JSE Journal of Systematics and Evolution

Journal of Systematics and Evolution 48 (6): 445–454 (2010) doi: 10.1111/j.1759-6831.2010.00104.x

Biosystematic studies on *Adenophora potaninii* Korsh. complex (Campanulaceae) V. A taxonomic treatment

Song GE* De-Yuan HONG

(*State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences,* Beijing 100093, China)

Abstract *Adenophora* is an extremely variable genus, and its taxonomy is very controversial. Of the genus, *Adenophora potaninii* complex, including *A. potaninii*, *A. bockiana*, *A. wawreana*, *A. lobophylla*, *A. biformifolia*, *A. polydentata*, and *A. wawreana* var. *lanceifolia*, is a typical group with different taxonomical treatments due to high level of morphological diversity. We carried out extensive biosystematic studies based on population sampling, transplantation experiments and offspring tests, cluster analysis, and a crossing experiment. The results reveal four main findings. (i) Leaf forms of the *A. potaninii* complex were extremely polymorphic; the leaf form of *A. potaninii* and *A. bockiana*, and that of *A. wawreana* and *A. biformifolia* could be found, respectively, on a single population or among the offsprings of a single plant. (ii) Cluster analysis and a crossing experiment indicated that *A. bockiana* and *A. polydentata* could not be separated from *A. potaninii*, nor *A. biformifolia* from *A. wawreana*. (iii) *Adenophora potaninii* and *A. wawreana* were gradational in morphology and their compatibility value was slightly reduced compared to that within each entity. (iv) *Adenophora lobophylla* was distinct from the other members of the complex in shape and size of corolla, relative length of style, and shape of capsule. This species was incompatible reproductively with the other members of the complex, but partly compatible with *A. stenanthina*, a species in another section. Therefore, we recognized only one species with two subspecies in the complex, *A. potaninii* subsp. *potaninii* and subsp. *wawreana*, moved *A. lobophylla* out of the complex, and reduced all the other names as new synonyms.

Key words *Adenophora potaninii*, biosystematics, populations, species complex, taxonomy.

The genus *Adenophora* is a group recently derived from the genus *Campanula*, from which it differs only in having a disc surrounding the base of style (Hong, 1983; Roquet et al., 2009). The genus is still actively differentiating, and extremely variable in nearly all morphological characters. Tsoong (1935) and Baranov (1963) realized the difficulty of the genus in taxonomy. Tsoong (1935) detected great variations not only in vegetative morphological characters, but also in floral characters, e.g. shape and size of corolla. Due to the great variation of morphological characters and difficulty in finding correlated character variation, the development of a taxonomic account of *Adenophora* is very complicated. Because of this fact the taxonomy of the genus is extremely controversial among authors. Tsoong (1935) and Federov (1957) considered the number of species to be approximately 70 and 50, respectively, whereas according to Bailey (1941) the number of species in Siberia, China, and Japan is no more than 14. Hong (1983) realized great variation of the genus in morphology, and thus reduced 32 specific names and 20 infraspecific names as new synonyms based on his taxonomic account of the genus in China on field observation and examination of a large number of herbarium specimens (Hong, 1983).

The *Adenophora potaninii* Korsh. complex is a representative of the genus showing the variability of morphological characters and the complexity of taxonomy (Ge & Hong, 1994a, 1995). *Adenophora potaninii* Korsh. (Korshinsky, 1894) is the earliest published species in the complex, and distinct from all the previously described *Adenophora* species. Zahlbruckner (1895) described *A. wawreana* as new one year later based on petioled leaves. Then *A. bockiana* was described by Diels (1901) based on linear leaves and exerted style. Hong (1983) stated that the material was not enough for him to judge if *A. bockiana* was a distinct species or just an entity in *A. potaninii*. Hong (1983) described *A. lobophylla* as a new species according to a number of collections from NW Sichuan with petioled and lobed leaves, verrucose-denticulate calyx-lobes, smaller corolla, and elongated capsule. Therefore, according to Hong's (1983) account the complex comprised four species. Thereafter, a number of new taxa were described: *A. biformifolia* by Zhao (1980, after Hong's manuscript was sent to Science Press in 1978) based on sessile and dimorphic leaves, that is,

Received: 15 March 2010 Accepted: 26 August 2010

* Author for correspondence. E-mail: gesong@ibcas.ac.cn; Tel.: 86-10-62836097; Fax: 86-10-62590843.

the lower leaves linear and entire, but the upper ones linear-lanceolate to lanceolate, with irregularly serrate or sparsely serrate margins; *A. wawreana* var. *lanceifolia* also by Zhao (1980) according to a single specimen with leaves lanceolate or oblong-lanceolate, caudate-acuminate at apex, cuneate at base; *A. polydentata* by Tu et al. (1990) based on a single specimen with leaves sessile or very shortly petioled, more dents on leaf margins, and calyx-lobes having more than two pairs of dents. Liu (1996) reduced *A. bockiana* Diels to varietal rank, *A. potaninii* var. *bockiana* (Diels) Liu.

Given the high variation in morphology both within and among species of the *A. potaninii* complex and inconsistent taxonomic treatments of different authors, we have carried out a comprehensive biosystematic study on this complex, including the phenotypic plasticity and variation of major taxonomic characters (Ge & Hong, 1994a, 1995), a crossing experiment between taxa (Ge & Hong, 1994b), and allozyme variation and differentiation of natural populations (Ge & Hong, 1998). These investigations provided both insights into the understanding of this complex and important bases for further revision on the taxonomy of the complex. As part of this project, we analyzed the morphological characters based on our population sampling across the whole distribution range of the complex. We also investigated the specimens from major herbaria in China. On these bases, in conjunction with the evidence from our previous studies, we made a taxonomic revision of *A. potaninii* complex. We showed that a reasonable taxonomic revision must be based on a better understanding of the characters, their variation and genetics, and the correlation between them. This study also highlights the importance of population-based study in better delimitation of species and taxonomy of complex plant groups such as *Adenophora*.

1 Material and methods

A total of 23 populations representing all the taxa in *A. potaninii* complex were sampled across its entire distribution. Twelve to 35 individuals were sampled randomly from each population and were subsequently maintained in a garden in Beijing. The locality, sample size and the habitat of these populations are shown in Table 1. One population of *A. stenanthina*, which is distinctly related to *A. potaninii* complex, was collected for

Table 1 Populations of the *Adenophora potaninii* complex sampled in this study

Population no.	No. of individuals sampled	Locality	Habitat	Abbreviation of specific names
01	28	Erdaogou, Jianchang, Liaoning, China	560 m, shaded grassy and stony slopes	WAW
02	18	Vicinity of Qinglong, Hebei, China	250 m, shaded grassy and stony slopes	WAW, BIF
03	20	Donghai Shi, Xinglong, Hebei, China	750 m, shaded grassy and stony slopes	WAW, BIF
04	18	Xiangshan, Beijing, China	550 m, semi-shaded slopes, thickets	WAW, BIF
05	16	Hengshan, Hunyuan, Shanxi, China	1650 m, shaded shrubby and stony slopes	WAW, BIF
06	23	Dongzhai, Ningwu, Shanxi, China	1680 m, semi-shaded shrubby and stony slopes	POT
07	31	Daqing Shan, Nei Mongol, China	1200 m, semi-shaded shrubby and stony slopes	WAW, BIF
08	30	Luluo, Xingtai, Hebei	700 m, semi-shaded shrubby slopes with grasses	WAW, BIF
09	26	Shibanyan, Linxian, Henan, China	620 m, shaded shrubby and sandy slopes with grasses	WAW, BIF
10	26	Nanniwan, Yan'an, Shaanxi, China	980 m, shaded shrubby slopes with grasses	WAW, BIF
11	35	Raoshan, Yuncheng, Shanxi, China	750 m, semi-shaded and stony grassy slopes	POL, POT
12	22	Gukuan, Longxian, Shaanxi, China	1300 m, shaded slopes, by the fields	POT
13	26	Lüergou, Tianshui, Gansu, China	1350 m, semi-shaded slopes, by the fields	POT, POL
14	12	Gantong, Dangchang, Gansu, China	2460 m, shaded shrubby slopes	POL, BOC
15	15	Jinjiahe, Lüeyang, Shaanxi, China	800 m, semi-shaded and stony shrubby slopes with grasses	POT, BOC, POL
16	25	Dingjun Shan, Mianxian, Shaanxi, China	620 m, shaded shrubby slopes with grasses	POT, POL
17	28	Funshun, Maoxian, Sichuan, China	1200 m, semi-shaded shrubby slopes	POT, POL
18	23	Qugu, Maoxian, Sichuan, China	3000 m, shaded and stony shrubby slopes	POT, BOC, POL
19	22	Zhabei, Barkam, Sichuan, China	2560 m, shaded slopes, by the fields	POT, BOC, POL
20	30	Dalangjiao valley, Barkam, Sichuan, China	2620 m, shaded shrubby slopes with grasses	POT, BOC, POL
21	25	Xueshan, Baoxing, Sichuan, China	950 m, shaded shrubby slopes	POT, POL
22	16	Baguadiaogou, Anning, Jinchuan, Sichuan, China	2450 m, shaded shrubby slopes, by forests	LOB
23	12	Tanchang Valley, Jinchuan, Sichuan, China	2780 m, shaded shrubby slopes, by forests	LOB
STE	24	Shanghenan Cun, Ningwu, Shanxi, China	1850 m, shaded and stony grassy slopes	STE

BIF, *Adenophora biformifolia*; BOC, *A. bockiana*; LOB, *A. lobophylla*; POL, *A. polydentata*; POT, *A. potaninii*; STE, *A. stenanthina*; WAW, *A. wawreana*.

Table 2 Variation index and standard deviation of 34 characters within population, and principal components

Character	Variation index within population (standard deviation)	Principal component I	Principal component II	Principal component III
Height of stems	0.3172 (0.0880)	−0.0027	0.1345	−0.0661
Length of inflorescene branches	0.5424 (0.1328)	−0.0409	0.0663	0.1236
Stem height/inflorescence branch length	0.4531 (0.1432)	−0.0700	−0.0321	0.1879
Indumentum of stems	0.7690 (0.3997)	0.0782	−0.2618	0.1217
Length of leaves	0.3158 (0.1167)	−0.0572	0.2236	−0.0948
Width of leaves	0.3461 (0.1179)	0.0050	−0.1680	−0.3837
Leaf length/leaf width	0.7482 (0.4282)	−0.0887	0.1913	0.2684
Length of petioles	1.2590 (1.0184)	−0.1446	−0.1443	−0.2933
Indumentum of leaf adaxial surface	0.9261 (0.4314)	0.0768	−0.2637	0.0819
Indumentum of leaf abaxial surface	0.9419 (0.6614)	0.1714	−0.2279	0.1413
Number of teeth of leaf margin	0.3338 (0.1447)	−0.1187	−0.0283	−0.3517
Tooth length of leaf margin	0.4136 (0.1559)	−0.0563	−0.3042	0.0888
Tooth length/leaf length	0.5456 (0.1996)	−0.0785	−0.2280	−0.3198
Length of corolla	0.1188 (0.0318)	0.2899	0.0342	0.1386
Diameter of corolla	0.1310 (0.0291)	0.3050	0.1014	−0.0374
Corolla length/corolla diameter	0.1165 (0.0273)	−0.2107	−0.1941	0.2102
Length of corolla-lobes	0.1473 (0.0311)	0.3027	0.0750	−0.0717
Width of corolla-lobes	0.1223 (0.0251)	0.2884	0.1402	−0.0555
Length/width of corolla-lobes	0.1274 (0.0675)	0.1016	−0.2246	−0.0820
Length of corolla-lobes/corolla length	0.1306 (0.0471)	0.2095	0.1241	−0.2250
Length of style	0.0901 (0.0204)	0.1556	−0.0170	0.1498
Corolla length/style length	0.0931 (0.0175)	0.2621	0.0574	0.0732
Length of disc	0.1623 (0.0344)	0.0670	−0.3202	−0.0057
Disc length/style length	0.1591 (0.0360)	0.0271	−0.3160	−0.0407
Diameter of disc	0.2289 (0.3365)	−0.0833	0.0035	−0.1742
Length/diameter of disc	0.2084 (0.0475)	0.0519	−0.3168	0.0856
Length of calyx-lobes	0.1496 (0.0340)	0.1730	−0.1474	−0.0736
Shape of calyx-lobes	0.1585 (0.0949)	0.2863	−0.0987	0.0447
Length of capsule	0.1176 (0.0273)	0.1262	−0.1313	0.1942
Diameter of capsule	0.1097 (0.0346)	0.2656	0.0017	0.0225
Length/diameter of capsule	0.1357 (0.0365)	−0.1095	−0.0977	0.1631
Length of seeds	0.0900 (0.0192)	0.2671	−0.0002	−0.0702
Width of seeds	0.0897 (0.0264)	0.2370	−0.0089	−0.1992
Length/width of seeds	0.1159 (0.0211)	−0.0188	0.0237	0.2014

comparison in statistical analyses. Some of these populations have been used in our previous studies (Ge & Hong, 1994a, 1994b, 1995, 1998).

Thirty-four morphological characters (Table 2), including all the taxonomic characters used in previous taxonomic treatments, were scored for 12 to 15 randomly chosen individuals. We scored all morphological characters by routine measurement (mean and its variance), and their variation within populations was measured by coefficient of variation and summarized by principal components analysis. Unweighted pair group method with arithmetic mean (UPGMA) clustering was carried out based on all 34 characters. These statistical analyses were carried out by the program NTSYS-pc (Rohlf, 1994).

2 Results

2.1 Character analysis

2.1.1 Leaves Figure 1 shows changing states of the leaves on a single individual with developmental stages. It is clear that the individual a2 has the lower leaves linear-lanceolate, with the upper ones lanceolate, and the individual a1 from the same population has the lower leaves petioled, with the upper ones sessile or cuneate-petioled. We can see the leaf character of *A. biformifolia* (leaves dimorphic) from these two individuals in the same population, a population of *A. wawreana*.

Polymorphism is very prominent in the genus *Adenophora*. Nearly all populations of *Adenophora* are found polymorphic, particularly for leaf forms, and the *A. potaninii* complex is not exceptional. Figure 2 shows two typical polymorphic populations in leaf form. We may find the phenotype of *A. bockiana* or *A. potaninii* var. *bockiana* (with linear leaves) from any of these two populations, **a** belonging to *A. wawreana* and **b** to *A. potaninii*.

Seeds were collected individually in the field, and sown in flower pots. The seedlings had only basal leaves in the first year, they grew mature in the second year. Fifteen to eighteen two-year-old offsprings from a single maternal individual were observed (Ge, 1993). As shown in Fig. 3, a wide range of segregation of leaf

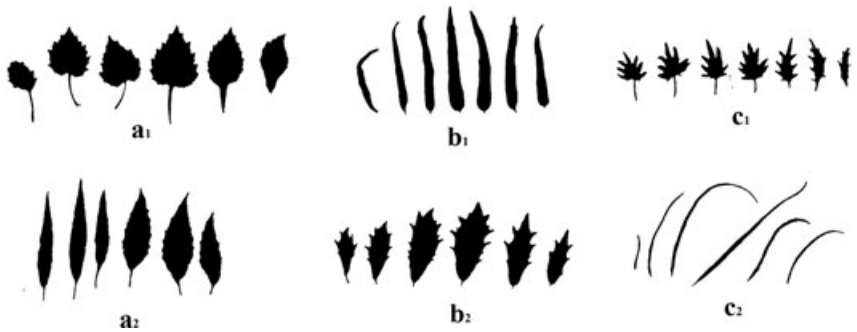

Fig. 1. Leaves at different developmental stages of six individuals in the *Adenophora potaninii* complex from three populations. **a1, a2,** From Mount Henshan, Shanxi; **b1, b2:** From Beicun village, Barkam, Sichuan. **c1, c2:** From Baguadiao valley, Jinchuan, Sichuan (from Ge 1993, with rearrangement).

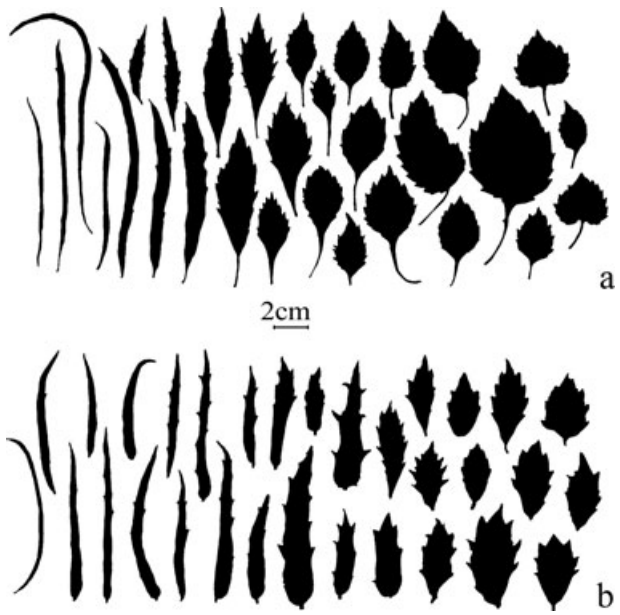

Fig. 2. Leaves at the lower-middle part of stems (1/4 from the base) in the *Adenophora potaninii* complex from two populations showing variation of leaf forms within population. **a:** From Daqing Shan, Nei Mongol (with 30 individuals). **b:** From Dalangjiao valley, Barkam, Sichuan (with 31 individuals) (from Ge & Hong, 1995).

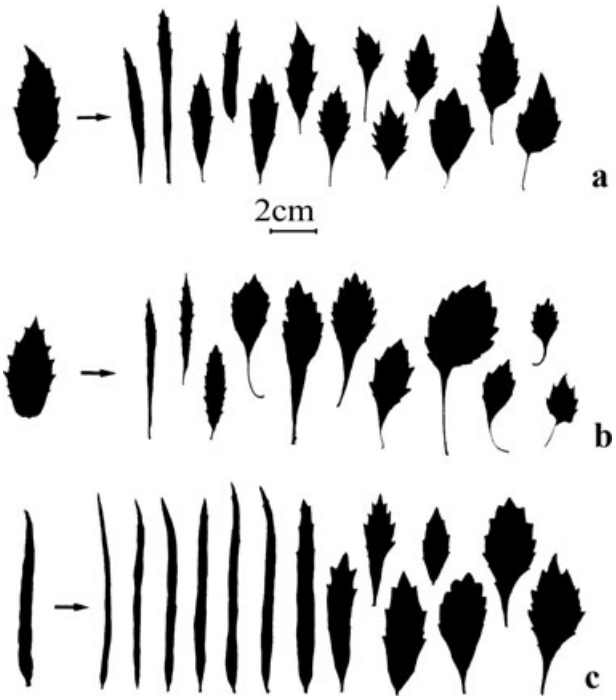

Fig. 3. Leaves of three maternal individuals in the *Adenophora potaninii* complex (left) and their offspring (right) from free pollination (each leaf representing one individual). **a:** From Daqing Shan, Nei Mongol. **b:** From Lüer valley, Tianshui, Gansu. **c:** From Dalangjiao valley, Barkam, Sichuan (from Ge & Hong, 1995).

form was found in offsprings. A mother with broad leaves gave her offspring various forms of leaves including linear leaves, and vice versa, a mother with linear leaves produced offspring with various leaf forms including ovate or obovate leaves. Any taxonomic delimitation based on leaf form is, therefore, unjustifiable in this complex.

2.1.2 Calyx-lobes The characters of calyx-lobes, including shape, absence or presence of teeth, number of teeth, and shape of teeth, are frequently used in taxonomic treatments in the genus *Adenophora*. Figure 4 shows various forms of calyx-lobes and their teeth and these characters are more stable than leaf form (Ge, 1993). However, they varied in a rather large range. We analyzed these characters on two populations, population 11 from Mount Raoshan, Yuncheng, Shanxi Province (based on 35 individuals), and population 20 from the Dalangjiao valley, Barkam, Sichuan Province (based on 31 individuals). It is clear from Fig. 5 that teeth are mostly three, four, or five in number, but one or seven could be found as extremes. It is based on the number of teeth on calyx-lobes (two to five pairs) that *A. polydentata* was described as new (Tu et al., 1990). Therefore, *A. polydentata* is in the range of variation in

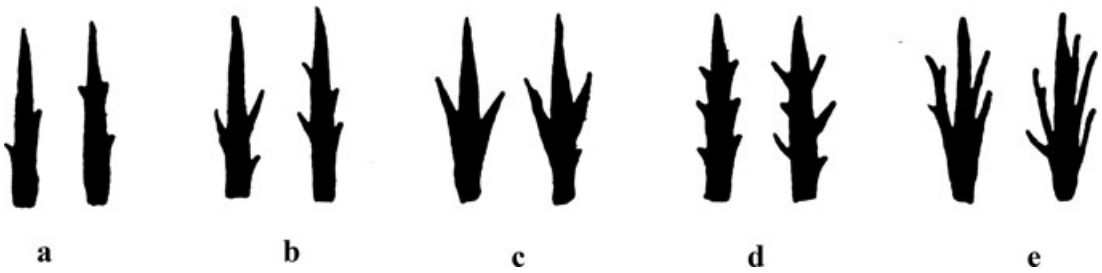

Fig. 4. Various forms of calyx-lobes in the *Adenophora potaninii* complex found in three populations. **a, b:** Population 7 from Daqing Shan, Nei Mongol. **c:** Population 18 from Qugu Township, Maoxian, Sichuan. **d, e:** Population 20 from Dalangjiao valley, Barkam, Sichuan, showing a wide range of variation in the number and shape of teeth on calyx-lobes.

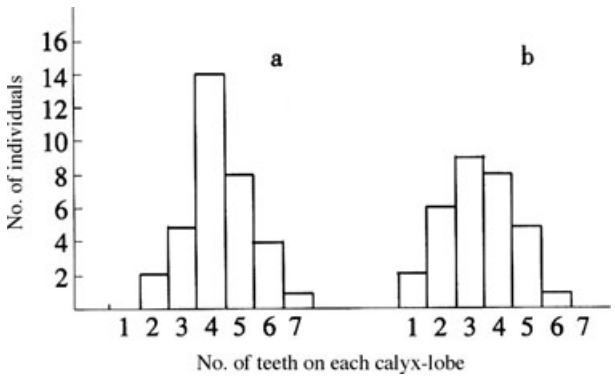

Fig. 5. Histogram showing variation of teeth of calyx-lobes in number within population in the *Adenophora potaninii* complex. **a:** From Mount Raoshan, Yuncheng, Shanxi (population 11). **b:** From Dalangjiao valley, Barkam, Sichuan (population 20) (from Ge & Hong, 1995).

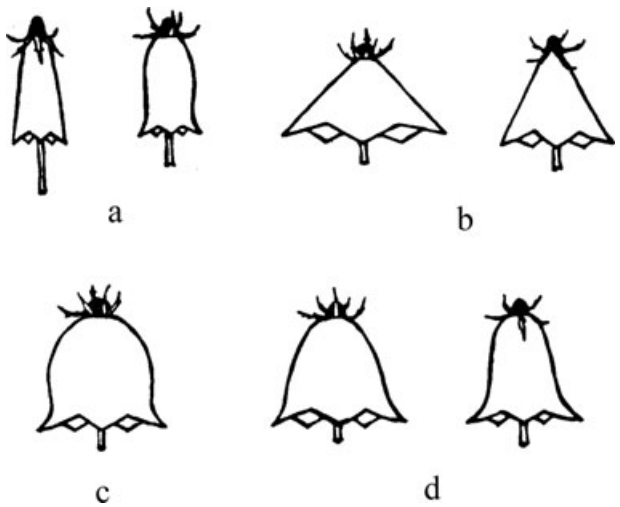

Fig. 6. Different forms of corolla in the *Adenophora potaninii* complex. **a:** From Bagua valley, Jinchuan, Sichuan (population 22). **b:** From Fushun township, Maoxian, Sichuan (population 17). **c:** From Erdao valley, Jianchang, Liaoning (population 01). **d:** from Mount Henshan, Shanxi (population 05).

population 11 (Fig. 5: a) and seems not justified as a new species.

2.1.3 Corolla The characters of corolla are the most stable ones and most frequently used for taxonomic treatments (Hong, 1983). Our analysis of principal components also shows that the characters of corolla, diameter, length of corolla-lobes, width of corolla-lobes and corolla length, are the four characters having the largest loads (Table 2). Figure 6 shows different forms of corolla in the complex. The statistical analysis of six floral characters based on samples of 20 populations is presented in Fig. 7. These results indicated that: (i) the populations in the northeast mostly have smaller corolla diameter, shorter corolla-lobes, and shorter corolla than those in the southwest, but the differences in corolla between the populations in these two regions are gradational rather than distinct; and (ii) Populations 22 and 23 (the type locality of *A. lobophylla*) are very special with very narrow corolla, very short and very narrow corolla-lobes, which make the populations distinct from all the others. In other words, *A. lobophylla* is distinctly different from all the other populations under study in the characters of corolla.

2.1.4 Style and disc The characters of style are often used in taxonomy of the genus. According to our analysis, the ratio of corolla length to style length holds a rather important position in the first principal component (eighth in the order of load, Table 2). According to our field observations, the style of populations 22 and 23 was always exerted above corolla. The results of analysis show that the style is nearly 1.5 times longer than corolla in populations 22 ($n = 16$) and 23 ($n = 12$) (Figs. 6, 7). Furthermore, the much exerted style is closely correlated with the characters of corolla, tubular, and corolla-lobes narrow and short.

Length and diameter of disc are two characters often used in taxonomy of the genus. Figure 7 shows that the disc in populations 22 and 23 is statistically much longer than that in all the others. The above analysis of the characters of both style and disc also indicates

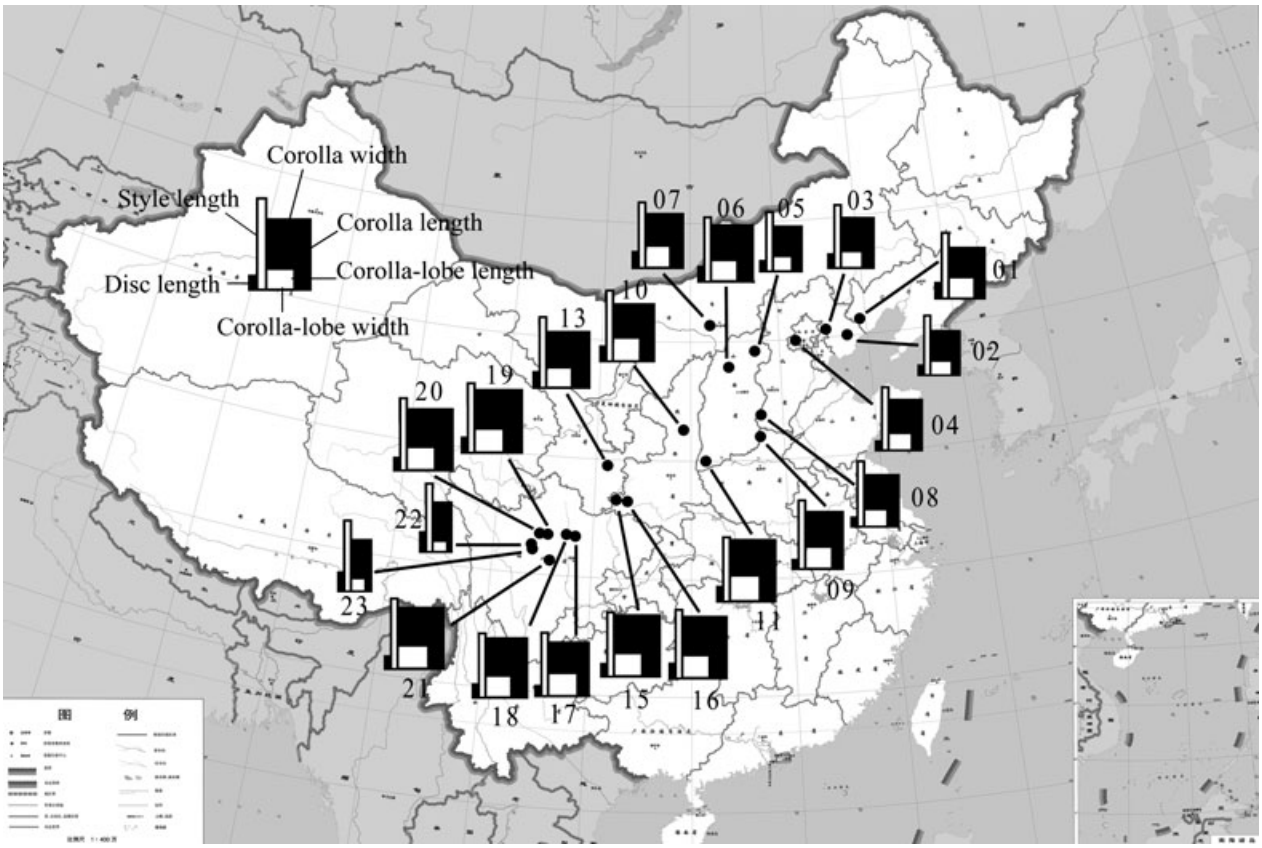

Fig. 7. Localities of populations in the *Adenophora potaninii* complex sampled in this study and the variation pattern of six floral characters among populations (see Table 1 for precise localities of the populations).

that populations 22 and 23 (*A. lobophylla*) are distinctly different from the other populations under analysis.

2.2 Cluster analysis

For the cluster analysis (UPGMA), we used 34 characters (Table 1) based on 21 populations with each population as an operational taxonomic unit. The result is shown in Fig. 8, which shows two major clades, the first consisting of populations 22 and 23, and the second made up of the remaining 19 populations. The distinctness of populations 22 and 23 from all the rest is consistent with the result of the above character analysis (Figs. 6, 7). The 19 populations except for populations 22 and 23 are grouped into two clusters. Populations 01, 02, 03, 04, 05, 08, and 09 form a cluster, and all the other populations form another cluster. These two clusters are not distantly differentiated as population 01 appears intermediate, but the differentiation is correlated with geographical distribution. The former occurs in the northeast of distribution range, whereas the latter is found in the southwest. As shown in Figs. 6 and 7, the former has narrower corolla, smaller corolla-lobes and longer style than those in the latter, but they cannot be distinctly distinguished.

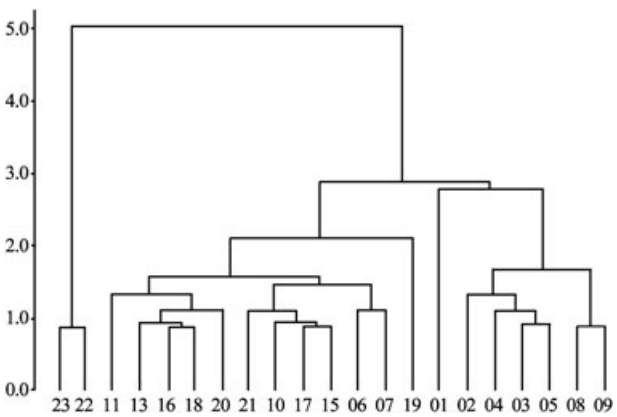

Fig. 8. Unweighted pair group method with arithmetic mean (UPGMA) of the *Adenophora potaninii* complex based on 34 morphological characters.

2.3 Crossing experiment

The relationship between crossing experiments and taxonomy has been stated, and the materials and

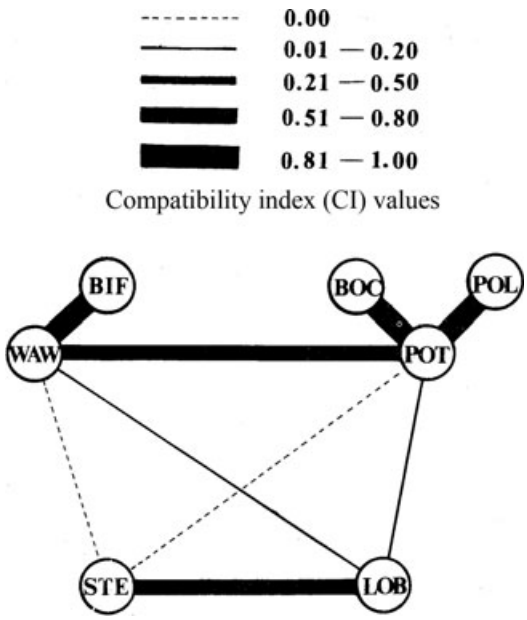

Fig. 9. Crossing diagram showing compatibility index (CI) values among six taxa within the *Adenophora potaninii* complex and *A. stenanthina* in another section. BIF, *A. biformifolia*; BOC, *A. bockiana*; LOB, *A. lobophylla*; POL, *A. polydentata*; POT, *A. potaninii*; STE, *A. stenanthina*; WAW, *A. wawreana*. CI = SI × PG where SI is the seed set index and PG is the percent germination of hybrid seeds (from Ge & Hong, 1994b).

methods we used have been provided before (Ge & Hong, 1994b). The result is summarized in Fig. 9. As stated before (Figs. 2, 4), the forms of *A. biformifolia (*BIF) and *A. wawreana* (WAW) coexisted on the same site; the form of *A. potaninii* (POT) was found to grow together with that of *A. bockiana* (BOC) in NW Sichuan, and also with that of *A. polydentata* (POL) in Gansu, Shaanxi, and Shanxi. In the crossing experiment three populations from WAW and BIF and four populations representing POT, BOC, and POL were used and one population each for *A. lobophylla* (Jinchuan, Sichuan) and *A. stenanthina* (Ningwu, Shanxi) (STE) were also involved. The crossing diagram (Fig. 9) states clearly that there is no reproductive barrier between *A. wawreana* and *A. biformifolia,* between *A. potaninii* and *A. bockiana*, nor between *A. potaninii* and *A. polydentata*. Crossing compatibility between them is largely the same as that between individuals within the same form. Therefore, the result of the crossing experiment does not support recognition of any of the three taxa, *A. bockiana, A. biformifolia*, or *A. polydentata*, as independent species. However, the compatibility index (CI) value 0.51–0.8 between the *A. potaninii* group (populations 10, 13, 18, and 19, in the southwest of the distribution area, Fig. 7) and the *A. wawreana* group (populations 01, 05 and 07 in the northeast of the area, Fig. 7) indicated the existence of a slight reproductive barrier between the two entities. The crossing behavior between the two groups makes us consider them as two subspecies, consistent with a consideration from external morphology. It is interesting to note that *A. lobophylla* D. Y. Hong is on one side of the diagram and all the rest of the taxa in the complex under study is on the other side. As shown in Fig. 9, the CI value between them is 0.01–0.20, indicating nearly incompatible in reproduction. This result is consistent with the morphological distinction of *A. lobophylla* from the other elements in the complex. We crossed *A. lobophylla* with *A. stenanthina* in another section from Ningwu County, Shanxi, and obtained hybrids that gave rise to fairly high average seed set and percent germination (CI = 0.624, Fig. 9). This result suggests that Hong's treatment of *A. lobophylla* as a member of the *A. potaninii* complex is unjustified (Hong, 1983).

2.4 Conclusion

Our character analysis shows (Figs. 1–3) that different forms of leaves as described for *A. potaninii* and *A. bockiana* can be found on a single site or in the offspings from a single maternal individual. This situation can also be found in the cases of *A. wawreana* and *A. biformifolia*. The individuals having polydentical calyx-lobes of *A. polydentata* were found to coexist with those having oligodentical calyx-lobes in the same populations (Fig. 5). The cluster analysis (Fig. 8) and crossing experiment (Fig. 9) do not support *A. bockiana, A. biformifolia*, or *A. polydentata* as independent species. *Adenophora lobophylla* was shown by our character analysis to be distinct from all the other members in the complex in corolla, style, and capsule (Figs. 6, 7). The crossing experiment further indicates that the relative of *A. lobophylla* is *A. stenanthina*, instead of the *A. potaninii* complex (Fig. 9). The character analysis and cluster analysis show that *A. potaninii* and *A. wawreana* are two entities, which are, however, not distinct enough as different species (Fig. 8). When we take the result of the crossing experiment into consideration, it seems more reasonable to recognize them as two subspecies. Our allozyme analysis also indicates that there was high genetic divergence between *A. lobophylla* populations and the *A. potaninii–A. wawreana* group, whereas no clear genetic difference existed between *A. potaninii* and *A. wawreana* populations (Ge & Hong, 1998).

3 Taxonomic treatment

Key to species

1a. Cauline leaves usually lobed and petioled; corolla tubular or tubular-urceolate, corolla-lobes 1/4–1/3 as long as corolla-tube; style

much exerted above corolla; capsule columnar-ellipsoid ..... **2. A. lobophylla**

1b. Cauline leaves serrated, never lobed, petioled or sessile; corolla campanulate, corolla-lobes 1/3–1/2 as long as corolla-tube; style as long as or exerted above corolla; capsule globose-ellipsoid or ellipsoid ..... **1. A. potaninii**

2a. Cauline leaves sessile or rarely lower ones shortly petioled; corolla broad-campanulate or infundibular; style nearly as long as or slightly exerted above corolla ..... **1a.** subsp. **potaninii**

2b. Cauline leaves petioled (except linear leaves); corolla narrow-campanulate; style obviously exerted above corolla ..... **1b.** subsp. **wawreana**

1. Adenophora potaninii Korsh., Mém. Acad. Imp. Sci. St.-Pétersbourg, ser. 7, 42(2): 39. 1894; D. Y. Hong in Hong (ed.): Fl. Reip. Pop. Sin. 73(2): 119. 1983. Type: China, Sichuan, "Provincia Szetschuan ad fl. Atulunva et Honton," 9–13 Aug. 1885, *Potanin s. n.* (holotype: LE).

Stems usually densely, less often sparsely retrorse-hispidulous, very rarely glabrous. Cauline leaves alternate, sessile or petioled; leaf blades from obovate, ovate-elliptic to linear, hispidulous on both surfaces, margins with two to several gross teeth or entire on linear leaves. Calyx glabrous; tube obovoid or globose-obovoid; lobes triangular-subulate, 3–7 mm long, with 1–4 pairs of teeth. Corolla campanulate or infundibular, 1.5–2.5 mm long; lobes ovate-deltoid, 5–8 mm long. Disc tubular, 2–2.6 (3) mm long, hairy at least at the apex. Style nearly as long as or exerted above corolla. Capsule globose-ellipsoid or ellipsoid, 7–11 × 4–6 mm. $2n = 34, 102$.

The species is rather widely distributed from NW Sichuan to SW Liaoning. Two allopatric subspecies can be recognized.

1a. subsp. **potaninii**

Adenophora bockiana Diels, Bot. Jahrb. Syst. 29: 605. 1901 = *A. potaninii* var. *bockiana* (Diels) S. W. Liu in Fl. Qinghaiica, 3: 317. 1996, syn. nov. Type: China, Sichuan, Lixian (Tsa ku lao), *BvR 2531* (fl. Aug.) (lectotype here designated: B).

Adenophora polydentata P. F. Tu & G. J. Xu, J. China Pharm. Univ. 21(1): 16. fig. 1A. 1990, syn. nov. Type: China, Shanxi, Yuncheng, 700–800 m, 18.08. 1987. *J. D. Yang 87056* (holotype: CPU).

Cauline leaves sessile, or rarely lower ones short-petioled. Corolla broad-campanulate or infundibular. Style nearly as long as or slightly exerted above corolla.

The subspecies is found in NW Sichuan, E Qinghai, SE Gansu, S Ningxia, Shaanxi, and W Shanxi. They grow on shaded or semi-shaded grassy slopes, less often in bushes, or forests, at an altitude of 1000–3300 m.

Additional representative specimens examined:

China. Gansu (甘肃): Gaolan, Dangchang, Huanghe Exped s. n. (PE); Xiaojingou, Huanghe Exped. 02736 (WUK); Heshui, Lianjiakeng, Caojiashi, J. H. Sun et al. 0246 (WUK); Huining, Hancha Township, Z. Y. Yu et al. 3808 (PE); Jonê, Dajia Shan, T. P. Wang 5458 (PE), T. P. Wang 5591 (PE); Lintao, Huanghe Exped. 155 (PE); Lupan Shan, Huanghe Exped. 02214 (PE); Pingliang, Kongtong Shan, J. H. Yang 5657 (WUK), J. H. Yang 5740 (WUK); Têwo (Dêngkagoin), Luodanan Shan, P. C. Kuo 5622 (WUK); Tianshui, Lüergou, C. L. Wu 20064 (PE); Wenxian, Dangbao Township, Z. Y. Zhang 9806 (WUK), Bikou Township, Z. P. Wei 3089 (WUK); Yuzhong, Xinglong Shan, Z. Y. Yu 3732 (WUK), Xinglong Shan, Liangdianwan, Huanghe Exped. 5927 (PE). **Ningxia (宁夏):** Guyuan, T. P. Wang 13669 (WUK); Jingyuan, Erlonghe, J. H. Yang 5650 (WUK), Hexi, S. Coll. Jing 0107 (PE); Yanchi, Pingyuan Station, Z. Y. Zhang et al. 174 (WUK). **Qinghai (青海):** Datong, K. C. Kuan 77312 (PE); Guide, Jiangla Forest Farm, S. Chen 2377 (PE, WUK); Huangyuan, Ala'ang Shan, P. C. Tsoong 8926 (PE); Huzhu, Qiaotou, P. C. Kuo 6711 (PE); Minhe, Bazhou, Gansu-Qinghai Exped. 1873 (WUK); Xining (Sining), K. S. Hao 816 (WUK); Tongren, T. P. Wang 6110 (PE); Zhugusi, P. C. Tsoong 10093 (PE, WUK). **Shaanxi (陕西):** Ansai, K. T. Fu 7537 (PE); Danfeng, Qipanmo, B. Z. Guo 3855 (WUK); Foping, Dajiangou Valley, B. Z. Guo 7737 (WUK); Huanglong, Nangouyu, Loess Exped. 1005 (WUK); Huashan, forest, K. S. Hao 3991 (WUK); Jingbian, between Yejipeng and Xiaozhanggu, Huanghe Exped. 8017 (PE); Longxian, Kuanshan Township, Sanjiagou, Z. Y. Yu 39 (WUK); Lüeyang, Xiantai, Xialiangekou, K. T. Fu 5993 (PE); Mianxian, Dingjun Shan, T. N. Liou 11980 (PE, WUK); Qingjian, Sanshilipu, K. T. Fu 7786 (PE); Wuqi, Huanghe Exped. 8791 (PE); Yan'an, Nanniwan, J. H. Yang 4597 (WUK); Zhidan, Haojiacha, Shaanxi-Gansu Exped. 10815 (PE). **Shanxi (山西):** Lanxian, Loess Plateau Exped. 932 (WUK); Lishi, Wucheng, Z. H. Wu 85453 (WUK); Luya Shan, W. Y. Hsia 1621 (WUK); Linxian, Gancaogou, Huanghe Exped. 2nd Group 1827 (WUK); Ningwu, Lüfang Township, X. Y. Liu 15315 (WUK); Pianguan, Nanbao, Loess Exped. 1005 (WUK); Wuzhai, Dianping, Huanghe Exped. 2nd Group 2332 (WUK); Xiangning, Shijin Forest Farm, K. T. Fu 18134 (WUK); Xingxian, Heicha Shan, Huanghe Exped. 2nd Group 2603 (WUK); Yuncheng, Xuehua Shan, Bao & Yan 0875 (HSIB); Zhongyang, P. Y. Li 10354 (WUK). **Sichuan (四川):** Baoxing, T. H. Tu 4772 (PE); Barkam, Dalangjiao valley, X. Li 72251 (PE, SZ); Dujiangyan (Guanxian), Qingcheng Shan, P. F. Tu 86031 (PE); Heishui, Lühua, X. Li 73809 (PE); Jinchuan, Anning, X. Li 78384 (PE, SZ); Kangding, Paoma Shan, Y. Q. He 7979 (WUK); Lixian, Miyaluo, P. He 45348 (WUK); Maoxian, Sanlong Township, Nahagou, Z. He 13311 (SZ); Nanping, Yuwa, Sichuan Econ. Exped. Aba Group 4034 (CDBI); Songpan, T. P. Wang 7743 (WUK); Tianquan, Z. X. Qu 4113 (SZ).

1b. subsp. **wawreana** (Zahlbr.) S. Ge & D. Y. Hong, stat. nov. *Adenophora wawreana* Zahlbr., Ann. Naturhist. Hofmus (Wien) 10 (notiz): 56. 1895; Nannf., Acta Horti Gothob. 5: 22. t. 12. 1929. Type: China, Hebei Prov. (Tschili), Tse-Tai-ssu, *Wawra 1057* (B?)

Adenophora biformifolia Y. Z. Zhao, Acta Sci. Nat. Univ. Intramongolicae 11(1): 57. 1980, syn. nov. Type: China, Nei Mongol, Daqing Shan, Baiyangou, 23. 09. 1976, *Y. Z. Zhao & X. Wang s.n.* (holotype: HIMC!).

Adenophora wawreana f. *oligotricha* Kitag., Rep. First Sci. Exped. Manch. sect. 4, 2: 114. 1935. syn. nov. Type: Hebei, Chengde (Jehol, Ch'eng-te), Chuanwayang, *Nakai, Honda & Kitagawa Aug. 24, 1933* (holotype: TI).

Adenophora wawreana f. *polytricha* Kitag., Rep. First Sci. Exped. Manch. sect. 4, 2: 115. 1935. Type: Hebei, Xinglong (Jehol, Hsing-lung-t'ang), Beiyingfang, *Nakai, Honda & Kitagawa Aug. 27, 1933* (holotype: TI).

Adenophora polymorpha Ledeb. var. *chanetii* H. Lév., Repert. Spec. Nov. Regni Veg. 12: 22. 1913, syn. nov. Type: Hebei (Pé-Tché-Li), 1904, *Chanet 570* (holotype: E).

Cauline leaves mostly petioled, but linear leaves often sessile. Corolla narrow-campanulate. Style obviously exerted above corolla.

The subspecies is distributed in E Shanxi, S Nei Mongol, Hebei, Henan, and SW Liaoning, growing on shaded or semi-shaded grassy slopes with or without shrubs.

Additional representative specimens examined:

Beijing (北京): Fangshan, Shangfang Shan, W. Y. Hsia 3290 (PE, WUK), T. N. Liou 8291 (PE); Changping, Xiakoucun, J. Zhang 2054 (PE); Xiaolongmeng, Dagou, C. G. Yang 566 (PE); Haidian, Xiangshan, 236–6 Group 312 (PE); **Hebei (河北):** Chicheng, Zheng'anbao, Inst. Bot. Herbarium 4395 (PE); Dahaituo Shan, Inst. Bot. Herbarium 6473 (PE); Fuping, Longquanguan, K. M. Liou L3292 (PE); Laiyuan, Hengshan, K. M. Liou L3177 (PE); Pingshan, Muchang, Dadi, 5th Exped. Team V1204 (PE); Neiqiu, Xiaolingdi, X. Y. Liu 1293 (PE); Qianxi, Hujiatan, K. M. Liou L3893 (PE); Weichang, G. Sato 10194 (PE); Xingtai, Luluo Township, Y. Liu 13879 (PE); Xinglong, Hongmei Shi to Zhongyuyuan, T. N. Liou & P. Y. Fu 4597 (PE); Daqing Shan, Inst. Bot. Herbarium 2574 (PE); Xiaowutai Shan, H. W. Kung 1055 (PE); Yangjiaping, H. Smith 529 (PE); Yixian, Langya Shan, Hebei Agricult. Univ. 302 (PE); Zhangjiakou, Gushi Village, Y. W. Tsui 1691 (PE); Zhuolu, Yangjiaping, C. G. Yang 1840 (PE); Zunhua: Loudicun Village, X. Y. Liu 848 (PE). **Henan (河南):** Linxian, Shibanyan, K. T. Fu 19024 (WUK); **Liaoning (辽宁):** Shanhaikuan, Jiaoshasi, G. Sato 6770 (PE). **Nei Mongol (内蒙古):** Liangcheng, Zhahan Shan, Y. C. Ma 165–16 (PE); Zhuozi, Zhuozi Shan, Y. W. Tsui 01137 (PE); Wula Shan, T. P. Wang 2512 (PE). **Shanxi (山西):** Heshun, Ziluowenyao, K. T. Fu 19321 (WUK); Hunyuan, Daciyao, Loess Exped. 01851 (WUK); Jiexiu, Jinshan, Loess Exped. 02781 (WUK); Huoxian, Huoshan, T. P. Wang 3926 (WUK); Lingchuan, Yetou, K. T. Fu 18798 (WUK); Pingding, Longfeng Shan, K. M. Liou 3968 (WUK); Pingshun, K. M. Liou 7961 (WUK); Wutai Shan, Jingangku, Y. L. Chen 1696 (PE); Xiyang, Pandaodi, Y. Liu 13505 (PE); Yangqian, between Yangqian & Shipeng, K. T. Fu 19526 (WUK).

2. Adenophora lobophylla D. Y. Hong in D. Y. Hong (ed.): Fl. Reip. Pop. Sin. 73(2): 186. pl. 17: 5–8. 1983. Type: China, NW Sichuan, Jinchuan, Anning, Baguadiaogou, 2400 m, 17. 08. 1958, *X. Li 78384* (holotype: PE!; isotype: SZ).

Stems mostly simple, sparsely retrorse-hirsute. Cauline leaves all petioled or only the lower and middle ones petioled; leaf blades ovate, ovate-lanceolate or linear, pinnatifid, rarely deeply dentate. Inflorescences with slender and ascending branches forming a panicle, or several flowers in a pseudo-raceme, rarely flowers solitary and terminal. Calyx usually glabrous; tube oblong or obovoid, base obtuse-rounded; lobes subulate, margins with 1–2 pairs of verrucose denticles. Corolla tubular or urceolate, 11–17 mm long; lobes ovate-deltoid, 3–5 mm long. Disc tubular, 2–3 mm long, sparsely puberulous above. Style obviously or strongly exserted from corolla. Capsule columnar-ellipsoid, base rounded, 6–8 mm long, ca. 3 mm broad. $2n = 34$, 34 +2B.

The species is confined to three counties in NW Sichuan, Barkam, Danba, and Jinchuan, growing in thickets, open woods or at the edges of forests at an altitude of 2000–3400 m.

Adenophora lobophylla is distinct in morphology from *A. potaninii*, and incompatible in reproduction with the latter species. Apparently Hong's placement of *A. lobophylla* in the *A. potaninii* complex is unjustifiable. The crossing experiment (Fig. 9) and the characters of corolla and style all indicate that the species is a relative of *A. stenanthina* (sect. *Adenophora*).

Additional representative specimens examined:

Sichuan (四川): Barkam, Dalangjiao Valley, H. F. Zhou & Z. Y. Zhang 22983 (SZ); Danba, Dongguhe Valley, D. Y. Hong et al. 95051 (PE); Jinchuan, Anning, Baguadiaogou Valley, S. Ge population 22 (PE); Tanchang Valley, S. Ge population 23 (PE); Zengda, D. Y. Hong et al. 95048 (PE).

Acknowledgements We thank Yi-Zhi ZHAO, Peng-Fei TU, Rui CAO, and Jun-Dao YANG for assistance in collecting materials in the field; Yan CHEN for help in cultivation and crossing experiments. We are also grateful to Xin-Hui ZOU for editing the manuscript. This work was supported by the National Natural Science Foundation of China (39600009).

References

Bailey LH. 1941. The standard cyclopedia of horticulture. Vol. 1. A–E. New York: Macmillan.

Baranov AI. 1963. Materials to the monograph of the species of *Adenophora* of NE China. Quarterly Journal of the Taiwan Museum 16: 143–179.

Diels L. 1901. Campanulaceae. In: Die Flora von Central-China. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 29: 604–607.

Federov AA. 1957. *Adenophora*. In: Komarov ed. Flora U.R.S.S. 24. Moskova & Leningrad: Akademiya Nauk SSSR.

Ge S. 1993. Biosystematic studies on *Adenophora potaninii* Korsh. complex (Campanulaceae). Ph.D. Dissertation. Beijing: Institute of Botany, Chinese Academy of Sciences.

Ge S, Hong DY. 1994a. Biosystematic studies on *Adenophora potaninii* Korsh. complex (Campanulaceae) I. Phenotypic plasticity. Acta Phytotaxonomica Sinica 32: 489–503.

Ge S, Hong DY. 1994b. Biosystematic studies on *Adenophora potaninii* Korsh. complex (Campanulaceae) II. Crossing experiment. Cathaya 6: 15–26.

Ge S, Hong DY. 1995. Biosystematic studies on *Adenophora potaninii* Korsh. complex (Campanulaceae) III. Genetic

variation and taxonomic value of morphological characters. Acta Phytotaxonomica Sinica 33: 433–443.

Ge S, Hong DY. 1998. Biosystematic studies on *Adenophora potaninii* Korsh. complex (Campanulaceae) IV. Allozyme variation and differentiation. Acta Phytotaxonomica Sinica 36: 481–489.

Hong DY. 1983. *Adenophora*. In: Flora Reipublicae Popularis Sinicae. Beijing: Science Press. 73(2): 92–139.

Korshinsky S. 1894. *Adenophora potaninii*. Memoirs of the Imperial Academy of Sciences in St.-Pétersbourg, Ser. 7, 42(2): 39.

Liu SW. 1996. Campanulaceae. In: Liu SW ed. Flora Qinghaiica. Xining: Qinghai People's Publishing House. 3: 306–317.

Rohlf FJ. 1994. NTSYS-pc, numerical taxonomy and multivariate analysis system. V.1.80. New York: Exeter Software.

Roquet C, Sanmartin I, Garcia-Jacas N, Saez L, Susanna A, Wikstrom N, Aldasoro JJ. 2009. Reconstructing the history of Campanulaceae with a Bayesian approach to molecular dating and dispersal-vicariance analyses. Molecular Phylogenetics and Evolution 52: 575–587.

Tsoong PC. 1935. Preliminary study on Chinese Campanulaceae– *Adenophora*. Contributions from the Institute of Botany, National Academy of Peiping 3: 66–83.

Tu PF, Xu GJ, Hong DY. 1990. New species of *Adenophora* from China. Journal of China Pharmaceutical University 21: 16–18.

Zahlbruckner A. 1895. *Adenophora wawreana* A. Zahlbr. nov. spec. Annalen des K. K. Naturhistorischen Hofmuseums 10 (in notiz.): 56.

Zhao YZ. 1980. A preliminary report on the taxonomy study of the genus *Adenophora* Fisch. of Inner Mongolia. Acta Scientiarum Naturalium Universitatis Intramongolicae 11: 53–61.