
A TAXONOMIC REVISION OF THE *PAEONIA ANOMALA* COMPLEX (PAEONIACEAE)¹

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ABSTRACT

Based on field observation, examination of over 350 sheets of exsiccatae, and investigation of all the relevant types, a taxonomic revision of the *Paeonia anomala* complex is presented. Typifications are clarified for *P. anomala*, *P. intermedia*, *P. hybrida*, *P. sinjiangensis*, *P. altaica*, and *P. veitchii*. The identity of three well-known taxa, *P. anomala*, *P. hybrida*, and *P. intermedia*, is also clarified. Two species, *P. anomala* and *P. intermedia*, are recognized, with the circumscription of *P. anomala* emended to include *P. veitchii* as its subspecies. *Paeonia anomala* includes two subspecies: subspecies *anomala* and subspecies *veitchii* with the former distributed in Central Asia, Siberia, and the northeastern European part of Russia, while the latter occurs in China southeast of the Gobi Desert. *Paeonia intermedia* is distributed in Central Asia, but with an isolated locality in Georgia. *Paeonia sinjiangensis* is treated as a synonym of *P. anomala*, and *P. hybrida* Pallas is treated as a synonym of *P. tenuifolia* L. The lectotypes of *Paeonia laciniata*, *Paeonia beresowskii*, and *Paeonia intermedia* are designated here in the present paper.

Key words: *Paeonia*, *Paeonia anomala* complex, *Paeonia hybrida*, *Paeonia intermedia*, Paeoniaceae.

The *Paeonia anomala* L. complex (Paeoniaceae) comprises a group of herbaceous peonies in Central Asia, Siberia, and adjacent northeastern European regions. They are characterized by leaves biennial with leaflets decurrent at the base, leaflets finely segmented, with segments of a lower (the best developed) leaf ranging from 70 to 100 in number and 4–32 mm in width, and by bristles along veins on the upper blade surface. The only species with which it may be confused is *Paeonia tenuifolia* L., but the latter has leaves even more finely segmented, with segments more than 130 in number and 0.5–6 mm in width.

Since the late 1970s, two new species in the *Paeonia anomala* complex have been described from Xinjiang, the Central Asian part of China: *P. sinjiangensis* K. Y. Pan (1979) and *P. altaica* K. M. Dai & T. H. Ying (1990). For a better understanding of the species group in Xinjiang, we made an expedition in 1993 to the Altai and the Tianshan in Xinjiang and found that morphological features of the group in Xinjiang were not consistent with the descriptions by Schipczinsky (1921, 1937) and Gamaulova (1961); Stern's (1946) treatments and nomenclature are different from theirs but do not reflect the reality of the group in Xinjiang, either. Thus, we realized that the *P. anomala* complex

needed a comprehensive taxonomic revision and review of the nomenclature. For this purpose, the first author examined all available specimens of this group in the herbaria at BM, HNWP, K, LE, NWTC, PE, SHI, SHMU, TBI, XJBI, XJNU, and XJU (see Appendix 1). In addition, the types of *P. anomala*, *P. hybrida*, *P. intermedia*, and the other six specific and varietal names were examined at LINN (Herbarium of the Linnean Society), BM, K, and PE, respectively.

HISTORICAL REVIEW

Within the *Paeonia anomala* complex the type species, *P. anomala*, was described from Siberia by Linnaeus (1771). Pallas (1789) described three additional species, *P. laciniata* and *P. sibirica* from Siberia, and *P. hybrida* from a plant raised from seeds of *P. tenuifolia* cultivated in the Botanic Garden of the St. Petersburg Academy in Russia. *Paeonia sibirica* Pallas (1789) shares an illustration (tabula) with *P. laciniata*, but does not have a description. In his monograph of *Paeonia*, Anderson (1818) recognized only *P. anomala*, reducing *P. hybrida* as a synonym of *P. tenuifolia* for the first time. De Candolle (1818) recognized *P. anomala*, *P. hybrida*, and *P. laciniata*, but later (1824) treated *P.*

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laciniata as a synonym of *P. anomala*. Meyer (1830) described the fourth species, *P. intermedia*, from the Altai Mountains. Ledebour (1842) cited *P. anomala*, *P. hybrida*, and *P. intermedia*, treating *P. laciniata* as a synonym of *P. anomala*. Trautvetter (1860) recognized only one species, reducing *P. hybrida* as a variety of *P. anomala*, and treating *P. intermedia* as a form of variety *hybrida*. Lynch (1890) cited *P. hybrida* and *P. anomala*, and stated that the former was native to the Caucasus. Huth (1892) adopted the widest species concept of *P. anomala*, which includes four varieties: var. *typica*, var. *hybrida* (= *P. intermedia*), var. *nudicarpa*, and var. *emodi* (= *P. emodi*, confined to the western Himalayas). A further treatment by Krylov (1901) divided the complex into two species, *P. anomala* and *P. hybrida*, and reduced *P. intermedia* as a variety of the latter, *P. hybrida* var. *intermedia* (C. A. Meyer) Krylov, in addition to the typical variety. In the area of West Tianshan (Kirghizia and Xinjiang, China), Trautvetter (1904) enumerated only *P. anomala*, treating *P. intermedia* as its subspecies. Schipczinsky (1921) basically followed Krylov (1901), recognizing two species, *P. anomala* (with two varieties, var. *anomala* and var. *nudicarpa*) and *P. hybrida* (with two varieties, var. *hybrida* and var. *intermedia*), and the same treatment was adopted for the Flora of the USSR (Schipczinsky, 1937). These two *Paeonia* species were grouped by him as series 4, *Dentatae* Kom. (Schipczinsky, 1937: 33, "leaf lobes incised or with dentate margin"). Roots of both species were described as tuberous. In contrast, Stern (1946) recognized only one species in his monograph of *Paeonia*, *P. anomala*, in which two varieties were recognized: variety *anomala* with glabrous carpels, and variety *intermedia* with tomentose carpels. He did not mention roots of this group. Stern (1946: 113) considered *P. hybrida* Pallas as an ambiguous name: "It is doubtful what species Pallas intended by this name and, as it is not possible to discover what he meant, this name of *P. hybrida* has been omitted." However, in the *Flora of Kazakhstan*, Gamaulova (1961), following Krylov (1901) and Schipczinsky (1921, 1937), described two species, and still recognized *P. hybrida* as a valid name.

While working on *Paeonia* for the *Flora Reipublicae Popularis Sinicae*, Pan (1979) found a specimen from Xinjiang whose roots were basipetally attenuate. According to Schipczinsky (1937) and Gamaulova (1961), *Paeonia anomala* and *P. hybrida* have tuberous or fusiform roots, so the plant was described by her as a new species, *P. sinjiangensis* K. Y. Pan; the plants with tuberous or fusiform roots were treated as *P. anomala* with two varieties: va-

riety *anomala* and variety *intermedia* (Pan, 1979). Also from Xinjiang, Dai and Ying (1990) described another new species, *P. altaica*, which was stated to have flowers larger than *P. sinjiangensis* and one or two underdeveloped flower buds in addition to the terminal blooming flower.

Interestingly, Schmitt (1999) failed to recognize the distinct differences between *Paeonia anomala* and *P. intermedia* in the root and calyx, and thus treated them as a single species, but still recognized *P. sinjiangensis* and *P. altaica* as distinct species.

From the above it is clear that *Paeonia hybrida*, *P. intermedia*, and *P. anomala* have been variously treated. With this paper we hope to clarify the biological attributes and variations of the *P. anomala* complex.

OBSERVATIONS AND DISCUSSION

To answer how many species were really present in Xinjiang and what biological features they have, the first author and coworkers (Hong et al., 1994) made an expedition to the Tianshan and Altai Mountains, conducting field observations and population samplings of *Paeonia* in 1993. Seven populations in total were observed, covering those character states previously described for the *P. anomala* complex (Table 1). We found there were only two species in Xinjiang that differed distinctly from each other in the root and calyx. One species had the roots basipetally attenuate (carrot-shaped) and sepals mostly caudate (Fig. 2), preferring relatively moist habitats in woods. This was treated as *P. sinjiangensis*. The other had roots tuberous or fusiform and sepals mostly (at least 2) rounded but not caudate at apex, growing on sunny, shrubby or grassy slopes, or in sparse woods. This latter was recognized as *P. anomala*. We also found the presence or absence of indumentum on the carpels in this species group to be a polymorphism, i.e., individuals with carpels either glabrous or from sparsely to densely pubescent could be found within a single population (Table 1). The indumentum on carpels was demonstrated as quite variable, although it was considered by the previous authors as taxonomically valuable. Therefore, any taxonomic division based on this character, such as that between *P. anomala* and *P. anomala* var. *nudicarpa* (by Huth, 1892) or *P. anomala* and *P. anomala* var. *intermedia* (by Stern, 1946), is artificial. Also not observed by the previous authors was the clear differentiation in root and calyx in this group, which are closely correlated with each other (Fig. 2).

We also found that in the form with carrot-shaped

Table 1. The populations sampled and their characters in the *Paeonia anomala* complex in Xinjiang, China (all the vouchers are in PE). The figures before parentheses indicate character states, while those in parentheses express totally glabrous, “1” extremely sparsely hairy, “5” entirely covered with hairs, while “2,” “3,” and “4” are in between.

Population	Locality and habitat	Roots	Leaf color	Indumentum on carpels	Number of non-caudate sepals on carpels
D. Y. Hong et al. 3	Altai: Mt. Halamaryi, NW of Altay City, 1200 m, <i>Populus</i> forest by stream	carrot-shaped (3)	pale green	0(2); 1(3)	0(2); 1(1); 5(1)
D. Y. Hong et al. 5	Altai: Xiaodong Gou Valley, NE of Altay City, 1060 m, <i>Populus-Betula-Picea</i> forest at valley bottom	carrot-shaped (3)	pale green	0(2)	0(1)
T. H. Ying 1006-1022	Altai: Habala County, 1200–1550 m, in <i>Betula</i> forests	carrot-shaped (2) fusiform to tuberous (3)	green	0(4); 1(1) 2(1); 3(5)	5(4); 0(2) 0(1); 2(1); 3(5)
D. Y. Hong et al. 2	Altai: Mt. Halamaryi NW of Altay City, 1300 m, S slope, rocky <i>Berberis-Spiraea</i> bushes	fusiform to tuberous (2)	green	2(1); 3(2)	0(2); 5(1)
D. Y. Hong et al. 0125	Altai: Mt. Halamaryi, NW of Altay City, 1000 m, sparse bushes	fusiform to tuberous (6)	green	3(2); 4(1)	0(1); 5(3)
D. Y. Hong et al. 4	Altai: Xiaodong Gou, NE of Altay City, 1060 m, W slope, rocky sparse <i>Spiraea-Berberis</i> bushes	fusiform to tuberous (5)	green	2(4); 3(1)	5(5)
D. Y. Hong et al. 1	Tianshan: Yining County, Yining Forest Farm, 1150–1200 m, N slope, sparse <i>Prunus-Malus</i> forest with <i>Cotoneaster</i> & <i>Spiraea</i>				

roots, the petals varied greatly in length, from 3.5 to 6.5 cm, and in the Altai Mountains some individuals of this form possessed one or two additional underdeveloped flower buds similar to *Paeonia veitchii*. This was again a polymorphism, and not considered by us to be a stable character, and therefore *P. altaica* was reduced to a synonym of *P. sinjiangensis* (Hong et al., 1994).

After examination of about 200 sheets of herbarium specimens in the Komarov Institute of Botany (LE) in 1999, the first author found that two species could also be distinguished in this complex: one with the roots carrot-shaped and sepals mostly caudate, while the other with the roots tuberous or fusiform, and sepals mostly non-caudate. These biological features match those on plants observed in Xinjiang (Hong et al., 1994). Gamaulova (1961, tab. 2) described roots of *Paeonia anomala* as fusiform-thickened, and those of *P. hybrida* as tuberous-thickened. However, roots of *P. intermedia* (= *P. hybrida* sensu Schipczinsky and Gamaulova) vary in shape from tuberous consistently to fusiform, and this variation could be found within populations or even on the same individual, whereas in *P. anomala* neither fusiform-thickening nor tuberous-thickening were found.

Contradictions exist between our natural observations (Hong et al., 1994) and earlier descriptions by Schipczinsky (1937) and Gamaulova (1961). Stern's (1946) treatment of this complex as one species with two varieties (*P. anomala* and *P. anomala* var. *intermedia*) is also at variance. For a clear taxonomic revision and correct nomenclature, one remaining issue ought to be resolved: the identity of *Paeonia anomala*, *P. hybrida*, and *P. intermedia*. The type specimen of *P. anomala*, with two visible sepals both caudate and relatively thin leaves, is perfectly consistent with the form with carrot-shaped roots. According to the type specimen at LINN [Siberia, no. 692. 3], field observation, and examination of over 350 sheets of exsiccatae, *P. sinjiangensis* and *P. altaica* should be treated as synonyms of *P. anomala*; the descriptions of roots of *P. anomala* by Schipczinsky (1937) and Gamaulova (1961) are erroneous. The type of *P. hybrida* (at BM), on which Pallas's (1789) tab. 86 was apparently based, has leaf segments 3–4 mm in width, and at least more than 100 in number, and is thus within the range of variation in *P. tenuifolia* L. (Hong & Zhou, 2003). Therefore, *P. hybrida* Pallas should be treated as a synonym of *P. tenuifolia*, as Anderson (1818) suggested nearly 200 years ago. The type specimen of *P. intermedia* at K possesses tuberous roots, mostly non-caudate sepals, and relatively thick and narrow leaf segments. The plants

that have tuberous or fusiform roots, are distributed widely from the Altai to Tadzhikistan and Uzbekistan, and were named *P. hybrida* by Schipczinsky (1921, 1937) and Gamaulova (1961) correspond to this type specimen very well.

Stern's (1946) statement concerning the name of *Paeonia hybrida* is not correct, confusing *P. intermedia* with *P. anomala*. Pan's (1979) treatment of the *P. anomala* complex (a new species, *P. sinjiangensis*, and *P. anomala* with var. *intermedia*) is also unjustifiable. Although Hong and his coworkers (Hong et al., 1994) properly described two species and clearly stated their morphological and ecological differences for this group, the nomenclature they used is misapplied.

The *Paeonia anomala* complex comprises two species: *P. anomala* and *P. intermedia*. *Paeonia emodi*, which was treated as a variety of *P. anomala* by Huth (1892), remains a distinct species, with leaves ternate, without bristles on the upper surface, leaflets much less segmented, segments no more than 40 in number and 1.5–4 cm wide, carpels usually two, less frequently one, very rarely three, and flowers white. *Paeonia veitchii* Lynch was described from Sichuan Province, China (Lynch, 1890), and was said (Stern, 1946; Pan, 1979) to differ from the *P. anomala* group in having several flowers instead of a single flower on a stem. According to our observation, one or two underdeveloped flower buds sometimes also exist in addition to one normal and terminal flower in *P. anomala*, while *P. veitchii* sometimes has flowers solitary (*P. veitchii* var. *uniflora*), although it has 3 or 4 flowers or 1 to 3 underdeveloped flower buds in addition to the terminal flower on a stem. Thus, *P. veitchii* was reduced to a subspecies of *P. anomala* (Hong et al., 2001).

KEY TO THE *PAEONIA ANOMALA* COMPLEX

- 1a. Roots carrot-shaped, never tuberous or fusiform; sepals all or mostly caudate, less frequently one or very rarely two non-caudate 1. *P. anomala*
- 2a. Flowers solitary, rarely 1 or 2 underdeveloped flower buds present in addition to terminal flower on a stem 1a. *P. anomala* subsp. *anomala*
- 2b. Flowers usually 2 to 4 on a stem or 1 to 3 underdeveloped flower buds present in addition to terminal flower, rarely flowers solitary on a stem 1b. *P. anomala* subsp. *veitchii*
- 1b. Roots fusiform or tuberous; inner 2 to 4 sepals rounded but non-caudate at apex 2. *P. intermedia*

TAXONOMIC TREATMENT

- 1. *Paeonia anomala* L., Mant. 2: 247. 1771.**
TYPE: Siberia, no. 692.3 (holotype, LINN!).
Figure 1A.

Paeonia laciniata Pallas, Fl. Ross. 1(2): 93, tab. 85, sub *P. sibirica*, 1789. TYPE: the illustration (tab.) cited in the protologue (lectotype, designated here!).
Paeonia sibirica Pallas, Fl. Ross. 1(2): tab. 85. 1789.

Pallas's (1789) illustration (tab.) 85 has only one name, *P. sibirica*, and apparently he used this illustration also for *P. laciniata* because one sees "Paeonia laciniata Tab. LXXXV" on p. 93. *Paeonia laciniata* was described in detail by Pallas, but no description of *P. sibirica* was given by him.

Perennials; tap roots \geq 50 cm long, carrot-shaped, basipetally attenuate, up to 2 cm diam., lateral roots slender, neither tuberous nor fusiform. Leaves biennial; leaflets finely segmented; lower leaves with segments 70 to 100 in number, 8–32 mm in width. Flowers solitary or 2 to 4 on a stem, often only terminal one fully developed and blooming; sepals 3 to 5, mostly caudate at apex, rarely 1 or very occasionally 2 non-caudate; carpels 2 to 5, from glabrous to densely tomentose.

The species prefers relatively moist habitats, growing in forests, on the edges of forests, or rarely in bushes. It is found at altitudes from 1100 to 3870 m.

This species is widely distributed from central China to the Kola Peninsula of Russia via Siberia and Central Asia. The species is of two allopatric subspecies, with the typical subspecies distributed northwest of the Gobi Desert, while subspecies *veitchii* is in China southeast of the Gobi Desert (Fig. 3).

1a. *Paeonia anomala* subsp. *anomala*

Paeonia sinjiangensis K. Y. Pan, Fl. Reipubl. Popularis Sin. 27: 603, fig. 12. 1979. TYPE: China. Xinjiang: Habahe County, Larix forests, 1973, Y. R. Ling 1141 (holotype, PE!).

Paeonia altaica K. M. Dai & T. H. Ying, Bull. Bot. Res. (Harbin) 10(4): 33, fig. 1. 1990. TYPE: China. Xinjiang: Habahe County, Wuzliti, 1550 m, in forests, 10 June 1980, T. H. Ying 1007 (holotype, SHMU; isotype, PE!).

The typical subspecies is usually found in deciduous or conifer forests, in valleys, less frequently in meadows, at altitudes from 1100 to 2200 m. Apparently it prefers relatively moist habitats. This subspecies is of very wide distribution: northeast Kazakhstan, northern Mongolia, from the Altai and Baikal to the Kola Peninsula in Russia, and in the Altai and adjacent regions in Xinjiang, China (Fig. 3).

Additional specimens examined. CHINA. Xinjiang: Altay, L. R. Xu s.n. (PE); Mt. Halamaryi, D. Y. Hong et al. Population No. 3 (PE), 0128 (PE); Xiaodong Gou valley, T. H. Ying 1001 (PE, SHMU). Burqin: Kem, N. R. Cui 86624 (XJNU). Emin: Shiyue Township, Wuerkehe'er,

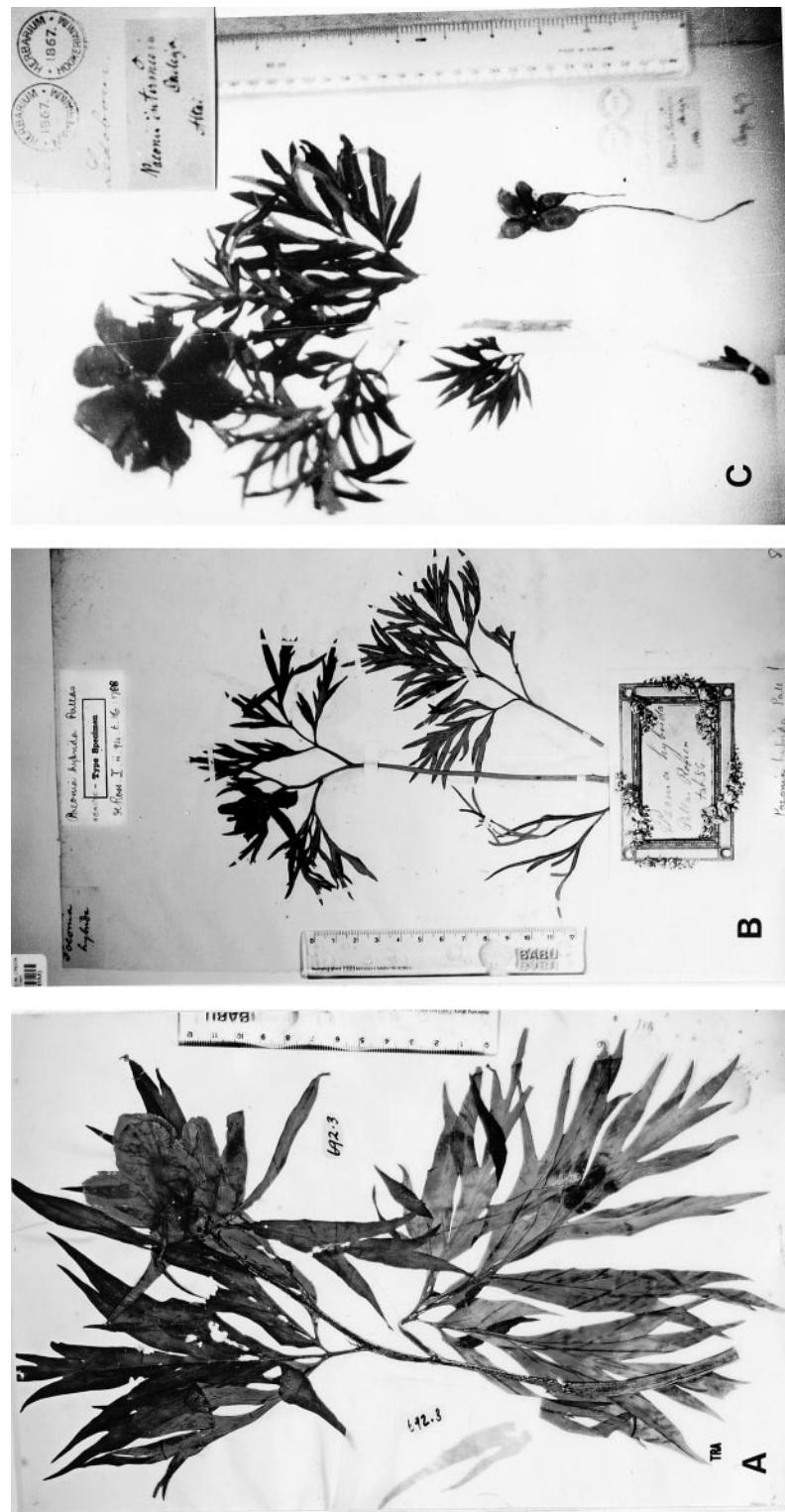


Figure 1. *Paeonia* holotype specimens: —A. *P. anomala* (LINN.). —B. *P. hybrida* Pallas (BM). —C. *P. intermedia* C. A. Meyer (BM); the insert at upper right is the enlargement of the label at lower right.

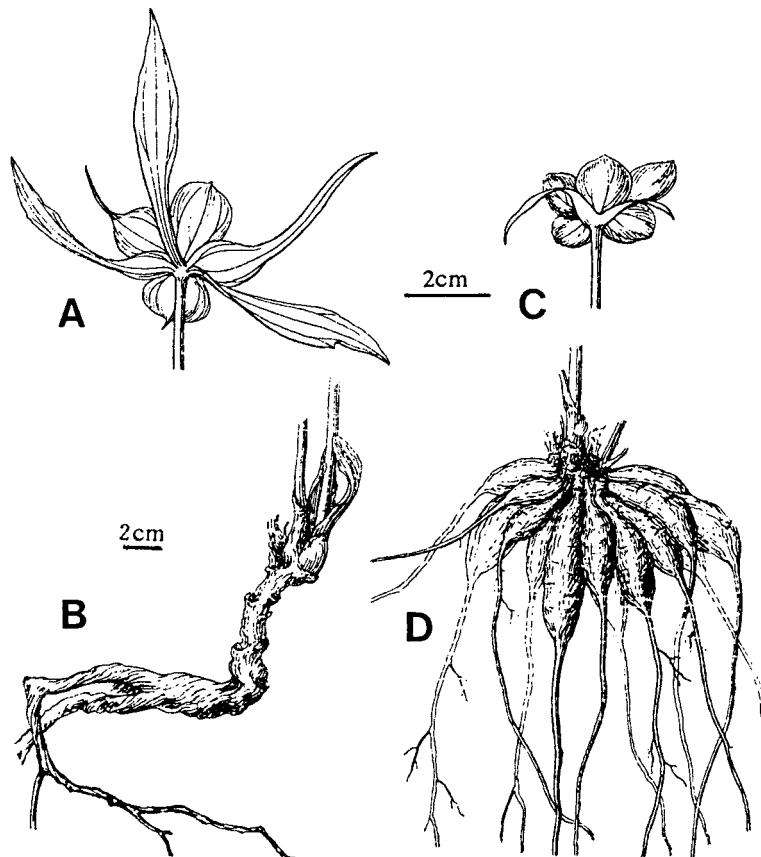


Figure 2. Diagnostic features of *Paeonia anomala* (A, B) and *P. intermedia* (C, D). Tuberous or fusiform roots are correlated with non-caudate sepals, while carrot-shaped roots correlated with usually caudate sepals.

right bank of Telikete River, *Xinjiang Branch Acad. Sinica* 012 (XJBI). Fuhai: Ahebai, glades, s. coll. 3867 (XJBI); Daqiao Forest Farm, *T. H. Ying* 1011 (PE, SHMU). Fuyun: *C. W. Chang* 11356 (XJBI). Hababe: Baihaba, *Z. M. Mao* 10413 (XJBI); Tielieke, Zamanashi Valley, *C. W. Chang et al.* 10255 (XJBI); Tiekeliti, *T. H. Ying* 1010 (PE, SHMU); Wuzlity, *T. H. Ying* 1022 (PE, SHMU). Jeminay: Xingfu Township, Sanxie Valley, *Integ. Exped.* 7305 (XJBI). Qinghe: Daqinghe, Mudeng Valley, *Integ. Exped.* 11829 (XJBI). Tacheng: Mt. Ba'erleike, *X. Y. Li* 870147 (SHI). Toli: Jiayi'er Gold Mine, *N. R. Cui* 091 (XJNU); Mt. Zayier, N slopes, *Integ. Exped. (Biology)* 630 (XJBI). Wenquan: A'erxiaoto Gou, *F. M. Zhang* 90-346 (XJNU). Yumin: Ku'erzhai, *Liu & Shen* 8308 (XJBI). KAZAKHSTAN. **Semipalatinsk Province:** Altai, near Altaiskaya Station, Mt. Narymsky region, gorge slopes, *Ladygin* 92 (LE). Southern Altai: Mt. Ivanovsky Range, near Gorno-Ulbinki, *I. Rohderi* s.n. (LE). Ustkamenogorsk region: Mt. Altai, Kunduzda River valley, *V. & A. Reznichenko* 360 (LE); Mt. Kalbinskie, Saryshbay River valley, *V. Reznichenko* 49 (LE); Mt. Kalbinskie, Ulansky, near Asybulak, by Tainta River, *P. Yurchenko* s.n. (LE); Mt. Narymsky, upper Urkar River, *V. Reznichenko* 58 (LE); near Ulbinsky gorge, *V. Iljin* s.n. (LE); Urunhaika River mouth, S banks of Marka-Kul Lake, *A. Sedelnikov* s.n. (LE). Zaisan region: Mt. Altai, Ulkunchumek River valley, upper Kaldzhir River, *V. Reznichenko* 106 (LE); Markakul Lake, *B. Keller* s.n.

(LE); Mt. Narymsky Range, Ak-tui River valley, *D. Yakovlev* 69 (LE); Mt. Saur, Chagan-obo River valley, *V. Reznichenko* s.n. (LE); Mt. Saurkie, Maly Dgewan River valley, *B. Keller* s.n. (LE). MONGOLIA. **Ulan Bator:** 10 mi. E of Ulan Bator, *P. Morgan* 23 (K). **Gloucester:** Mongolia-Chinese Turkestan Exped. *M. P. Price* 293 (K). **North Mongolia:** Mt. Saldzharsky Pass, *E. Clements* 11a (LE). RUSSIA. **Altai Region:** Altai: between Charga & Shabolina, mtn. slopes, *E. K. Clements* 4d (LE); Chuja road, Saadak-lary, *Vereshagin* 296 (LE). West Altai: Mt. Listvennitchny, near Nizhne-Uimonskoye, *S. Kolomoitseva* 236 (LE). **Buryato-Mongolian Autonomous State:** Baikal, Tunkam, *Turczaninow* s.n. (LE); Zabaikalje, upper Toreika River, 130 km W of Troitskosavsk, *P. Mihno* s.n. (LE). **Eubinsk Region:** West Sayan, Mt. Alan Range, Golots Taskalyk, *I. Krasnoborov* 6765 (LE); near Buiba Station, by river, *Krasnoborov & Sannikova* s.n. (LE). Tuva: Tandinsky distr., East Mt. Tannudla Range, near Shurmak, *V. Hanminchun* 515 (LE); Ulug-Hemsky distr., Uluksky Mtn. Range, Bajan-Kol River valley, Orto-Hem tributary, *Lomonosova & Ivanova* 89 (LE). **Irkutsk Region:** Irkutsk Prov.: Lena River valley, upper Gulm River, *I. Kuznetsov* 114 (LE). Balagansk distr.: near Bazheevskoye, *N. Matsev* 79 (LE). Nizhneudinsky distr.: by Angara River, opposite Yandov, *S. Ganeshin* s.n. (LE); Mt. Hariba-bim Range, Angara River valley, Karpovskoye, *A. Korovkin* 290 (LE); by Oka River, *A. Krishtofovich* s.n. (LE); near

Vidimka, Vidim River, *S. Kucherovskaya* 282 (LE). Tunkin distr.: Mt. Sayany, near Nylova Pustyn, *V. Komarov s.n.* (LE); Nizhnaya Tunguska valley, near Nizhnaya Korelina, *S. Kokulin* 254 (LE). Tunkinsky distr.: Kuren Arshan, *V. Smirnov s.n.* (LE). Verholensky distr.: Biriulka, near Yushina, *P. Alexandrov* 179 (LE); Harat, *G. Dolenko* 108 (LE); Lena River & Kirenga valley, Toptykan, *M. Tomin* 67 (LE); Tutura, *P. Alexandrov* 219 (LE). **Kola Peninsula:** Ponoi River, left bank, 8 km from its mouth, *E. Chernov* 3 (LE); Ponoi River, near its mouth, *N. Orlova* 240 (LE). **Krasnoyarsk Region:** Belsk distr.: near Alshat, *I. Kuznetsov* 4661 (LE); Chadobets, *G. Borowikow s.n.* (LE); Rybnoe, *Dranitsyn & Kochubei s.n.* (LE). Enisei Prov., Achinsk distr.: near Ingol Lake, *A. Suhareva s.n.* (LE); near Maloye Lake, *M. Ermolajeva s.n.* (LE); Bolshe-Uluiskaya, near Bobrovki, *I. Kuznetsov* 53 (LE); Chuksha River Valley, *I. Tolmatschew* 247 (LE); Katanga, *G. Borovikov s.n.* (LE); Vyezhi Log, *A. Tugarinov s.n.* (LE). Kansk distr.: Gutar River valley, by Kamenka tributary, *W. Troitsky s.n.* (LE); near Kansk, *A. Shliahtin s.n.* (LE); Rybnaya River valley, Perovskoye, *I. Kuznetsov* 193 (LE); near Nazimovskoye, *Z. Euseeva* 4406 (LE). Krasnoyarsk Prov.: Chunia River, right bank opposite mouth of Muturai River, *A. Rubin s.n.* (LE); Hakassia, Shirinsky distr. Bolshaya Iusa River valley, NW slopes, *Polozhii & Kandasova s.n.* (LE); near Krasnoyarsk, by Mohovaya River, *V. Verhovskaya & M. Mishin* 104 (LE); Minusinsk, Bolshoy Kysylkul Lake, *K. Golubeva et al. s.n.* (LE); Nizhnaya Tunguska River valley, near mouth of Hurkakut River, *Rubin & Maskil s.n.* (LE); between Salba & Grigorievka, *P. Krylov s.n.* (LE); Shushensky distr. near Tanzyben, by Black Tanzyben River, *Kuminova & Alexeeva s.n.* (LE); near Sorokino Station, N slopes, *Cherepnin s.n.* (LE). **Novosiberia Region:** Altai: Elikmanar, upper Karakol River, *V. Vereshagin* 345 (LE). Kuznetsky Alatau: Kondoma River valley, Kazany Mine, Mt. Kyon, *B. Klopotov s.n.* (LE); upper Sary-Chumysh River, near Ulus Munai, *A. Vydrin s.n.* (LE); Tom River valley, Mt. Tohpantai, *B. Klopotov s.n.* (LE). Mariinsky Prov.: Biisk, Black Anuj, Talitskiebelky, to Kazanda, *Pobedimova* 697 (LE); Biisk, Lebed River valley, by Chuja River, *B. Klopotov* 180 (LE); Biisk, between Tulatinskaya & Sentelek, *N. Kuznetsov* 1991 (LE); Kainsk, Verhnaya Nazarova, *B. Klopotov* 113 (LE); Narym, Ixa River, *S. Genina s.n.* (LE); Sofronova, *P. Krylov s.n.* (LE); Tomsk distr.: Chulym & Chet River valley, *P. Sokolov* 13a (LE). Moshkovsky Prov. (Distr.): Uskorniha River valley, *Kuwajev & Sabitov s.n.* (LE). Toguchinsky distr., near Mirny, *Lashinsky & Ronginskaya* 973 (LE). **Omsk Region:** Tobolsk Province: Berezov distr., Lopsia River, tributary of Severnaya Sosva, *s. coll. s.n.* (LE); Tobolsk distr., Landinka River valley, *E. Vislouh* 73 (LE). **Ural:** Arctic Ural: Lyapin tributary, upper Manja River, *V. Sochava* 100 (LE); Severnaya Sosva River valley, Lyapin tributary, upper Khulga River, *B. Gorodkov* 512 (LE). Mariinsky distr., Beket River valley, Kolosnokoye, *N. Kuznetsov* 199 (LE). Tobolsk Province: Berezovsky distr., Berezov, *Pohle & Rozhdestvensky s.n.* (LE); Tarsky distr., Rybinsk, near Pustynnoye, *V. Varentsov s.n.* (LE). **Yakutsk Autonomous State:** Yakutia, Suntarsky distr., upper Viluy River, Tuoikhai, by Chona River, *I. Kildushevsky* 150/22 (LE).

**1b. *Paeonia anomala* subsp. *veitchii* (Lynch) D. Y. Hong & K. Y. Pan, Novon 11: 317. 2001.
Paeonia veitchii Lynch, Gard. Chron. ser. 3, 46: 2 tab. I. 1909. TYPE: China. W. Sichuan:**

Tatien-lu (Kangding), 8–10,000 ft., *E. H. Wilson* (for James Veitch & Sons) 3034 (holotype, K!, photo, PE!).

Paeonia beresowskii Komarov, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 2: 5. 15 Jan. 1921. *Paeonia veitchii* var. *beresowskii* (Komarov) Schipczinsky, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 2: 46. 26 Mar. 1921. TYPE: “China Occid, Szechuan (Sichuan), Sun-pan-tin (Songpan), Guichua,” 9 June 1894, *M. Beresowskii s.n.* (lectotype, designated here, LE not seen).

Paeonia veitchii var. *woodwardii* (Stapf ex Cox) Stern, J. Roy. Hort. Soc. 68: 130. 1943. *Paeonia woodwardii* Stapf ex Cox, Pl. Introd. Farrer 43. 1930. TYPE: China. Gansu: Zone (Chuoni), *R. Farrer* 67 (holotype, E not seen).

Paeonia veitchii var. *leiocarpa* W. T. Wang & S. H. Wang, Fl. Reipubl. Popularis Sin. 27: 603. 1979. TYPE: China. Sichuan: Jinchuan, Kasa Township, Yinchanggou, forests by stream, 2700 m, 26 Apr. 1958, X. Li 77248 (holotype, PE!).

Paeonia veitchii var. *uniflora* K. Y. Pan, Fl. Reipubl. Popularis Sin. 27: 603. 1979. TYPE: China. Sichuan: Gaze, Xiongjiling, 3600 m, mtn. summit, bushes, 18 June 1974, *Qinghai-Xizang Exped. Veget. Group 034* (holotype, PE!).

This subspecies, though distantly isolated from *Paeonia anomala* subsp. *anomala* by the huge deserts of the Gobi, still very much resembles the latter. The only remarkable difference between them is the number of flowers on a stem. *Paeonia anomala* subsp. *veitchii* usually possesses 2 to 4 blooming flowers in addition to up to 2 underdeveloped flower buds. Very rarely only the terminal flower blooms in addition to up to 3 flower buds. *Paeonia anomala* subsp. *anomala* possesses only a single terminal blooming flower, without or infrequently with 1 to 3 underdeveloped flower buds.

The subspecies is widely distributed in China: southeastern and central Gansu, southern Ningxia, eastern Qinghai, the Qinling Range of Shaanxi, Shanxi, western Sichuan, and the eastern extreme of Xizang (Tibet) (Fig. 3). Like subspecies *anomala*, *Paeonia anomala* subsp. *veitchii* prefers relatively moist habitats, growing in forests, grasses on the edges of forests, bushes, or subalpine and alpine meadows with shrubs, at altitudes from 1800 to 3870 m.

Phenology. The subspecies flowers from late April to early June, and fruits in August and September.

Chromosomes. $2n = 10$ (Hong et al., 1988).

Additional specimens examined. CHINA. **Gansu:** Dingxi, *s. coll. s.n.* (CPB). Hezheng: Xinuang, *Gansu Herbs Group s.n.* (NWTC). Hezuo: Mt. Dalinke, *Q. R. Wang* 7034 (NWTC). Jiangcha: *S. Gansu Grassland Exped.* 681 (NWTC). Kangle: Mt. Taizi, *G. L. Zhu* 80006 (NWTC); Mt. Lianhua, *M. S. Yan* 1843 (NWTC). Kangxian: s. loco,

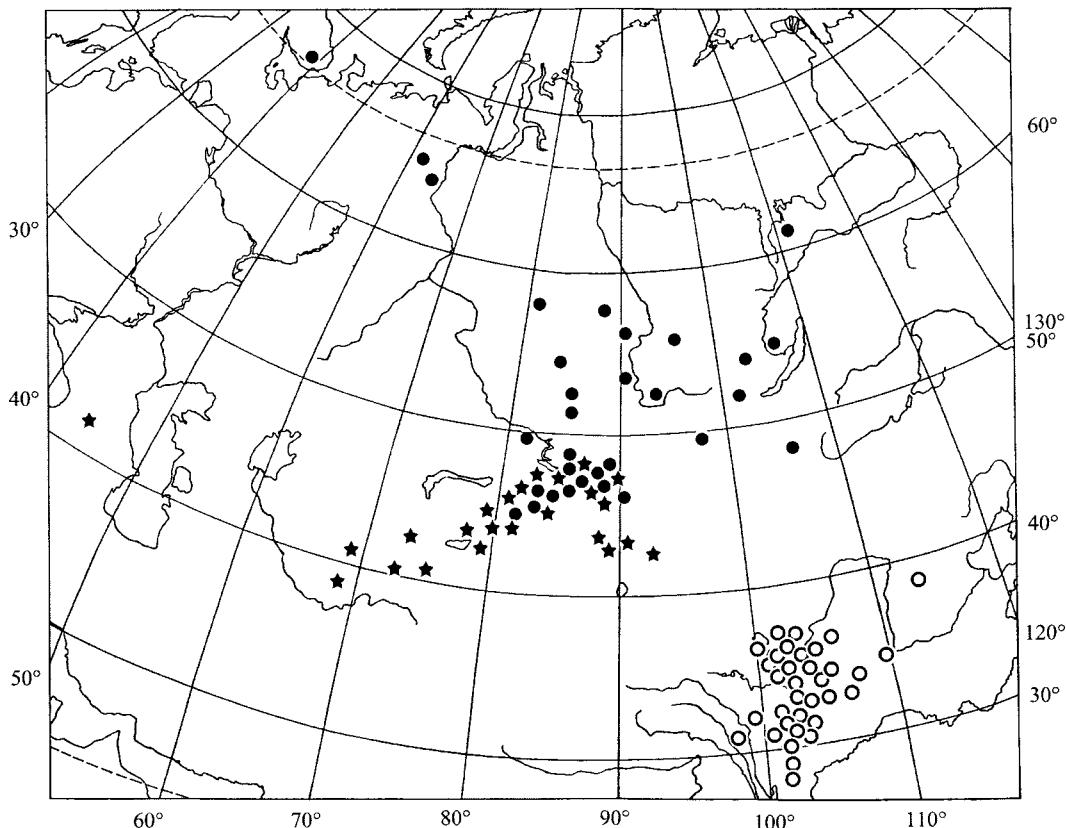


Figure 3. Distribution map of the *Paeonia anomala* species complex. Black circles: *Paeonia anomala* subsp. *anomala*; white circles: *P. anomala* subsp. *veitchii*; stars: *P. intermedia*. Each site in the map is supported by a single or several vouchers cited in the text.

s. coll. s.n. (NWTC). Lanzhou: Mt. Xinlong, *s. coll.* 84 (NWTC); Mt. Tiandu, *s. coll. s.n.* (NWTC). Linxia: near Senanpa, by river, T. K. Fu 834 (PE). Longdie: Dacaopo, H. J. Zhou 708 (NWTC). Minxian: Lujing, Zhongchuan-gou, J. Q. Wang 197 (NWTC); Mt. Luodadoujiedela, T. P. Wang 15240 (PE); near Mawu, T. P. Wang 4594 (PE); between Lintao and Yuzhong, *Huanghe Exped.* 1689 (PE); Mt. Wutai, *Taohe Exped.* 3243 (PE); Lamathan, K. S. Hao 604 (PE). Taohe: *J. F. Rock* 12829 (PE). Tsaluku to Shimen, *J. F. Rock* 13127 (PE). Tianshui: Mt. Xinjia, W. Y. Hsia 5707 (PE). Tianzhu: Anyuan, Y. Q. He 4516 (PE); Zhucha, Y. Q. He 4915 (PE); Jinqiang Township, Mt. Maomao, Q. R. Wang 1869 (NWTC). Xiahe: Chingshui, T. P. Wang 6944 (PE); Tangar'ang, Longwagou, Q. R. Wang 7270 (NWTC). Yongdeng: Liancheng, Tulugou, J. L. Bai 8613 (NWTC). Yuzhong: Xinlong, near Yangdaowan, *s. coll. s.n.* (PE). Zhangxian: Caotan distr., *Huanghe Exped.* 03183 (PE); Mt. Guiqing, *Huanghe Exped.* 4735 (PE); Hediling, Mt. Kehu, *Huanghe Exped.* 4655 (PE); Shichuan Forest Farm, Jinhuachi, Lian, Wang et al. 79197 (NWTC). Zhouqu: Taozhou Forest Farm, Jiang & Jin 00386 (PE). Zone (Chuoni): Kache Forest Farm, Lian & Chen 31 (NWTC); Wanchang, Sangtanagou, Lian & Chen 72 (NWTC). **Ningxia:** the Liupan Mountain Range, Y. W. Cui 10281 (PE). **Qinghai:** Datong: Kuanghuizu, K. M. Liou 6019 (PE); near Anchiapu, K. M. Liou 5970 (PE); Dongxia, Yu, Lu, Gu & Li 68 (PE); Mt. Laoye, Liang et al. 378 (HNWP); Baoku, Z. H. Zhang et al. 4291 (HNWP). Huangyuan: Mt. Banjie, P. C. Tsoong 8842 (PE). Huangzhong: Sanhei Forest Farm, S. X. Wang 1065 (HNWP); 40 km W of Xining, S. X. Zhen 0351 (PE). Huzhu: Beishan Forest Farm, Guo & He 9012 (HNWP); Qiaotou, Guo & Wang 6717 (HNWP). Jainca: near Angla, Liu & Luo 1040 (HNWP). Ledu: Maying Township, Kongjiazui, B. Z. Guo 6767 (HNWP). Golog: Markog Forest Farm, Hongjungou, W. Y. Wang 26818 (HNWP). Menyuan: Semnyi, betw. Lihua & Dalong, Z. Y. Qing 1218 (HNWP, PE); Semnyi, Zhugusi, Xielong, B. Z. Guo 7396 (HNWP); Semnyi, Hankegou, *Gansu-Qinghai Exped.* 2493 (PE). Minhe: Gushan, Nanxia, L. H. Zhou 2528 (HNWP); Xin'erbeishan, B. Z. Guo 7010 (HNWP). Tongren: Rongwo, B. Z. Guo 10232 (HNWP); Shuangfengxi, B. Z. Guo 10186 (HNWP). Xining [Sining]: Shangwuchuang, K. S. Hao 779 (PE). Xunhua: Mengda Forest Farm, Guo & Wang 25058 (HNWP); Mt. Dalijia, G. Z. Zhang 005 (HNWP). **Shaanxi:** Huxian: Taipingyu, Hualingwan, *Pharmac. Exped.* 2019 (PE). Hwainhsien [Huayin]: Qinglongbei, W. Y. Hsia 4539 (PE). Mt. Taibai: near Dadian temple, W. Y. Hsia 4571 (PE); Sanchaixia, K. J. Fu 4441 (PE); Dadian temple to Dumugong temple, Hong & Zhu PB85065 (PE). **Shanxi:** Shiziping, Xigou, *Shanxi Exped.* Wang & Tian 594 (PE). Mt. Wutai: Xitai, Xiachantan village, Xiejiagou, *Shanxi Exped.* 684 (PE). **Sichuan:** Baoxing: Raozhi, Nibagou, Hong & Zhong PB82105 (PE);

Longdong distr., Zhonggan, Mt. Daping, *Sichuan-Econom.* A59-0246 (PE); Ganyanggou, *T. T. Yu* 2200 (PE); Dengchigou, *T. H. Tu* 4329 (PE); Lianghekou, Mahuangpo, *Zhang & Ren* 5572 (PE). Barkam: near Puyajiao, *X. Li* 71029 (PE); near Kanzhugou, by river, *X. Li* 70441 (PE); Pu'ermagou, 209 Lumbering Ground, *X. Li* 70867 (PE); Bu'ermagou, *X. Li* 70903 (PE); near Matan, *X. Li* 71645 (PE); Dalongjiaogou, *X. Li* 70685 (PE); near Kafeiqiao, *X. Li* 71196 (PE); Zonggag, *X. Li* 70719 (PE); Nazhugou, *X. Li* 71087 (PE). Emei: Jieyindian, *T. H. Tu* 362 (PE). Dege: *S. X. Jia* 229 (PE). Garze: S bank of Yalongjia River, *Y. W. Cui* 4348 (PE). Heishui: Shidiaolou Township, *Sichuan-Econom.* A59-1208 (PE); Sandougou, *Sichuan-Econom.* A59-1001 (PE). Jinchuan: Zosijia, *P. X. Li* 10137 (PE). Jiulong: Mt. Baitai, between Niupo & Baitai village, *J. S. Ying* 3869 (PE). Kangding: Yulingong, Yingbapo, *Hu & He* 10463 (PE); Yulin Township, Simaqiao, *Jiang & Xiong* 35625 (PE); Yulin Township, Laoyulin, *X. C. Jiang* 36014 (PE); Taiyangshan distr., *Hu & He* 10373 (PE); Niugu village, *W. Sichuan Exped.* *Kuan et al.* 243 (PE); Xinduqiao, *W. Sichuan Exped.* *Kuan et al.* 732 (PE); Shade distr., Mi'Along, *Nanshui-Beidiao Exped.* 02912 (PE); Zhonggu village, Dagaigou, *W. Sichuan Exped.* *Kuan et al.* 352 (PE); between Kangding & Dawu, *P. C. Tsoung* 5004 (PE). Lixian: Longxi, Yiduo village, *Z. He* 12339 (PE); Miyaluo, Misugou, *S. Jiang* A-7162 (PE); Shuanjingsi, *P. X. Li* 10100 (PE); Shuanjingsi, 333 km milestone of Chengdu-Aba highway, *Zhang & Zhou* 23742 (PE); Somang, 42 km milestone of Shuanjingsi-Barkam highway, *Zhang & Zhou* 22675 (PE). Luhuo: *P. C. Tsoung* 5024 (PE); Zhehor, by river, *J. S. Ying* 4582 (PE). Mabian: *F. T. Wang* 22930 (PE). Maowen: Mt. Mafang, *Sichuan Econom.* (A-59) 2554 (PE); Xiang-Naha, Sanlonggou, *He & Zhou* 13338 (PE). Mianning: Yejin Township, *S. F. Zhu* 20491 (PE); Huning distr., Jieyingou, *S. Jiang* 5768 (PE). Muli: Wa-chin, *T. T. Yu* 6137 (PE). Qianning: S of town, *Jiang & Jin* 2113 (PE); to Dawu, *Zhang & Lang* 57 (PE). Sertar: 1 km S of Wungda, *S. Jiang* 9082 (PE). Songpan: Housigou, *S. Jiang* A-7275 (PE); Mont. Occid. *H. Smith* 2499 (PE). Tianquan: Mt. Erlong, Xiaoniujiangou, around Xiashan, *Hu & He* 10088 (PE). Wenchuan: Wolong Township, *Sichuan-Econom.* A59-2290 (PE); Wolong Nature Reserve, Mt. Balang, *Hong & Zhu* PB85019 (PE). Xiaojin: Xihekou, Niuchanggou, *Zhang & Ren* 6322 (PE); Luobigou, Yangpingkou, *Zhang & Ren* 6082 (PE). Yajiang: Mt. Ermin, *Sichuan Plants Collection* 0905 (PE); Tanjiao to Malangcuo, *J. S. Ying* 3113 (PE). Zamtang: Lukesi Temple, right bank, *S. Jiang* 8930 (PE); 10 km W of Gangmuda, *S. Jiang* 8965 (PE). Xizang (Tibet): Jomda: Gamtog distr., *Qinghai-Xizang Exped.*, Vegetation Group 9893 (PE).

2. *Paeonia intermedia* C. A. Meyer, in Ledebour, Fl. Altaic 2: 277. 1830. *Paeonia anomala* var. *hybrida* f. *intermedia* (C. A. Meyer) Trautvetter, Enum. Pl. Songor. 88. 1860. *Paeonia hybrida* var. *intermedia* (C. A. Meyer) Krylov, Fl. Altaya 1: 47. 1901. *Paeonia anomala* subsp. *intermedia* (C. A. Meyer) Trautvetter, in B. Fedtschenko, Trudy Imp. S. Petersburg. Bot. Sada 23: 351. 1904. *Paeonia anomala* var. *intermedia* (C. A. Meyer) O. & B. Fedtsch., Beih. Bot. Centralbl. 18: 216.

1905. TYPE: the Altai Mountains, *Lebedour s.n.* (lectotype, designated here, Kl!).

Paeonia majko N. Ketschoweli, Notul. Syst. Geogr. Inst. Bot. Tiphlis. fasc. 21: 17. 1959. TYPE: Georgia. Kartly, between Igoeti and Lamitskali, 16 May 1958, N. Ketschoweli s.n. (holotype, TBII!).

Paeonia intermedia subsp. *pamiroalaica* P. N. Ovchinnikov, in Fl. Tadzhikistskoi SSR. 4: 6-10 & 531. 1975. TYPE: Tadzhikistan: declivitas australis jugi Hissarcic, ad ripam dextram fl. Maichura, 5 km ab ostio, 2500 m, 12.06.1971, A. A. Glebova 6 (holotype, TAD not seen).

The species has long been identified as *Paeonia anomala* (Pan, 1979), treated as a variety of *P. hybrida* (Krylov, 1901; Schipczinsky, 1921, 1937; Gamaulova, 1961), a variety of *P. anomala* (Fedtschenko, 1905; Stern, 1946; Pan, 1979), a subspecies of *P. anomala* (Trautvetter, 1904), or even as a form of *P. anomala* var. *hybrida* (Trautvetter, 1860). These diverse and erroneous assignments were made because: (1) the identity of *P. anomala*, *P. intermedia*, and *P. hybrida* was not previously clear; (2) previous authors emphasized the taxonomic value of indumentum on carpels; and (3) the characters of roots and calyces and their correlation were not considered. Examination of the types of the three taxa and extensive observations on herbarium specimens and natural populations (Table 1) show that *P. intermedia* C. A. Meyer is an independent species, distinctly differing from *P. anomala* by its lateral roots tuberous to long-fusiform, sepals mostly (at least 2) rounded at apex but not caudate. Also different from *P. anomala*, *P. intermedia* prefers relatively sunny and dry habitats. Carpels vary from 1 to 5 in number, and from glabrous to densely tomentose. Ovchinnikov (1975) properly treated the peony in Tadzhikistan as *P. intermedia*, but his description of the new subspecies *pamiroalaica* is unjustifiable. His description and our extensive observations have not revealed any significant difference.

This species is widely distributed in northern Xinjiang, China (south to the Tianshan), Kazakhstan, Kirghizia, Tadzhikistan, Uzbekistan, and the Altai of Russia. One small isolated population was found in Georgia (Hong & Zhou, 2003) (Fig. 3). It grows in grassy and shrubby slopes, meadows, steppes, or in sparse woods, at altitudes from 900 to 3250 m.

Phenology. This species flowers from late May to late June and fruits from August to September.

Chromosomes. $2n = 10$ (Hong et al., unpublished).

Additional specimens examined. CHINA. Xinjiang: Altai Mt.: Acad. Sinica Xinjiang Integr. Exped. 10657

(PE). Altay: Qiao'ati, *G. L. Zhu et al.* 6325 (PE); to Halamarzi, *Acad. Sinica Xijiang Exped. 10227* (PE); Klasz Gou, *R. C. Ching 2433* (PE); Haxiong Gou, *T. Y. Chou 652100* (XJBI); Mt. Halamarzi, *D. Y. Hong et al. Population No. 2* (PE); Xiaodong Gou, *D. Y. Hong et al. Population No. 4* (PE). Barkol: Nanshan, *s. coll.* 780 (XJBI). Fuhai: Fuhai Forest Farm, *G. L. Zhu 5665* (PE); N slopes, *T. Y. Chou et al.* 652150 (PE, XJBI). Fukang: Tienci, Shimen, *D. Y. Hong et al. 0190* (PE). Fuyun: Mica No. 3 Mine, *Integr. Exped. s.n.* (XJBI); Mica No. 4 Mine, *Integr. Exped. s.n.* (XJBI). Habahe: Tielieke, *Kelimu 10171* (XJBI); Wuzlitz, *Kelimu 10614* (XJBI). Hoboksar: *Songshu Gou s. coll.* 7385 (XJBI); Mt. Qiaganebo, *Integr. Exped. 10563* (PE, XJBI). Huocheng: Aksu Commune, *Y. R. Ling 74848* (PE); Daxigou, *Acad. Sinica Exped. 10402* (PE); Xin'ertai, Yeguolin, *C. W. Chang et al. 3316* (XJBI); Xiaoxigou, *A. R. Li & J. N. Zhu 10414* (PE, XJBI). Mori: Nangou, *S. L. Chen 0040* (PE). Qapqal: 58 km from Yining to Zhaoxiu, *Inst. Biology and Pedology 66* (XJBI). Qitai: Biliuhe, *J. C. Zhao 82-4288* (PE, XJU); Kuangou, *Biology 81-8381574* (XJBI); Tangfangmen Forest Farm, *Integr. Inst. Bio. Res. 5788* (XJBI); Yuejin Commune, *S. Q. Lin et al. 34* (XJBI). Tacheng: Mt. Baerleike, N slope, *Integ. Exped. 1200* (XJBI). Toli: Mt. Albakzin, mountain slope, *K. C. Kuan 2611* (PE, XJBI). Xinyuan: Nanshan, *T. Y. Chou et al. 650392* (PE). Yining: Yining Forest Farm, Jirttoulong valley, *D. Y. Hong et al. Population 1 & 092* (PE). Yumin: The Wild Bada *Prunus* Nature Reserve, *J. C. Zhao 85-293* (PE, XJU). GEORGIA. **Kartly:** between Lamistskali and Igoeti, *Hong & Zhou H99033* (PE). KAZAKHSTAN. **Ili-Pribalkhash:** NW ridges of Mt. Kirgizsky Range, upper Sugata River, *V. Golos-Kokov s.n.* (LE); Issyk-Kul Province, Santash, Dongulsky garden, *Aidarova & Kashenko s.n.* (LE); Semirechensk Province, N slope of Alatau, between Verny to Kastek mountain pass, *V. Ladyshev s.n.* (LE); SW Songorian Alatau, Mt. Emelsky Range, Mt. Matai, *V. Goloskokov s.n.* (LE); Taldy-Kurgan Province, Mt. Altyn-Emel Range, Mt. Engi-Altyn-Emel pass to road Sary-Ozek-Dzharkent, *Grubov & Luboarsky 229* (LE); Zailiinsky Alatau, Usun-Kargali River Valley, W Sukonnaya Fabrika, *Y. Goloskokov* (LE). **E. Kazakhstan:** Mt. Kalbinsky Range, Mt. Kok-tau, near Sabinsk Lake, *A. Yunatov 24* (LE); Semipalatinsk Province, Zaisan distr., Kusto Gorge, *B. Shishkin s.n.* (LE); Zaisan distr., near Kenderlyk, *B. Shishkin s.n.* (LE); near Zaisan, Mt. Kichken-tau, *Tatarowa & Borsowa 52* (LE). **Mountain Kazakhstan:** Semirechensk Prov., Songorian Alatau, S of Lepisinsk, *R. Rozhevits 55* (LE); W ridges of Songorian Alatau, Koksu Gorge, near Koksuisky, *V. Goloskokov* (LE); Tarbagatai, Chenarak, steppes, *Grigoriev & Buhaeva 298* (LE); Mt. Tsarytsynsky Pass, deep gorge from the pass, *Schipczinsky 125* (LE). **S. Kazakhstan:** Mt. Chatkalsky Range, Chatkal Valley, Mt. Piazak, *O. Knorring 60* (LE); Prichuisky Mijun(Kum), Sulunger Gorge, *F. Zapriagaev 66* (LE). KIRGHIZIA. **Dzhalalabad Province:** Bazar-Kurgan distr., Mt. Fergansky Range, S slopes, near AK-Terek, *Lebedeva & Faleeva s.n.* (LE); Kara-Alma, Toguz (Bulak), N slopes, *Poniatovskaya, s.n.* (LE); Tianshan, Mt. Ketmen Range, Mt. Elchin-Ustriuk, Kizilbulak Gorge, *s. coll. s.n.* (LE). **Fergana Province:** Kirgizsky Alatau, Makbal Gorge, Ty-Karyn River, *G. Igolkina 97* (LE); Oshsky distr., Ak-Bura valley, Mt. Kanida Pass, *O. Knorring 25* (LE). **Semirechensk Province:** Pishpeksky distr., Uzungyrskaya Volost, Mt. Aleksandrovsky Range, Mt. Shekule N slope, *A. Savenkova 29* (LE). RUSSIA. **Altai:** *Alex Shrenk s.n.* (LE); Altai, Barnaul Province, between Kalmyskies Mysy & Mahanova, *P. Krylov s.n.* (LE). TADZHIKISTAN.

Gissarsky Mountain Range: Buhara, Gissar, Mtn. Zar-kamar Pass, *V. Lipsky 1697* (LE), Darvazsky Mtn. Range, N slopes, left bank of Zarako River, opposite Havdak, *Shinova & Kinzikaeva 1550* (LE). Imam-Askari, Mt. W of Darai-Imam, *Bochantsev & Egorova 1014* (LE). Peter I Range, N slopes, Nazarak Valley, upper reaches, 15 km S of Tadzhikabad, *Ladygina, Ikonnikov & Fridman 1337* (LE). Vahshsky Mtn. Range, Mt. Hozreshi-Sho, above Sary-Hosor, *Sidorenko 185* (LE). Varzob Valley, right bank of Maihir Gorge, NE slope, *Stepanenko & Kudriashova 2514* (LE); Mountain pass between rivers Havag & Kets-gug, N. *Gontscharow 2051* (LE); upper Horanchon, *Zapriagaev 351* (LE). UZBEKISTAN. **Tashkent Province:** Bolshoy Chimgan, *Z. von Minkwitz 1190* (LE); Bolshoy Chimgan, N stony slopes, *V. Bochantsev 547* (LE).

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APPENDIX 1

INDEX TO EXSICCATAE EXAMINED

The figures in parentheses represent: 1a = *Paeonia anomala* subsp. *anomala*; 1b = *P. anomala* subsp. *veitchii*; 2 = *P. intermedia*.

Acad. Sinica Bot. Inst. Exped. Xinjiang 1803 (PE, XJBI) (2); Acad. Sinica Exped. 10402 (PE) (2); Acad. Sinica Xinjiang Exped. 2496 (PE, XJBI) (1a), 10227 (PE) (2); Acad. Sinica Xinjiang Integr. Exped. 10657 (PE) (2); Agr. College 1051 (PE) (2); Aidarova & Kashenko s.n. (LE) (2); Alexandrov, P. 179 (LE) (1a), 219 (LE) (1a); Alex Shrenk s.n. (LE) (2).

Bai, J. L. 8613 (NWTC) (1b); Beresowskii, M. s.n. (LE) (1b, type of *Paeonia beresowskii* Komarov); Biology Exped. 79250198 (XJBI) (2), 81–8330478 (XJBI) (2); Bochantsev, V. 547 (LE) (2); Bochantsev & Egorova 1014 (LE) (2); Borovikov, G. s.n. (LE) (1a); Borovikov et al. s.n. (LE) (1a).

Chang, C. W. 11356 (XJBI) (1a); Chang, C. W. et al. 3316 (XJBI) (2), 4037 (XJBI) (2), 4357 (XJBI) (1a), 10255 (XJBI) (1a); Chen & Ju s.n. (NWTC) (1b); Chen, S. L. 0040 (PE) (2); Cherepnin s.n. (LE) (1a); Ching, R. C. 1803 (PE) (1a), 2433 (PE) (2), 2496 (PE) (1a); Chou, T. Y. 652100 (XJBI) (2); Chou, T. Y. et al. 650392 (PE) (2), 650868 (PE, XJBI) (2), 652150 (PE, XJBI) (2); Cui, N. R. 091 (XJNU) (1a), 86624 (XJNU) (1a); Cui, Y. W. 4348 (PE) (1b), 10281 (PE) (1b).

Dolenko, G. 108 (LE) (1a); Dranitsyn & Kochubei s.n. (LE) (1a).

Ermolajeva, M. s.n. (LE) (1a); Evseeva, Z. 4406 (LE) (1a).

Fang, W. P. 4213 (LE) (1a), 6037 (LE) (1a); Farrer, R. 67 (E) (1b, type of *Paeonia woodwardii* Stapf ex Cox); Fedorov & Iljina 72 (LE) (2), 128 (LE) (2); Fu, K. J. 4441 (PE) (1b); Fu, T. K. 834 (PE) (1b).

Ganeshin, S. s.n. (LE) (1a); Gansu Herbs Group s.n. (NWTC) (1b); Genina, S. s.n. (LE) (1a); Gansu-Qinghai Exped. 2493 (PE) (1b); Goloskokov, V. s.n. (LE) (2); Gontcharow, N. 2051 (LE) (2); Gorodkov, B. 512 (LE) (1a); Grigoriev & Buhaeva 298 (LE) (2); Grubov & Luboarsky 229 (LE) (2); Guo, B. Z. 6767 (HNWP) (1b), 7010 (HNWP) (1b), 7396 (HNWP) (1b), 10186 (HNWP) (1b), 10232 (HNWP) (1b); Guo & He 9012 (HNWP) (1b); Guo & Wang 6008 (HNWP) (1b), 6717 (HNWP) (1b), 25058 (HNWP) (1b); Guo & Yang 9608 (HNWP) (1b).

Hanminchun, V. 515 (LE) (1a); Hao, K. S. 779 (PE) (1b); He, Y. Q. 4516 (PE) (1b), 4915 (PE) (1b); He, Z. 12339 (PE) (1b); He & Zhou 13338 (PE) (1b); Hong D. Y. et al. Population 2 (PE) (2), Population 3 (PE) (1a), Population 4 (PE) (2), Population 5 (PE) (1a), Population 1 (PE) (2), Population 0190 (PE) (2); Hong D. Y. & Zhong PB82105 (PE) (1b); Hong D. Y. & Zhu PB85019 (PE) (1b), PB85040 (PE) (1b), PB85065 (PE) (1b); Hong, Luo & He H95034 (A, CAS, K, MO, PE, US) (1b); Hong & Zhou H99033 (PE) (2); Hsia, W. Y. 4539 (PE) (1b), 4571 (PE) (1b), 5707 (PE) (1b); Hu, W. G. 13050 (PE) (1b); Huanghe Exped. 1689 (PE) (1b), 3183 (PE) (1b), 4655 (PE) (1b), 4735 (PE) (1b); Hu & He 10083 (PE) (1b), 10373 (PE) (1b), 10463 (PE) (1b), 11173 (PE) (1b); Huang, Luo & Jiang 730 (PE) (1b).

Igolkin, G. 97 (LE) (2); Ikonnikov & Fridman 892 (LE)

(2); Iljin, V. s.n. (LE) (1a); Integr. Exped. 630 (XJBI) (1a), 1200 (XJBI) (2), 7305 (XJBI) (1a), 10563 (PE, XJBI) (2), 11829 (XJBI) (1a), s.n. (XJBI) (2); Integr. Inst. Hydrol. Pedol & Biol. Res. 5788 (XJBI) (2).

Jia, S. X. 229 (PE) (1b); Jiang & Jin 00386 (PE) (1b), 2113 (PE) (1b); Jiang & Xiong 34242 (PE) (1b), 34319 (PE) (1b), 35625 (PE) (1b); Jiang, S. 5768 (PE) (1b), 8874 (PE) (1b), 8930 (PE) (1b), 8965 (PE) (1b), 9082 (PE) (1b), A-7162 (PE) (1b), A-7275 (PE) (1b); Jiang, X. C. 36014 (PE) (1b), 36433 (PE) (1b).

Kelimu 10171 (XJBI) (2), 10369 (XJBI) (2), 10614 (XJBI) (2); Keller, B. s.n. (LE) (1a); Ketzchoweli, N. s.n. (TBI) (2, type of *Paeonia majko* N. Ketzchoweli); Kildushewsky, I. 150/22 (LE) (1a); Klements, E. 4d (LE) (1a), 11a (LE) (1a); Klopotov, B. 113 (LE) (1a), 180 (LE) (1a); Knorrung, O. 25 (LE) (2), 66 (LE) (2); Kokulin, S. 254 (LE) (1a); Kolomoitseva, S. 236 (LE) (1a); Komarov, V. s.n. (LE) (1a); Korovkin, A. 290 (LE) (1a); Krasnobarov, I. 6765 (LE) (1a); Krishtofowich, A. s.n. (LE) (1a); Krylov, P. s.n. (LE) (2); Kuan, K. C. 2611 (PE, XJBI) (2), 77309 (PE) (1b); Kuan et al. 243 (PE) (1b), 352 (PE) (1b); Kuchurovskaya, S. 282 (LE) (1a); Kuminova & Alexeeva s.n. (LE) (1a); Kuvajev & Sabitov s.n. (LE) (1a); Kuznetsov, I. 53 (LE) (1a), 114 (LE) (1a), 193 (LE) (1a), 4661 (LE) (1a); Kuznetsov, N. 199 (LE) (1a), 1991 (LE) (1a).

Ladygin 92 (LE) (1a), s.n. (LE) (2); Ladygina et al. 1337 (LE) (2); Lashinsky & Ronginskaya 973 (LE) (1a); Lebedeva & Faleeva s.n. (LE) (2); Ledebour, s.n. (K) (2, type of *Paeonia intermedia* C. A. Meyer); Li, A. R. & Zhu, J. N. 10414 (PE, XJBI) (2); Li, P. X. 10100 (PE) (1b), 10137 (PE) (1b), 10143 (PE) (1b); Li, X. 70247 (PE) (1b), 70441 (PE) (1b), 70510 (PE) (1b), 70685 (PE) (1b), 70719 (PE) (1b), 70867 (PE) (1b), 70903 (PE) (1b), 71029 (PE) (1b), 71087 (PE) (1b), 71196 (PE) (1b), 71645 (PE) (1b), 74842 (PE) (1b), 74936 (PE) (1b), 77248 (PE) (1b, type of *Paeonia veitchii* var. *leiocarpa* W. T. Wang & S. H. Wang); Li, X. Y. 870147 (SHI) (1a), 870169 (SHI) (2); Lian & Chen 31 (NWTC) (1b), 72 (NWTC) (1b); Lian et al. 378 (HNWP) (1b), 79179 (NWTC) (1b); Licent, P. 2022 (PE) (1b); Lin, S. Q. et al. 34 (XJBI) (2); Ling, Y. R. 1141 (PE) (1a, type of *Paeonia sinjiangensis* K. Y. Pan), 74243 (PE) (2), 74848 (PE) (2), 74849 (PE) (2); Liou, K. M. 5659 (PE) (1b), 5970 (PE) (1b), 6019 (PE) (1b), 6178 (PE) (1b); Lipsky, V. 1697 (LE) (2); Liu & Luo 1040 (HNWP) (1b); Liu & Shen 8308 (XJBI) (1a); Liu, S. W. 2115 (HNWP) (1b); Lomonosova & Ivanova 89 (LE) (1a); Long, X. F. 85 (NWTC) (1b).

Maltsev, N. 79 (LE) (1a); Mao, Z. M. 10413 (XJBI) (1a); Mihno, P. s.n. (LE) (1a); Minkwitz Z. von 1190 (LE) (2); Morgan, P. 23 (K) (1a).

Nanshui-Beidiao Exped. 02912 (PE) (1b).

Pharmac. Exped. 2019 (PE) (1b); Pobedimova 697 (LE) (1a); Pohle & Rozhdestvensky s.n. (LE) (1a); Polozhii & Kandasova s.n. (LE) (1a); Poniatovskaya s.n. (LE) (2); Price, M. P. 293 (LE) (1a).

Qing, Z. Y. 1218 (HNWP, PE) (1b); Qinghai-Xizang Exped. Veget. Group 034 (PE) (1b, type of *Paeonia veitchii* var. *uniflora* K. Y. Pan), 9893 (PE) (1b); Qu, Z. X. 2792 (PE) (1b).

Reznichenko, V. 49 (LE) (1a), 58 (LE) (1a); Reznichenko, V. & A. 106 (LE) (1a), 360 (LE) (1a), s.n. (LE) (1a); Rock, J. F. 12260 (PE) (1b), 12829 (PE) (1b), 13127 (PE) (1b); Rohderi, I. s.n. (LE) (1a); Rozhevits, R. 55 (LE) (2); Rubin, A. s.n. (LE) (1a); Rubin & Maskil, s.n. (LE) (1a).

Sanadze et al. s.n. (TBI) (2); Savenkova, A. 29 (LE) (2); Schipczinsky 125 (LE) (2); s. coll. Siberia, (LINN) (1a, type of *Paeonia anomala* Linnaeus); Sedelnikov, A. s.n.

- (LE) (1a); S. Gansu Grassland Exped. 681 (NWTC) (1b); Shanxi Exped. 684 (PE) (1b); Shanxi Exped. Wang & Tian 594 (PE) (1b); Shinova & Kinzikaeva 1550 (LE) (2); Shishkin, B. s.n. (LE) (2); Shliahtin, A. s.n. (LE) (1a); Shukin, S. s.n. (LE) (1a); Sichuan-Econom. A59-0246 (PE) (1b), A59-1001 (PE) (1b), A59-1208 (PE) (1b), A59-2554 (PE) (1b); Sichuan-Econom. & Ya 838 (PE) (1b); Sichuan Plants Collection 0905 (PE) (1b); Sidorenko 185 (LE) (2); Smirnov, V. s.n. (LE) (1a); Smith, H. 2499 (PE) (1b); Sochava, V. 100 (PE) (1b); Sokolov, P. 13a (LE) (1a); Song, Z. P. 38544 (PE) (1b), 39107 (PE) (1b); Stepanenko & Kudriashova 2514 (LE) (2); Suhareva, A. s.n. (LE) (1a).
Tang, T. 938 (PE) (1b); Taohe Exped. 3243 (PE) (1b); Tatarova & Borsowa 52 (LE) (2); Tolmatschew, I. 247 (LE) (1a); Tomin, M. 67 (LE) (1a); Tripolitova, T. s.n. (LE) (2); Troitsky, W. s.n. (LE) (1a); Tsoong, P. C. 5004 (PE) (1b), 5024 (PE) (1b), 8842 (PE) (1b); Tu, T. H. 362 (PE) (1b), 4329 (PE) (1b); Tugarinov, A. s.n. (LE) (1a); Turczaninow, s.n. (LE) (1a).
Varentsov, V. s.n. (LE) (1a); Vereshagin, V. 296 (LE) (1a), 345 (LE) (1a); Verhovskaya & Mishin 104 (LE) (1a); Vislouh, E. 73 (LE) (1a); Vydrin, A. s.n. (LE) (1a).
Wang, F. T. 22930 (PE) (1b); Wang, J. Q. 197 (NWTC) (1b); Wang, Q. R. 1869 (NWTC) (1b), 7034 (NWTC) (1b), 7270 (NWTC) (1b); Wang, S. X. 1065 (HNWP) (1a); Wang, T. P. 197 (NWTC) (1a), 15240 (NWTC) (1a), 4594 (NWTC) (1a), 6944 (PE) (1b); Wang, W. Y. 26771 (HNWP) (1b), 26818 (HNWP) (1b), 27060 (HNWP) (1b); Wang, W. Y. et al. 27347 (HNWP) (1b); Wang & Zhou 19 (HNWP) (1b), 198 A (HNWP) (1b).
Xinjiang Branch Acad. Sinica 012 (XJBI) (1a); Xu, L. R. s.n. (PE) (1a).
Yakovlev, D. 69 (LE) (1a); Yan, M. S. 1843 (NWTC) (1b); Ying, J. S. 3113 (PE) (1b), 3869 (PE) (1b), 4582 (PE) (1b), 4591 (PE) (1b); Ying, T. H. 995 (PE, SHMU) (1a), 1001 (PE, SHMU) (1a), 1006 (PE, SHMU) (1a), 1007 (SHMU, PE) (1a, type of *Paeonia altaica* K. M. Dai & T. H. Ying), 1008 (PE) (1a), 1009 (PE, SHMU) (1a), 1010 (PE, SHMU) (1a), 1011 (PE, SHMU) (1a), 1014 (PE, SHMU) (1a), 1022 (PE, SHMU) (1a); Yu et al. 68 (PE) (1b); Yu, T. T. 2200 (PE) (1b), 6137 (PE) (1b); Yunatov, A. 24 (LE) (2); Yurchenko, P. s.n. (LE) (1a).
Zapriagaev, F. 66 (LE) (2), 351 (LE) (2); Zhang, F. M. 90-346 (XFNU) (1a); Zhang, G. Z. 005 (HNWP) (1b); Zhang & Lang 57 (PE) (1b); Zhang & Li 0502 (HNWP) (1b); Zhang & Ren 5572 (PE) (1b), 6082 (PE) (1b), 6322 (PE) (1b); Zhang, Z. H. et al. 0097 (HNWP) (1b), 0414 (HNWP) (1b), 4291 (HNWP) (1b), 4317 (HNWP) (1b), 4320 (HNWP) (1b); Zhang & Zhou 22092 (PE) (1b), 22155 (PE) (1b), 22675 (PE) (1b), 23742 (PE) (1b); Zhao, J. C. 82-293 (PE, XJU) (2), 82-4288 (PE, XJU) (2), s.n. (PE, XJU) (2); Zhen, S. X. 0351 (PE) (1b); Zhou, H. J. 708 (NWTC) (1a); Zhou, L. H. 2528 (HNWP) (1b); Zhu, G. L. 5665 (PE) (2), 5755 (PE) (1a), 6345 (PE) (1a), 80006 (NWTC) (1b); Zhu, G. L. et al. 6325 (PE) (2), 6386 (PE) (2); Zhu, S. F. 20491 (PE) (1b).