The Genus *Circaea* (Onagraceae) in Japan

David E. BOUFFORD*

D. E. ブーフォード：日本産ミズタマソウ属

The genus *Circaea* (Onagraceae) has been a source of confusion in Japan, resulting in varying taxonomic treatments of the genus by different authors (MAEKAWA et al., 1962; HARA, 1934, 1954; OHWI, 1965; KITAMURA & MURATA, 1977). Part of the problem has been due to the failure to recognize two distinct subspecies within *C. alpina*, and part to the lack of a full appreciation of the many, often abundant hybrids in the genus, even though several of these were discussed by HARA (1959). The following discussion and treatment is based on extensive field and herbarium studies in Japan in 1977 and on subsequent studies of Japanese collections in American and European herbaria.

Circaea consists of seven species and an additional seven subspecies with the greatest diversity and center of distribution in eastern Asia, where 11 of the 14 taxa occur. Five species and an additional subspecies occur in Japan. Distributional patterns of individual taxa of *Circaea* are highly interesting and are similar to those found in other groups of plants. FERNALD (1915) was the first to point out that the closely related *C. lutetiana* subspp. *canadensis* and *quadrisulcata* exhibit the classic pattern of disjunction between eastern Asia and eastern North America; this was later discussed by HARA (1939, 1952). It is now known that the Asian *C. lutetiana* subsp. *quadrisulcata* is not restricted to eastern Asia but extends westward to eastern Europe (SKVORTSOV, 1979; BOUFFORD, 1982). On the Asian mainland it is common in northeastern China, North Korea and the Soviet Far East. From here it extends westward between 50°–60° N. latidude to the vicinity of Moscow where it intergrades with *C. lutetiana* subsp. *lutetiana*. Except for these intergrading populations *C. lutetiana* subsp. *quadrisulcata* is most similar to subsp. *canadensis* of eastern and central North America and differs from it only in the absence of bracteoles and in the generally smaller floral parts.

Circaea cordata and *C. mollis* represent examples of a Himalayan-Sino-Japanese distribution and their ranges match closely some of the other examples of this pattern pointed out by HARA (1966) such as *Hydrocotyle nepalensis* HOOKER, *Helwingia japonica* (THUNB.) DIETRICH, *Peracarpa carnosa* (WALL.) HOOK. f. & THOMSON and others. *C. erubescens* belongs to the Sino-Japanese pattern of distribution and ranges from southwest-

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* The Arnold Arboretum of Harvard University, 22 Divinity Ave., Cambridge, MA 02138, U. S. A.

ern China in Yunnan and Sichuan to South Korea and all of the major islands of Japan. Both *C. cordata* and *C. erubescens* occur also on Taiwan. *C. alpina* subsp. *alpina* is circumboreal in distribution and in Japan it extends southward from near sea level in Hokkaido to the high mountains of Yaku-shima. On the Asian mainland it occurs in northeastern China, Korea, northern Mongolia and from the Soviet Far East on Kamtchatka to the Atlantic Ocean. In North America it ranges across the northern United States and southern Canada to western Canada and Alaska and southward in the Appalachian and Rocky Mountains. It is replaced in the Himalayas by the closely related *C. alpina* subsp. *micrantha* (SKVORTSOV) BOUFFORD. *C. alpina* subsp. *caulescens*, which occurs as disjunct populations in Japan, exhibits the most interesting distribution pattern. It is fairly common in northeastern China, Korea and the Soviet Far East but then occurs as small, disjunct populations in the Soviet Union south of Lake Baikal, in the Altai Mountains and in the Caucasus Mountains! It has also been collected in north central Mongolia. The range of this subspecies in the Soviet Union has been mapped by SKVORTSOV (1979), who also pointed out that this rare type of distribution is similar to that of *Osmorhiza aristata* (THUNB.) MAKINO & YABE.

The species of *Circaea* in Japan can be placed in two, clearly defined groups. One group, consisting of *C. cordata, C. erubescens, C. lutetiana* subsp. *quadrisulcata* and *C. mollis,* is primarily outcrossing, has bilocular ovaries and fruit and lacks tuberous thickenings on the rhizomes. The other group, containing only *C. alpina,* is mainly self pollinating, has unilocular ovaries and fruits and has rhizomes terminated by tuberous thickenings. *C. repens* WALL. ex ASCH. & MAG. of the Himalayan region and the mountains of southwestern and south central China is intermediate between the two groups in being unilocular with a trace of a second locule and appearing to be outcrossing. This taxon provides a link between the two groups and thus precludes the formal recognition of two distinct infrageneric taxa.

Reproduction: Two main types of sexual reproduction are found in *Circaea.* The primarily inbreeding *C. alpina* often sheds pollen directly on the stigma before the buds open (RAVEN, 1963; HABER, 1977; BOUFFORD, 1982) especially under unfavorable weather conditions or when the air temperature is below about 16.5°C. During favorable weather or at higher temperatures the buds may open as, or just after, the pollen is shed, allowing for some outcrossing. All other species are primarily outcrossing and shed their pollen only after the flowers open and when the stigma and stamens are widely separated from each other. The chief visitors to the flowers of *Circaea* in Japan are Syrphidae (Diptera) and Halictidae (Hymenoptera). These same insect groups are also the major visitors to *Circaea* in North America (BOUFFORD, 1982) and Europe (KUGLER, 1938).

Even though *Circaea alpina* is primarily self pollinating, some outcrossing occurs. This is evidenced by the abundant hybrids between it and *C. lutetiana* in North America and Europe and between *C. alpina* and *C. erubescens* in Japan. With the exception of *C. cordata,* all of the outcrossing species exhibit an adaption to insect pollination in the elevated, ring-like nectary which protrudes beyond the opening of the floral tube. The exserted nectary is well suited to visits by Syrphidae which alight on the flowers to lick nectar. In doing so they make frequent contact with the anthers and stigma and no doubt transfer pollen from one plant to another. Halictidae usually gather only pollen from the flowers of *Circaea*, but often come in contact with both anthers and stigmas and probably also serve as pollinating agents.

In *Circaea cordata* and *C. alpina* the nectariferous tissue is located at the base of the floral tube. *C. alpina* produces only minute quantities of nectar. However, the flowers of *C. alpina* subsp. *alpina* open on erect or ascending pedicels before the raceme elongates, and the several flowers that are open at one time are held in a cluster at the apex of the inflorescence, similar to most Cruciferae. This clustering of several flowers may provide enough nectar to make it worthwhile for visits by some insects. In *C. alpina* subsp. *caulescens* and all of the bilocular species of *Circaea*, the flowers open after the raceme elongates and after the pedicels drop to a spreading position. Each flower then acts as a separate visitation unit for insects.

Even though all species of *Circaea* exhibit abundant fruit set, it may be that single colonies represent only one or a few different individuals. All species produce abundant rhizomes and there is no doubt that vegetative reproduction is one of the major means by which *Circaea* populations increase in size. New populations may be started when pieces of rhizomes from the parent plant are carried into new areas by natural agencies or through the actions of man. RAVEN (1963) has pointed out that in the British Isles the highly sterile *C.* × *intermedia* occurs as a garden weed well south of its main area of distribution, suggesting that the rhizomes were probably introduced with soil. Naturally distributed plants can be seen in the morphologically similar hybrids which occur for several kilometers along streams in the absence of one or both parents. A particularly good example of such a population occurs along the Okoppe-gawa River on Hokkaido. Here, *C.* × *dubia* extends for several kilometers along the river bank, growing in the zone where debris is deposited during high water. All of the hybrids within this population are morphologically similar suggesting that they were the result of a single hybridization. Evidently rhizomes from the original hybrid colony have been transported by water to the sites where the plants are now found. If, on the other hand, these plants were the result of multiple hybridizations it would be expected that they would show a greater degree of variability. Despite considerable searching in this area I was unable to locate either of the parental species, *C. cordata* or *C. erubescens*. It is most likely that these hybrids were formed sometime in the past, far upstream from where the hybrids now occur and where the parents once, or still do, grow together. The high degree of variation within individual hybrid taxa, however, indicates that they have been produced on numerous occasions in widely scattered parts of Japan.

Hybridization: Seven hybrid combinations are known to occur naturally in Japan (fig. 1). In addition, a single collection from Miyagi Prefecture, Narugo, Kawatabi,

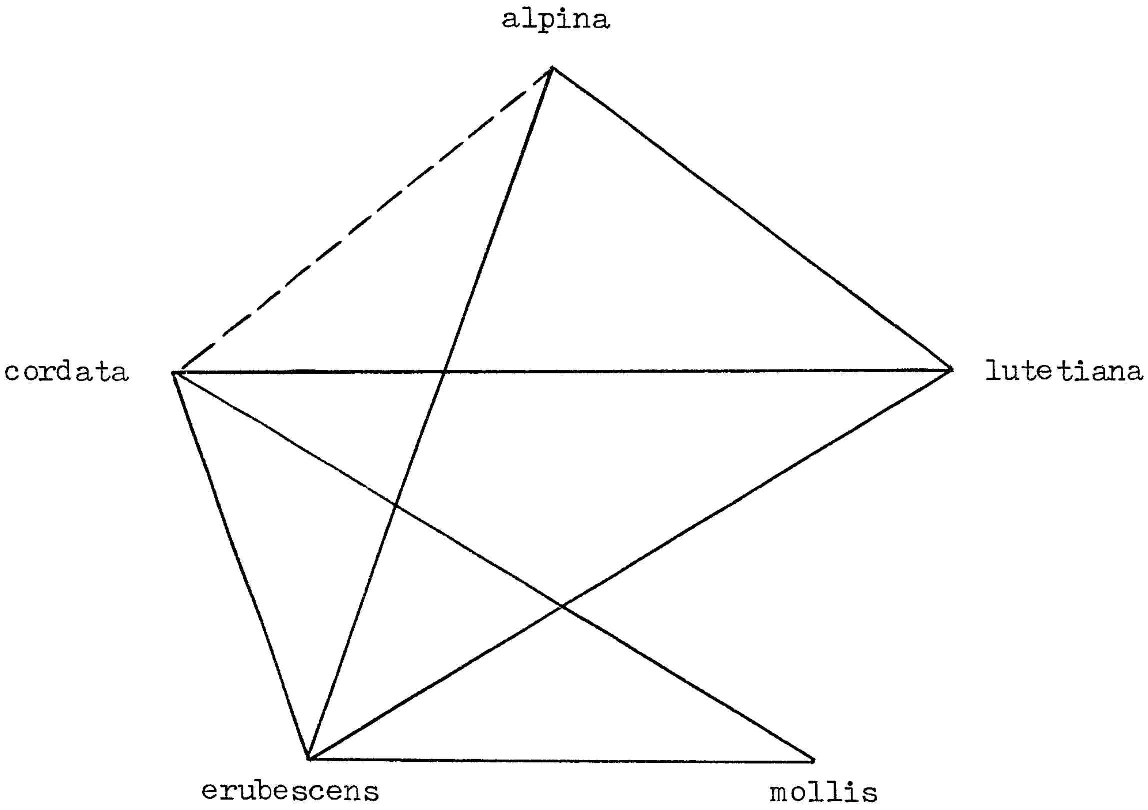

Figure 1. Hybridization in the genus *Circaea* in Japan. Known hybrids are represented by solid lines. The broken line represents a possible hybrid.

K. Sugawara s. n. (MO), may represent a hybrid between *Circaea alpina* and *C. cordata.* This combination is known to occur in China, but is very rare. Hybrids between *C. alpina* and *C. mollis* and between *C. lutetiana* subsp. *quadrisulcata* and *C. mollis* should be sought. The latter is certainly to be expected in Hokkaido where the ranges of the two species overlap. I never saw *C. alpina* and *C. mollis* growing close to each other and perhaps they are separated from each other altitudinally throughout their entire range. Hybrids involving *C. alpina* subsp. *caulescens* may not be morphologically different from those involving *C. alpina* subsp. *alpina* and it might be impossible to determine which subspecies was the parent.

Hybrids in *Circaea* are completely intermediate between the parents morphologically and are highly sterile. The lack of fruit set on plants in the field is a good indication of hybrid origin. The ovaries abort shortly after anthesis leaving a naked inflorescence axis topped by recently opened flowers and buds. Pollen in hybrids in highly sterile and rarely are more than 10% of the pollen grains well filled. Hybrids involving *C. alpina* often have 98–100% unfilled or shriveled pollen (Cooperrider, 1962; Raven, 1963; Haber, 1977; Boufford, 1982). In contrast, pollen in the parents is usually more than 85% fertile and fruit set is nearly 100%.

Circaea hybrids usually occupy habitats intermediate between those of the parents. They are often found in disturbed places where other vegetation has been removed or reduced, such as along streams. Once established, hybrid colonies vigorously increase in size through vegetative reproduction.

Taxonomic Treatment

Circaea L., Sp. Pl. 8. 1753. ASCH. & MAG., Bot. Zeit. **28**: 47. 1870. H. LEV., Bull. Geogr. Bot. **22**: 217. 1912. GAGNEPAIN, Bull. Soc. Bot. France **16**: 39. 1916. HAND.-MAZZ., Symb. Sin. **7**: 602. 1933.

Erect, perennial, rhizomatous herbs. Leaves opposite, petiolate, becoming alternate, sessile and bractlike at the base of the inflorescence, denticulate to serrate or occasionally subentire. Inflorescence a raceme or a branched panicle of racemes, terminal on the main stem and sometimes at the tips of the uppermost, short axillary branches. Flowers 2-merous, the stamens opposite the sepals. Petals (in the Japanese plants) notched or cleft at the apex. Style elongate, terminated by a bilobed stigma. Ovary uni- or bilocular with a single seed in each locule. Fruit an indehiscent capsule covered with stiff, uncinate hairs (unique in the Onagraceae). Floral tube deciduous after anthesis. Pollen shed as monads, with viscin threads. Chromosome number, $n=11$.

A genus of seven species and an additional seven subspecies. Circumboreal in moist deciduous and coniferous forests, rarely in broad leaved evergreen forests, from sea level to 5000 meters. Six taxa in Japan. The synonymy under each species deals only with names which have been applied directly or indirectly to Japanese plants. For complete synonymy and full descriptions of the taxa see BOUFFORD (1982).

Care should be taken when collecting *Circaea* to facilitate identification. Underground parts should be carefully collected and fruit shape and sculpturing, which are sometimes obscured in pressing, should be noted. The presence or absence of an exserted nectary is also critical and can be observed most easily in fresh material.

Key to the Species

1. Ovaries and fruit bilocular; rhizomes not terminated by tuberous thickenings..............................2
  2. Nectary wholly included, not projecting as a cylindrical or ring-like disc above the opening of the floral tube; axis of the inflorescence with short falcate, glandular and long, straight or slightly curved patent hairs ....1. *C. cordata*
  2. Nectary exserted beyond the opening of the floral tube as a cylindrical or ring-like disc; axis of inflorescence glabrous or glandular, sometimes with short falcate hairs, never with long, straight or slightly curved patent hairs 3
    3. Petals obovate to depressed broadly obovate, with the apical notch 1/4 or more the length of the petal; axis of inflorescence pubescent; mature capsules with deep longitudinal grooves and broadly rounded ridges 4
      4. Stem pubescent, often densely so, with falcately recurved hairs; leaves cuneate, rarely rounded at the base; inflorescence subglabrous or with glandular and falcately recurved hairs...2. *C. mollis*
      4. Stem glabrous; leaves rounded to subcordate at the base; inflorescence densely glandular pubescent, without falcately recurved hairs..................................3. *C. lutetiana* subsp. *quadrisulcata*
    3. Petals obtrullate, with the apical notch 1/5 or less the length of the petal; axis of inflorescence

glabrous; mature capsules without deep grooves and rounded ridges ....4. *C. erubescens*

1. Ovaries and fruits unilocular; rhizomes terminated by tubers ....5. *C. alpina*

1. **Circaea cordata** Royle, Illustr. Bot. Himal. 211, t. 43, fig. 1, a-i. 1834. Type: India, Kotgarh, *J. F. Royle s. n.* (Lectotype: LIV; photograph MO. Possible isolectotype: K). *C. mollis* sensu Maximowicz, non Sieb. & Zucc., Prim. Fl. Amur 105. 1859. *C. cardiophylla* Makino, Bot. Mag. Tokyo **20**: 42. 1906. Type: Japan, Honshu, Tokyo Prefecture, Dokan-yama, *T. Makino s. n.* (Lectotype: MAK 6904). *C. kitagawae* Hara, J. Jap. Bot. **10**: 595. 1935. Type: China, Hebei (Hopeh), Ch'engte ("Manchuria, Jehol"), between Hsing-lung-t'ang and Pei-ying-fang, 27 August 1933, *T. Nakai, M. Honda & M. Kitagawa s. n.* (Holotype: TI).

Circaea cordata is easily distinguished from other species of the genus by the long, spreading hairs on nearly all parts of the plant. From other bilocular species it can be recognized by the absence of an exserted nectary. The flowers of *C. cordata* are more closely spaced than in *C. erubescens, C. lutetiana* and *C. mollis* and are borne on short (0.7–2.8 mm long), clustered pedicels at the apex of the raceme. The fruits are obliquely obovoid to lenticular and dorsally flattened, rounded at the apex and either truncate or, more commonly, obliquely rounded to the pedicel. *C. cordata* ranges from Japan and southeastern Siberia through Korea and northeastern China southwestward to Sichuan and Yunnan, China, and Assam, India; Nepal; northwestern India to Kashmir and Pakistan; Taiwan. Chromosome number, $n=11$.

Hybrids between *Circaea cordata* and *C. erubescens* are *C.* × *dubia* Hara, described in Bot. Mag. Tokyo **50**: 306. 1936. Type: Japan, Hokkaido, Hidaka-shicho, forests near Shoya, 11 August 1934, *H. Hara* (Holotype: TI). These plants are morphologically intermediate between the two parents. A short, ring-like, exserted nectary is present and there are at least a few, long, straight or slightly curved hairs on some part of the plants, especially on the buds. This is the most common *Circaea* hybrid in eastern Asia. In Japan it is known from scattered localities on Hokkaido and Honshu.

Hybrids between *Circaea cordata* and *C. lutetiana* subsp. *quadrisulcata* are *C.* × *skvortsovii* Boufford (Ann. Missouri Bot. Gard. in press. Type: Sakhalin, Moneron Island (Kaibato) 16 August 1973, *L. Alexeeva s. n.*–Holotype: MHA). It isinteresting that the only collection which appears to be this hybrid from Japan (Honshu, Iwate Prefecture, Shimohei-gun, Mt. Hayachine, *T. Makino s. n.* (MAK 6953) is from an area outside of the range of *C. lutetiana* subsp. *quadrisulcata.* This is similar to the situation in North America and Europe where *C.* × *intermedia* occurs outside the range of one or both parents. Either of two possibilities may explain these cases: 1. that the hybrid was formed at some time in the past when conditions were favorable for both parents to grow here; 2. that the hybrids were formed outside of this area and seeds were transported here, possibly through the epizoochoric fruits becoming attached to migrating birds.

Circaea × *skvortsovii* is intermediate between the two parents in degree and nature of the pubescence, color and morphology of the floral parts and in the spacing of the flowers.

It is similar to *C. cordata* in the long, spreading hairs, sporadically distributed on all parts of the plants and in the relatively close spacing of the flowers. The exserted ring-like nectary, reddish color of the buds and sepals and the densely glandular pubescent inflorescence are characteristic of *C. lutetiana* subsp. *quadrisulcata.*

Hybrids between *C. cordata* and *C. mollis* are *C.* × *ovata* (HONDA) BOUFFORD, based on *C. quadrisulcata* (MAXIM.) FRANCH. & SAV. var. *ovata* HONDA (Bot. Mag. Tokyo **46**: 3. 1932). HARA (1934) called these plants *C. mollis* SIEB. & ZUCC. var. *ovata* (HONDA) HARA. The type (Japan, Tochigi Prefecture, Kimitsuga-gun, Higashioashi-mura, Mt. Futamata, *H. Sekimoto* 13 (Holotype: TI) lacks fruit and pollen and is presumably sterile. I found plants similar to the type growing in mixed populations of *C. cordata* and *C. mollis* in Yamagata Prefecture, near Makino, *D. E. Boufford & E. W. Wood 19881* (K, KYO, MO, NY, P, UC) and on Hokkaido near the base of Mt. Maru-yama in Sapporo, *D. E. Boufford & E. W. Wood 19855* (K, KYO, MHA, MO, S, SHIN). Those plants have only about 10% well-filled pollen grains. The plants from Yamagata Prefecture set no fruits while those from Hokkaido averaged less than one mature fruit per plant. It was not determined whether the fruits were fertile. *C.* × *ovata* has darkened nodes, intermediate between the green nodes of *C. cordata* and the reddened nodes of *C. mollis.* The leaves are ovate and intermediate between the commonly cordate leaves of *C. cordata* and the elliptic to nearly ovate leaves of *C. mollis.* An exserted ring-like nectary is always present in *C.* × *ovata.*

The one collection (mentioned above) which may represent a hybrid between *Circaea cordata* and *C. alpina* is almost totally glabrous and has the nectary wholly within the floral tube, as do the putative parents. It resembles *C. cordata* in habit but the lower leaves have rather sharp, low teeth as in *C. alpina.* This possible hybrid needs more study and should be sought wherever the parental species grow together.

2. **Circaea mollis** SIEB. & ZUCC., Abh. Akad. Muench. **4**: 134. 1843. Type: Japan ("Nipponia"), *P. Siebold s. n.* (Lectotype: L; photograph P. Isolectotypes: L, 2 sheets).

Circaea mollis most closely resembles *C. leutetiana* subsp. *quadrisulcata* in Japan but differs in having pubescent stems, green buds and sepals, cuneate leaf bases, and generally shorter pedicels and smaller floral parts. *C. mollis* is usually more robust and produces more inflorescence branches than *C. lutetiana* subsp. *quadrisulcata. C. mollis* is a more southern plant, common on Honshu, Shikoku and Kyushu and less common on Hokkaido. *C. lutetiana* subsp. *quadrisulcata* is a more northern plant common on Hokkaido but known from only a single collection from Honshu. *C. mollis* differs from the remaining species by the globose to pyriform fruits with deep grooves and raised rounded ridges. Outside of Japan *C. mollis* ranges from Korea and northeastern China to south central China, then westward across southern China and the northernmost parts of Vietnam, Cambodia, Laos and Burma to eastern Assam, India. Chromosome number, $n=11$.

Hybrids between *Circaea mollis* and *C. erubescens* are known but have not been given a formal name. These plants are intermediate between the parents in several critical features, but in habit they usually resemble one parent more than the other. The petals in the hybrids are more deeply notched than in *C. erubescens* and are often minutely crenulate at the apex of the truncate or broadly rounded lobes. The leaf bases are rounded and the leaves vary from lanceolate to nearly ovate. The pedicels are shorter than in *C. erubescens* and nearly as short as in *C. mollis*. *C. erubescens* and *C. mollis* often grow in close proximity in many places in Japan and it would be expected that hybridization between the two would be a fairly frequent event, yet these hybrids appear to be relatively rare. Experimental attempts to produce these hybrids should be carried out to see whether or not barriers to hybridization exist.

3. **Circaea lutetiana** L. subsp. **quadrisulcata** (MAXIM.) ASCH. & MAG. Bot. Zeit. **28**: 787. 1870. Based on *C. lutetiana* L. forma *quadrisulcata* MAXIM., Prim. Fl. Amur 106. 1859. Type: U. S. S. R.?, Amur, "forma fructa 4-sulcata", *C. Maximowicz s. n.* (Lectotype: LE, not seen. Isolectotypes: GH; K; P, 2 sheets). *C. lutetiana* L. var. *quadrisulcata* (MAXIM.) FRANCH. & SAV., Enum. Pl. Jap. **1**: 169. 1873. *C. mollis* SIEB. & ZUCC. var. *maximowiczii* H. LEV., Bull. Geogr. Bot. **22**: 223. 1912. Based on *C. lutetiana* L. forma *quadrisulcata* MAXIM. *C. maximowiczii* (H. LEV.) HARA, J. Jap. Bot. **10**: 598. 1934. *C. maximowiczii* (H. LEV.) HARA var. *viridicalyx* HARA, J. Jap. Bot. **10**: 600. 1934. Type: Korea, Keiki Province, Koryo, 2 September 1930, *T. Nakai s. n.* (Holotype: TI). *C. maximowiczii* (H. LEV.) HARA forma *viridicalyx* (HARA) KITAGAWA, Fl. Manshur. 328. 1939.

When I was in Japan in 1977 I believed that *Circaea lutetiana* subspp. *quadrisulcata* and *canadensis* represented members of a single species distinct from the primarily European *C. lutetiana* subsp. *lutetiana*. My annotations on specimens in Japanese herbaria reflect my thoughts at that time. Since then I have been able to examine specimens in European herbaria from the Soviet Union and have become convinced that the eastern Asian plants of subsp. *quadrisulcata*, which ranges from Far Eastern Asia to the vicinity of Moscow, intergrade with plants of subsp. *lutetiana* in the western part of the Soviet Union, where the ranges of both subspecies overlap. SKVORTSOV (1979) has also noticed these intergrading populations and because of them he prefers not to recognize subspecies within *C. lutetiana*. However, since the plants from Far Eastern Asia and Siberia are clearly distinct from the European plants in several characters and occupy large parts of geographically distinct regions it seems best to treat these differences taxonomically. *C. lutetiana* L. subsp. *canadensis* (L.) ASCH. & MAG. of North America represents a third subspecies.

Circaea lutetiana subsp. *lutetiana* has pubescent stems and clavate to obovoid fruits which taper smoothly to the pedicels. *C. lutetiana* subsp. *quadrisulcata* has glabrous stems and thick, pyriform to subglobose fruits which are usually rounded obliquely to the pedicels. In general, the floral parts of subsp. *lutetiana* tend to be larger than in subsp. *quadrisulcata*.

Circaea lutetiana subsp. *quadrisulcata* hybridizes with *C. erubescens* producing *C.* × *decipiens*

BOUFFORD (Ann. Missouri Bot. Gard. in press. Type: Japan, Hokkaido, Hidakashicho, Samani-gun, Samani-cho, Okada, *D. E. Boufford & E. W. Wood 19717*–Holotype: MO. Isotypes: CM; GH; K; KYO; MHA; MICH; NCU; NY; P; SHIN; UC). This hybrid differs from *C. erubescens* by having the petals more deeply notched and obovate and from *C. lutetiana* subsp. *quadrisulcata* by having sparsely glandular pubescent or glabrous inflorescences. From *C.* × *dubia* it differs in having the stem glabrous below the inflorescence. It is apparently rare and local and is known only from Hokkaido. At the type locality the plants grow in a disturbed area downstream from where the two parents grow side by side. In 1977 the hybrids were fairly extensive, occurring for nearly 10 meters along the streambank, but in 1980, when I revisited the site, the hybrids were being choked out by coarser, more aggressive plants.

Circaea lutetiana subsp. *quadrisulcata* also hybridizes with *C. alpina* and these plants are *C.* × *intermedia* EHRH. (Beitr. zur Naturkunde **4**: 42. 1789. Type: Germany, Diester Gebirge, *F. Ehrhart 101* (Lectotype: GOET. Isolectotypes: L; W). This hybrid is very rare in Japan, having last been collected on Rishiri Island in 1903. HARA called these plants *C. canadensis* (L.) HILL, sensu FERNALD, var. *rishiriensis* HARA (J. Jap. Bot. **34**: 317. 1959. Type: Japan, Hokkaido, Rishiri Island, Oshidomari, August 1903, *T. Makino s. n.* (Holotype: MAK 6954. Isotype: TI). Although *C.* × *intermedia* is the result of crosses between *C. alpina* and all three subspecies of *C. lutetiana*, the International Code of Botanical Nomenclature does not allow for the use of different hybrid names when different infraspecific taxa are involved as one of the parents. The Code does allow for the naming of nothomorphs for hybrids where different infraspecific taxa are involved, but in the case of *C.* × *intermedia* this seems unwarranted. The morphological characteristics of *C.* × *intermedia* in Japan fall well within the range of variability of *C.* × *intermedia* from other parts of the world and it would be impossible to consistently separate these plants from their European and American counterparts.

Circaea lutetiana subsp. *quadrisulcata* ranges from Korea, northeastern China and the Soviet Far East to the vicinity of Moscow. In Japan it is common on Hokkaido but known from only a single collection on Honshu (Tochigi Prefecture, Nikko, *H. Ito 310* (TI)). Chromosome number, $n=11$.

4. **Circaea erubescens** FRANCH. & SAV., Enum. Pl. Jap. **2**: 370. 1879. Type: Japan, Kanagawa Prefecture, Mt. Hakone, August 1866–1874, *P. Savatier 413* (Holotype: P).

Circaea erubescens can be easily recognized by the shallowly notched, obtrullate petals which are unique in the genus. Plants from Japan and Cheju-do (Quelpaert Island), Korea, may have either glabrous or minutely pubescent stems. Plants from the Asian mainland are always completely glabrous. I could find no geographic or altitudinal correlation for this difference in pubescence in Japanese plants, but perhaps ecological differences may be involved.

Hybrids between *Circaea erubescens* and *C. alpina* are *C.* × *mentiens* BOUFFORD (Ann.

Missouri Bot. Gard. in press. Type: Japan, Hokkaido, Ishikari-shicho, Sapporo city, Maru-yama, 17 August 1977, *D. E. Boufford & E. W. Wood 19633*–Holotype: MO. Isotypes: CM; KYO; SHIN; UC). These plants resemble *C. alpina* but are larger and more spindly. The nectary is present as a low, ring-like disc projecting beyond the opening of the floral tube. From *C. erubescens* these plants differ in having petals which more closely resemble those of *C. alpina*. The leaves are prominently toothed in the hybrid, as in *C. alpina* subsp. *alpina*, but the nodes are purple as in *C. erubescens*.

Circaea erubescens is common throughout Japan and reaches the northern limit of its range on Hokkaido. On the Asian mainland it occurs in South Korea and in China from Jiangsu (Kiangsu) and Zhejiang (Chekiang) Provinces through the Changjiang (Yangtze) drainage system to Sichuan, Yunnan and Guizhou (Kweichow). Chromosome number, $n=11$.

5. **Circaea alpina** L., Sp. Pl. 9. 1753. Lectotype: Sheet 25-2 (LINN).

Two subspecies of *Circaea alpina* occur in Japan and can be separated as follows:

1. Stems pubescent with short, recurved hairs; flowers opening on spreading or slightly ascending pedicels after the racemes elongate; bracteoles absent beneath pedicles...5a. *C. alpina* subsp. *caulescens*
1. Stems glabrous; flowers opening on erect or ascending pedicels before the racemes elongate; bracteoles present beneath pedicels ....5b. *C. alpina* subsp. *alpina*

5a. **Circaea alpina** L. subsp. **caulescens** (KOMAROV) TATEWAKI, Vegetation Shikotan Is. 44. 1940; BOUFFORD, Ann. Missouri Bot. Gard. in press. Based on *C. alpina* L. var. *caulescens* KOMAROV, Fl. Manshur. **3**: 99. 1905. Type: China, in the valley of the Yalu River, 10 July 1897, *V. Komarov s. n.* (Lectotype: LE). *C. alpina* L. var. *imaicola* ASCH. & MAG., pro parte, Bot. Zeit. **28**: 750. 1870. *C. imaicola* (ASCH. & MAG.) HAND.-MAZZ., pro parte, Symb. Sin. **7**: 603. 1933. *C. caulescens* (KOMAROV) NAKAI ex HARA, J. Jap. Bot. **10**: 588. 1934. *C. caulescens* (KOMAROV) NAKAI ex HARA var. *robusta* NAKAI ex HARA, J. Jap. Bot. **10**: 589. 1934. Type: Korea, Kogen Province, Mt. Kongo-san, 7 August 1916, *T. Nakai s. n.* (Holotype: TI). *C. caulescens* (KOMAROV) NAKAI ex HARA var. *pilosula* HARA, J. Jap. Bot. **10**: 589. 1934. Type: Japan, Nagano Prefecture, Wada-toge, 23 July 1880, *J. Matsumura s. n.* (Holotype: TI). *C. alpina* L. var. *pilosula* (HARA) HARA, J. Jap. Bot. **20**: 326. 1944. *C.* × *dubia* HARA var. *makinoii* HARA, J. Jap. Bot. **34**: 317. 1959. Type: Japan, Tokyo Prefecture (Musashi Province), Mt. Takao, in 1921, *T. Makino s. n.* (Holotype: MAK 6955. Isotypes: S; TI).

From the above synonymy, and that under subsp. *alpina*, it is obvious that *Circaea alpina* has been a source of confusion in Japan. The situation becomes clear when it is seen that *C. alpina* is represented here by two distinct subspecies which can easily be separated by the above key. *C. alpina* subsp. *caulescens* appears to be the more primitive of the two. As in the bilocular species, it has thicker leaves, flowers that open on spreading pedicels and it prefers warmer sites or lower elevations than *C. alpina* subsp. *alpina*. However, the two can sometimes be found growing together in intermixed populations. SKVORTSOV (1970, 1979) reported similar findings in the Soviet Far East and stated that he had not seen any intermediates. Based on his observations he considers these plants to be two distinct species. However, plants which are morphologically intermediate between the two are found both in Japan and in Korea. These plants appear fertile with abundant fruit set. Because of similar intergrading populations in different subspecies of *C. alpina* in other parts of the world, it seems best to regard subspp. *alpina* and *caulescens* as ecologically separated subspecies of *C. alpina*.

Circaea alpina subsp. *caulescens* occurs as scattered populations on Hokkaido and Honshu and is known from a single collection from Shikoku. It is most common in Nagano Prefecture (see BOUFFORD, 1982, for specimen citations). Chromosome number, $n=11$.

5b. **Circaea alpina** L. subsp. **alpina**.

C. caulescens (KOMAROV) NAKAI ex HARA forma *rosulata* HARA, J. Jap. Bot. **10**: 591. 1934. Type: Sakhalin, Tonnai, August 1906, *G. Nakahara s. n.* (Holotype: TI). *C. caulescens* (KOMAROV) NAKAI ex HARA var. *glabra* HARA, J. Jap. Bot. **10**: 590. 1934. Type: Japan, Nagano Prefecture, Mt. Yatsuga-dake, 19 August 1902, *Y. Yabe s. n.* (Holotype: TI). *C. caulescens* (KOMAROV) NAKAI ex HARA forma *ramosissima* HARA, J. Jap. Bot. **10**: 591. 1934. Type: Japan, Shikoku, Ehime Prefecture (Iyo Province), Mt. Ishizuchi, 9 August 1898, *R. Yatabe? s. n.* (Holotype: TI).

Circaea alpina subsp. *alpina* can be recognized by its glabrous stems, which are usually flattened in pressing, by the flowers which open in a cluster on erect or ascending pedicels before the racemes elongate, by the prominently toothed leaves and by the presence of bracteoles at the base of the pedicels. *C. alpina* subsp. *alpina* grows near sea level in Hokkaido and is found at increasing elevations southward through Honshu, Shikoku and Kyushu to Yakushima. It is often found on moist, moss covered rocks and logs or in loose soils, commonly in coniferous forests. Chromosome number, $n=11$.

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摘要 ミズタマソウ属の分類は混乱していて人によって取り扱いが違っている。日本産種についていえば，混乱の原因のうち大切なものが2つあり，その1つはミヤマタニタデの2亜種をはっきり認識していなかったことであり，他の1つは雑種についてよく調べられていなかったことである。筆者はミズタマソウ属についての比較研究を行って，この属には7種7亜種が認められることを確かめた。この研究の成果は Annals of Missouri Botanical Garden に掲載される予定である。

ミズタマソウ属は東亜に分布の中心があり，日本にも多様な型が見られる。筆者は1977年に日本各地で詳細な野外観察を行ない，1980年にも補足的な調査を行なったほか，日本や欧米のハーバリウムにある標本も丁寧に検討した。これらの研究によって，日本のミズタマソウ属には5種1亜種が認められることを確かめた。これらを識別するための人為検索表をつくると，

1 子房と果実は2室で，根茎は塊茎状にはならない……………………………………………………2
  2 密腺は花筒部内にあり，円筒状または環状のディスクになって突出することはない。花序の軸には，短かくて鎌状に曲がる腺毛と，長くて真直ぐか少し曲がる開出毛がつく…………… 1 ウシタキソウ
  2 密腺は花筒の開口部より外へ突出し，円筒状か環状のディスクとなる。花序の軸は無毛か，腺毛あるいは短かくて鎌状に曲がる毛がつくが，長くて真直ぐか少し曲がる開出毛はつかない ………………3
    3 花弁は倒卵形または広卵形，先へ伸びる部分は花弁の全長の1/4かそれ以上。花序の軸は有毛。さく果は熟するとたてに深い溝が入り，稜は鈍円形 ……………………………………………………4
      4 茎は有毛で，鎌状に曲がる毛が密に生じることが多い。葉は基部がクサビ形または稀に円形。花序はほとんど毛がないか，腺状で鎌状に曲がる毛がつく………………………… 2 ミズタマソウ
      4 茎は無毛。葉は基部は円形からやや心形。花序は腺状で鎌状に曲がる毛が密生する ……………………………………………………………………………… 3 ヤマタニタデ
    3 花弁はコテ形で，先へ伸びる部分は花弁の全長の1/5かそれ以下。花序の軸は無毛。さく果は熟しても深い溝や円形の稜をもたない………………………………………………………………… 4 タニタデ

1 子房と果実は１室で，根茎は塊茎状になって終る ……………………………………………………………5

5 茎には短かくて反曲した毛がつく。花は総状花序が展開してから開出するか少し斜上する柄の上で咲く。小花柄には小包葉がない。………………………………………………………5a ケミヤマタニタデ

5 茎は無毛。花は総状花序が展開する前に直立か斜上する柄の上で咲く。小花柄には小包葉がある ………………………………………………………………………… 5b ミヤマタニタデ（狭義）

ミズタマソウ属は日本で図１に示すような組み合せで７通りの雑種を作っている。この他，ミヤマタニタデとウシタキソウの雑種と思われる標本が１点だけある。この組み合わせの雑種は，稀ではあるけれども中国では知られている。その他の組み合わせの雑種も探がしてみる値打ちがある。特に，ヤマタニタデとミズタマソウの雑種は北海道にありそうである。ミズタマソウ属では雑種は形態的に両親の完全な中間型となり，不稔である。野外では果実のつかないものがあれば雑種である可能性が高い。花粉も普通なら80%以上も成熟するが，雑種では10%以上が完熟することは珍らしい。雑種は生育場所でも母種の中間となり，川沿いのような場所に繁茂することが多い。雑種がつくられると，あとは栄養繁殖をして大きな群落をつくっていることが多い。

1 ウシタキソウ Circaea cordata Royle

日本・台湾・朝鮮・中国・南東シベリア・アッサム・ネパール・パキスタンに分布し，染色体数は $n=11$。

オオタニタデ C. ×dubia Hara はウシキタソウとタニタデの雑種である。

ウシキタソウとヤマタニタデの雑種（C. ×skvortsovii Boufford）らしいものが早池峰山でも採られている（*T. Makino MAK 6953*）が，ここにはヤマタニタデが生えていない。片親が現在分布していない地域に雑種が生育する例はアメリカでもある。これはその地域にかっては両種が分布していたか，他の地域から動物によって雑種種子が運ばれてきた可能性を推定させる。

ヒロハノミズタマソウはウシタキソウとミズタマソウの雑種で，学名を C. ×ovata (Honda) Boufford とする。

2 ミズタマソウ Circaea mollis Sieb. & Zucc.

日本・朝鮮・中国・インドシナ北部・ビルマ北部・アッサムに分布し，染色体数は $n=11$。

ミズタマソウとタニタデは相接して生育している所が多いけれど雑種はあまり見つかっていない。

3 ヤマタニタデ Circaea lutetiana L. subsp. quadrisulcata (Maxim.) Asch. & Mag.

ヨーロッパの subsp. lutetiana, アメリカの subsp. canadensis と地理的に分かれており，東アジアからシベリアに分布している。染色体数は $n=11$。

ヤマタニタデとタニタデの雑種が北海道で見つかり C. ×decipiens Boufford と命名する。

ヤマタニタデとミヤマタニタデの雑種（C. ×intermedia Ehrh.）は原（1959）のエゾミズタマソウである。

4 タニタデ Circaea erubescens Franch. & Sav.

日本，朝鮮南部，中国に分布し，染色体数は $n=11$。

タニタデとミヤマタニタデの雑種も北海道で見つかり C. ×mentiens Boufford と命名する。

5 ミヤマタニタデ Circaea alpina L.

これは狭義のミヤマタニタデ subsp. alpina とケミヤマタニタデ subsp. caulescens (Komarov) Tatewaki とに区別されるが，これまでそれらが混同されていた（検索表参照）。ケミヤマタニタデは北海道と本州に生育するが，多いものではない。四国では１ケ所知られているのみである。染色体数は $n=11$。ミヤマタニタデは北海道では海岸に，本州以南では山地に生じ，屋久島にも生育している。染色体数は $n=11$。