

Plant Syst Evol (2009) 280:167–174
DOI 10.1007/s00606-009-0175-7

ORIGINAL ARTICLE

Pollen brush of *Astragalus* L. subgenus *Pogonophace* Bunge (Leguminosae) and its systematic significance

Yun Kang · M.-L. Zhang

Received: 6 August 2008 / Accepted: 9 March 2009 / Published online: 8 May 2009
© Springer-Verlag 2009

Abstract The style morphologies of *Astragalus* subgenus *Pogonophace* (Leguminosae) were examined using the scanning electron microscope. The results showed that in most species, there are erect and upwardly pointed trichomes on the style. This kind of structure is exactly a pollen brush. The style of *A. craibianus* Sims. is glabrous, and there are finger-like projections formed by the epidermal cells only on the stigma. *A. hoantchy* Franch. has a penicillate stigma. The three types of styles are not homologous. These supported the exclusion of sect. *Sesbanella* and *A. craibianus* from *Pogonophace*. In molecular studies, some *Pogonophace* species are nested within the Coluteinae clade. This study found that those species rightly have the structure of pollen brush. Therefore, the pollen brush is likely to be a synapomorphy of *Pogonophace* and Coluteinae. The close relationship between *Pogonophace* and subtribe Coluteinae (tribe Galegeae) can be supported by the pollen brush.

Keywords *Pogonophace* · *Astragalus* · Coluteinae · Galegeae · Leguminosae · Pollen brush

Introduction

Astragalus L. (Leguminosae) is usually cited as the largest genus of angiosperms (Polhill 1981). There are about 2,000–3,000 species in this genus (Lock and Simpson 1991; Mabberley 1997; Maassoumi 1998). Distributed mainly in drier parts of the Northern Hemisphere, many species of *Astragalus* are narrow endemics, often occurring in marginal habitats or with special edaphic requirements, while relatively few are widespread. It is especially diverse in Southwest Asia (ca. 1,000–1,500 spp.), the Sino-Himalayan region (ca. 500 spp.), western North America (ca. 400–450 spp.) and along the Andes in South America (ca. 100 spp.) (Wojciechowski et al. 1999). It is also diverse in Mediterranean climatic regions, such as the Pacific coasts of North and South America, southern Europe and northern Africa.

As a subgenus of *Astragalus*, *Pogonophace* was established by Bunge (1868, 1869), and it is characterized by the bearded stigma. This subgenus is mainly distributed in China (Zhang 2002). There are different opinions about the classification of *Pogonophace* (Weninger 1991; Zhang 2002; Kang 2004). Fu's (1993) treatment is adopted in this paper for the convenience of discussion. The 32 species (including 1 subspecies, 8 varieties and 1 form) recorded in Flora Reipublicae Popularis Sinicae were classified into four sections (Fu 1993). The four sections are *Sesbanella* (5 spp.), *Bibracteola* (23 spp.), *Phyllobium* (1 spp.), and *Trichostylus* (3 spp.).

The type species of *Pogonophace* is *Astragalus complanatus* (Fu 1993). Barneby (1964) had pointed out the similarities between this species and subtribe Coluteinae and suggested that they may be treated as a large genus. Recent molecular studies (Sanderson and Liston 1995; Sanderson and Wojciechowski 1996; Wojciechowski et al. 1999;

Y. Kang
School of Pharmacy, Fudan University, 200032 Shanghai, China
e-mail: ykang123@yahoo.com.cn

M.-L. Zhang (✉)
Laboratory of Evolution and Biodiversity Conservation in Arid Region, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, 830011 Urumqi, China
e-mail: zhangml@ibcas.ac.cn

M.-L. Zhang
Institute of Botany, Chinese Academy of Sciences, 100093 Beijing, China

Wojciechowski et al. 2000; Kang et al. 2003) also showed that *A. complanatus* and several *Pogonophace* species do have a close relationship with subtribe Coluteinae. Therefore, the systematic position of *Pogonophace* is questionable, further study is needed to resolve this problem.

In the classification of Galegeae, subtribe Coluteinae is separated from the rest by the bearded style (Polhill 1981). As mentioned above, *Pogonophace* is characterized by the bearded stigma. However, the “bearded style” and “bearded stigma” are not precise terms for the description of the the style and stigma that bear trichomes. Lavin and Delgado (1990) proposed four types of bearded styles or stigmas in Leguminosae subfamily Papilionoideae. The pollen brush pertains to a dense aggregation of erect trichomes borne directly on the style toward the distal end; the ciliate style refers to ovarian trichomes loosely trailing into the proximal portion of the style; the ciliate and penicillate stigmas refer to lax trichomes emanating from the stigmatic region, whereas the latter have longer trichomes (Lavin and Delgado 1990).

The so-called “bearded style” of subtribe Coluteinae is a pollen brush (Lavin and Delgado 1990). Because the pollen brush can be morphologically distinguished from similar conditions, unclear definitions of the trichomes on style or stigma may lead to conflicting taxonomies. Our earlier study (Kang and Zhang 2004) has shown that the “bearded stigma” of three *Pogonophace* species is the pollen brush. In this paper we want to find out how many species of *Pogonophace* have the pollen brush, and to accumulate morphological evidence for the systematic study of *Pogonophace*.

Materials and methods

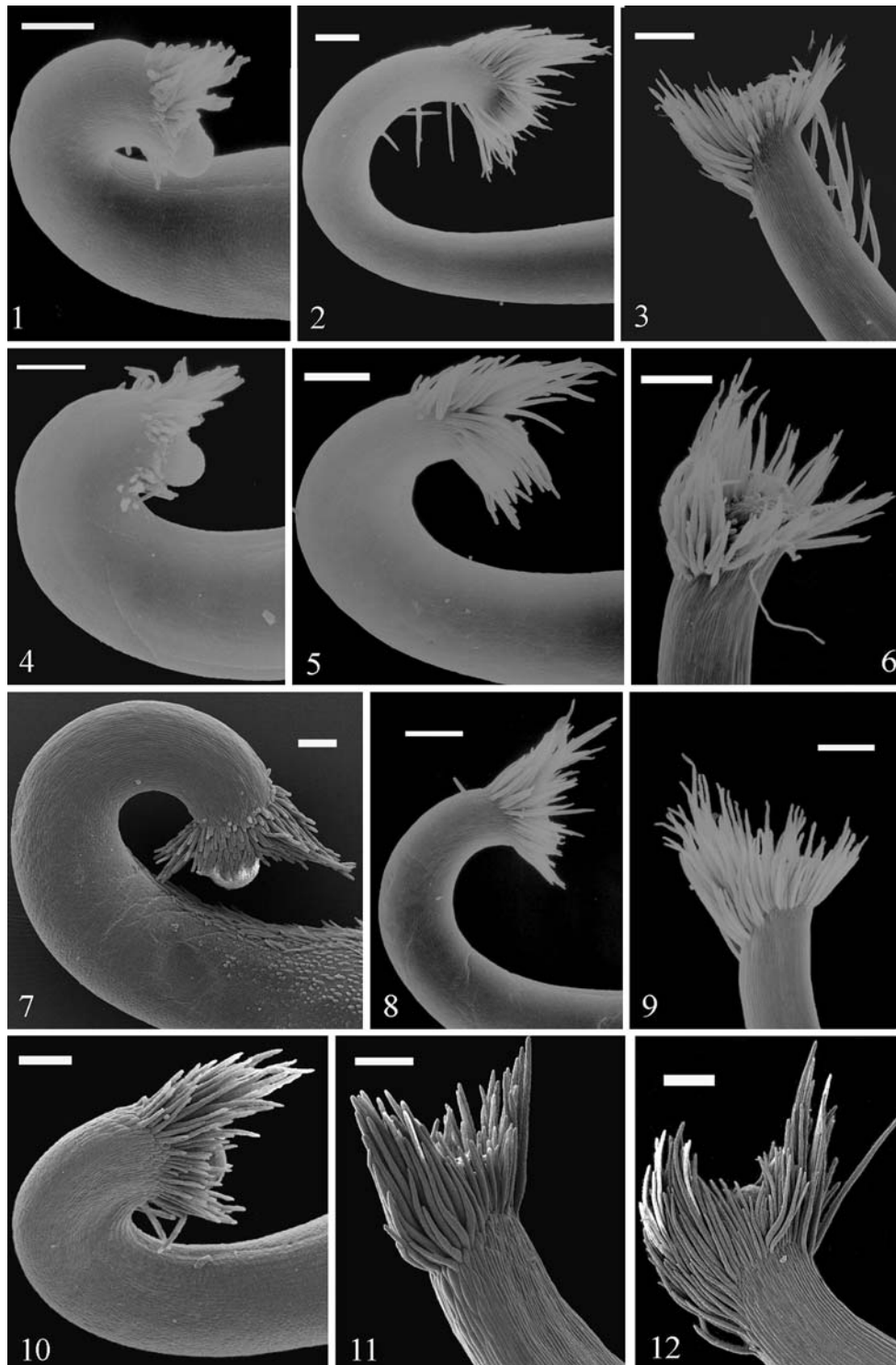
The *Pogonophace* species are mainly distributed in Tibet and the Hengduan Mountains of China. Because of the extreme natural environment and difficult communications, it was very difficult to obtain material. In 2006 and 2007, mainly thanks to support of the National Natural Science Foundation of China (30500035), we could obtain material from Gansu, Sichuan, Yunnan and Tibet. Vouchers (see Table 1) are deposited in the Medicinal Herbarium of Fudan University (SHMU). In the field, fresh material (flowers and flower buds) were fixed in formalin–acetic acid–alcohol (FAA, 70% ethanol:glacial acetic acid:40% formalin = 18:1:1). Various stages of gynoecia were dissected in 70% ethanol and dehydrated in an ethanol/amyacetate series (80% ethanol 1.5 h, 95% ethanol 1.5 h, 100% ethanol 2 h 2 times, 100% ethanol:100% amyacetate (3:1,1:1,1:3) each step 2 h, 100% amyacetate 2 h 2 times); amyacetate was then removed in a Hitachi HCP-2 Dryer. Dried gynoecia were mounted on metal stubs and sputter coated with gold. Prepared samples were then examined with a Hitachi S-800 Scanning Electron Microscope (SEM) and photographed.

Results

In this study, most species of *Pogonophace* have trichomes on the style (Figs. 1–31, 34–36). In these species, like *A. balfourianus* Sims. (Figs. 1–3) and *A. camptodontoides* Sims. (Figs. 4–6), the style bends to the adaxial side, and

Table 1 Origin of materials studied

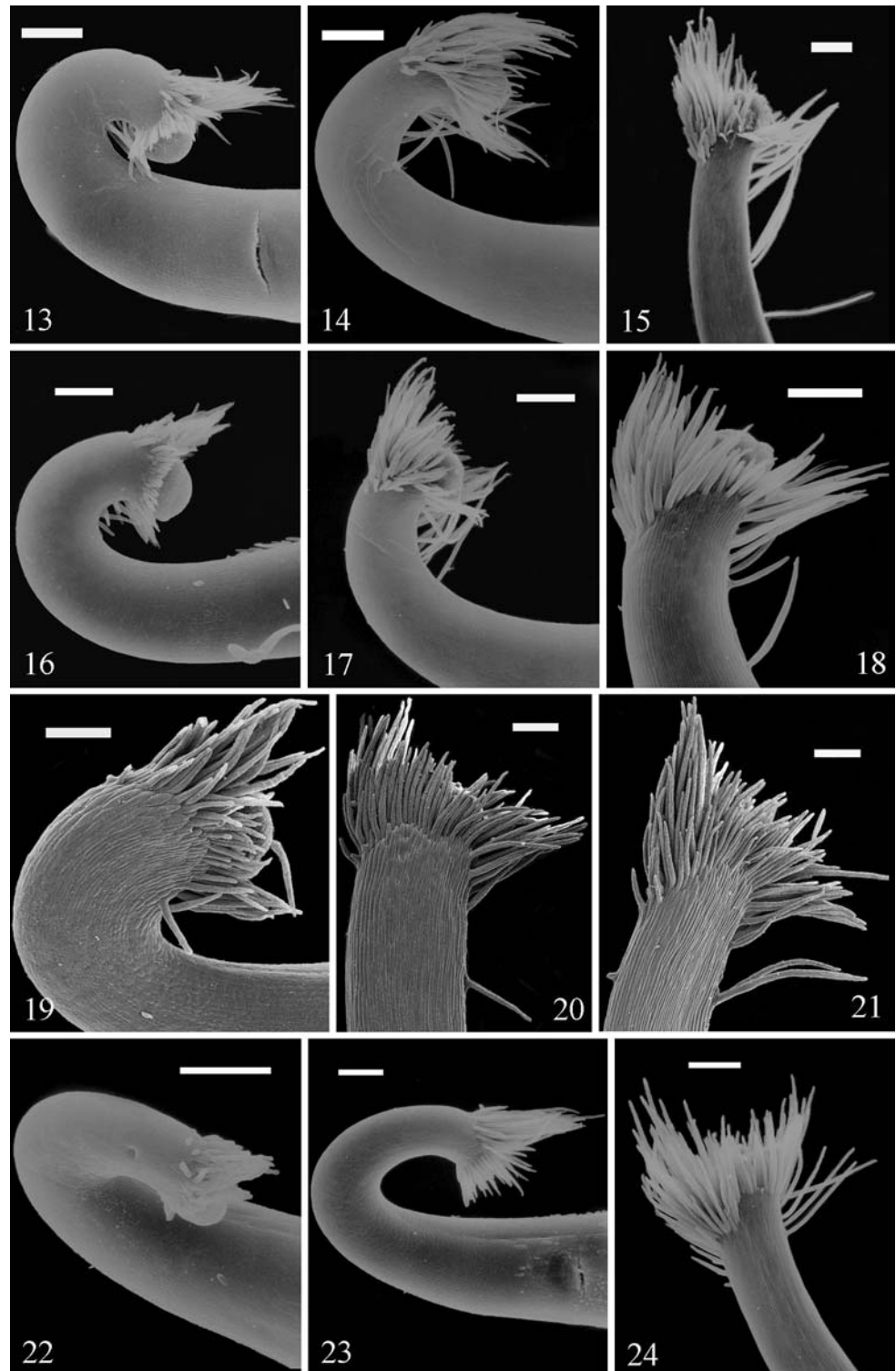
Species	Section	Origin	Voucher
<i>Astragalus balfourianus</i> Sims.	<i>Bibracteola</i>	Lijiang, Yunnan, China	Kang Yun 06-08
<i>A. camptodontoides</i> Sims.	<i>Bibracteola</i>	Eryuan, Yunnan, China	Kang Yun 06-06
<i>A. lasaensis</i> Ni et P. C. Li	<i>Bibracteola</i>	Lhasa, Xizang, China	Kang Yun 07-05
<i>A. milingensis</i> Ni et P. C. Li	<i>Bibracteola</i>	Nyingchi, Xizang, China	Kang Yun 07-01
<i>A. pastorius</i> Tsai et Yü	<i>Bibracteola</i>	Zhongdian, Yunnan, China	Kang Yun 06-11
<i>A. pastorius</i> Tsai et Yü var. <i>linearibracteatus</i> K. T. Fu	<i>Bibracteola</i>	Xiangcheng, Sichuan, China	Kang Yun 06-16
<i>A. prodigiosus</i> K. T. Fu	<i>Bibracteola</i>	Lhasa, Xizang, China	Kang Yun 07-03
<i>A. siccanus</i> P. C. Li	<i>Bibracteola</i>	Yanyuan, Sichuan, China	Kang Yun 06-03
<i>A. tanguticus</i> Batalin	<i>Bibracteola</i>	Daofu, Sichuan, China	Kang Yun 07-09
<i>A. tribulifolius</i> Benth.	<i>Bibracteola</i>	Lhasa, Xizang, China	Kang Yun 07-04
<i>A. hendersonii</i> Baker	<i>Trichostylus</i>	Damxung, Xizang, China	Kang Yun 07-07
<i>A. heydei</i> Baker	<i>Trichostylus</i>	Litang, Sichuan, China	Kang Yun 06-17
<i>A. donianus</i> DC.	<i>Bibracteola</i>	Yadong, Xizang, China	Kang Yun 07-06
<i>A. turgidocarpus</i> K. T. Fu	<i>Bibracteola</i>	Wudu, Gansu, China	Kang Yun 06-01
<i>A. craibianus</i> Sims.	<i>Bibracteola</i>	Deqen, Yunnan, China	Kang Yun 07-08
<i>A. sanbilingensis</i> Tsai et Yü	<i>Bibracteola</i>	Batang, Sichuan, China	Kang Yun 06-18



Figs. 1–12 Pollen brush of *Astragalus balfourianus* Sims. (Kang Yun 06-08, SHMU); **Fig. 1** at inception; **Fig. 2** prior to anthesis; **Fig. 3** at anthesis. **Figs. 4–6** Pollen brush of *A. camptodontoides* Sims. (Kang Yun 06-06, SHMU); **Fig. 4** at inception; **Fig. 5** prior to anthesis; **Fig. 6** at anthesis. **Figs. 7–9** Pollen brush of *A. lasaensis*

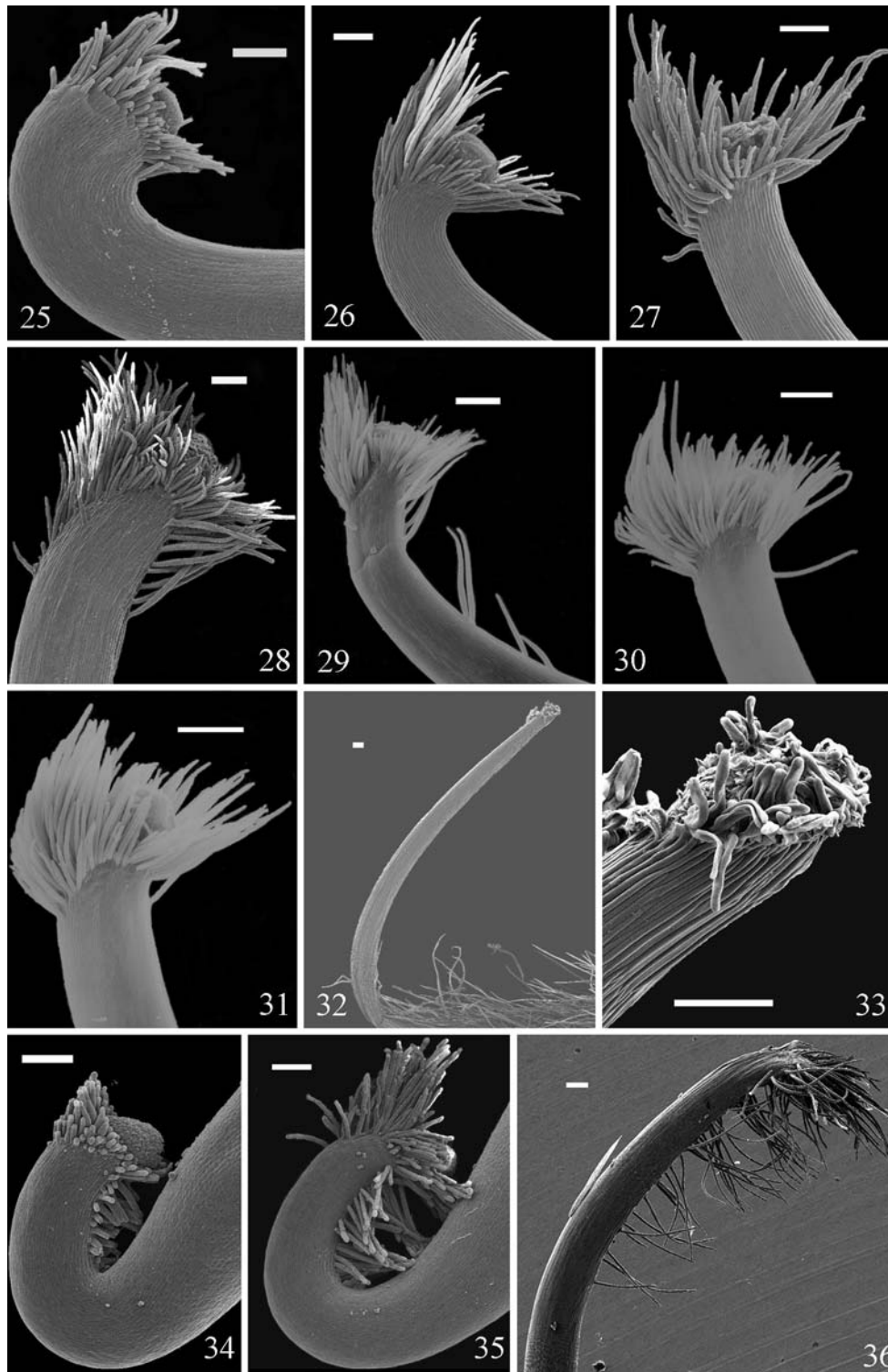
Ni et P. C. Li (Kang Yun 07-05, SHMU); **Fig. 7** at inception; **Fig. 8** prior to anthesis; **Fig. 9** at anthesis. **Figs. 10–12** Pollen brush of *A. milingensis* Ni et P. C. Li (Kang Yun 07-01, SHMU); **Fig. 10** at inception; **Fig. 11** prior to anthesis; **Fig. 12** at anthesis

Figs. 13–15 Pollen brush of *A. pastorius* Tsai et Yü (Kang Yun 06-11, SHMU); **Fig. 13** at inception; **Fig. 14** prior to anthesis; **Fig. 15** at anthesis. **Figs. 16–18** Pollen brush of *A. pastorius* var. *linearibracteatus* K. T. Fu (Kang Yun 06-16, SHMU); **Fig. 16** at inception; **Fig. 17** prior to anthesis; **Fig. 18** at anthesis. **Figs. 19–21** Pollen brush of *A. prodigosus* K. T. Fu (Kang Yun 07-03, SHMU); **Fig. 19** at inception; **Fig. 20** prior to anthesis; **Fig. 21** at anthesis. **Figs. 22–24** Pollen brush of *A. siccanus* P. C. Li (Kang Yun 06-03, SHMU); **Fig. 22** at inception; **Fig. 23** prior to anthesis; **Fig. 24** at anthesis



the stigma is located on the adaxial side of the style top. The stigma is only about half the size of the style top, and this can be clearly seen when the trichomes begin to appear (Figs. 1, 4, 7, 13, 16, 22, 25, 34). The trichomes appear at the very top of the style, first on the abaxial side (Figs. 1, 4,

7, 10, 13, 16, 19, 22, 25), then followed by those on the lateral and the adaxial sides (Figs. 2, 3, 5, 6, 8, 9, 11, 12, 14, 15, 17, 18, 20, 21, 23, 24, 26). At anthesis, the stigma is surrounded by the trichomes (Figs. 3, 6, 9, 12, 15, 18, 21, 24, 26–31), and the abaxial side always has more, longer,



Figs. 25–36 Pollen brush of *A. tanguticus* Batalin (Kang Yun 07-09, SHMU); **Fig. 25** at inception; **Fig. 26** at anthesis. **Fig. 27** Pollen brush of *A. sanbilingensis* Tsai et Yü (Kang Yun 06-18, SHMU); **Fig. 27** at anthesis. **Fig. 28** Pollen brush of *A. hendersonii* Baker (Kang Yun 07-07, SHMU); **Fig. 28** at anthesis. **Fig. 29** Pollen brush of *A. heydei* Baker (Kang Yun 06-17, SHMU); **Fig. 29** at anthesis. **Fig. 30** Pollen

brush of *A. tribulifolius* Benth. (Kang Yun 07-04, SHMU); **Fig. 30** at anthesis. **Fig. 31** Pollen brush of *A. turgidocarpus* K. T. Fu. (Kang Yun 06-01, SHMU); **Fig. 31** at anthesis. **Figs. 32, 33** The style and stigma of *A. craibianus* Simps. (Kang Yun 07-08, SHMU); **Fig. 32, 33** at anthesis. **Figs. 34–36** Pollen brush of *A. donianus* DC. (Kang Yun 07-06, SHMU); **Figs. 34, 35** at inception; **Fig. 36** at anthesis

Figs. 37–39 Penicillate stigma of *A. hoantchy* Franch. (Kang Yun 02-05, PE); **Fig. 37** at anthesis. **Fig. 38** Pollen brush of *Sphaerophysa salsula* (Pall.) DC. (Kang Yun 02-01, PE); **Fig. 38** at anthesis. **Fig. 39** Stigma of *Astragalus englerianus* Ulbr. (Zhu Shi-xin and Kang Yun 24, PE); **Fig. 39** at anthesis. **Figs. 37–39** modified from Kang and Zhang (2004)

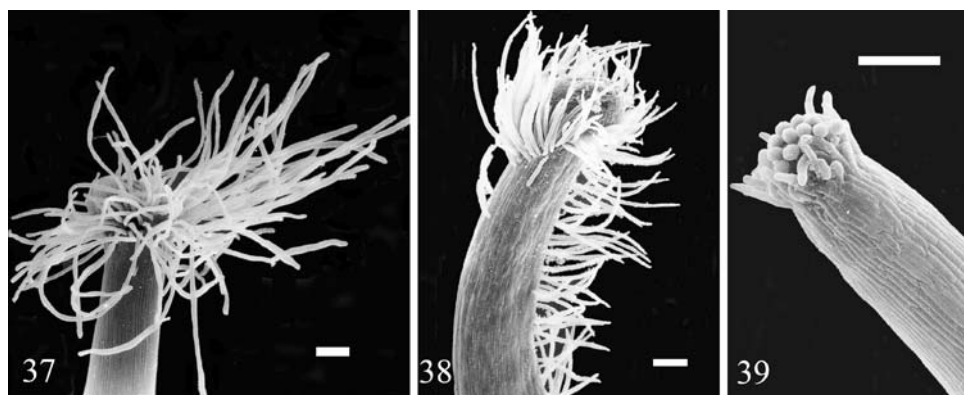


Table 2 Main morphological features of the species studied (–, trichomes absent)

Species	Style thickened	Stigma size (cf. style)	Trichome around the stigma	Trichomes trail to the proximal portion of the style
<i>A. balfourianus</i> Simps.	Yes	Small	Yes	Yes
<i>A. camptodontoides</i> Simps.	Yes	Small	Yes	No
<i>A. lasaensis</i> Ni et P. C. Li	Yes	Small	Yes	No
<i>A. milingensis</i> Ni et P. C. Li	Yes	Small	Yes	No
<i>A. pastorius</i> Tsai et Yü	Yes	Small	Yes	Yes
<i>A. pastorius</i> var. <i>linearibracteatus</i> K. T. Fu	Yes	Small	Yes	Yes
<i>A. prodigosus</i> K. T. Fu	Yes	Small	Yes	Yes
<i>A. siccanus</i> P. C. Li	Yes	Small	Yes	Yes
<i>A. tanguticus</i> Batalin	Yes	Small	Yes	No
<i>A. tribulifolius</i> Benth.	Yes	Small	Yes	Not clear
<i>A. hendersonii</i> Baker	Yes	Small	Yes	Yes
<i>A. heydei</i> Baker	Yes	Small	Yes	Yes
<i>A. donianus</i> DC.	Yes	Small	Yes	Yes
<i>A. turgidocarpus</i> K. T. Fu	Yes	Small	Yes	Not clear
<i>A. craibianus</i> Simps.	No	The same	–	–
<i>A. sanbilingensis</i> Tsai et Yü	Yes	Small	Yes	No
<i>A. hoantchy</i> Franch. ^a	No	Slightly swollen	Yes	No
<i>S. salsula</i> (Pall.) DC.	Yes	Swollen	Yes	Yes
<i>A. englerianus</i> Ulbr.	No	Slightly swollen	–	–

^a The following species are cited from Kang and Zhang (2004)

and denser trichomes than the adaxial side. Sometimes the trichomes may loosely trail into the proximal portion of the style (Fig. 3, 15, 18, 21, 24, 28, 29).

Compared with those species mentioned above, *A. donianus* DC. differs in the morphology of its style (Figs. 34–36). It also has trichomes on the style, but when the trichomes begin to appear, the proximal portion of the style also has many trichomes, except for the abaxial side of the style top (Fig. 34). So at anthesis, there are also many trichomes on the proximal portion of the style (Fig. 36).

In the present study, *A. craibianus* Simps. is the only species that has no trichomes on the style and stigma

(Fig. 32). Unlike the above species, the stigma of *A. craibianus* is not clear, and it has the same size of the style top. When the stigma was magnified 200 times, we could see some finger-like projections formed by the epidermal cells on it (Fig. 33).

For the convenience of comparison, the observations of three species in our former study (Kang and Zhang 2004) are included in this paper (Fig. 37. *A. hoantchy* Franch.; Fig. 38. *Sphaerophysa salsula* (Pall.) DC.; Fig. 39. *Astragalus englerianus* Ulbr.). The stigma of *A. hoantchy* is slightly swollen and the lax and curved trichomes emanate from the base of stigma (Fig. 37). The trichomes

of *S. salsula* appear at the abaxial side of the style top and the proximal portion of the style (Fig. 38). There are no trichomes on the style of *Astragalus englerianus*, and the epidermal cells around the stigma form short hairs (Fig. 39). Detailed descriptions can be seen in Kang and Zhang (2004).

Discussion

Our data demonstrate that in *Pogonophace*, *A. craibianus* has no trichomes on the style and stigma, and that the trichomes of *A. hoantchy* are on the stigma, while all other species of *Pogonophace* have trichomes on the style. Although the trichomes emanate from the style top, the stigma is smooth and surrounded by the trichomes. Most importantly, trichomes are erect and pointed upwards. This is the essential functional feature of the pollen brush in secondary pollen presentation (Faegri and van der Pijl 1979; Leppik 1966; Lavin and Delgado 1990). According to our observation, some of the characteristics correlated with the pollen brush (Lavin and Delgado 1990) also exist in these species, such as thickened style and non-interlocking keel and wing petals (i.e. the absence of bosses on the keel and matching sockets on the wings). Therefore, according to Lavin and Delgado's (1990) criteria, this kind of structure can be recognized as a pollen brush. *S. salsula* is a species that has been confirmed to have the structure of pollen brush (Lavin and Delgado 1990; Kang and Zhang 2004). We can see that in this species, there are more trichomes on the proximal portion of the style (Fig. 38), while in the *Pogonophace* species, trichomes are mainly clustered around the stigma, and sometimes scattered on the proximal portion of the style (see Table 2). But one species of *Pogonophace*, *A. donianus*, also has many trichomes on the proximal portion of the style (Figs. 34–36). Therefore, the pollen brush of this species is very similar to that of *S. salsula* (Fig. 38).

In molecular studies (Sanderson and Liston 1995; Sanderson and Wojciechowski 1996; Wojciechowski et al. 1999; Wojciechowski et al. 2000; Kang et al. 2003; Kang et al. unpublished), some *Pogonophace* species are always nested within the Coluteinae clade. From this study combined with our former study (Kang and Zhang 2004), we can see that it is the species with the pollen brush that would be nested within the Coluteinae clade, while other species such as *Astragalus hoantchy* and *A. craibianus* remain within the *Astragalus* clade. Because the pollen brush is the key character to distinguish subtribe Coluteinae from the rest of Galegeae (Lavin and Delgado 1990), it is also likely to be a homologous character of *Pogonophace* and Coluteinae. Therefore, the proposal to separate *Pogonophace* from *Astragalus* and transfer it to Coluteinae

(Kang and Zhang 2004) can be supported by the pollen brush.

Astragalus hoantchy belongs to section *Sesbanella*. Unlike the above species, the trichomes emanate from the base of the stigma (Fig. 37). Meanwhile, the trichomes of this species are lax and curved, and they have no uniform direction. Because of these differences, the style morphology of *A. hoantchy* can be recognized as a penicillate stigma. Morphologically, section *Sesbanella* is a distinctive group in *Pogonophace* for its erect habit, flattened fruit (bilaterally compressed) and long fruit stalk (longer than the calyx). And as mentioned above, in molecular studies the *Sesbanella* species are still nested within the *Astragalus* clade (Kang et al. 2003; Kang et al. unpublished). Therefore, the separation of *Sesbanella* from *Pogonophace* (Weninger 1991; Kang 2004) can be supported by the penicillate stigma.

A. craibianus is a problematic species of *Pogonophace*. It has many characteristics that are quite dissimilar from the other species that have the structure of pollen brush. For example, the fruit with dense trichomes is highly inflated, and the fruit stalk is longer than the calyx tube. Moreover, the stipules of this species are membranous. Because of these differences, Kang (2004) considered that *A. craibianus* should be separated from *Pogonophace*. We only had late flowering material at our disposal. Because of this, an extra part can be seen on the abaxial side of the style top, just below the stigma (Figs. 32, 33). This is caused by the splitting of the style top (may also including the stigma). However, our study still shows that the style of this species is glabrous (Fig. 32). The original description of its stigma mentioned "stigma minute capitatum" (Simpson 1915). Finger-like projections could be seen on the stigma when it was magnified 200 times (Fig. 33). The projections are like the short hairs around the stigma of *A. englerianus* (Fig. 39, *A. englerianus* is a *Astragalus* species); both are formed by the epidermal cells. Because there are no trichomes on the style and stigma, this is not a pollen brush, and it does not belong to the other three style morphologies proposed by Lavin and Delgado (1990). In molecular studies, *A. craibianus* is still nested within the *Astragalus* clade (Kang et al. unpublished). Therefore, the stigma morphology of *A. craibianus* can also support its exclusion from *Pogonophace*.

Section *Phyllobium* has been studied before and is confirmed to have the pollen brush (Kang and Zhang 2004). Adding the species of section *Trichostylus* (see Table 1) in the present study, the four sections of *Pogonophace* have been investigated so far. We can see that except section *Sesbanella* and *A. craibianus*, the remaining *Pogonophace* species all have the structure of pollen brush. Combined with other morphological and molecular data, the pollen brush can support the exclusion of *Sesbanella*

and *A. craibianus* from *Pogonophace*. Meanwhile, it may be a morphological argument for the close relationship between *Pogonophace* and Coluteinae. The suggestion to transfer *Pogonophace* from *Astragalus* to Coluteinae (Kang and Zhang 2004) can also be supported by this structure.

In addition, some closely related species are slightly different in the pollen brush. For example, *A. hendersonii* and *A. heydei* are morphologically similar and are sometimes treated as one species (Wenninger 1991). The former has more trichomes on the abaxial side, and the trichomes on the proximal side are clustered together (Fig. 28). In the latter, the trichomes on the proximal side are scattered (Fig. 29). Therefore, the pollen brush may provide significant information for the classification of those species.

The present study shows that most species of *Pogonophace* have a pollen brush. When analyzed with other data, especially with molecular studies, this structure can be of important systematic significance. But in order to get a satisfying classification of *Pogonophace*, further morphological and molecular studies are still needed to accumulate enough data.

Acknowledgments The authors wish to express their deep gratitude to two anonymous reviewers and the Associate Editor Louis Ronse De Craene for valuable comments on the manuscript and for language corrections. We would like to thank Yang Ao for assistance in the field. We are grateful to Xiao Yin-hou for his technical assistance and to Chen Zhi-duan for valuable comments on an earlier version of this manuscript. Craig Brough is thanked for providing an important reference. National Natural Science Foundation of China (30500035) and the Young Teacher Science Foundation of Fudan University (CHF301005) supported this research.

References

- Barneby RC (1964) Atlas of North American *Astragalus*. Mem New York Bot Garden 13:1–1188
- Bunge A (1868) Generis Astragali species gerontogae. Mém Acad Imp Sci Saint Pétersbourg ser. 7 11(16):1–140
- Bunge A (1869) Generis Astragali species gerontogae. Pars Altera: Specierum enumeratio. Mém Acad Imp Sci Saint Pétersbourg ser. 7 15(1):1–245
- Faegri K, van der Pijl L (1979) The principles of pollination ecology. Pergamon, Oxford
- Fu KT (1993) *Astragalus*. In: Fu KT (ed) Flora Reipublicae Popularis Sinicae, vol 42 (1). Science Press, Beijing, pp 78–349 (In Chinese)
- Kang Y (2004) Taxonomic revision of *Astragalus* L. subgenus *Pogonophace* Bunge (Leguminosae) and a preliminary study of its systematic position. Ph.D. Dissertation. Beijing: Institute of Botany, the Chinese Academy of Sciences (In Chinese with English abstract)
- Kang Y, Zhang ML (2004) Study of pollen brush in selected species of *Astragalus* subgenus *Pogonophace* Bunge (Leguminosae). Plant Syst Evol 249:1–8
- Kang Y, Zhang ML, Chen ZD (2003) A preliminary phylogenetic study of the subgenus *Pogonophace* (*Astragalus*) in China based on ITS sequence data. Acta Bot Sin 45:140–145
- Lavin M, Delgado SA (1990) Pollen brush of Papilionoideae (Leguminosae): morphological variation and systematic utility. Amer J Bot 77:1294–1312
- Leppik EE (1966) Floral evolution and pollination in Leguminosae. Ann Bot Fenn 3:299–308
- Lock JM, Simpson K (1991) Legumes of West Asia, a check-list. Royal Botanic Gardens, Kew
- Maassoumi AAR (1998) Old world check-list of *Astragalus*. Research Institute of Forests and Rangelands, Tehran
- Mabberley DJ (1997) The plant-book a portable dictionary of the vascular plants. Cambridge University Press, Cambridge
- Polhill RM (1981) Galegeae. In: Polhill RM, Raven PH (eds) Advances in legume systematics, Part 1. Royal Botanic Gardens, Kew, pp 357–363
- Sanderson MJ, Liston A (1995) Molecular phylogenetic systematics of Galegeae, with special reference to *Astragalus*. In: Crisp MD, Doyle JJ (eds) Advances in legume systematics, Part 7. Royal Botanic Gardens, Kew, pp 331–350
- Sanderson MJ, Wojciechowski MF (1996) Diversification rates in a temperate legume clade: are there so many species of *Astragalus* (Fabaceae)? Amer J Bot 83:1488–1502
- Simpson ND (1915) A numeration of the Chinese Astragali. Notes R Bot Gard Edinburgh 8:239–264
- Wenninger J (1991) Revision von *Astragalus* L. sect. Chlorostachys Bunge, sect. *Phyllolobium* Bunge und sect. Skythropos Simpson (Leguminosae). Mitte der Bot Staatssammlung München 30:1–196
- Wojciechowski MF, Sanderson MJ, Hu JM (1999) Evidence on the monophyly of *Astragalus* (Fabaceae) and its major subgroups based on nuclear ribosomal DNA ITS and chloroplast DNA *trnL* intron data. Syst Bot 24(3):409–437
- Wojciechowski MF, Sanderson MJ, Steele KP, Liston A (2000) Molecular phylogeny of the “temperate herbaceous tribes” of Papilionoid legumes: a supertree approach. In: Herendeen PS, Bruneau A (eds) Advances in legume systematics, Part 9. Royal Botanic Gardens, Kew, pp 277–298
- Zhang ML (2002) Systematics of *Astragalus* subgenus *Pogonophace* (Leguminosae). Acta Botanica Yunnanica 24(5):543–553