

A Preliminary Phylogenetic Study of the Subgenus *Pogonophace* (*Astragalus*) in China Based on ITS Sequence Data

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Abstract: The internal transcribed spacers (ITS) (including ITS1, 5.8S rRNA gene and ITS2) of *Cara-gana roborovskyi* and eight species of subgenus *Pogonophace* (*Astragalus*) were sequenced, and analyzed together with other ITS data (from GenBank) of 48 species representing *Astragalus* and 12 related genera. The results of phylogenetic analyses suggest that the subgenus *Pogonophace* is not a monophyletic group. Sect. *Sesbanella* (*Astragalus hoantchy* and *A. dshimensis*) and other species of *Pogonophace* are nested within different major clades in the phylogenetic tree. The species of sections *Bibracteola*, *Phyllobium* and *Trichostylus* compose a monophyletic group with a close relationship to subtribe Coluteinae instead of *Astragalus*. *Astragalus tribulifolius* and *A. tanguticus* might be a vicariant species pair as inferred by the ITS data.

Key words: *Pogonophace*; *Astragalus*; Coluteinae; ITS; phylogeny

The subgenus *Pogonophace* is essentially distinguished from other subgenera of the genus *Astragalus* by the occurrence of a ciliate style (Fu, 1993). It consists of about 50 species distributed mainly in the cold and droughty mountainous areas of Asia, especially the Hengduan Mountains (Zhang, 2000). According to Fu's treatment (Fu, 1993) of Chinese *Pogonophace*, there are four sections (i.e. *Sesbanella*, *Bibracteola*, *Phyllobium*, and *Trichostylus*) in this subgenus based on morphological characters of pod. The species of the four sections reflect an extensive pattern of variation. Most species in *Pogonophace* have such characters: prostrate habit, depressed fruit (dorsi-ventrally pressed conditions) and short carpopodium (shorter than the calyx). Wenninger (1991) concluded that a ciliate style was not very phylogenetically informative, and there might have been several parallel gains of this trait within *Astragalus*. In his recent revision of *Astragalus*, sect. *Sesbanella* was excluded from *Pogonophace* (Wenninger, 1991). Barneby (1964) stated *Astragalus complanatus* in *Pogonophace* "agrees in all important characters with *Sphaerophysa* except that the pod is not inflated", and suggested combining them with the genus *Swainsona*, genus *Lessertia* and other members of *Pogonophace* which share the characteristic of non-interlocking keel and wing petals (for the absence of bosses on the keel and matching sockets on the wings) as a large genus. A series of molecular data have shown that *A. complanatus* and the members of subtribe Coluteinae share a common ancestor (Liston and Wheeler, 1994; Sanderson and Liston, 1995; Sanderson and Wojciechowski, 1996; Wojciechowski *et al.*, 1999). Because of high levels of homoplasy, there are few monophyletic groups within *Astragalus* (Wojciechowski *et al.*, 1999). So the systematic problems associated with *Pogonophace* are its circumscription, monophyly, and infrasubgeneric

division.

The internal transcribed spacers (ITS) region of nuclear ribosomal DNA is a valuable source of evidence for angiosperm phylogeny (Baldwin *et al.*, 1995). Although ITS sequences of many *Astragalus* species and related genera have been reported (Wojciechowski *et al.*, 1999), few of them belong to *Pogonophace*. In this study we analyze the ITS sequences to explore the following questions: (1) Can *Pogonophace* form a monophyletic group? (2) Can Wenninger's treatment of sect. *Sesbanella* be supported by molecular data? (3) Is it a universal phenomenon that *Pogonophace* species and subtribe Coluteinae share a common ancestor?

1 Materials and Methods

The origin of materials is provided in Table 1. Total genomic DNA was extracted from silica gel dried leaf material following a modification of the CTAB procedure (Wang and Li, 1998) of Rogers and Bendich (1988). The two internal transcribed spacers (ITS-1, ITS-2) and 5.8S rDNA were amplified using the primers "ITS1" (5' AGA AGT CGT AAC AAG GTT TCC GTA GC 3') and "ITS4" (5' TCC TCC GCT TAT TGA TAT GC 3'). The amplification reaction was performed in 25 μ L volumes containing about 10 ng genomic DNA, 2 mmol/L dNTP, 15 mmol/L Mg^{2+} , 6.25 pmol of each primer, and 0.75 U DNA polymerase. The following temperature profile was used in the amplification of the Polymerase Chain Reaction (PCR): 70 $^{\circ}$ C for 4 min; 2 cycles of 94 $^{\circ}$ C for 1 min, 52 $^{\circ}$ C for 20 s, 72 $^{\circ}$ C for 50 s; linked to 35 cycles of 94 $^{\circ}$ C for 20 s, 52 $^{\circ}$ C for 20 s, 72 $^{\circ}$ C for 50 s; linked to 72 $^{\circ}$ C for 4 min; held at 4 $^{\circ}$ C. Anneal temperature can be altered between 50 $^{\circ}$ C and 55 $^{\circ}$ C. The amplified double stranded DNA fragments were purified using Pharmacia Biotech aFXTmper DNA and Get Band purification

Table 1 Taxa sampled, their collection information and accession numbers of sequences in this study

Species	Location	Voucher	Accession number
<i>Astragalus hoanitchy</i> Franch.	Helan Mt., Nei Mongol	Y. Kang 01-01 (PE)	AF521952
<i>A. complanatus</i> Bunge	Fangshan, Beijing	Y. Kang 01-03 (PE)	AF521950
<i>A. balfourianus</i> Simps.	Lijiang, Yunnan	M. L. Zhang 99-303 (PE)	AF521951
<i>A. tribulifolius</i> Benth. ex Bunge	Lhasa, Xizang	H. N. Qin <i>et al</i> 608 (PE)	AF521953
<i>A. milingensis</i> Ni et P. C. Li	Linzhi, Xizang	H. N. Qin <i>et al</i> 608 (PE)	AF521954
<i>A. yatungensis</i> Ni et P. C. Li	Nielamu, Xizang	H. N. Qin <i>et al</i> 701 (PE)	AF521955
<i>A. tanguticus</i> Batalin	Dazi, Xizang	Y. Kang 01-02 (PE)	AF521956
<i>A. hendersonii</i> Baker	Nielamu, Xizang	H. N. Qin <i>et al</i> 644 (PE)	AF521957
<i>Caragana roborovskiyi</i> Kom.	Wuhai, Nei Mongol	M. L. Zhang 200037 (PE)	AF521958
* <i>Sphaerophysa salsula</i> (Pall.) DC.	Asia	Yoder-williams 78-120A-1 (RENO)	U56011, U56012
<i>Smirnovia turkestanica</i> Bge.	(former) USSR	anonymous (A)	U51218, U51219
<i>Eremosparton flaccidum</i> Litw.	(former) USSR	Leontief 10.5.35 (US)	U56013, U56014
<i>Lessertia brachystachya</i> DC.	South Africa	USDA 208172	U56005, U56006
<i>Sutherlandia frutescens</i> L.	Mexico	W and S 266	U50516, U50517
<i>Colutea arborescens</i> L.	(former) USSR	USDA 369222, W and S 406	U56009, U56010
<i>C. istria</i> Miller		DELEP 890385	U69544, U69545
<i>Lessertia herbacea</i> DC.	South Africa	USDA 207923, W and S 299	AF121752
<i>Swainsona pterostylis</i> (DC.) Bakh. f.	Australia	DLEG 900185, W and S 296	U56007, U56008
<i>Camichaelia stevensonii</i> (Cheeseman) Heenan	New Zealand	Sanderson 1551	AF121751
<i>C. williamsii</i> Kirk	New Zealand	Sanderson 1550	U50520, U50521
<i>Clianthus puniceus</i> (G. Don) Lindley	New Zealand	T and M 7140 (Liston, 960, OSC)	L10800, L10801
<i>Astragalus cysticalyx</i> Ledeb.	(former) USSR	USDA 440146 (Liston 961, OSC)	AF121687
<i>A. dshimensis</i> Gontsch			AF359755
<i>A. lehmannianus</i> Bunge			AF359756
<i>A. chinensis</i> Linn. f.	Switzerland	USDA 415802	AF121681
<i>A. aksuensis</i> Bunge			AF359753
<i>A. membranaceus</i> (Fisch.) Bunge	China	Hu 1131	AF121675
<i>A. umbellatus</i> Bunge	AK, USA	Parker 88-78 (COLO)	AF121683
<i>A. atropilosulus</i> (Hochst.) Bunge var. <i>venosus</i> (Hochst.) Gillett	Kenya	USDA 193735, W and S 301	U50504, U50505
<i>A. austrosibiricus</i> Schischk.			
<i>A. adsurgens</i> Pall.	China	USDA 462310, W and S 267	AF121674
<i>A. pulchellus</i> Boiss.	Iran	USDA 384778, W and S 168	L10786, L10787
<i>A. asterias</i> Stev. ex Ledeb	Morocco	USDA 516491, W and S 169	L10764, L10765
<i>A. nuttallianus</i> DC. var. <i>nuttallianus</i>	Pima Co., AZ, USA	Wojciechowski 102	L10816, L10817
<i>A. eremiticus</i> Sheld	Humboldt Co., NV, USA	Wojciechowski 520	AF121736
<i>A. peristereus</i> Boiss. & Hausskn. (syn. <i>Astracantha peristerea</i> (Boiss. & Hausskn.) Podl.)	Iran	DLEG 880051	U50494, U50495
<i>A. echidnaeformis</i> Sirj. (syn. <i>Astracantha echidnaeformis</i> (Sirj.) Podl)	Iran	DLEG 880044, W and S 411	U50512, U50513
<i>A. cerasocrenus</i> Bunge (syn. <i>Astragacantha cerasocrena</i> (Bge.) Podl.)	Iran	DLEG 880043	U50514, U50515
<i>A. polycladus</i> Bur. et Franch.	China	Donoghue 094 (1996)	AF121676
<i>A. alpinus</i> L.	WY, USA	USDA 232536, W and S 183	L10760, L10761
<i>A. edulis</i> Bunge	Isreal	USDA 244273, W and S 293	AF121677
<i>A. boeticus</i> L.	France	USDA 41423, W and S 300	AF121679
<i>A. falcatus</i> Lam.	Boulder Co., CO, USA	Weber 15359 (COLO)	U50488, U50489
<i>A. canadensis</i> L. var. <i>breviens</i> (Gand.) Barneby	Nye Co., NV, USA	W and S 302	U50496, U50497
<i>A. corrugatus</i> Bertol.	Iran	USDA 227441, W and S 164	L10774, L10775
<i>A. eucomus</i> Robinson	AK, USA	Walker 81-86 (COLO)	AF121684
<i>A. robbinsii</i> (Oakes) A. Gray var. <i>minor</i> (Hook.) Barneby	Lincoln Co., WY, USA	Holmgren and Holmgren 9605 (RM)	U50490, U50491

Table 1 (To be continued)

Species	Location	Voucher	Accession number
<i>A. australis</i> (L.) Lam. var. <i>aboriginum</i> (Richardson) Welsh	Eureka Co., NV, USA	Tiehm 11985 and Williams (RM)	AF121686
<i>A. williamsii</i> Rydb.	Yukon, Canada	Calder and Gillett 25825 (A)	AF121685
<i>Oxytropis campestris</i> (L.) DC. var. <i>johannensis</i> Fern.	ME, USA	USDA 504535, W and S 174	L10802, L10803
<i>O. viscida</i> Nutt.	Sevier Co., UT, USA	W and S 231	AF121758
<i>O. sericea</i> Nutt. var. <i>sericea</i>	Dagget Co., UT, USA	W and S 255	AF121757
<i>O. oreophila</i> A. Gray var. <i>juniperina</i> Welsh	Wayne Co., UT, USA	W and S 229	AF121755
<i>O. splendens</i> Dougl.	Cororado Native Plant Teller Co., CO, USA Society 112 (COLO)		AF121761
<i>O. multiceps</i> Torr. & Gray	Teller Co., CO, USA Mullineaux, Root, Richards and Yeatts 5360 (COLO)		AF121760
<i>O. besseyi</i> (Rydb.) Blank. var. <i>ventosa</i> (Greene) Bameby	Dagget Co., UT, USA	W and S 253	AF121756
<i>O. pilosa</i> (L.) DC.	(former) USSR	USDA 420696, W and S 306	AF121759

* The following ITS sequences analyzed in this study were from GenBank, for more information please see Wojciechowski *et al* (1999).

Kit, and directly sequenced on an ABI 377 automated sequencer (PE Applied Biosystems, Inc.). Primers were the same as those of the initial PCR and used singly in forward and reverse reactions. Each base position was examined for agreement between complementary strands.

2 Results

The boundaries of the ITS region were determined by comparing with those of *A. complanatus* (Sanderson and Wojciechowski, 1996). Sequences were automatically aligned using Clustal W (Higgins, 1994) with manual correction. The length of the aligned ITS sequence is 636 bp. Of the 239 variable nucleotide positions within ingroup, 165 are phylogenetically informative. Thirty-four most parsimonious trees were generated using PAUP version 4.0b4a (Swofford, 2000). Their strict consensus tree was shown in Fig.1 with 585 steps, a consistent index (CI) of 0.631, and a retention index (RI) of 0.837. Bootstrapping was adopted to quantify the support of the clades on the cladogram. The number of bootstrap replicates was 1 000. Subtribe Coluteinae and the three sections of subgenus *Pogonophace*, i. e. *Bibracteola*, *Phyllolobium*, and *Trichostylus*, form Clade A. Clade B consists of the majority of *Astragalus*, and the representatives (*A. hoantchy* and *A. dshimensis*) of sect. *Sesbanella* of *Pogonophace*. Clade C comprises the species of genus *Oxytropis*.

3 Discussion

As a cosmopolitan and the largest genus of angiosperms, *Astragalus* is well known for its complex variation patterns. Although it consists of both aneuploid and euploid species, recent molecular phylogenetic studies show that the majority of *Astragalus* is monophyletic (with the exception of “outlier” species) (Wojciechowski *et al*,

1999).

There are three major clades in Fig.1: (1) the so-called “Coluteoid clade” (Clade A), comprising all of Galegeae subtribe Coluteinae sensu Polhill (1981), some members of *Astragalus* subgenera *Pogonophace* and *Calycocystis*, and tribe Carmichaelieae (Wagstaff *et al*, 1995); (2) Clade B, comprising the majority of *Astragalus*; (3) Clade C, a monophyletic *Oxytropis*. *Pogonophace* is separated into two distant clades: the first one (Clade D, 99% bootstrap support), including the species of sections *Bibracteola*, *Phyllolobium*, and *Trichostylus*, is nested within Clade A (81% bootstrap support); the second (Clade G, 91% bootstrap support), comprising the representatives of sect. *Sesbanella* (*A. hoantchy*, *A. dshimensis*), is nested within Clade B (82% bootstrap support). Therefore, the results from the present study strongly support that *Pogonophace* is not monophyletic. Morphologically, sect. *Sesbanella* is distinctive from other groups with its erect habit, flattened fruit (bilaterally pressed conditions) and long carpopodium (longer than the calyx). It was moved out from subgenus *Pogonophace* by Wenninger (1991) and his treatment is supported by the ITS sequence data of the present study.

Three major clades (Clade E, Clade D and Clade F) are recognized in “Coluteinae clade” (Clade A). Clade E at the basal of Clade A, including genera *Carmichaelia*, *Clianthus*, and *Swaiaona*, was proposed into tribe Carmichaelinae (Wagstaff *et al*, 1995). Clade D and Clade F are sister group. Based on the analyses of *rpoC* and ITS sequences (Sanderson and Wojciechowskj, 1996; Wojciechowski *et al*, 1999), *A. complanatus* and other species in *Pogonophace* were placed to Coluteinae (Sanderson and Liston, 1995; Sanderson and Wojciechowski, 1996; Wojciechowski *et al*, 1999), which

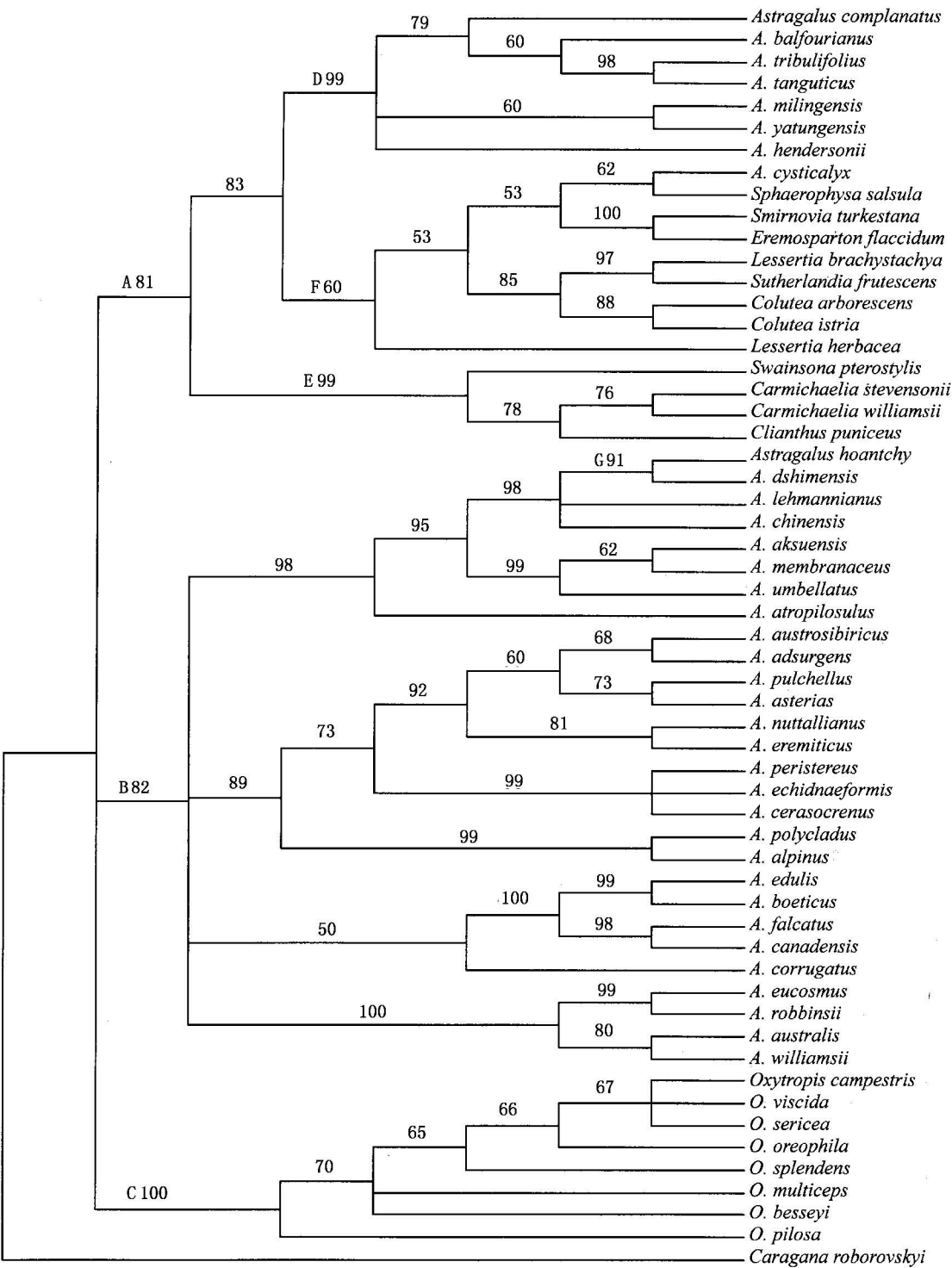


Fig.1. The strict consensus tree of 34 most parsimonious trees from ITS sequences when *Caragana roborovskiyi* is the designated outgroup and gap is treated as missing data. Numbers above the branches are bootstrap data values. The tree has 585 steps, with CI = 0.631 and RI = 0.837. A. Subtrib. Coluteinae and outlier species of *Astragalus*; B. The majority of *Astragalus*; C. *Oxytropis*; D. *Pogonophace* I; E. Subtrib. Carmichaelinae; F. Subtrib. Coluteinae; G. *Pogonophace* II.

is similar to the results of this study. Therefore, the monophyly of the subtribe Coluteinae sensu Polhill (1981) needs to be further investigated. From Fig.1, if we add the species in *Pogonophace* and *A. cysticalyx*,

Coluteinae (Clade A excluding Clade E), as a monophyletic group, receives a moderate bootstrapping support (83%). Polhill presented the distribution area of subtribe Coluteinae, i.e. the droughty mountains of the Old

World, including Africa, Australia and New Zealand (Polhill, 1981; Lavin and Delgado, 1990). *Pogonophace* is mainly distributed in cold and droughty mountains of Asia. Furthermore, the members of the subgenus possess a ciliate style similar to the diagnostic pollen brushes of subtribe Coluteinae (Lavin and Delgado, 1990). Barneby (1964) firstly pointed out that *Astragalus complanatus* "agrees in all important characters with *Sphaerophysa* except that the pod is not inflated", and he suggested to put genera *Sphaerophysa*, *Swainsona*, *Lessertia*, *A. complanatus*, and the other members of *Pogonophace* into a large genus. The evidence of ITS sequences in the present study does not support his viewpoint; however most species in *Pogonophace* are supposed to be closely related to coluteoid groups by our ITS sequence data. Morphologically, *Pogonophace* is really a peculiar group in *Astragalus*. Rather than being exceptional *Astragalus*, most species of *Pogonophace* are more likely specialized members of the coluteoid clade exhibiting morphological convergence to *Astragalus*. However, the close relationship between Coluteinae and *A. cysticalyx* is surprising. No obvious morphological characters link these taxa. Data from the ITS and sampling of additional members of subgenus *Calycocystis* are needed to confirm this association (Wojciechowski *et al.*, 1999).

Within Clade D, one moderate-supported clade (79% bootstrap support) contains *A. complanatus* (sect. *Phyllobium*), *A. tribulifolius* (series *Ebracteola*, sect. *Bibracteola*), *A. tanguticus*, and *A. balfourianus* (series *Bibracteolati*, sect. *Bibracteola*). A close relationship is shown between sections *Phyllobium* and *Bibracteola*, which is consistent with their morphological variation. *A. tribulifolius* and *A. tanguticus*, with non-overlapping distribution respectively, form a clade with 98% bootstrap support. *A. tribulifolius* is distributed in central and southwestern Tibet, Sikkim, and Kashmir, while *A. tanguticus* in eastern Tibet, northwestern Sichuan, eastern and southern Qinghai, and southern Gansu. *A. tribulifolius* and *A. tanguticus* are so similar that Wenninger (1991) believed that they should be combined. The ITS sequences data show that *A. tribulifolius* and *A. tanguticus* are similar and they might be a pair of vicariant species. The results also show that sect. *Bibracteola* is not a monophyletic group. *A. yatungensis* and *A. milingensis* (sect. *Bibracteola*) form one clade with 60% bootstrap support. The relationship between *A. hendersonii* (sect. *Trichostylus*) and rest taxa of clade D is not resolved. The three species have special morphological characters: *A. yatungensis* (sect. *Bibracteola*) with 10 united stamens has indumentum on the upper part of its style; even in the same population, different individuals of *A. milingensis* represent a wide-ranging pattern of variation; while *A. hendersonii* is only about 10 cm tall.

Because bracteoles are not always present in sect. *Bibracteola*, this section is divided into two series, *Ebracteola* and *Bibracteolati* (Fu, 1993). Sometimes bracteoles are absent during flowering. We also noticed this status from the specimens. In the phylogenetic tree

(Fig.1), the two species of different series, *A. tribulifolius* (series *Ebracteola*) and *A. tanguticus* (series *Bibracteolati*), show a close relationship. Morphological traits and ITS sequence data do not support the series' division of sect. *Bibracteola* (Fu, 1993).

Evidence from ITS sequences provides strong support to the monophyly of the majority of *Pogonophace*. Further work is needed to assess the relationships between *Pogonophace* and the members of subtribe Coluteinae, in particular, focusing on the character of style brush, which may be a synapomorphy of subgenus *Pogonophace* and subtribe Coluteinae.

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基于 ITS 序列对中国簇毛黄耆亚属(黄耆属)系统学问题的初步研究

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摘要: 测定了簇毛黄耆亚属(*Pogonophace*)4组8种和外类群 *Caragana roborovskiyi* 的 ITS 序列, 从 GenBank 中调出相关 12 属 47 种的 ITS 序列, 组成数据矩阵, 应用 PAUP 程序中的最大简约法构建了系统发育树状图。扁荚组(Sect. *Sesbanella*)与亚属其余类群在系统树上处于不同的分支, 亲缘关系较远, 这个亚属不是一个单系类群; 蓼果组(Sect. *Bibracteola*), 背扁组(Sect. *Phyllolobium*)和袋果组(Sect. *Trichostylus*)作为一个单系类群能得到 ITS 序列的支持, 但与鱼鳔槐亚族比与黄耆属其他类群的关系更近; *Astragalus complanatus* 和 *A. tribulifolius* 可能为一对替代种; 亚属下的分组以及蓼果组下系的划分都得不到 ITS 序列分析的支持。

关键词: 簇毛黄耆亚属; 黄耆属; 鱼鳔槐亚族; ITS 序列; 系统发育

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