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青藏高原一新特有属——异型株属及其传粉模式*

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摘要: 胚胎学和分子证据表明广义獐牙菜属的异形花组应该独立为一个新属。在重新检查该属唯一种在各居群的形态变化时, 发现该物种具有异形植株和异形花; 前一性状在以前的研究中被忽略了, 同时还发现该物种主要是采用闭花受精结实, 这一繁殖特点可能是对青藏高原极端环境生存适应的结果。这些特征明显不同于獐牙菜属的其余种和相关属。综合其它证据讨论了该种的系统位置, 认为其与花锚属有最近的亲缘关系, 这一物种独特的形态性状和系统位置支持其独立为属, 并正式描述和发表这一新属——异型株属。但是必需指出的是, 广义獐牙菜属排除这一物种后, 分子证据表明其还是一个复系属。分类上处理这种由于快速物种多样化和性状趋同进化导致的复系属仍面临巨大的挑战, 还有待今后更详细的研究。

关键词: 异型株属; 异型植株; 异型花; 传粉式样
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A New Qinghai-Tibet Plateau Endemic Genus *Sinoswertia* and Its Pollination Mode*

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Abstract: Available data from both embryological and molecular studies of the monotypic section *Heteranthos* within the genus *Swertia* s. l. suggested that this taxon should be erected as a separate genus. We examined morphological variations of the only species across multiple populations and found that it has two types of individuals and one type contains both large and small flowers while the other only small flowers. However, all small and most large flowers set seeds through a cleistogamous pollination mode, which may have evolved in response to the reproductive adaptation to the arid habitats of the Qinghai-Tibet Plateau. However, this pollination mode is different from the outcrossing breeding system observed for the other *Swertia* species. Dimorphic plants and flowers distinguish this species from the other *Swertia* species and related genera. We further discussed the systematic position of this species based on the comprehensive data and the current data support its close relationship with *Halenia*. The morphological distinctness and systematic position of this species from all comparisons justified its generic status. We here place this species in a new genus *Sinoswertia*, and describe and illustrate it. However, after excluding this species, *Swertia* s. l. is still polyphyletic based on the molecular evidence. The taxonomic treatment of this polyphyletic genus possibly due to the recent radiative diversification and convergent evolution poses an extreme challenge at the present and pends further detailed studies.

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Kew words: *Sinoswertia*; Dimorphic individuals; Dimorphic flowers; Pollination mode

With more than 160 species accepted, *Swertia* is one of the large genera in the tribe Gentianinae of the family Gentianaceae (Struwe and Albert, 2002). It is widely distributed in Asia, Africa, North America and Europe. This genus was defined based on the rotate corolla and diverse nectaries not surrounded by fringes or appendages (Ho, 1988; Ho and Pringle, 1995). However, all phylogenetic analyses based on the molecular data suggested that *Swertia* in its present circumscription is polyphyletic and that the rotate corolla as well as fringed nectaries may have derived from homoplastic evolutions due to the radiative diversifications of the common ancestor together with the related genera or taxa (Yuan and Küpfer, 1995; Chassot *et al.*, 2001; Liu *et al.*, 2001; Hagen and Kadereit, 2002). It is necessary to use distinct morphological traits to define these identified monophyletic lineages inferred from molecular data.

Within this in mind, we aimed to examine morphological traits and taxonomic rank of a special taxon, sect. *Heteranthos* within the genus *Swertia*, which is endemic to the Qinghai-Tibet Plateau. The only species of this monotypic section, *S. tetraptera*, was found to cluster with *Halenia* with spurred flowers (Yuan and Küpfer, 1995; Chassot *et al.*, 2001; Liu *et al.*, 2001; Hagen and Kadereit, 2002). The embryological comparisons also suggested that unique characters united these two taxa together and the exclusion of this taxon from *Swertia* s. l. was further inferred (Xue *et al.*, 1999a, b). In the present study, we reported dimorphic plants and flowers found across all populations of this species and we also found that most flowers of this species set seeds through a cleistogamous pollination mode. All these traits clearly distinguish this species from the other *Swertia* species and related genera. Therefore, this species should be elevated to a separate genus and the new genus is described here for the first time.

1 Materials and methods

1.1 Morphology

The previously collected specimens in HNWP were initially examined and two types of individuals were found. We explored this morphological variation in the field populations between 2002 and 2010. In total, we visited 14 populations at altitudes between 2 420 m and 4 310 m. We randomly collected 100 individuals and examined the distribution of two types of individuals in each population.

1.2 Pollination mode

In 2008, we subjected three types of flowers found in *S. tetraptera*, i. e., small flowers of the homogeneous individuals, large and small flowers of the heterogeneous individuals for the following five treatments: (1) control; (2) bagged isolation; (3) isolation without emasculation; (4) emasculation for natural pollination; and (5) emasculation and hand-pollination with pollen grains from the other individuals. We marked flowers for treatments (1), (2) and (3) at the bud phase while emasculations in treatment for (4) and (5) were completed before stigma lobe opened. In order to provide enough space for flower opening and closing, we isolated all flowers with paper bags with at least two sizes of flowers. All these experiments were finished at one population in Datong, Qinghai (2 700 m) and we also monitored how many flowers had opened in this population through the total growing season. We used one-way ANOVA and Post hoc-LSD to examine seed sets associated with different treatments.

1.3 Systematic position inferred from molecular evidence

We examined the sequence variations between different populations and two different individuals from three populations. The extracting of the total DNA and amplifying and sequencing of three DNA fragments (*trn*L-F, *trn*S-*Ycf*9, and ITS) followed the previous standard procedures and primers (Yuan and Küpfer, 1995; Chassot *et al.*, 2001; Liu *et al.*,

2001; Hagen and Kadereit, 2002). We also downloaded the corresponding sequences for the other genera or species (Table 1). Two *Gentiana* species were chosen as outgroups. Phylogenetic analyses of cpDNA and ITS sequences were performed by MrBayes 3.0 (Ronquist and Huelsenbeck, 2003). All gaps (indels) were excluded. For Bayesian analyses, four chains were used per run (three heated and one cold), and each analysis was repeated three times, twice for two million generations, with the final analyses running for 10 million generations. We used Bayesian posterior probabilities to assess branch support and the supports were calculated from 1000 replicates using a heuristic search with simple addition with TBR and MULPARS options on in PAUP*(Swofford, 2002).

2 Results

2.1 Morphology

Swertia tetraptera was described by Maximowicz in 1881 and he described only one type of individuals. We firstly examined the specimens kept in the herbaria and found that most sheets comprised only one heterogeneous type of individuals with large and small flowers. However, in a few sheets, two types of individuals, one heterogeneous type and the other homogeneous individuals with only small flowers. In all examined populations in field, plants conspicuously have formed two types: heterogeneous and homogeneous plants. Heterogeneous plants are tall and stout, with a distinct erect main stem and few to numerous, procumbent, weak branches at stem base. Inflorescence is a panicle of cymes, few- to many-flowered, spreading. However, flowers are dimorphic. On main stem or rarely also on terminal flowers of basal weak branches, flowers are large-sized; nectaries are linear-oblong, canaliculate, with a very narrow scale and few irregular divisions; capsules are large (10–14 mm), narrowly ellipsoid with seeds 13–18 (–27) in number. On weak branches, flowers are small-sized, 1/4–1/3 as large as those of main stem; nectaries have broadly oblong, entire, elevated scales and indistinct flat gland patches; capsules are small-sized (4–5 mm), broadly ovoid to subglobose with seeds (2–) 4–6 (–7) in number. Homogeneous plants are dwarf; stems are flaccid, slender, few-branched without basal weak branches at stem base. Cymes are lax, few-flowered. All flowers are uniform and small-sized, their calyx, corolla, nectaries, stamens, pistil, capsules and seeds (in shape, size, color, structure and number) are the same as those of the small-sized flowers on heterogeneous plants. The ratio of the two plant types changes with the altitudes and a highly significant negative correlation was found between frequencies of heterogeneous versus homogeneous

Table 1 Accession numbers of the sequences used for constructing phylogenetic relationships of *Sinoswertia tetraptera*

Species	*trn*L-*trn*F		*trn*S-*Ycf*9	ITS	
Halenia brevicornis	GI: 15149891	GI: 15209270	GI: 15149919	GI: 21261681	GI: 21261650
Halenia weddelliana	GI: 15149893	GI: 15209272	GI: 15149921	GI: 15149957	GI: 15149986
Halenia elliptica	GI: 15149892	GI: 15209271	GI: 15149920	GI: 15384520	
Sinoswertia tetraptera	GI: 15150018	GI: 15209307	GI: 15150036	GI: 1486469	GI: 1486470
Swertia bimaculata	GI: 15149903	GI: 15209282	GI: 15149931	GI: 15149967	GI: 15149996
Veratrilla baillonii	GI: 15150001	GI: 15209266	GI: 15150019	GI: 13507073	
Swertia punicea	GI: 15150014	GI: 15209299	GI: 15150032	GI: 15150050	GI: 15150069
Swertia pubescens	GI: 15150013	GI: 15209298	GI: 15150031	GI: 15150049	GI: 15150068
Swertia crassiuscula	GI: 15150004	GI: 15209288	GI: 15150022	GI: 15150040	GI: 15150059
Comastoma pulmonarium	GI: 15149908	GI: 15209303	GI: 15149936	GI: 15384516	
Swertia cordata	GI: 15150003	GI: 15209287	GI: 15150021	GI: 18152465	GI: 18152482
Swertia volkensii	GI: 15150016	GI: 15209301	GI: 15150034	GI: 15150052	GI: 15150071
Gentiana frigida	GI: 4092155	GI: 15209309	GI: 15149941	GI: 13235130	GI: 13235177
Gentiana phyllocalyx	GI: 15149888	GI: 15209267	GI: 15149916	GI: 15149952	GI: 15149981

individuals in the 14 examined populations (correlation index $r=-0.582$; $P<0.05$). With the altitudinal increases, homogeneous plants with only small flowers occurred more frequently at high altitude.

2.2 Pollination mode

The seed sets of five pollination treatments were listed in the Table 2. The direct isolations with the bags indicated that both large flowers and small flowers of the heterogeneous individuals and all small flowers of the homogeneous plants always set numerous seeds with high rates (>98%). The seed sets of these isolation treatments showed no distinct difference from the control treatments ($P>0.1$). However, the emasculation and hand-pollination treatments still produced high rates of seeds, indicating that outcrossing in this species is still fertile. The emasculation and bagged isolation produced no seeds, which suggested that the agamospermy does not exist in this species (Table 2). Our pollination treatments together suggested that all flowers from both types of individuals have developed a perfect self-pollination mechanism. In the field, we found all flowers have nectaries, which can produce sweet secretions. However, most flowers did not open, and only 1–3% of the large flowers of the heterogeneous plants were open in one monitored population when they became mature with their pistil and stamens equal in height. We found that only ants and thrips visited these open flowers with very low frequency (four times within the monitored 12 hours for two open flowers). Because most flowers of this species are self-pollinated without being open, it seems to be a cleistogamous pollination mode (Lord, 1981).

2.3 Systematic position inferred from molecular evidence

We examined the sequence variations among 12 heterogeneous or homogeneous individuals at the *trn*L-F, *trn*S-*Ycf*9, and ITS. We found no variation in these sequenced fragments between different individuals of *S. tetraptera*, and all sequences were the same as those obtained before (Table 1). We constructed the phylogeny trees based on two chloroplast DNA fragments (*trn*L-F and *trn*S-*Ycf*9) and nuclear ITS respectively. Both phylogenetic trees (Fig. 1) suggested that *S. tetraptera* is closely related to *Halenia* with high supports while the other *Swertia* representative species clustered with the other genera as indicated before (Yuan and Küpfer, 1995; Chassot *et al.*, 2001; Liu *et al.*, 2001; Hagen and Kadereit, 2002).

3 Discussions

In this study, we found two different types of individuals in *S. tetraptera*, one heterogeneous type with both large and small flowers and the other homogeneous individuals with only small flowers. This dimorphic species was firstly recorded in the *Swertia* and also rarely found in the family Gentianaceae.

Table 2 Seed sets under various treatments on both large and small flowers of the heterogeneous individuals and small flowers of the homogeneous ones found in *Sinoswertia tetraptera*

Flower types		Natural pollination	Bagged isolation	Emasculation for natural pollination	Emasculation and bagged isolation	Emasculation and hand-pollination
Lf	Seed numbers per flower (Mean ± SE)	13.2 ± 0.5^{a}	13.1 ± 0.3^{a}	2.2 ± 0.2^{b}	0	6.8 ± 1.2^{c}
	Seed set ratios (Mean ± SE%)	>98%^{a}	>98%^{a}	<20%^{b}	0	51.8 ± 6.5%^{a}
	Numbers of flowers examined	159	151	15	12	18
Sf	Seed numbers per flower (Mean ± SE)	5.2 ± 0.2^{a}	5.3 ± 0.9^{a}	0	0	1.8 ± 0.2^{b}
	Seed set ratios (Mean ± SE%)	>98%^{a}	>98%^{a}	0	0	<10%^{b}
	Numbers of flowers examined	224	10	12	10	14
Shf	Seed numbers per flower (Mean ± SE)	5.6 ± 0.2^{a}	5.8 ± 0.8^{a}	0	0	1.0 ± 0.2^{b}
	Seed set ratios (Mean ± SE%)	100%^{a}	100%^{a}	0	0	<10%^{b}
	Numbers of flowers examined	108	25	8	10	8

Lf = large flowers on a main stem of a heterogeneous individual; Sf = small flowers on basal weak branches of a heterogeneous individual; Shf = small flowers of the homogeneous individuals.

Values with the same superscript letter in the same column, or the same superscript number in the same row, do not differ significantly at the 0.05 level

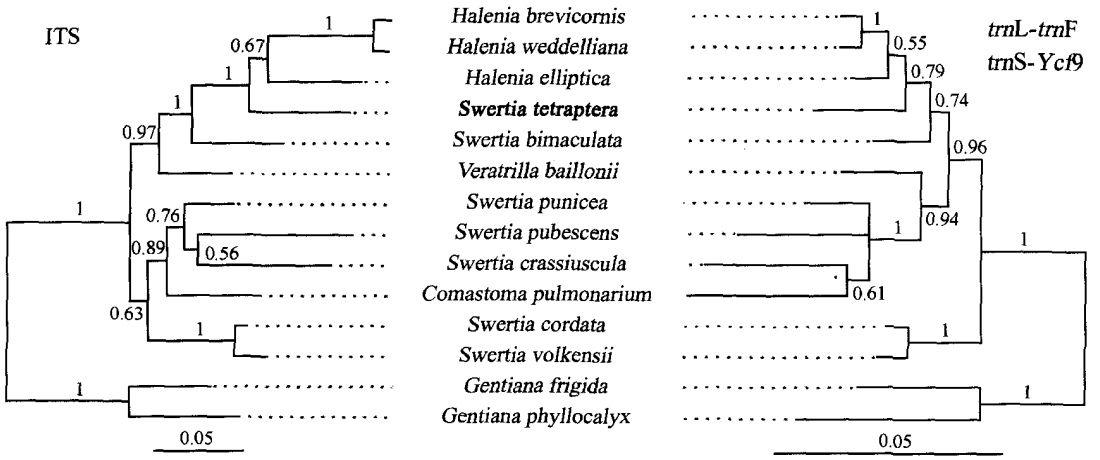

Fig. 1 Two phylogenetic trees constructed for *Sinoswertia tetraptera* and related genera based on chloroplast DNA fragments and ITS sequences

We further found that most flowers were self-pollinated through a cleistogamous mode with flowers closed. This pollination mode and the increase of the homogeneous individuals with altitude may have the survival advantages for this species to occur in the arid habitats (He *et al.*, 2006; Duan *et al.*, 2007, 2010) although such a probability needs further tests. However, no dimorphic individual was recorded for the other *Swertia* species and all species with pollination mode studied in this genus were found to be outcrossing with all flowers open at the flowering stage (Duan and Liu, 2007 and references cited within it). All molecular phylogenies based on different DNA sequences suggested that *S. tetraptera* is sister to *Halenia*, a genus distributed in Asian mountains but with its great diversification in the southern America (Yuan and Küpfer, 1995; Chassot *et al.*, 2001; Liu *et al.*, 2001; Hagen and Kadereit, 2002). In addition, as pointed out by Xue *et al.* (1999a, b), *S. tetraptera* and *Halenia* share two important embryological characters: orthotropous ovules and well-developed hypostase. However, in the remaining studied *Swertia* species, ovules are anatropous or ana-campylotropous and both placenta intrusion and hypostase are not distinctly developed (Xue *et al.*, 2002a, b). All these lines of evidence suggest that *S. tetraptera* should be established as one separate genus, sister to the well-defined *Halenia*. However, *Halenia* differs from this new monotypic genus with spurred corolla.

After excluding *S. tetraptera*, the remaining species or sections in the genus *Swertia* seem still to be polyphyletic. The representative species sampled from this genus for phylogenetic studies, clustered respectively with the other well-circumscribed genera, for example, *Comastoma* and *Veratrilla* (Fig. 1 and also see Chassot *et al.*, 2001 and Hagen and Kadereit, 2002). Although the clade represented by *S. bimaculata* is sister to *Halenia-S. tetraptera*, it is similar to the other *Swertia* species or sections with rotate corolla and nectaries surrounded by fringed or tubular appendages. *Swertia* is also similar to *Lomagogonium*, but the latter differs from it with decurrent stigma (Ho and Pringle, 1995). In addition, all these genera differ from one another in both morphological and embryological traits (Xue *et al.*, 1999a, b, 2002a, b and references in them) (Table 3). The rotate and deeply lobed corolla and diverse nectaries shared by *S. tetraptera*, the other *Swertia* species and the other genera may have resulted from the convergent evolutions due to common selection pressure during the rapid diversification of *Swertia* in the Qinghai-Tibet Plateau and adjacent regions. In fact, such a scenario was also found for other genera. For example, in the *Ligularia-Cremanthodium-Parasenecio* complex (Asteraceae), intergeneric circumscriptions are extremely difficult because these three species-abundant genera with dia-

gnostic morphological traits are polyphyletic because of radiative diversification and common selection pressure (Liu *et al.*, 2006). The taxonomic treatment of the polyphyletic *Swertia* in the current circumscription is still a challenge at the present and pends further studies in the future.

4 Taxonomic treatments

Sinoswertia T. N. Ho, S. W. Liu & J. Q. Liu **gen. nov.**

—Type: *Sinoswertia tetraptera* (Maximowicz) T. N. Ho & S. W. Liu

Swertia sect. *Heteranthos* T. N. He & S. W. Liu, Acta Phytotax. Sin. **18** (1): 85 (1980). Type: *S. tetraptera* Maxim.

This new genus is closely related to *Swertia* s. l. and *Halenia*. It differs from the latter by spurless corolla and from both by dimorphic plants and dimorphic flowers (Fig. 2).

A monotypic genus endemic to the northeastern Qinghai-Tibet Plateau (Fig. 3).

Sinoswertia tetraptera (Maximowicz) T. N. Ho, S. W. Liu & J. Q. Liu, **comb. nov.**

=*Swertia tetraptera* Maxim., Bull. Acad. Imp. Sci. St. -Pétersbourg **27**: 503 (1881). Type: China, Gansu (Kansu), in shrubs, in 1872–1880, Przewalski s. n. (LE-holotype, not seen; PE! -isotype).

=*Swertia dimorpha* Batalin, Act. Hort. Petrop. **13**: 379 (1894). Type: China, N Sichuan (Szechuan), [Nanpin-Songpan-Pingwu], Dshangla, Nereku, 25 July 1885, G. N. Potanin s. n. (LE-holotype, not seen; HNWP! -photo.).

=*Swertia pusilla* Diels, Notizbl. Bot. Gart. Berlin **11**: 215 (1931), non Pursh (1814). Type: China, W Ningxia (Kansu), Mt. Helan Shan (Ho Shan), He-lan-wu-kou, 2 000 m, 11 May 1923, R. C. Ching 70 (US! -holotype).

=*Anagallidium dimorpha* (Batalin) Ma. Acta Phytotax. Sin. **14**: 65 (1976).

Additionalis description homogeneae plantae:

Plantae homogeneae nanae, (1–) 3–8 (–15) cm. Caules flaccidi, graciles, fere quadrangulares, pauco-ramosi. Folia 2–4-binata, late disposita; petioli usque 1 cm; laminae 5–10×3–8 mm, apice obtusae, base angustatae, nervis 1–3, prominentibus. Cymae pauciflorae. Pedicelli 5–50 mm. Flores uniformes, parvi. Calyx corollaque lobata fere ad bases; tubus calycis 0.3–0.5 mm, lobis 1.5–4 mm, late ovatis, apice acutis, costis prominentibus; corolla viridis usque flavido-viridis, interdum purpurato-tingens, tubo 0.3–0.5 mm, lobis 2.5–5 mm, obovato-oblongis usque oblongis, apice subroundatis erosisque, base contractis; nectaria 2 in unoquoque lobo corollae, una squama integra late oblonga et maculis indistinctis instructa; filamenta 1–1.5 mm, linearia, complanata, base una squama semiorbiculata ornata; antherae 0.5–1 mm, ellipsoideae, flavidae; pistillum 1.2–1.7 mm; stylus indistinctus; lobi stigmatis capitati. Capsulae 4–5 mm, late ovoideae usque subglobosae. Semina numero (2–) 4–6 (–4) variantia, (0.8–) 1.2–1.5×0.9–1.1 mm, flavida, late ellipsoidea usque subglobosa, tenuiter reticulata usque fere laevia.

Plantae homogeneae a eis heterogeneis caulibus nanis, pauci-ramosis, absque debilibus ramosis, omnibus floribus parvis et uniformibus recedit.

Table 3 Diagnostic features of *Sinoswertia*, the other *Swertia* sections, *Halenia* and *Lomatogonium*

Characters	*Sinoswertia*	Other *Swertia*, sections	*Halenia*	*Lomatogonium*
Dimorphic individuals	Yes	No	No	No
Dimorphic flowers	Yes	No	No	No
Corolla spur	No	No	Distinct	No
Stigma	Normal	Normal	Normal	Decurrent
Placenta intrusion	Strong	No	Strong	No
Ovule	Orthotropous	Anatropous (ana-campylotropous)	Orthotropous	Campylotropous
Hypostase	Developed	No	Developed	No
Pollination model	Complete cleistogamy	Outcrossing	Outcrossing or self-pollination	Outcrossing

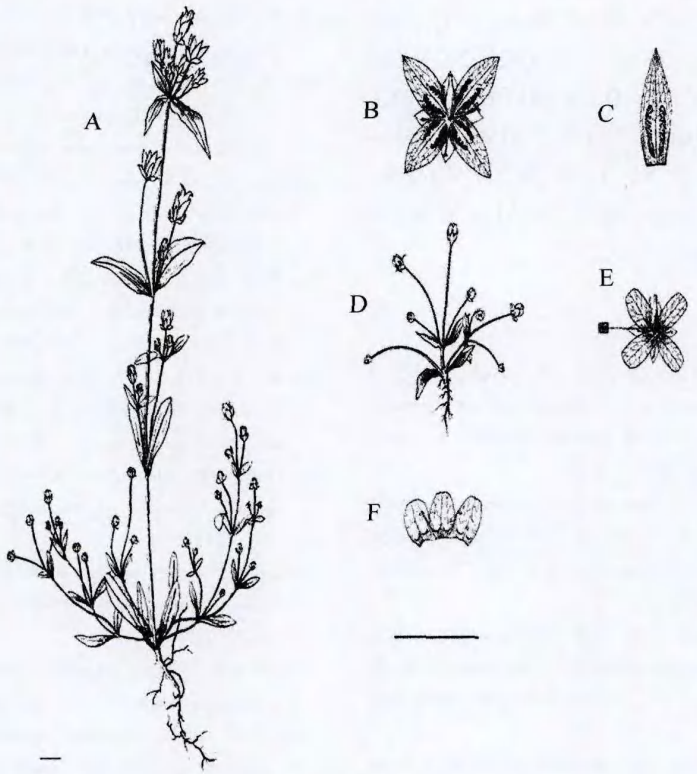

Fig. 2 *Sinoswertia tetraptera*. A. a heterogeneous individual with large and small flowers; B: a large flower of the heterogeneous individual; C: a corolla lobe; D: a homogeneous plant only with small flowers; E: a small flower of a homogeneous individual; F: a part of opened corolla lobes of a small flower

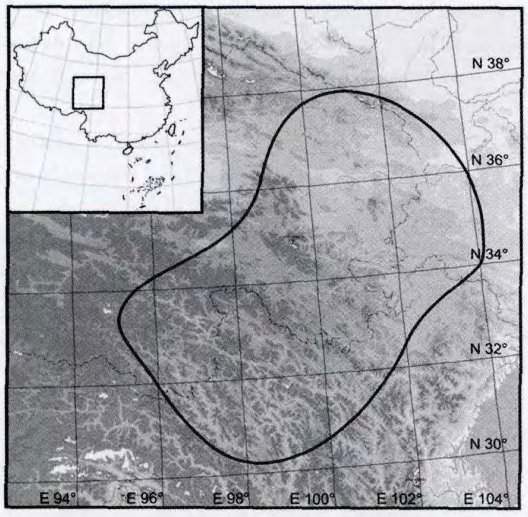

Fig. 3 Distributional range of *Sinoswertia tetraptera* in the Qinghai-Tibet Plateau

Distribution and habitat: endemic to Qinghai-Tibet Plateau (Fig. 3), including northeastern Tibet, eastern and southwestern Qinghai, northwestern Sichuan, and Gansu, It grows in diverse environments, i. e., alpine meadows, alpine shrub-meadows, shrubs, scattered forests, grasslands, wet places near to the river, stream or gutter, roadsides, gravelly lands, and stone pits, mainly at elevations between 2 000 m and 4 310 m.

Representative specimens. CHINA, Qinghai: Minhe, Ho T. N., Liu S. W. & Wang Z. Q. 110 (HNWP); Datong, =Ho T. N., Liu S. W. & Wang Z. Q. 18 (HNWP); Ping'an, Ho T. N., Liu S. W. & Wang Z. Q. 34 (HNWP); Xunhua, Ho T. N., Liu S. W. & Wang Z. Q. 91 (HNWP); Huangyuan Ho T. N., Liu S. W. & Wang Z. Q. 117 (HNWP); Gonghe, Ho T. N., Liu S. W. & Wang Z. Q. 41 (HNWP); Chindu, Ho T. N., Liu S. W. & Wang Z. Q. 31 (HNWP); Yushu, Ho T. N., Liu S. W. & Wang Z. Q. 135 (HNWP). **Tibet**:

Jomda, Ho T. N., Liu S. W. & Wang Z. Q. 166 (HNWP). **Gansu**: Zuoni, LiuJQ-2012-GN-162 (LZU, KIB); Maqu, LiuJQ-GN-2011-011 (LZU, KIB); Hezuo, LiuJQ-GN-2011-022 (LZU, KIB); **Sichuan**: Serxu, Ho T. N., Liu S. W. & Wang Z. Q. 168 (HNWP); Dege, Ho T. N., Liu S. W. & Wang Z. Q. 167 (HNWP).

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