *Sugerok*? s. n., ca. 1867 (U? holo.), fide Fenderson (1986).

2a. var. **jesoana**

Japanese name: O-sakuraso, Miyama-sakuraso. オオサクラソウ，ミヤマサクラソウ

"O-sakuraso" means "large *Primula" and* "Miyama-sakuraso" means "deep mountains *Primula*". These Japanese names appropriately express the morphological and ecological features of this species.

Description. Perennial herbs with thickened short creeping rhizomes, covered with membranaceous scales. Leaves 2-6, radical, membranaceous, orbicular, 3-9 cm long, 3-11 cm wide, shallowly 7- to 9-lobed, lobes irregularly acute-serrulate, glabrous above, thinly puberulent beneath, petioles 5-30 cm long, glabrous. Scapes 15-50 cm tall, sparsely to subdensely glandular puberulent above. Inflorescence 1-2(-4)-tiered raceme, each tier with 2-8 flowers. Bracts linear, 2-8 mm long. Pedicels 2-15 mm long, round-tipped punctate hairy. Calyx 6-10 mm long, sparsely round-tipped punctate hairy, deeply 5-lobed; lobes lanceolate, 4-6 mm long. Corolla salverform, rose-purple, with a yellow eye, tube 8-10mm long, deeply 5-lobed; lobes obcordate, 8-10 mm long, notched. Capsules broadly oblong, 7-10 mm long, 5 mm across, nearly as long as persistent calyx. Flowers May to July. 2n=24. SW. to E. Hokkaido (mainly Oshima- and Hiyama-sicho; moderately moist deciduous forest on mountain slopes; lowlands to 1000 m) and N. to C. Honshu (sunny moderately moist meadows; 500-2600 m). Endemic to Japan.

Remarks. The white flowered form has been named forma **leucantha** Hara (Japanese name: Shirobana-miyama-sakuraso) in Bot. Mag. Tokyo 50: 569 (1936). Kawano (1957) described *Primula jesoana* var. *glabra* forma *minor* Kawano (Japanese name: Koezo-sakuraso), dwarf type from Prov. Iburi.

2b. var. **pubescens** (Takeda) Takeda et Hara ex Hara in Bot. Mag. Tokyo 50: 569 (1936). —*Primula jesoana* Miq. forma *pubescens* Takeda in Not. Bot. Gard. Edinb. 8(37): 86 (1913). —Type: not cited. [Plate 2]

Japanese name: Ezo-o-sakuraso, Ezo-sakuraso. エゾオオサクラソウ, エゾサクラソウ

This is a hairy variant of *P. jesoana*. "Ezo (or Yezo)" is the old name of Hokkaido, so this variety mainly occurs in Hokkaido, norhtern Japan.

Description. Scapes and petioles densely to subdensely long-pubescent. 2n=24. C. to E. Hokkaido (moderately moist deciduous forests; lowlands to 1000 m); Korea and S. Manchuria.

Remarks. The white flowered form has been named forma **albiflora** Tatewaki (Japanese name: Shirobana-o-sakuraso) in Res. Bull. Exper. For. Hokkaido Univ. 5: 105, 131 (1928) —Type: Oshikoshigawa, near Fuyushima, Prov. Hidaka, *M. Tsushima,* May, 1928, fl. (SAPT! holo.; collector name, *M. Tsushima* is not written on the label of the herbarium specimen).

Remarks. Differences between the two varieties of *P. jesoana* are not distinct and intermediate phases are often found. *Primula jesoana* var. *pubescens* forma *nudiuscula* (Nakai et Kitagawa) Hara (Japanese name: Usuge-no-ezo-zakura) in Bot. Mag. Tokyo 50: 569 (1936), may be one of such intermediate phases between the two varieties.

3. **Primula hidakana** Miyabe et Kudo [in Tatewaki in Res. Bull. Exper. For. Hokkaido Univ. 5: 105, f. 14 (1928), nom. nud.] ex Hara in Icon. Pl. Asia.-Or. I, 16, t. 8 (1935). —Syntypes: Mt. Apoi, Prov. Hidaka, *M. Tatewaki* 9040, May 22, 1927, fl. (SAPT! lecto.); *H. Hara* , July 9, 1933, fr. (TI). [Plate 3]

Japanese name: Hidaka-iwazakura, Hidaka-kozakura. ヒダカイワザクラ, ヒダカコザクラ

This is a fascinating tiny primula, but it is somewhat difficult to maintain it in gardens for a long time. The Japanese "Hidaka" was named after the Hidaka Mountains where this endemic species grows. "Iwa-zakura" in Japanese means "rock *Primula*", so its rocky habitat is well expressed in this name.

Ligneous stout rhizomes of this species are regarded as a primitive character shared with the next species (Inoue, 1977).

Description. Perennial herbs with creeping ligneous rhizomes, densely covered with chartaceous persistent brown scales. Leaves 2-4, radical, membranaceous, orbicular, 1-2.5 cm long and wide, deeply cordate at base, shallowly 7-lobed, irregularly toothed, glabrous above, glabrous or sparsely long pilose beneath, petiole 2-9 cm long, glabrous. Scapes 4-10 cm tall, glabrous, 1(-2)

-flowered in an umbel. Bracts linear-lanceolate, 3-7 mm long, glabrous. Pedicels 0.5-4 cm long, glabrous. Calyx 5-8 mm long, glabrous or sparsely pilose, deeply 5-lobed; lobes linear-lanceolate, 3-4 mm long, with round-tipped short pilose hairs on margin. Corolla salverform, rose-purple, with a yellow eye, 2.5-3 cm across, tube 8-10 mm long, 5-lobed; lobes obcordate, 10-13 mm long, notched. Capsules cylindric, 10-15 mm long, 4 mm across, 1.5-2 times as long as persistent calyx. Flowers May to June. Hokkaido (Hidaka Mountains; on moderately moist rocky cliffs in valleys and on the mountain slopes). Endemic to the Hidaka Mountains.

Remarks. Plants with the petioles, scapes and calyx lobes more densely long pilose hairy are named var. **kamuiana** (Miyabe et Tatewaki) Hara (Japanese name: Kamui-kozakura), Enum. Sperm. Jap. 1: 90 (1948) —*Primula hidakana* Miyabe et Kudo ex Tatewaki forma *kamuiana* Yamazaki in Flora of Japan 3a: 91 (1993) —*Primula kamuiana* Miyabe et Tatewaki, Trans. Sapporo Nat. Hist. Soc. 16: 4, f. 1 (1939) —Syntypes: Yezo, Bot. Gard., Sapporo, cult. from Mt. Kamuiekuushi-kaushi, *K. Miyabe*, May 14, 1938, fl. (SAPT!); June 2, 1939 (not found in SAPT); Prov. Tokachi, Mt. Kamuiekuushikaushi, *Y. Tochinai & B. Ishida,* Aug. 13, 1937, sterile (SAPT!). In addition to these specimens, *K. Miyabe*, May 20, 1938 is found in SAPT and this specimen includes two plants and one sketch used in the protologue.

4. **Primula takedana** Tatewaki in J. Jap. Bot. 5: 29, photo., f. 1-4 (1928). —Syntypes: Upper Nupuromapporo, a branch of the Teshio River, Prov. Teshio, *M. Tatewaki* 10765, June 4, 1928, fl. (SAPT! lecto., SAPT! iso.); *M. Tatewaki* 9424, July 17, 1927, fr. (SAPT!). [Plate 4]

Japanese name: Teshio-kozakura. テシオコザクラ

This species occurs on serpentine rock areas and endemic to northern Hokkaido. We use the serpentine rockstones for the cultivation in Hokkaido gardens. Japanese name means small primula native to Teshio province of Hokkaido. Specific epithet is dedicated to Dr. Hisayoshi Takeda (1883-1972), an alpinist as well as a plant taxonomist.

Inagaki and Toyokuni (1966) recognized endemic section *Takedana* composed of only this species. Kitamura (1957) considered that this species is related to *P. jesoana.* But now it is usually considered to be related to *P. hidakana* (Inoue, 1977) and included in new section *Hidakanae* (Yamazaki, 1993). Distylous flower condition of this species is reported by Tsukui et al. (1994) in this volume.

Description. Perennial herbs with thick creeping ligneous rhizomes, densely covered with many chartaceous brown persistent scales. Leaves 2-3, radical, thinly chartaceous, reniform-orbicular, 2-4 cm long, 2.5-5.5 cm wide, deeply cordate at base, deeply incised, each lobe with 1-2 -paired tooths, sparsely brownish pilose hairy above, densely long pilose hairy on nerves beneath, petioles 3-12 cm long, brownish long pilose hairy. Scapes 10-15 cm tall, sparsely brownish pilose hairy, (1-)2-4(-5)-flowered in an umbel. Bracts narrowly lanceolate, 3-8 mm long, punctate pilose. Pedicels 10-25 mm long at flowering, to 35 mm long at fruiting, sparsely long pilose. Calyx 5-7 mm long, punctate pilose, deeply 5-lobed; lobes lanceolate, 3-5 mm long, punctate pilose. Corolla white, with a yellow eye, salverform, glabrous; tube about 10 mm long, 5-lobed; lobes ascending, not spreading, oblong-obovate, 5-7 mm long, shallowly notched. Capsules cylindric, 7-12 mm long, 3-4 mm wide, about twice as long as persistent calyx. Flowers May to June. $2n=24$. N. Hokkaido (Teshio region; eroded serpentine stony places along the streams and on the heads of valleys).

Endemic to N. Hokkaido.

5. **Primula japonica** A. Gray in Mem. Amer. Acad. Arts Sci. (Boston), new ser. 6: 400 (1859), in note. —Type: C. Wright s. n., 1853-1856 (GH holo.), fide Fenderson (1986). [Plate 5]

Japanese name: Kurinso. クリンソウ

This species is the most robust *Primula* in Japan, and is commonly cultivated by the stream in rock gardens. Several cultivars have been produced especially in England. "Ku-rin" in Japanese means "nine wheels" symbolizing several flower tiers in inflorescence.

This species is regarded as a tetraploid (2n=44) and a self-fertile secondary homostyle (Wedderburn and Richards, 1992; Richards, 1993). But Yamazaki (1993) noted 2n=22 for this species, thus hetero/homostyly and chromosome numbers should be reexamined in the wild. *Primula miyabeana* (Ito) Ito et Kawakami from Taiwan is regarded as a relative of *P. japonica* (Richards, 1993).

Description. Perennial herbs with thickened short rhizomes, covered with membranaceous scales. Leaves radical, membranaceous, more or less fleshy, oblong-oblanceolate to oblong-ovate, 8-40 cm long, 3-10 cm wide, obtuse, gradually narrowed to base, forming winged petiole, with many short deltoid teeth, glabrous on both surfaces, a raised midrib beneath. Scapes terete, 30-80 cm tall, glabrous. Inflorescence 1-5-tiered raceme, each tier with 5-12 flowers. Bracts linear, 0.5-2 cm long, glabrous. Pedicels 7-20 mm long at flowering, to 35 mm long at fruiting, glabrous. Calyx 5-10 mm long, glabrous, 5-lobed; lobes triangular-ovate, 3-5 mm long. Corolla salverform, rose-purple, with a yellow eye, 2-2.5 cm across; tube about 1.5 cm long, 5-lobed; lobes orbiculate-obcordate, 8-10 mm long, shallowly notched. Capsules globose, 5-6 mm long, 5-7 mm across, as long as or slightly shorter than persistent calyx. Flowers May to June. 2n=22, 44. Hokkaido (wet sandy meadows along streams; lowlands to 1000 m), Honshu and Shikoku (wet meadows along streams; 800-1800 m). Endemic to Japan.

6. **Primula sorachiana** Miyabe et Tatewaki in Trans. Sapporo Nat. Hist. Soc. 13: 2, t. 1, f. 4 (1933). —Type: Along the River Sorachi, near Kanayama, Ishikari, *M. Tatewaki*, May 15, 1933, fl. (SAPT! holo.). [Plate 6]

Japanese name: Sorachi-kozakura. ソラチコザクラ

This is an endemic species to the Hidaka and Yubari Mountains of central southern Hokkaido. Both Japanese and scientific names "sorachi" originated in the River Sorachi where it was first collected.

This species was sometimes regarded as a lowland variant of *P. yuparensis* (Ohwi, 1965; Richards, 1993), but is clearly distinguished from the latter species by several characters noted in the key. Detailed description and geographical distribution were noted by Ito (1971). It is more easy to cultivate this species than *P. yuparensis*.

Description. Perennial herbs with short thickened rhizomes, covered with many withered leaves of the previous season. Leaves radical, ovate or elliptic, rounded, cuneate at base, attenuate into petiole, 1-3 cm long, 0.8-2 cm wide, with many irregular small apiculate denticules on margin, yellowish to white farinose beneath, petiole 0.5-5 cm long or inconspicuous. Scapes 3-5 cm tall, yellowish white farinose, with 2-10-flowered in an umbel. Bracts linear, 2-8 mm long, farinose, slightly saccate at base. Pedicels 10-25 mm long, yellowish white farinose. Calyx 3-5 mm long, farinose, 5-lobed; lobes linear-lanceolate, about twice as long as calyx-tube. Corolla salverform, rose-purple, with a white eye, about 10 mm across; tube 5-7 mm long, about 1.5 times as long as calyx, 5-lobed; lobes obovate-cuneate, about 5 mm long and wide, usually widely notched. Capsules oblong, about 5 mm long, 2 mm across, nearly as long as persistent calyx. Flowers May. 2n=18. Hokkaido (Ishikari-, Kamikawa- and Hidaka-sicho; on rocky cliffs in the valleys). Endemic to the Hidaka and Yubari Mountains.

7. **Primula modesta** Bisset et Moore in J. Bot. 16: 134 (1878). —Type: Japan, Nikko, *Bisset* s. n., mid May, 1877 (BM? K? holo.), fide Fenderson (1986).

Japanese name: Yukiwari-so. ユキワリソウ

"Yukiwari" in Japanese means "cutting snow", expressing its early flowering season. This species is sometimes treated as a variety or subspecies of *P. farinosa* L., but treated here as a distinct and an east Asian counterpart species of Eurasian *P. farinosa*. All varieties of this species are tiny and fascinating, and they are commonly cultivated in Hokkaido gardens and nurseries.

Description. Perennial herbs with short thickened rhizomes, covered with withered leaves of the previous season. Leaves radical, membranaceous, oblanceolate, 2-13 cm long, 0.5-2.5 cm wide, obtuse to rounded, gradually narrowed to a petiole-like base, minutely depressed-denticulate, green and glabrous above, prominently yellowish farinose beneath. Scapes 5-15 cm tall, slightly farinose, (1-)2-10(-15) flowered in an umbel. Bracts linear-lanceolate, 3-7 mm long, slightly saccate at base, farinose. Pedicels 0.5-2 cm long, slightly farinose. Calyx 4-5 mm long, yellowish farinose, 5-lobed; lobes oblong-ovate, 1.5-2 mm long, about as long as calyx tube. Corolla salverform, 10-15 mm across, pale rose-purple, with a yellow eye, tube 5-7 mm long, 1-1.5 times as long as calyx, 5-lobed; lobes 5-6 mm long, notched. Capsules cylindric, 5-8 mm long, 2 mm across, slightly longer than persistent calyx. Flowers late May to early July. 2n=18.

7a. var. **matsumurae** (Petitm.) Takeda in Bot. & Zool. (Tokyo) 4: 185 (1936) in text. —*Primula matsumurae* Petitm. in Bull. Herb. Boiss. ser. 2, 7: 528, fig. 4 (1907). —Type: *Faurie* 8467 (G holo.), fide Fenderson (1986). [Plate 7]

Japanese name: Rebun-kozakura. レブンコザクラ

"Rebun" was named after the Island Rebun situated at the northern Hokkaido. This island is famous for its rich flora composed of boreal and alpine flowering plants.

Description. Leaves large, oblanceolate, appressedly and obscurely denticulate, gradually narrowed to base. Inflorescence with 2-15 flowers. Scapes 9-15 cm tall at fruiting. S. Kuriles and C. to N. and E. Hokkaido (sunny rocks; lowlands to 1300 m). Endemic to N. Japan.

Remarks. The white flowered form has been named forma **alba** Hara (Japanese name: Shirobana-rebun-kozakura), Enum. Sperm. Jap. 1: 93 (1948).

7b. var. **fauriei** (Fr.) Takeda in Not. Bot. Gard. Edinb. 8(37): 88 (1913), ut *β. faurieae*. —*Primula fauriei* Fr. in Bull. Soc. Philom. Paris, 7 ser. 10: 146 (1886). —Type: *Faurie* 722 (P holo.), fide Fenderson (1986).

Japanese name: Yukiwari-kozakura. ユキワリコザクラ

"Yukiwari" in Japanese means "cutting snow" as stated already and "kozakura" a "little primula". Scientific name is dedicated to a famous French plant collector Mr. U. Faurie (1847-1915).

Description. Leaves broadly ovate, abruptly cuneate at base, with coarse depressed irregular dentate teeth, reflexed on margin; petiole 1-4.5 cm long. Inflorescence with 2-10 flowers. Scape 4-6 cm tall at fruiting. S. Kuriles, C. to E. Hokkaido (Hidaka-, Kushiro- and Nemuro-sicho; sunny, moderately moist meadows on cliffs near the sea) and N. Honshu (mountains at 500-800 m); the C. Kuriles.

Remarks. The white flowered form has been named forma **leucantha** Hara (Japanese name: Shirobana-yukiwari-kozakura), Enum. Sperm. Jap. 1: 93 (1948).

7c. var. **samanimontana** (Tatewaki) Nakai, Veg. Apoi: 65 (1930). —*Primula fauriei* Fr. var. *samanimontana* Tatewaki in Res. Bull. Exper. For. Hokkaido Univ. 5: 105, 131 (1928). —Syntypes: Mt. Apoi, Samani, Prov. Hidaka, *M. Tatewaki,* May 29, 1927, fl. (SAPT! holo., here selected); May 22, 1927, fl. and Aug. 10, 1927, fr. (SAPT!).

Japanese name: Samani-yukiwari. サマニユキワリ

Japanese name means *Primula modesta* native to Samani, a local name of Hidaka-sicho of Hokkaido.

Description. Leaves oblanceolate or oblong, prominently reflexed on margin, gradulally narrowed to base, petioles 0.5-4 cm long. Inflorescence with 3-10 flowers. Scapes 3-8 cm tall at fruiting. C. Hokkaido (southern regions of the Hidaka Mountains; sunny rocks). Endemic to C. Hokkaido.

Remarks. The white flowered form has been named forma **nivea** Hara (Japanese name: Shirobana-samani-yukiwari), Enum. Sperm. Jap. 1: 93 (1948).

Key to the varieties of *P. modesta.*

A. Leaves with inconspicuous petiole with broadly wing, not or slightly reflexed on margin ....7a. var. *matsumurae*

A. Leaves with distinct and slender petiole even at flowering, more or less reflexed on margin.

B. Leaves membranaceous, ovate, abruptly cuneate to base, reflexed on margin ....7b. var. *fauriei*

B. Leaves thick membranaceous, lanceolate or oblong, much reflexed on margin ....7c. var. *samanimontana*

8. **Primula yuparensis** Takeda in Not. Bot. Gard. Edinb. 8(37): 94, pl. 26 (1913). —Type: in montibus Yuparo. ins. Yezo, *H. Yanagisawa,* Aug. 9, 1913 (Herbarium?, not found in SAPT). [Plate 8]

Japanese name: Yubari-kozakura, Yupari-kozakura. ユウバリコザクラ, ユウパリコザクラ

Both Japanese and scientific names indicate Mt. Yubari (or Yupari) where this endemic species grows. Habitat of *P. yuparensis* is confined to serpentine stony areas of Mt. Yubari, and it is difficult to maintain this species in Hokkaido gardens. Mt. Yubari is famous for its occurrence of endemic species; e. g., *Saxifraga nishidae* Miyabe et Kudo, *Saxifraga yuparensis* Nosaka, *Viola yubariana* Nakai, and so on.

This species was regarded as being related to *P. sorachiana* (Ohwi, 1965; Hotta and Yamaguchi, 1975). On the other hand Inoue (1977) noted that this species is a relict having a distinct phylogenetic pathway. This primula is a tetraploid homostyle species (Wedderburn and Richards, 1992; Richards, 1993), thus it is regarded as a secondary homostyle.

Description. Perennial herbs with short thickened rhizomes, covered with withered petioles of the previous season. Leaves 10-15, radical, broadly lanceolate, elliptic, or oblanceolate, 10-25 mm long, 5-10 mm wide, subacute, gradually narrowed forming a winged petiole, with 10-20 subacute small denticules on margin, slightly white farinose beneath. Scapes 2-5 cm tall at flowering, to 8 cm tall at fruiting, white farinose, (1-)2-3 flowered in an umbel. Flowers homostyly. Bracts linear, 3-6 mm long, saccate at base, sparsely farinose. Pedicels 5-12 mm long at flowering, to 20 mm long at fruiting, white farinose. Calyx 5-7 mm long, white farinose; tube about 3 mm long, 5-lobed; lobes linear-lanceolate, about 1-1.5 times as long as calyx tube. Corolla salverform, about 10 mm across, pale rose-purple, with a whitish yellow eye; tube 10-12 mm long, about twice as long as calyx, 5-lobed; lobes about 5 mm long, notched. Capsules cylindric, about 8 mm long, 3 mm across, about 1.5 times as long as persistent calyx. Flowers July. 2n=36. Hokkaido (Mt. Yubari [Yupari]; serpentine stony, moist slopes; about 1400 m). Endemic to Mt. Yubari.

9. **Primula cuneifolia** Ledeb. in Mem. Acad. Sci. St.-Pet. 5: 522 (1814). —Collection: E. Siberia, 1803-1806, *Tilesius*? s. n., (LE), fide Fenderson (1986).

var. **cuneifolia** [Plate 9]

Japanese name: Ezo-kozakura. エゾコザクラ

This is a tiny fascinating plant, but it is very difficult to maintain it over two or three years in Hokkaido gardens. This species is a main component of alpine snowbed vegetation of central to northern Japan. Three varieties; *hakusanensis* (Japanese name: Hakusan-kozakura) from C. Honshu, *heterodonta* (Japanese name: Michinoku-kozakura) from N. Honshu and *cuneifolia* from Hokkaido, are serially distributed from south to north. According to Wedderburn and Richards (1992) and Richards (1993), north American subspecies *saxifragifolia* has homostylous flowers.

Description. Glabrous, rahter fleshy perennial herbs with short thickened rhizomes, covered with withered petioles. Leaves 5-10, radical, fleshy, obovate-cuneate, 1-4.5 cm long and 0.5-1.5 cm wide at flowering, 3-7 cm long and 1-2 cm wide at fruiting, acute, more or less abruptly cuneate to a petiole-like base, upper half with 2-5 pairs of coarse teeth, sparsely minute punctate hairs on both surfaces. Scapes 3-10 cm tall at flowering and 8-15 cm tall at fruiting, sparsely minute punctate hairy, 1-3(-7)-flowered in an umbel. Bracts linear-lanceo-late, 2-5 mm long, sparsely minute punctate hairy. Pedicels 5-13 mm long at flowering, to 15 mm long at fruiting, minute punctate hairy. Calyx 4-6 mm long, 5-lobed; lobes linear-lanceolate, about 1.5 times as long as calyx-tube, minute punctate hairy. Corolla salverform, rose-purple, with a yellow eye, 15-20 mm across; tube 5-6 mm long, 5-lobed; lobes 6-10 mm long, deeply notched. Capsules ellipsoid, about 5 mm long, 3 mm across, nearly as long as persistent calyx. Flowers July to August. 2n=22. S. Kuriles and Hokkaido (wet alpine meadows; 1200-2100 m); the Kuriles, Sakhalin, E. Siberia, Kamchatka and the Aleutians.

Remarks. The white flowered form has been named forma **leucantha** Hara (Japanese name: Shirobana-ezo-kozakura), Enum. Sperm. Jap. 1: 89 (1948). The laciniate leaved form has been named forma **laciniata** Tatewaki (Japanese name: Kireha-ezo-kozakura), in Jub. Publ. Com. Sixtieth Birth Prof. Tochinai & Prof. Fukushi 203 (1955).

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Miyabea 2 : 13-18 (1994)

Polymorphic flowers and pollinators of *Primula*

Takahiro Tsukui and Hideki Takahashi

Heterostyly is a polymorphism among angiosperm flowers that ensures cross-fertilization through pollination by visiting insects. Since Darwin's work (1877), distylous flowers of *Primula* which are composed of the long-styled "pin" and the short-styled "thrum", have been a well-known example. Many botanists have focused their attention on this topic from various standpoints. In this report we illustrate the mating system and the pollinators in the heterostylous flowers of *Plimura.*

Distyly

Figure 1 diagrammatically shows typical *Primura* flowers. The pin has long styles with long stigma papillae and low anthers containig small pollen (Fig. 1a). In contrast, the thrum has short styles with short stigma papillae and high anthers containing large pollen (Fig. 1b). Furthermore

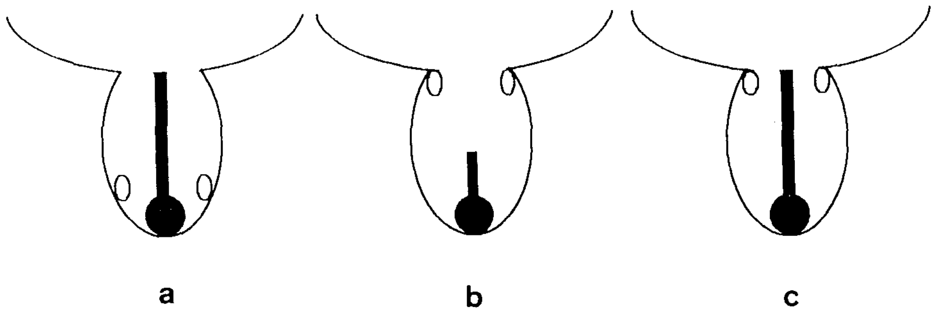

Fig. 1. Diagrams of typical flower morphs of *Primula.*

thrum's anthers contain larger but fewer pollen grains than those of pin.

Darwin (1877) conducted the artificial pollination experiments between the two flower morphs and noted that "ligitimate crosses" (pin × thrum or thrum × pin) are much more fertile in produced capsules and seeds than "illegitimate crosses" (pin × pin or thrum × thrum). The illegitimate crosses cause the sporophytic incompatibility between pollen and stigma/style (Wedderburn and Richards, 1990). But the levels of within-morph fertility show considerable differences between pins and thrums, and between species (Richards and Ibrahim, 1982; Wedderburn and Richards, 1990; Richards, 1993), thus we should examine a relationship between the self-fertility and the flower morphs in all other species.

Distyly of *Primula* is regarded as controlled by a single gene S/s, although in fact the genetic control is more complex which we will see later (Mather, 1950; Dowrick, 1956). The dominant allele S give rise to the thrum morph and the s the pin morph. Consequently, the thrum is usually a dominant heterozygote Ss and the pin is a recessive homozygote ss. Richards (1993) assumes that where 1) G/g controls gynoecial heteromorphy and female mating type, 2) P/p controls pollen size and male mating type and 3) A/a controls anther position. Short-styled thrums are regarded as heterozygotes GPA/gpa and long-styled pins as homozygotes gpa/gpa (Wedderburn and Richards, 1992).

Homostyly

In addition to the two flower morphs the third morph is well-known in *Primula*. The morph is called (long) homostyle which has high thrum-type anthers containing large pollen grains and high pin-type stigma covered in long papillae (Fig. 1c) (Darwin, 1877; Crosby, 1940; Ernst, 1955; Piper et al., 1984; Curtis and Curtis, 1985). Darwin noted seven species as homostyle; *P. elata, P. longifolia, P. mollis, P. scotica, P. sibirica* var., *P. stricta* and *P. verticillata*. Among 426 species of *Primula*, 40 species (about 9 %) are confirmed as partly or completely long homostyle (Richards, 1993). Homostyle is self-fertile and combine the pin's female and the thrum's male characters, thus the seed production is possible by pollen from homostyle and thrum plants.

Homostyle is controlled by S^h that is produced by genetic recombination within the 'S' complex linkage group (Dowrick, 1956; Wedderburn and Richards, 1992). A gene S^h is recessive to thrum's gene S and dominant to pin's gene s. Hence the genotypes of homostyle are heterozygote (S^hs) and/or homozygote (S^hS^h). According to Dowrick's model self-fertile long homostyle should have the linkage group gPA, derived by recombination from a short-styled thrum GPA/gpa. These homostyles were secondarily derived from heterostyles ("secondary homostyles"). In contrast "primary homostyles" are thought to represent survivors from a time before heterostyly evolved in *Primula* (Wedderburn and Richards, 1992).

Wedderburn and Richards (1992) reported that 54 % of homostyle species are polyploid and in contrast only 4 % of heterostyle species are polyploid in *Primula*. And most secondary homostyles are polyploid (Richards, 1993). Self-fertile polyploid homostyles may be buffered against the harmful effects of repeated selfing (Wedderburn and Richards, 1992).

Casual homostylous plants are also recognized in some distylous species. Crosby (1940) suggested that homostyle's self-fertility caused the spread of homostyles in the *P. vulgaris* population if the homostyle homozygote is viable. Piper et al. (1984) reported that in *P. vulgaris* self-compatible homostyle produce more seeds than those of the two morphs.

In spite of the expected advantages, secondary homostyle has remained localized and rare in the populations (Bodmer, 1984; Piper et al., 1984; Curtis and Curtis, 1985; Washitani et al., 1991). The emergence of homostyle relies on infrequent genetic recombination, and besides, the self-fertility would be handicapped by inbreeding depression, a decrease in viability of progeny due to selfing (Charlesworth and Charlesworth, 1979) and limited self-pollination due to protogyny (Bodmer, 1958, 1984).

In any case, the frequency of outcrossing may vary consederably according to the ecological condition and from year to year as a fluctuation of climate (Bodmer, 1984). The long-term studies have to be conducted as stated by Piper et al. (1984).

Pollinator

Evolution and maintenance of distyly and homostyly in *Primula* premise the gene (pollen) flow by mediating insect visitors. Table 1 summarizes visiting insects on the *Primula* flowers in

Table 1. A list of visiting insects on the *Primula* flowers in England and Japan.

Dermaptera
- Forficulidae
  - *Forficula*[2)]

Lepidoptera
- Hasperiidae
  - *Daimio*[5)], *Parnara*[5)]
- Noctuidae
  - *Cucullia*[1)]
- Nymphalidae
  - *Polygonia*[4)], *Vanessa*[1)]
- Pieridae
  - *Gonepteryx*[1)], *Pieris*[1)] (*Artogeia*[4)])

Diptera
- Bombyliidae
  - *Bombylius*[1),2),3),5)]
- Syrphidae
  - *Metasyrphus*[4)], *Rhingia*[2),4),5)], *Symphyta*[4)]

Coleoptera
- Nitidulidae
  - *Meligethes*[1),2),3)]
- Staphylinidae
  - *Eusphalerum*[1),2)], *Tachyporus*[2)]
- Thripidae
  - *Taeniothrips*[1),3)]

Hymenoptera
- Andrenidae
  - *Andrena*[1),3)]
- Apidae
  - *Anthophora*[1),2)], *Apis*[1)], *Bombus*[1),2),3),5)]
- Halictidae
  - *Lassioglossum*[4)], *Halictus*[1)]
- Megachilidae
  - *Osmia*[1)]

1) Flower visitors of *P. elatior*, *P. veris* and *P. vulgaris* (Christy, 1922).
2) Flower visitors of *P. vulgaris* (Marsden-Jones, 1927).
3) Flower visitors of *P. elatior*, *P. veris*, *P. vulgaris* (Woodell, 1960).
4) Flower visitors of *P. sieboldii* (Washitani et al., 1991).
5) Flower visitors of *P. sieboldii* (Takahashi et al., 1992).

England and Japan. Many visiting insects have been observed on British primulas (Christy, 1922; Marsden-Jones, 1926; Woodell, 1960), especially Christy (1922) summarized 57 insect species visiting three British primulas; *P. elatior, P. veris* and *P. vulgaris* based on his observation and earlier records by others.

Woodell (1960) classified visiting insects of British primulas into the following three groups based on their body size and foraging behavior.

1) large insects with long proboscis to reach the nectar.
2) pollen-gathering bees.
3) very small insects which inhabit the flowers.

It is too simple to clarify the variation of food habit and foraging behavior of pollinating insects and sometimes difficult to classify these insects into any of the three groups. In spite of these defects, his classification may be a useful key to explain the role of the insects in the pollination of primulas.

The *Primula* flowers have two food sources; the nectar at the bottom of corolla tube and the pollen near the mouth of it in thrum or deep of it in pin. Pollination of *Primula* is influenced by the insect's posture in foraging, which is decided by body size, mouth part shape and food habit compared with the corolla-tube diameter and anther position relative to stigma in the flower.

The first group includes long-tongued insects like bumblebees (*Bombus*), bee flies (*Bombylius*), syrphids (*Rhingia*), moths and butterflies. These insects may carry the pollen legitimately from pin to thrum and the reverse because the long mouth part can brush and take away the pollen from the anthers of both the morphs. The tubular flowers of *Primula* are adapted for pollination by long-tongued insects.

Darwin (1877) assumed that primrose (*P. vulgaris*) is pollinated by noctuid, *Cucullia verbasci* at night. He concluded that night flying moths were favored as pollinators rather than bee because the latters visited occasionally and stole nectar biting corolla tube in an improper pollinating manner. Dallman (1921) and Marsden-Jones (1926) denied the Darwin's prediction, however his prediction may be accepted by Christy (1922), Woodell (1960) and Boyd et al. (1990).

Since many daytime visiting insects were recognized on the flower of various *Primula* species, the effects of these insects on the pollination should not be neglected. Marsden-Jones (1926) suggested that diurnal insect was more effective as pollinator than nocturnal ones because the plants exposed in the daytime fruited well but those exposed at night produced little capsules in the field.

A main component of the diurnal insects with long-mouth part consists of bumblebees (*Bombus*) and bee flies (*Bombylius*) in Britain (Christy, 1922; Marsden-Jones, 1926; Ornduff, 1979).

Bumblebees, bee flies and butterflies (*Daimio, Parnara*) were recorded as visiting insects on *P. sieboldii* at a mountanous district in Japan (Washitani et al., 1991; Takahashi et al., 1992).

Pollen-gathering bees (e. g., *Andrena, Halictus*) constituting the second group, would also play an important role in pollination. When they creep into the flower to forage, many pollen grains adhere to their body. Especially these insects might transfer the pollen from thrum or homostyle plant to pin's stigma because they tend to gather pollen from the anthers at the mouth of the corolla (Woodell, 1960; Richards, 1984).

The third group is composed of herbivorous insects inhabiting the flower like thripses (*Taeniothrips*) and small beetles (*Meligenthes*) (Christy, 1922; Woodell, 1960). Darwin concluded that these insects might promote the self-pollination.

Cross-pollination of *Primula* would occur uneffectively by the paucity of visiting insects during the flowering period in some natural habitats. Washitani et al. (1991) investigated the floral morphs, seed production and pollination in distylous *P. sieboldii* whose habitat is surrounded by urban area in Japan. They reported that insects were not observed except a few butterflies (*Polygonia* and *Artogeia*) and casual self-compatible homostyle flowers preserved their high fertility independent of pollinator activity.

Richards (1993) suggested that self-fertile homostyle species have tendency to distribute the arctic and alpine region where the climate is very unreliable at flowering and *Primula* species can not rely on insects to the cross-pollination. The evolution of homostyly has been driven by a fitness advantage associated with selfing in these harsh habitats.

It is generally believed that insects affect the mating system of *Primula* by mediating pollination. But as Christy (1922) and Woodell (1960) stated, contribution of the insect visitors to the pollination have not been sufficiently clarified. Pollination efficiency of the insects in the *Primula* species have only been estimated by inconsecutive observations on visiting insects and their foraging mode.

Quantitative parameters of pollination by each insect, for example, visiting frequency in the field, number and morph of pollen grains on the insect bodies and stigmas should be examined in order to elucidate the pollinator efficiency and actual pollen flow of *Primula*. The most studies on the mating and pollination systems of *Primula* are regionally confined to Europe, the critical studies in eastern Asia will provide us invaluable information concerning the evolution of heterostylous flowers in the genus Primula.

We thank Yukiko Ejima for her critical comments on the manuscript.

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Miyabea 2 : 19-26 (1994)

Distyly in *Primula takedana* Tatewaki (Primulaceae) —population composition, flower morphology, pollen size and ovule number

Takahiro Tsukui, Yukiko Ejima and Hideki Takahashi

Primula takedana Tatewaki is a perennial herb with thick creeping ligneous rhizomes, reniform-orbicular leaves having brownish pilose hairs, and bell-shaped white flowers. It is a localized and endemic species to the Teshio district, northern Hokkaido (Tatewaki, 1928; Tatewaki and Igarashi, 1971). Kitamura (1957) thought that *P. takedana* is related to *P. jesoana* and is a serpentinimorphosed species derived from the latter. But Inagaki and Toyokuni (1966) noted that this is a well defined species differing from any other Japanese species. They recognized new section *Takedana* composed of only this species (Inagaki and Toyokuni, 1966). Inoue (1977) noted that *P. takedana* is related to *P. hidakana*, and Fenderson (1986) and Richards (1993) regarded the former species as included in section *Reinii* together with *P. hidakana, P. reinii* and *P. tosaensis*. Recently Yamazaki (1993) separated new section *Hidakanae* Yamazaki including the two species; *Primula hidakana* and *P. takedana*, from section *Reinii* (see Table 2 in Takahashi and Tsukui, 1994).

Primula species generally segregate for two self-incompatible but inter-fertile flower morphs; the long-styled "pin" and the short-styled "thrum", and the intermorph pollen flow depends on insect visitors (Darwin, 1877). The mating system of primulas will be certainly associated with the pollinator-insect fauna and pollinator behavior which are related to various ecological factors of the habitat (Ornduff, 1980; Piper et al., 1984; Boyd et al., 1990; Washitani et al., 1991). *Primula takedana* is restricted to open serpentine stony areas of northern Hokkaido and no other *Primula* species grow sympatrically. This species is regarded as a relatively poor competitor with peculiar habitat preference, therefore it is to be expected that special selection pressures should accompany the development of specialized mating system.

Most descriptive floras have noted the distyly state in the flowers of the Japanese *Primula* (Kitamura and Murata, 1961; Ohwi, 1978; Yamazaki, 1981; Ohwi and Kitagawa, 1983), but all these do not include any detailed description on the different morphological characters of the distylous flowers. As the first step to make sure of the mating system of *P. takedana* in the wild, population composition of the pin and the thrum plants, flower morphology, pollen size and ovule number were analyzed.

MATERIALS AND METHODS

Field sites—The study area is located at Teshio Experiment Forest, Hokkaido University, northern Hokkaido (Fig. 1). Three populations from 17-, 30- and 35-rinpan of Experiment Forest were examined. Figures 2 and 3 show collection sites of *Primula takedana*. From preliminary observation on the field populations, the two flower morphs were recognized; the pin with the stigma sitting at the mouth of the corolla and the thrum with the anthers attached near the mouth of the corolla (Fig. 4). The ratio of pin to thrum plants was estimated in each population based on several quadrats (1 × 1 m) arranged in crossing a population from upper to lower slope. Associated

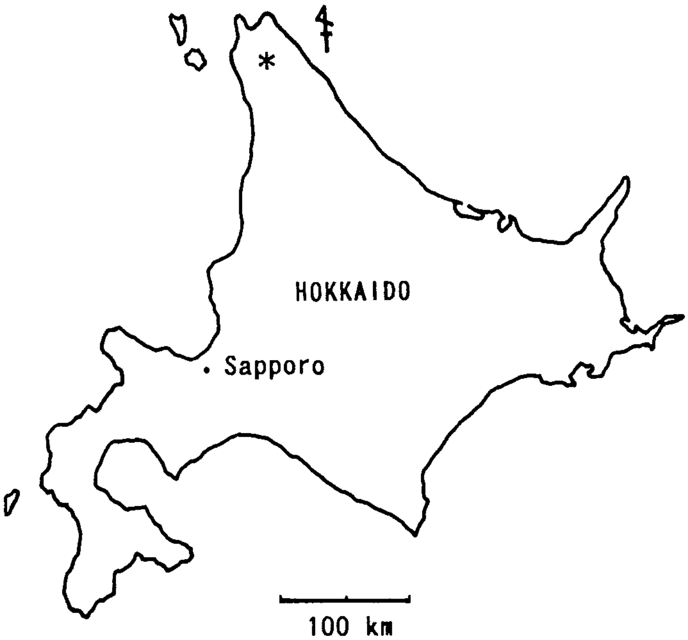

Fig. 1. Study site (*) of *Primula takedana* in Hokkaido.

Fig. 2. Habitat of *Primula takedana* on the serpentine slope beside the river.

plant species were also recorded.

Measurements-Flower specimens were randomly collected from the three sites in order to examine the detailed floral characters of the two flower morphs. At least three flowers were sampled from each plant, and fixed with FAA (5 parts stock formalin : 5 parts glacial acetic acid : 90 parts 70 % ethanol). In total we examined 121 flowers, which were classified into pin and thrum. The following six characters were measured with a stereoscope: 1) corolla tube length, 2)

Fig. 3. *Primula takedana* plants and a quadrat (1×1 m) on the serpentine slope.

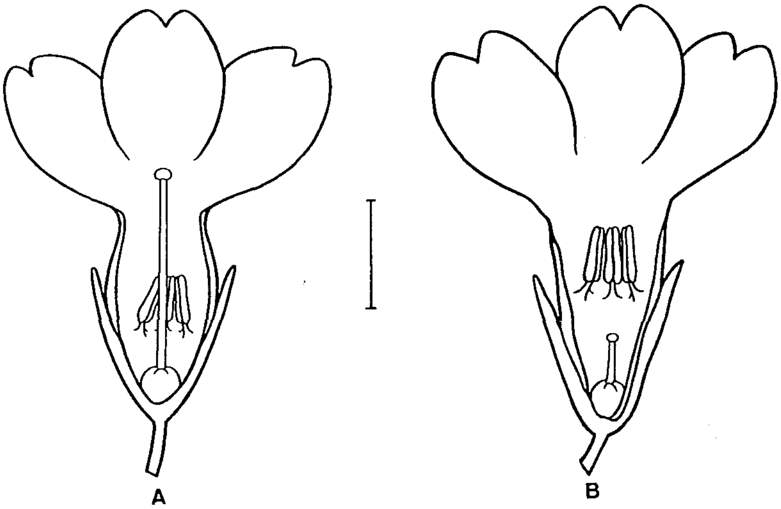

Fig. 4. Longitudinal sections of distylous flowers of *Primula takedana*. A. long-styled flower (pin), B. short-styled flower (thrum). Scale bar=5 mm.

stigma height (length from corolla base to the top of stigma), 3) style length, 4) stigma width, 5) anther height (length from corolla base to the top of anther), 6) anther length.

For measurement of pollen size, pollen grains from fixed anthers were stained with 1 % cotton blue in lactophenol solution and the diameter of pollen grains was measured with a microscope using ocular micrometer. Using young undehiscent capsules, ovule number per flower was determined.

RESULTS

Field study-Primula takedana grows on moist serpentine sandy slopes (an inclination of about 30 degrees) by the streams and on the heads of valleys. Characteristic serpentine plants; *Berberis amurensis, Crepis gymnopus, Euphorbia sieboldiana* var. *montana, Japonolirion osense* and *Viola sachalinensis* var. *alpina*, were included among the associated plants (Table 1). The ratio of pin to thrum plants was not significantly different from 1:1 in the two collection sites (17-and 30-rinpan), but significantly different in 35-rinpan ($P<0.005$). Significantly more thrum plants (56 %) occur in this population (Table 2).

Flower morphology-All measurements differed significantly between the two flower morphs ($P<0.001$; Table 3). On average the stigma position of the pin was 2.2 times as high as that of the thrum and the style of the pin was 2.8 times as long as that of the thrum. The ranges of these two character measurements did not overlap between the two morphs. Although there was overlap of

Table 1. Associated plant species on the *Primula takedana* habitat.

Alnus maximowiczii Call.
Aruncus dioicus (Walt.) Fern. var. *tenuifolius* (Nakai) Hara
Berberis amurensis Rupr.*
Carex blepharicarpa Franch.
Crepis gymnopus Koidz.*
Drosera rotundifolia L.
Euphorbia sieboldiana Morr. et Decne var. *montana* Tatewaki*
Geranium erianthum DC.
Geum pentapetalum (L.) Makino
Ilex crenata Thunb. var. *paludosa* (Nakai) Hara
Japonolirion osense Nakai*
Ledum palustre L. subsp. *diversipilosum* (Nakai) Hara
Miscanthus sinensis Andress
Parnassia palustris L. var. *multiseta* Ledeb.
Petasites japonicus (Sieb. et Zucc.) Maxim. subsp. *giganteus* (Fr. Schm.) Kitam.
Sanguisorba tenuifolia Fisch. ex Link var. *alba* Trautv. et Mey.
Sasa sp.
Solidago virgaurea L. subsp. *leiocarpa* (Benth.) Hulten forma *japonalpestris* Kitam.
Spiraea betulifolia Pall.
Viola sachalinensis H. Boiss. var. *alpina* Hara*

* Plants characteristic to serpentine rock areas.

Table 2. Pin and thrum composition in the three populations examined.

Place	Pin	Thrum	Total	χ^2 for deviation from 1 : 1	P
17-rinpan	241	255	496	0.39	>0.05
30-rinpan	130	166	296	4.37	>0.025
35-rinpan	230	295	525	8.04	<0.005

Table 3. Comparison of floral characters between the two morphs of *Primula takedana*. All values in mm. $\bar{X}$, mean; SD, standard deviation; N, sample size.

Character (t value and significance level)	Thrum (N=65) $\bar{X}\pm$SD (range)	Pin (N=56) $\bar{X}\pm SD$ (range)
Corolla tube length (t_{119}=4.62, $P<0.001$)	10.4±1.4 (7.7−13.3)	9.3±1.2 (5.6−12.7)
Stigma height (t_{119}=43.15, $P<0.001$)	4.0±0.5 (3.3−5.1)	8.9±0.8 (7.1−10.9)
Style length (t_{119}=50.51, $P<0.001$)	2.8±0.4 (2.1−3.5)	7.7±0.6 (5.9−9.2)
Stigma width (t_{119}=12.35, $P<0.001$)	0.5±0.1 (0.3−0.8)	0.7±0.1 (0.5−1.1)
Anther height (t_{119}=28.91, $P<0.001$)	8.2±0.7 (6.8−9.7)	5.1±0.4 (4.0−6.1)
Anther length (t_{119}=5.67, $P<0.001$)	2.4±0.3 (1.7−3.0)	2.1±0.3 (1.3−2.6)

Table 4. Comparison of ovule number per flower between the two morphs. $\bar{X}$, mean; SD, standard deviation; N, sample size. The mean ovule number for the thrum and pin flower not significantly different.

	Thrum (N=93)	Pin (N=99)
Ovule number	$\bar{X}\pm$SD (range)	$\bar{X}\pm$SD (range)
	32±7 (12−48)	32±7 (19−54)

the measurement ranges in the following four morphological characters, differences of the means were significant between the two morphs ($P<0.001$). Average stigma width of the pin was 1.4 times as broad as that of the thrum. On the other hand, the thrum flowers produce higher and longer anthers than the pin flowers. Corolla tube of the thrum is significantly longer than that of the pin.

Pollen size and ovule numbers-Figure 5 shows pollen grain size distributions for the two morphs. There was substantially no overlap in the distributions. The mean pollen grain size of the

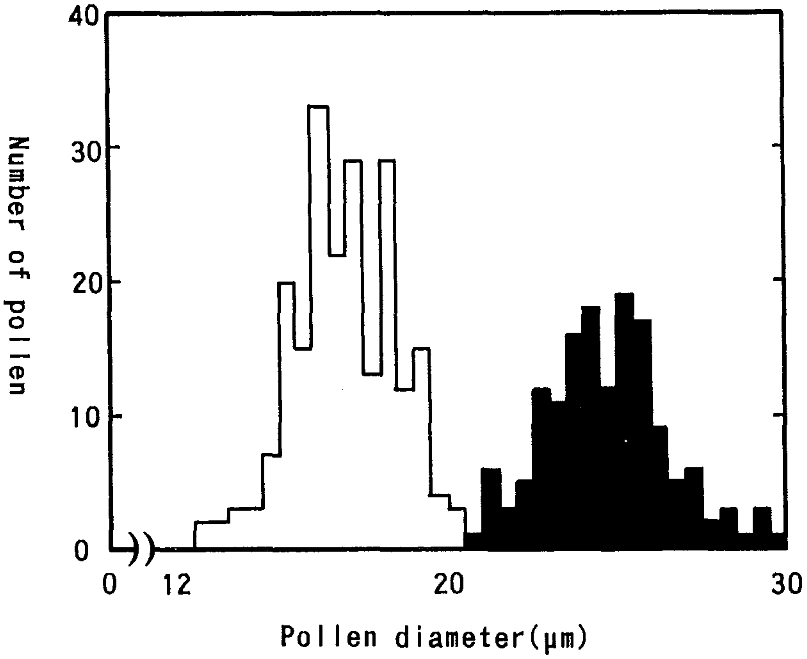

Fig. 5. Pollen grain size distributions for the two flower morphs. Open bars indicate the thrum's pollen grains and solid ones the pin's grains. The mean of pollen grain size from the thrum ($\bar{X}=24.4$ μm, SD=1.8, $N=150$) was significantly larger than that from the pin ($\bar{X}=16.7$ μm, SD=1.5, $N=210$) ($P<0.001$).

thrum (24.4 μm) was significantly larger ($P<0.001$) and 1.5 times as long as that of the pin (16.7 μm). Therefore pollen grain volume of the thrum is about 3.3 times as much as that of the pin. Pollen production per flower was not measured in this study.

Ovule number per flower is given in Table 4. There was no difference in ovule number between the two morphs (mean 32 ovules in each flower morph).

DISCUSSION

The floral features reveal that *P. takedana* is a distylous species, like most *Primula* species (91 %, according to Richards, 1993). The pin flower has a high stigma at the top of corolla tube and the anthers at the middle of corolla tube. In the thrum flower the sites of stigma and anthers take reciprocal positions. Until now homostyle which has high thrum-type anthers and high pin-type stigma have not been found in this species.

The reciprocal positioning of the sites of anthers and stigma of this species is considered to be preventive of self-pollination and efficient to cross-pollination if the pollen travel relies on the insect visitors. Artificial pollination experiment within and among the two flower morphs should be conducted because in fact the levels of within-morph fertility show considerable differences between pins and thrums, and between species (Wedderburn and Richards, 1990; Richards, 1993).

We currently cannot explain why significantly larger number of the thrum plants (56 %) occur in one population. Richards and Ibrahim (1982) noted that the departures from 1 : 1 ratios of pin to thrum are small (from 44 to 54 % of plants as pin) and either morph can predominate in *P. veris* and *P. vulgaris*. The ratio revealed in this study is not so different from the measurement range of these two species. Mortality, clonal growth, seedling survivorship, seed setting, pollinator efficiency of the two morphs should be also examined in the natural habitats of this species.

Christy (1922) noted that corolla tubes of the thrum flowers are, on average, considerably deeper than those of the pin flowers in British primulas. But afterwards this fact had been overlooked by most botanists, and was not supported by Mazer and Hultgård (1993) in northern European heterstylous *P. farinosa*. A significant difference of corolla tube length between the two morphs was detected in *P. takedana* and it is longer in the thrum than the pin as stated by Christy (1922).

Longer stigma papillae in the pin have been reported in some *Primula* species; *P. sinensis* (Mather, 1950) and *P. obconica* (Dowrick, 1956), and it is regarded as the case in all heterostylous *Primula* species (Richards, 1993). In *P. takedana*, significant wider stigma surface in the pin was newly recognized. This character may enhance the pollen number accepted by the pin flowers.

In addition to the flower morphology, primary sexual characters (pollen grain volume, pollen production, and ovule production) should be considered. Although pollen production per flower was not measured in this study, pollen size of thrum was significantly larger than that of pin (Fig. 5). This size difference of pollen between the two flower morphs in *Primula* has been recorded by many botanists; e. g., Mather (1950) for *P. sinensis,* Ernst (1955) for *P. floribunda,* Dowrick (1956) for *P. obconica,* Washitani et al. (1991) for *P. sieboldii* and Al Wadi and Richards (1992) for *Primula* subgenus *Sphondylia.* Generally the pins produce smaller but more pollen grains than the thrums in heterostylous species (Mazer and Hultgård, 1993). This negative relationship between pollen number and volume has been supported in some heterostylous *Primula* species; e. g., in *P. vulgaris* (Ornduff, 1979; Piper and Charlesworth, 1986), *P. veris* (Ornduff, 1980) and *P. farinosa* (Mazer and Hultgård, 1993).

Ovule number does not differ between the pin and the thrum in *P. takedana.* Although there are not much data of ovule number for *Primula,* no difference of ovule number between the two morphs has been also recorded in *P. vulgaris* (Ornduff, 1979) and *P. farinosa* (Mazer and Hultgård, 1993). It seems that there is a distinct difference of male production between the pin and thrum but not of female production. Interestingly, ovule number per flower of *P. takedana* (average 32) seems to be much lower than those of northern European *Primula* species studied by Mazer and Hultgård (1993)(average about 75-175) and 52 species of *Primula* studied by Wedderburn and Richards (1990) (range 50-100).

In the present study, a dipteron of Bibionidae was collected on a pin flower and it will be certainly one of the effective pollinators for this species. In order to clarify the mating system of *P. takedana,* the pollen flow mediated by pollinators between the two flower morphs should be assessed in the natural habitats and artificial pollination experiment with and among the two morphs should be conducted in the garden.

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BOOK REVIEWS

Flora of Japan vol. IIIa, Angiospermae-Dicotyledoneae: Sympetalae (a). K. Iwatsuki, T. Yamazaki, D. E. Boufford and H. Ohba (eds.), 496pp., Kodansha Ltd., Tokyo. 1993. ISBN4-06-153420-3, ¥50,000.

Since Ohwi's "Flora of Japan in English" in 1963, descriptive floras of Japan in English have not been published. There are over 100 new names proposed in this book and the plants of the Ryukyu and Bonin Islands are newly incorporated. The latest taxonomic treatment is found, especially in Ericaceae, Symplocaceae, Scrophulariaceae and so on. This book is the same title as Ohwi's "Flora of Japan", but the contents are completely different and sufficiently revised and up-to-date. This Flora will be certainly a standard of Japanese vascular plants flora, so I hope the following volumes will be published accodring to original plan.

"Flora of Japan" is composed of four volumes, seven fascicles in total. A fascicle is published each year and the last fascicle will be published in 1999. Next volume IIIb composed of the latter half of Sympetalae will be published on July, 1994. Over 40 taxonomists contribute to the "Flora of Japan".

The Flora covers all species found in Japan; the southern Kuriles, Hokkaido, Honshu, Shikoku, Kyushu, and the Ryukyu and Bonin islands. This first fascicle (vol. IIIa) include the first half of Sympetalae according to the Engler system. Families treated in this fascicle are arranged here in alphabetical order: Acanthaceae, Adoxaceae, Apocynaceae, Asclepiadaceae, Bignoniaceae, Boraginaceae, Buddlejaceae, Callitrichaceae, Campanulaceae, Caprifoliaceae, Clethraceae, Convolvulaceae, Diapensiaceae, Dipsacaceae, Ebenaceae, Empetraceae, Ericaceae, Gentianaceae, Gesneriaceae, Globulariaceae, Goodeniaceae, Lamiaceae(Labiatae), Lentibulariaceae, Loganiaceae, Menyanthaceae, Myoporaceae, Myrsinaceae, Oleaceae, Orobanchaceae, Phrymaceae, Plantaginaceae, Plumbaginaceae, Polemoniaceae, Primulaceae, Pyrolaceae, Rubiaceae, Sapotaceae, Scrophulariaceae, Solanaceae, Styracaceae, Symplocaceae, Theligonaceae, Trapellaceae, Valerianaceae, Verbenaceae. (Hideki TAKAHASHI)

Proceedings of first symposium on joint Siberian permafrost studies between Japan and Russia in 1992. M. Fukuda (ed.), 112 pp., Institute of Low Temperature Science, Hokkaido University, Sapporo, 1993.

The first symposium on joint Siberian permafrost studies between Japan and Russia was held on 27th January, 1993 at the Institute of Low Temperature Science (ILTS), Hokkaido University, Sapporo Japan. In total 25 papers are compiled in the proceedings and some botanical papers are included. They are carbon storage and carbon dioxide budget in forest ecosystem, dendroclimatological analysis, photosynthesis of woody species, pteridophytes and spermatophytes flora analysis, leaf survivorship of *Ledum palustre*, and so on. The proceedings give us a good introduction to physical and botanical nature of Siberia, and we can know a recent movement of joint studies between Japan and Russia. (Hideki TAKAHASHI)

Primula sieboldii
サクラソウ

Primula jesoana var. *pubescens*
エゾオオサクラソウ

Primula hidakana
ヒダカイワザクラ

Primula takedana
テシオコザクラ

Plate 5

YASUKO SUDA

Primula japonica
クリンソウ

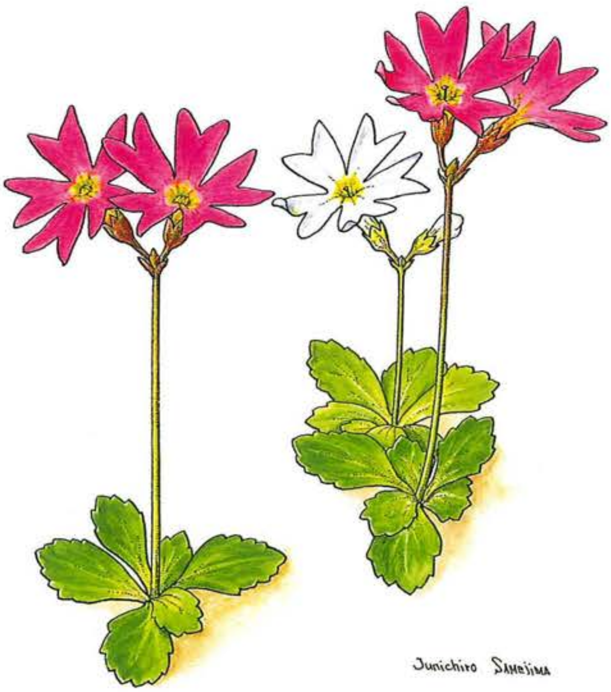
SAYOKO MATSUSHIMA

Primula sorachiana
ソラチコザクラ

Primula modesta var. *matsumurae*
レブンコザクラ

Plate 8 SAYOKO MATSUSHIMA

Primula yuparensis
ユウバリコザクラ



Primula cuneifolia
エゾコザクラ