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Authors: Tang, Ya, and Xie, Jia-sui

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A Pollination Ecology Study of *Pedicularis* Linnaeus (Orobanchaceae) in a Subalpine to Alpine Area of Northwest Sichuan, China

Ya Tang*† and

Jia-sui Xie*

*Department of Environmental Science,
Sichuan University, No. 24,
South Section 1, First Ring Road,
Chengdu, Sichuan 610065, China.

†Corresponding author.
tangya999@gmail.cn

Abstract

Pollination ecology and habitat preference of *Pedicularis* species were studied in a transitional zone between subalpine coniferous forests and alpine meadows in north-western Sichuan of China. *Pedicularis* species exhibited apparent preferences for different microhabitats. Species with long rostrate and contorted galea were nectarless and their mean corolla tube length ranged from 7 to 50 mm while species without long rostrate and contorted galea produced nectar and their corolla tube length averaged from 8 to 18 mm. Bumblebees were the sole pollinators of the studied species and five bee species pollinated seven *Pedicularis* species with one species pollinating all the *Pedicularis* species. Pollinators that visited nectariferous species had longer tongues than those that visited nectarless species and they spent longer time on nectariferous than on nectarless species. All *Pedicularis* species except for *P. rex* subsp. *lipskyana* were pollinated by worker bees. *Pedicularis rex* subsp. *lipskyana* was pollinated nototribically by worker, male and queen bumblebees through stigmatic contact with residual pollen on the left side of the bee's head. Morphology of pollinators, rather than pollinator species, may play the key role in diversification of *Pedicularis*. Microhabitats rather than pollination may be the separation barrier in propagation. Factors contributing to high diversity of *Pedicularis* need further study.

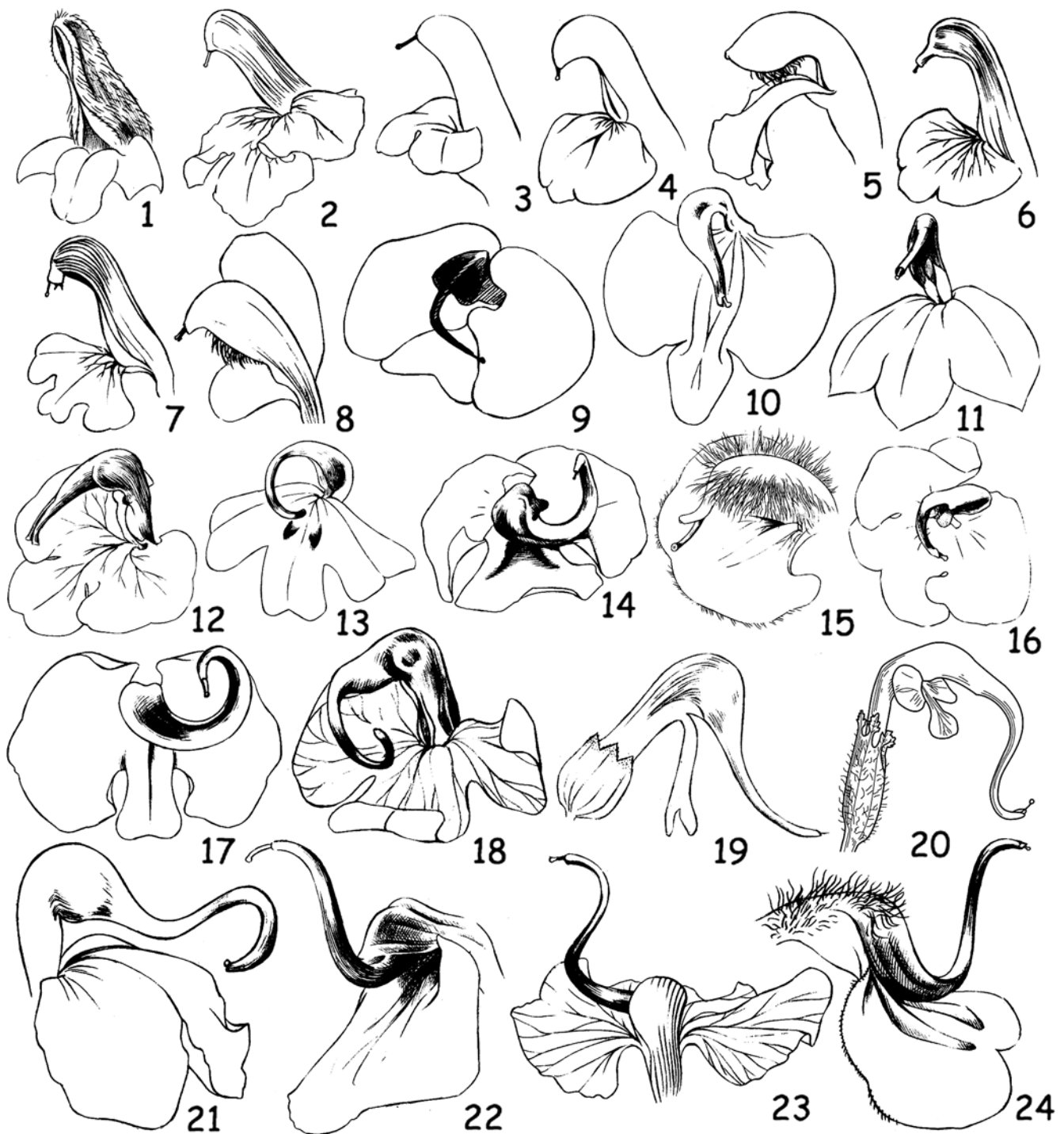
Introduction

Pedicularis Linnaeus (Orobanchaceae), with around 600 species, is one of the largest genera of flowering plants in the Northern Temperate region and most species are confined to alpine and arctic areas. Over half of the species are concentrated in the subalpine and alpine areas from the eastern Himalayas to the mountains of south-western China and 352 species have been recorded for China alone (Yang et al., 1998), excluding some newly described and reported taxa. *Pedicularis* is characterized by the extremely high floral diversity and is likely the flowering plant genus that exhibits the most diverse flora morphology in flowering plants (Pennell, 1943; Li, 1948, 1951). The corolla is variously colored and is the most variable floral part. The corolla consists of a basal tube, an upper lip, and a lower lip. The tube varies considerably in length. The upper lip is formed by a fusion of two dorsal petals, forming a compressed hood (galea) which contains the anthers and styles. The lower lip is formed by a fusion of three ventral petals and is spreading trifid. The four anthers are enclosed in the galea and the stigma usually extrudes out of the galea. The greatest diversity of floral morphology is found with the upper lip or galea, especially beaks (Figs. 1–24). The beaks vary from very short to very long; they may be erect, bending or coiled, and straight or twisted to one side. Despite the great number of species and high degree of floral diversity, *Pedicularis* is a bona fide genus and it seems impossible to divide it into subgenera (Pennell, 1943; Li, 1951; Tsoong 1955–1956, 1963; Yang et al., 1998). The presence of two corolla lips, two petals forming the upper lip and three forming the lower lip, is characteristic of the majority of Lamiales s. l. (Endress, 1999), but no other taxa have exhibited such a highly diverse corolla morphology as in *Pedicularis* (Endress, 2001). We are interested in the high diversity of species and corolla morphology of *Pedicularis*, whether it is intrinsic or extrinsic, that is developmental or ecological in nature.

Floral mechanism prevents self-pollination in *Pedicularis* and pollination pressure is considered to be the most important factor responsible for the highly divergent species and corolla forms in *Pedicularis* (Pennell, 1943; Li, 1948, 1951; Macior, 1982). The great variation in floral morphology led Pennell (1948) and Li (1948) to speculate that pollinators of this genus would be as diverse as the floral morphology in *Pedicularis* and that the pollination of some long-tubed species would depend on specific lepidoperan insects with very long probosces. However, studies in North America (Macior, 1968a, 1968b, 1969, 1970, 1982), Europe (Kwak, 1977, 1979; Eriksen et al., 1993), Japan (Macior, 1988), Indian Himalaya (Macior, 1990; Macior et al. 1991), and China (Macior et al., 1997; Wang, 1998; Wang et al., 1998; Macior et al., 2001) revealed that bumblebees are the prime pollinators. While the pollination ecology of almost all the species in North America has been studied, pollination ecology studies have been carried out on only a few species in China, where over half species of *Pedicularis* occur. The present study relates the pollination ecology of seven species in northwest Sichuan, part of the diversity center of *Pedicularis*, and the aims of the study are 1) to study whether the same pollination mechanism found in North America applies to the species in the studied area; 2) whether differences of corolla form are related directly to processes of pollination and; 3) whether pollination plays a vital role in diversification of the *Pedicularis* species in the region.

Materials and Methods

The study was carried out in the summers of 2002 and 2003 on the eastern slope of the Zhugu Shan in Lixian County, Aba Autonomous Prefecture, northwestern Sichuan Province, China. This area belongs to the transitional zone between subalpine coniferous forests and alpine meadows. The elevation varies from 2700 to 4200 m above sea level. Main vegetation types in the region are coniferous



FIGURES 1–24. Galea diversity in selected *Pedicularis* species. Fig. 1. *P. mollis* Wall. ex Benth; Fig. 2. *P. verticillata* Linnaeus; Fig. 3. *P. muscoides* Li subsp. *himalayca* Yamazaki; Fig. 4. *P. floribunda* Franchet; Fig. 5. *P. princeps*; Fig. 6. *P. chenocephala* Diels; Fig. 7. *P. oederi* Vahl; Fig. 8. *P. ingens* Maximowicz; Fig. 9. *P. cyathophylla*; Fig. 10. *P. geosiphon* H. Smith & Tsoong ex Tsoong; Fig. 11. *P. alopecuroides* Franchet; Fig. 12. *P. przewalskii* Maximowicz; Fig. 13. *P. longiflora* Rudolph var. *tubiformis* (Klotzsch) Tsoong; Fig. 14. *P. siphonantha* Don; Fig. 15. *P. rhodotricha* Maximowicz; Fig. 16. *P. cranolopha* Maximowicz; Fig. 17. *P. torta*; Fig. 18. *P. rhinanthoides* subsp. *labellata*; Fig. 19. *P. angustilabris* Li; Fig. 20. *P. macrorhyncha* Li; Fig. 21. *P. integrifolia* subsp. *integerrima* (Pennell & Li) Tsoong; Fig. 22. *P. oliveriana* Prain; Fig. 23. *P. streptorhyncha*; Fig. 24. *P. fetissowii* Regel.

forests, shrubland, regenerated shrubland after forest clearing, fallow farmland, alpine shrubland, and pasture.

Sites at different elevation, with different land uses, and with different *Pedicularis* species with different floral types, were selected after a preliminary survey of *Pedicularis* species and land uses. The characteristics of the selected study sites and species studied in each

site are provided in Table 1. Twelve *Pedicularis* species or subspecies were found in the study area: *P. semitorta* Maximowicz, *P. torta* Maximowicz, *P. szetschuanica* Maximowicz, *P. rex* C. B. Clarke subsp. *lipskyana* (Bonati) Tsoong, *P. davidii* Franchet, *P. cyathophylla* Franchet, *P. stenocorys* Franchet, *P. streptorhyncha* Tsoong, *P. princeps* Bureau & Franchet, *P. rhinanthoides* Schrenk subsp.

TABLE 1
Characteristics of the study sites.

Site	Latitude	Longitude	Elevation (m)	Vegetation	Studied species
1	31.7766°N	102.7094°E	3186	Shrubland	<i>P. rex</i> subsp. <i>lipskyana</i> , <i>P. torta</i> , <i>P. princeps</i>
2	31.7890°N	102.7184°E	3160–3195	Cultivated fodder	<i>P. szetschuanica</i> , <i>P. torta</i>
3	31.7965°N	102.6923°E	3458	Grassy slope	<i>P. cyathophylla</i> , <i>P. davidii</i> , <i>P. stenocorys</i> , <i>P. semitorta</i> , <i>P. szetschuanica</i>
4	31.8521°N	102.6722°E	4164	Steep grassy slope among rhododendron scrubland	<i>P. streptorhyncha</i> , <i>P. angularis</i> , <i>P. metasetschuanica</i>

labellata (Jacquin) Tsoong, *P. angularis* Tsoong, and *P. metasetschuanica* Tsoong. Among them, *P. streptorhyncha* has only been reported from the study area (Tsoong, 1963) while the other species have a wider geographical distribution.

Length of time of a floral visit, weather conditions, and duration of observation were recorded. Apart from direct observations of their behavior, pollinators were also collected. The behavior of pollinators was recorded both with a video camera and on 35 mm film. In order to determine whether there was an obligate relationship between pollinators and *Pedicularis* species, the collected pollinators were separated for each species of *Pedicularis*. Bumblebees were also collected from other sympatric plant species.

Bumblebees were identified to species and caste by Dr. Paul H. Williams of Department of Entomology, the Natural History Museum, London. The *Pedicularis* species were identified by the senior author. Voucher specimens of bumblebees and plants are deposited at the Herbarium of Laboratory for Biodiversity and Environmental Studies, Sichuan University. Duplicates of plant specimens are deposited at the herbarium of the Sichuan University and duplicates of bumblebees are stored at the herbarium of the Institute of Zoology, the Chinese Academy of Sciences and the Natural History Museum, London.

Results

FLORAL MORPHOLOGY, COLOR, AND FLOWERING PHENOLOGY

Twelve species of *Pedicularis* occurred in the study area and seven were in full bloom, three in full to late bloom, one past full bloom, and one in early to full bloom during the study period. These species differed in color, phenology, and corolla tube length (Table 2).

TABLE 2
Colors and phenology of various taxa of *Pedicularis*.

Taxa	Flower color	Phenology	Corolla tube length
<i>P. rex</i> subsp. <i>lipskyana</i>	Purplish to purple	Full bloom	15–20 (18)
<i>P. szetschuanica</i>	Red	Full bloom	6–9 (8)
<i>P. torta</i>	Yellow with purple galea beak	Full to late bloom	6–10 (7)
<i>P. semitorta</i>	Yellow	Full to late bloom	6–9 (8)
<i>P. cyathophylla</i>	Red	Full to late bloom	45–55 (50)
<i>P. davidii</i>	Pink with whitish parts	Full bloom	6–7 (7)
<i>P. stenocorys</i>	Pink to pinkish	Past full bloom	Na
<i>P. streptorhyncha</i>	Dark red	Full bloom	10–11 (11)
<i>P. princeps</i>	Yellow to yellowish	Early to full bloom	11–12 (11)
<i>P. angularis</i>	Red	Full bloom	6–10 (8)
<i>P. rhinanthoides</i> subsp. <i>labellata</i>	Pink to red	Full bloom	15–18 (17)
<i>P. metasetschuanica</i>	Red	Full bloom	5–9 (7)

Figures in parentheses are average of 15 measurements.

Five species, namely, *Pedicularis szetschuanica*, *P. cyathophylla*, *P. streptorhyncha*, *P. angularis*, and *P. metasetschuanica* had red corolla colors; while *P. torta*, *P. semitorta*, and *P. princeps* had yellowish-yellow corolla colors and galea of *P. torta* was purple, and *P. stenocorys* was pinkish to whitish; *Pedicularis davidii* and *P. rhinanthoides* subsp. *labellata* were pink with white spots, and *P. rex* subsp. *lipskyana* was purplish to purple (Table 2).

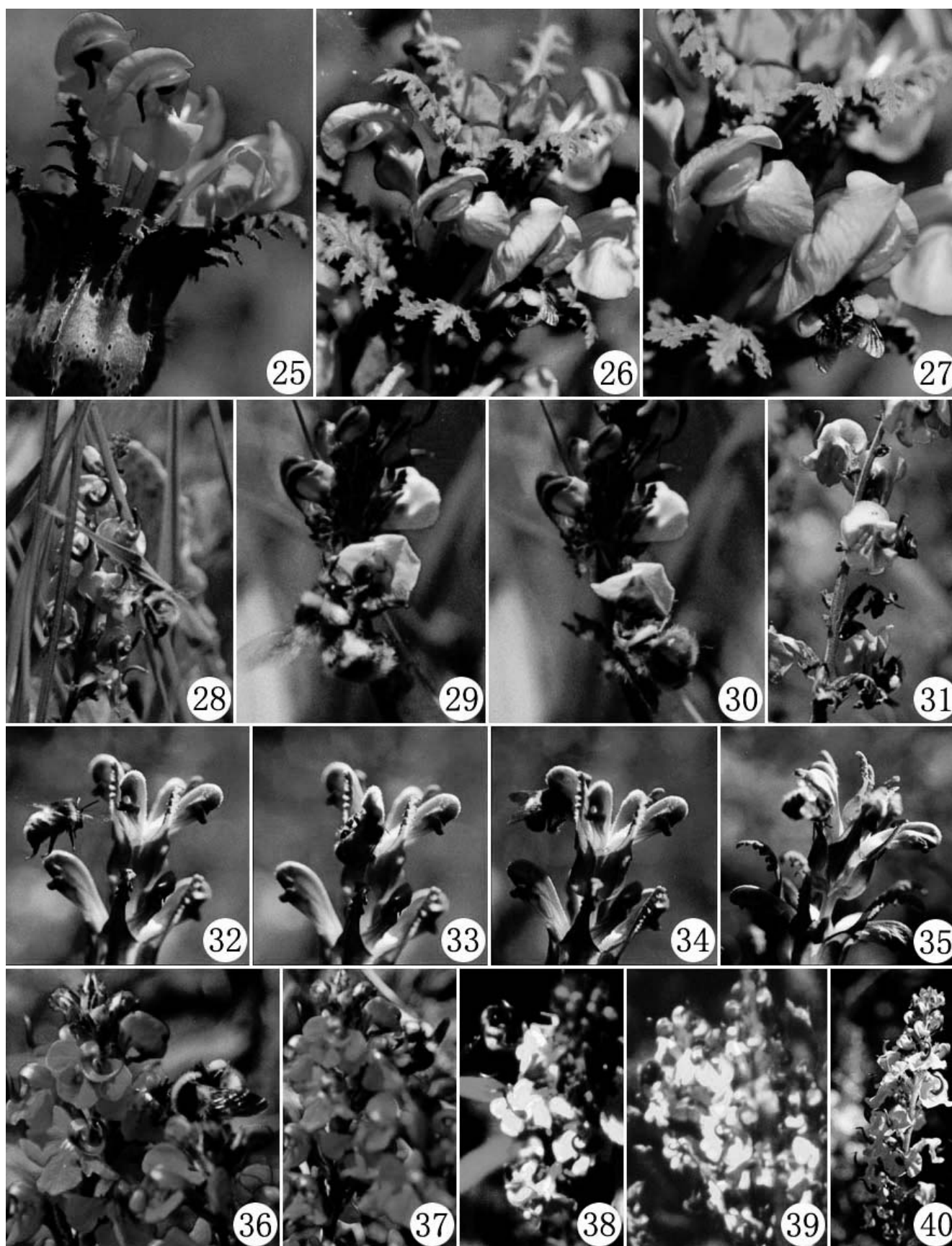
Corolla tube length varied by up to 10 times in the different species; it was short in eight species, ranging from 5 mm to 12 mm, medium (15–20 mm) in *P. rex* subsp. *lipskyana* and *P. rhinanthoides* subsp. *labellata*, and long (45–55 mm) in *P. cyathophylla*. Corolla morphology varied considerably as well. Based mainly on galea morphology, the studied species were classified into five groups. *Pedicularis cyathophylla* constituted the first group. Its lower lip was not spreading but the left was somewhat erect. Its galea was only moderately twisted. *Pedicularis davidii*, *P. semitorta*, *P. torta*, *P. rhinanthoides* subsp. *labellata*, and *P. streptorhyncha* comprised the rostrate and contorted group. They all had long and contorted galea beaks (Figs. 25, 40) and a spreading lower corolla lip. The third group consisted of four species, *P. angularis*, *P. metasetschuanica*, *P. szetschuanica*, and *P. stenocorys* which had a short and uncontorted galea beak, and a spreading lower corolla lip. The fourth group consisted of *P. rex* subsp. *lipskyana*. The lower corolla lip was reflexed slightly at the tip and its galea had a very short beak. As a result, the corolla mouth was partly opened. The fifth group consisted of *P. princeps*. The galea did not have a beak and the lower lip was longer than the galea, reflexed and slightly pendulous.

Seven species, namely, *P. cyathophylla*, *P. davidii*, *P. rhinanthoides* subsp. *labellata*, *P. princeps*, *P. semitorta*, *P. streptorhyncha*, and *P. torta* did not contain nectar at the base of corolla tube, while nectar was found at the base of the corolla tube of *P. angularis*, *P. metasetschuanica*, *P. rex* subsp. *lipskyana*, *P. stenocorys*, and *P. szetschuanica*.

POLLINATORS OF PEDICULARIS SPECIES AND OTHER SYMPATRIC PLANTS

Bumblebees (*Bombus* Latr. spp.) were the only pollinators of *Pedicularis* in the study area. Colonies of honey bees, both exotic *Apis mellifera* Linnaeus and native *Apis cerana* Fabricius, were common in the study area, especially in the forested area at lower altitude, but no honey bees were observed visiting flowers of *Pedicularis*, despite seven taxa of *Pedicularis* producing nectar. At study sites 1 to 3, butterflies and flies were common but they did not visit *Pedicularis*. Very occasionally they landed on flowers of *Pedicularis* species but without pollinating them.

A total of 154 bumblebees were collected from the study area with only 22 of these from *Pedicularis*. Bumblebees were observed pollinating *P. stenocorys* but were not captured. Visits to five *Pedicularis* species by bumblebees were not observed (Table 3). Five *Bombus* species, namely, *B. convexus* Wang, *B. impetuosus* Smith, *B. lepidus* Skorikov, *B. friseanus* Skorikov, and *B. modestus*



FIGURES 25–40. Fig. 25. Flower of *P. cyathophylla*; Figs. 26–27. Bumblebees collecting pollen on and sternotribically pollinating *P. cyathophylla*; Fig. 28. Bumblebee approaching *P. davidii*; Fig. 29. Bumblebees landing on *P. davidii*; Figs. 30–31. Bumblebees collecting pollen on and sternotribically pollinating *P. davidii*; Fig. 32. Bumblebee approaching *P. rex* subsp. *lipskyana*; Figs. 33–35. Bumblebee sucking nectar and nototribically pollinating *P. rex* subsp. *lipskyana*; Figs. 36–37. Bumblebee collecting pollen on and sternotribically pollinating *P. streptorhyncha*; Figs. 38–39. Bumblebee sternotribically pollinating *P. torta*. Fig. 40 Inflorescence of *P. torta*.

TABLE 3

Species, foraging behavior and frequency of bumblebees on *Pedicularis*.

<i>Pedicularis</i> taxa	<i>Bombus</i>	Caste	Foraging	Bees hour ⁻¹
<i>P. rex</i> subsp.	<i>B. friseanus</i> .	W	Upright, extracting	3.7
<i>lipskyana</i>	<i>B. modestus</i>	W	nectar	
	<i>B. lepidus</i>	W		
<i>P. szetschuanica</i>	<i>B. convexus</i>	W	Upright, extracting	3.0
	<i>B. impetuosus</i>		nectar	
	<i>B. lepidus</i>			
<i>P. cyathophylla</i>	<i>B. lepidus</i>	W	Inverted, collecting	2.0
			pollen	
<i>P. streptorhyncha</i>	<i>B. lepidus</i>	W	Inverted, collecting	2.9
			pollen	
<i>P. torta</i>	<i>B. lepidus</i>	W	Inverted, collecting	4.0
			pollen	
<i>P. davidii</i>	<i>B. lepidus</i>	W	Inverted, collecting	3.2
			pollen	
<i>P. stenocorys</i>	?	W	Upright, extracting	0.3
			nectar	
<i>Vicia villosa</i> var.	<i>B. modestus</i>	W, M, Q	Upright, extracting	50.0–60.0
<i>glabrescens</i> ,	<i>B. friseanus</i>	W	nectar	
<i>V. unijuga</i> ,	<i>B. remotus</i>	W		
<i>Lathyrus pratensis</i>	<i>B. lepidus</i>	W		
	<i>B. convexus</i>	W		
	<i>B. impetuosus</i>	W		
<i>Salvia</i>	<i>B. hypnorum</i>	W	Whole insect	1.5
<i>maximowicziana</i>			entering corolla	

W: worker; M: male; Q: queen.

Eversmann foraged on various *Pedicularis* species. *Bombus lepidus* was the most common pollinator and it foraged on all the six *Pedicularis* species from which pollinators were collected. It was also the sole pollinator of *P. cyathophylla*, *P. streptorhyncha*, *P. torta*, and *P. davidii*, all species with long rostrate and contorted beaks. In addition, each of the two nectariferous species, *P. rex* subsp. *lipskyana* and *P. szetschuanica*, were pollinated by other two different bumblebee species, respectively: *Pedicularis rex* subsp. *lipskyana* by *B. friseanus* and *B. modestus*; *P. szetschuanica* by *B. convexus* and *B. impetuosus*.

Field observations of bumblebees visiting flowers of *Pedicularis* and identification of the captured bumblebees revealed that, apart from *B. modestus*, only worker bees visited flowers of *Pedicularis* species. Three castes, namely, queen, male and worker bees of *B. modestus*, pollinated *P. rex* subsp. *lipskyana*. Of the captured *B. modestus* bees, 59% were male, 33% workers, and 8% queens. At site 1, the bumblebees visiting *P. torta* were obviously smaller than those visiting *P. rex* subsp. *lipskyana*, probably due to the smaller flowers and tender and smaller galea of *P. torta*.

At study site 2, a common green winter vetch, *Vicia villosa* Roth var. *glabrescens* Koch was cultivated in the fallowed land; mixed with this were another two common leguminous plants, *Vicia unijunga* A. Braun and *Lathyrus pratensis* Linnaeus. To some extent their corolla looked similar to that of *Pedicularis*. Six bumblebee species visited these three leguminous species. Five of these species also visited *Pedicularis* and only *B. remotus* (Tkalcu) did not visit *Pedicularis* species. More than half of the captured bees were *B. friseanus* and 30% were *B. modestus*, and only 10% were *B. lepidus*, the most common species pollinating *Pedicularis*.

Of the six bumblebee species, *B. convexus*, *B. lepidus*, *B. friseanus*, and *B. modestus* had shorter tongues, while *B. impetuosus* and *B. remotus* had longer tongues (Williams, personal communication).

FREQUENCY AND BEHAVIOR OF POLLINATORS

The frequency of bumblebees visiting flowers varied for different *Pedicularis* species (Table 3), ranged from 2.0 to 4 times per hour. The lowest frequency, 0.3 times per hour, was observed for *P. stenocorys*, possibly because many flowers withered during the study.

At site 4, bumblebees visiting *Pedicularis* species and other sympatric plants varied considerably in species and abundance. Frequency of bumblebees visiting *Pedicularis* and other plants were different in 2002 and 2003. In 2002, there were more bumblebees visiting *Pedicularis* species and fewer visiting other plants, especially a very short flowering species of *Sedum* sp. (Crassulaceae). Whereas in 2003 very few bumblebees visited *Pedicularis* species but many visited *Sedum* sp. In 2003, bumblebees were observed visiting *Pedicularis* species on only three occasions during a period of four man-hours but 34 bees were collected from *Sedum* sp. in 1.5 man-hours. In mid-July 2002, bumblebees visited *P. streptorhyncha* and *P. szetschuanica* at a frequency of 5.5 times per hour and 2.0 times per hour, respectively, but in late July 2003 at a frequency of 0.5 times per hour and 0.25 times per hour, respectively. The difference might be caused by a change in weather (or flowering phenology). Some *P. szetschuanica* and *P. torta* were mixed with the cultivated fodder plant, *Vicia villosa* var. *glabrescens*. Compared to *Pedicularis* species, the fodder plants were overwhelmingly abundant. The highest pollination frequency in 2002 was associated with cultivated fodder, up to 50 to 60 times per hour. But frequency of bumblebees visiting *P. szetschuanica* and *P. torta*, which grew together, was only 4 times per hour.

The bumblebees visiting *Pedicularis* species were usually active in the morning while those visiting other plants were active in the afternoon, both much less active during noon. Foraging behavior was different in *Pedicularis* species. Previous studies have shown that bumblebees visited flowers of various species of *Pedicularis* for either pollen or nectar. Careful observation on all the species did not find any indication of nectar robbing.

When a bumblebee was visiting a particular species, it visited only that species or visited different sympatric species. In the first case, it did not visit other species even though other species were in full bloom and very abundant. This was observed on *P. szetschuanica* and three leguminous species growing together. *Pedicularis szetschuanica* was common but scattered in the study area. Only the plants growing in a fodder community of *Vicia villosa* var. *glabrescens* were visited by bumblebees. Two other leguminous species, *Vicia unijunga* and *Lathyrus pratensis* were also common. When a bumblebee was visiting *P. szetschuanica*, it did not visit other legumes although the *Pedicularis* species was very sparse. Similarly, when a bumblebee was visiting *Lathyrus pratensis*, it passed by *P. szetschuanica* which grew together with *L. pratensis*. In the second case, however, the same bumblebee species that visited red flowered *P. streptorhyncha* also visited yellow-flowered *Salvia maximowicziana* Hemsley, although the captured bumblebee species were different for *S. maximowicziana* (Table 3).

For the species with long rostrate and contorted beak, including *P. cyathophylla*, *P. davidii*, *P. streptorhyncha*, and *P. torta*, workers of bumblebees foraged these species in an inverted position (Figs. 26–31, 36–39). Since the flowers of these species did not contain nectar, pollen was the only pollination reward. Bumblebees first landed on the lower lip or galea (Figs. 28–29, 36–37), then turned upside down, embracing the contorted galea (Figs. 30–31, 38–39). They next vibrated the galea concealing the four stamens. The vibration made pollen fall on the ventral part of the bumblebees. During the course of vibration, the stigma rhythmically protruded out of the galea, touching the ventral parts of the bumblebees, where residual pollen was stored, through which pollen transfer was realized. Therefore, the species with long

rostrate and contorted beak were pollinated sternotribically (Figs. 25–31, 36–40).

Bumblebee workers visited flowers of *P. szetschuanica* in an upright position for nectar deposited in the base of corolla tube. They plunged their heads into the corolla tube to remove nectar at the base. As a result of the activity of bumblebee workers to remove nectar, the stigma situated in the galea protruded out and touched the midline of the bumblebees' back. The residual pollen would be deposited on the stigma, resulting in pollination. This species was pollinated nototribically. Only workers were involved in pollination of this species.

Pollination of *Pedicularis rex* subsp. *lipskyana* was completed mainly by worker and male bumblebees. The corolla mouth of this subspecies was only slightly open. Bumblebees approached and landed on the lower lip of the flowers (Figs. 32–33). The weight of the workers forced the mouth of flowers to open so that bumblebees could insert their heads into the tube from the right side of the mouth (Figs. 33–34). The bees inserted their heads into the corolla tube to extract nectar deposited at the base of the tube (Figs. 34–35). While the bees extracted nectar from the base of the corolla tube, the stigma situated in the galea rhythmically “shot out” and touched the front left part of the head and back of bumblebees. The residual pollen on the head and back of the bumblebees completed the pollination. This subspecies was pollinated nototribically. No pollen loads were found on the hind legs of the captured bumblebees, indicating they foraged mainly for nectars. Visiting time per flower of pollinators was different in different *Pedicularis* species. It was shorter in visiting nectarless species than in visiting nectariferous species.

HABITAT PREFERENCES OF SPECIES

Species of *Pedicularis* exhibited different habitat preferences (Table 4). At site 1, *Pedicularis rex* subsp. *lipskyana* grew abundantly in a disturbed shrubland dominated by *Quercus aquifolioides* Rehder & Wilson between fallowed farmland and coniferous forests dominated by *Abies recurvata* Masters. *Pedicularis princeps* grew under coniferous forest, and *P. torta* in forest edges and in gaps in scrubland. These species did not grow together. The plant height varied between species. *Pedicularis rex* subsp. *lipskyana* and *P. princeps* grew to a height of 60–100 cm whereas *P. torta* only grew to a height of 30 cm. These three species were often found in forested areas. At site 2, *P. szetschuanica* grew on open grassy slope and in fallowed farmland whereas *P. torta* only grew on the boundary between the fallowed farmland and scrubland. At site 3, *P. cyathophylla* and *P. davidii* grew together in some patches but not always so. *Pedicularis semitorta* often grew in open and dry habitats with a poorly developed vegetation, while *P. stenocorys* usually grew in dense grassy vegetation. But *P. szetschuanica* grew on dry slopes with poor vegetation. At site 4, *P. streptorhyncha* grew with *P. angularis* and *P. metaschetschuanica* in a more or less wet habitat in a gully, surrounded by dense rhododendron scrubland, but the latter two were more frequently found in dry habitats.

Discussion

In North America, all long-tubed species are nectariferous whilst all rostrate species are nectarless and have short tubes (Macior, 1982). In this study, the rostrate species with long contorted beaks are nectarless but their corolla tube length varies from short (average 7 mm) to long (average 50 mm); both longest and shortest floral tubes were found with nectarless and rostrate species. Similarly, floral tubes in nectariferous species also vary considerably, averaging from 8 to 18 mm. Furthermore, the longest corolla tube of the genus is found in

TABLE 4
Habitats of different *Pedicularis* taxa.

Taxa	Habitats
<i>P. rex</i> subsp. <i>lipskyana</i>	Scrubland dominated by <i>Quercus aquifolioides</i> but mainly occurring in between individual plants of <i>Q. aquifolioides</i> , higher than shrubs
<i>P. szetschuanica</i>	Fallowed cropland, among leguminous fodder plants or other plants; also on steep grassy slope with very short plants
<i>P. angularis</i>	Dry slope and wet grassy slope
<i>P. metaschetschuanica</i>	Grassy slope
<i>P. torta</i>	Shrubland, under roadside trees or on forest edge
<i>P. semitorta</i>	On roadside dry slopes, dry and sparsely grassy slope or on shrubland edge
<i>P. cyathophylla</i>	Alpine grassy slope with dense vegetation
<i>P. davidii</i>	Alpine grassy slope, with sparse vegetation
<i>P. streptorhyncha</i>	Steep wet grassy slope among scrub of rhododendron
<i>P. rhinanthoides</i> subsp. <i>labellata</i>	Always in wet habitats with saturated soil moisture
<i>P. stenocorys</i>	Alpine grassy slope in dense vegetation
<i>P. princeps</i>	Under subalpine coniferous forest dominated by <i>Abies recurvata</i>

nectarless species with long and strongly contorted beaks (Li, 1948; Tsong, 1963). Unlike that of North American species, the floral tube length of Chinese species is therefore not related to whether flowers contain nectar. Nonetheless, species of *Pedicularis* can be classified into two groups, nectarless or nectariferous. These two groups of species have different types of corolla morphology. The nectarless species have rostrate and contorted galea while the nectariferous species either do not have a beak, or have only a short beak. Foraging behavior of pollinators is different in these two groups. Primarily, pollinators foraged the species with rostrate and contorted galea for pollen and the species without rostrate galea for both nectar and pollen. Nectar-foraging bumblebees pollinate *Pedicularis* nototribically and pollen-scraping bumblebees pollinate *Pedicularis* sternotribically. Therefore, nectarless species can only be pollinated sternotribically. Nectariferous species can be pollinated both sternotribically and nototribically and nototribical pollination is completed by nectar foraging pollinators with longer tongues, and sternotribical pollination by pollen-foraging pollinators with shorter tongues (Macior et al., 2001). In the present study, four nectarless species were pollinated by only one shorter-tongued bumblebee species (*Bombus lepidus*) while two nectariferous species were pollinated by three bumblebee species including both shorter- and longer-tongued species.

For North American species, successful pollination critically depends upon stigmatic contact with residual pollen along the midline of the anterior, dorsal and ventral regions of the insect because insects cannot remove pollen from these areas when it grooms its middle legs, sweeping both forward and backward (Macior, 1982). In the present study, the stigma of some species like *P. rex* subsp. *lipskyana* and *P. streptorhyncha* could not contact the midline of the insects. The stigmatic contact areas of the insects may not necessarily be the midline area. The residual pollen on other regions of the insects may be sufficient for successful pollination, but further study is needed to confirm this.

Visitation frequency was very low for some species in 2002 and at one site in 2003. Previous studies in subalpine and alpine meadows of Sichuan, China, also found that frequency of bumblebees' visits to some *Pedicularis* species was very low (Macior et al., 1997, 2001).

Our previous field observations show that activities of bumblebees in northwestern and western Sichuan were closely related to ambient temperature. Bees did not fly below a certain temperature. Furthermore, when temperature dropped below certain level, bumblebees that were active in the field stopped their activities and landed on the ground. They resumed activities when the temperature rose. This phenomenon was observed most frequently on days when weather was not stable. This was observed in different regions of northwestern and western Sichuan (Tang et al., unpubl.). The very low visitation frequency of this study might be also due to climatic factors. This, however, needs further study.

The observation on *P. rex* subsp. *lipskyana* in the present study was different in some important respects from Wang's (1998) observation on *P. rex* subsp. *rex*. Wang reported that this subspecies was nectarless and that *Bombus friseanus* and *B. lucrorum* visited *Pedicularis rex* in both upright and inverted positions, both for collecting pollen. It was found in the present study that *P. rex* subsp. *lipskyana* was nectariferous. The foraging behaviors of the bumblebees on *Pedicularis* could be divided into two types, namely, upright or inverted position, each corresponding to a specific type of pollination mechanism. The upright foraging position is always associated with nototribical pollination and the inverted foraging position with sternetribical pollination. The upright foraging bumblebees forage for nectar accumulating at the base of the corolla tube whereas the bumblebees foraging in an inverted position scrape pollen from anthers concealed in the galea, which has been shown in many studies (Macior, 1982; Macior et al., 1997, 2001; this study). While the bumblebees that visited *Pedicularis rex* subsp. *rex* in an inverted position were certainly collecting pollen, the bumblebees which visited *Pedicularis rex* in an upright position were foraging for nectar only. Based on our own observations on over 30 species in Sichuan (Tang et al., unpubl.) and studies in the past (Macior, 1968a, 1968b, 1969, 1970, 1973, 1975, 1977, 1978, 1980, 1982, 1983, 1986a, 1986b, 1986c, 1988, 1990, 1993, 1995a, 1995b, 1996; Macior et al., 1991, 1997, 2001), bumblebees foraging in an upright position were reported only from nectariferous species. In addition, previous observations (Macior, 1982; Macior et al., 1997, 2001) suggested that the *Pedicularis* species with a relatively deep corolla tube are pollinated either nototribically by nectar sucking pollinators with longer tongues, or sternetribically by pollen-scraping pollinators with shorter tongues. But Wang's observation was just the opposite. The bumblebees that visited *P. rex* in an upright position had shorter tongues and those in an inverted position had longer tongues. Part of Wang's (1998) observation might therefore need to be re-examined in the field.

Pedicularis have extremely variable floral forms, especially their corolla morphology (Li, 1948; 1951; Tsoong, 1955–1956; Tsoong, 1963; Tsoong et al., 1963). Pressure of pollination was considered to be the most important contributing factor to the highly diverse floral morphology (Pennell, 1943; Li, 1948, 1951) and pollinators on this genus would be as much diverse as floral morphology of *Pedicularis* (Pennell, 1943). Further, Li (1951) thought that many of the species with less differentiated corolla forms can be pollinated by bees but other species with highly specialized beaked or long-tubed corollas requires specific pollinators, such as butterflies, moths, or other insects with a very long proboscis (Li, 1948). Thus far, however, pollination ecology studies have revealed that bumblebees are the primary and effective pollinators of this genus although honey bees (Macior et al., 1997, 2001), hummingbirds (Macior, 1986a) and hawk moths (Tang et al., unpubl.) were also pollinating some species of this genus. Furthermore, those species pollinated by honey bees, hummingbirds and hawk moths were pollinated mainly by bumblebees (Macior, 1982; Macior, 1986a; Macior et al., 1997, 2001; Tang et al., unpubl.). No single species has been reported to be pollinated solely by non-bumblebee insects. This implies that it is not diversity of pollinators

but bumblebees with different morphology and foraging behavior that may play a role in diversification of *Pedicularis* species and corolla morphology. The region with most numerous species of *Pedicularis*, from the eastern Himalayas to the mountains of southwestern China, also has the highest number of bumblebee species (Williams, 1998). The co-existence of high levels of species diversity of both *Pedicularis* and bumblebees in this region indicates well-developed co-adaptation between these two groups of organisms. However, the research thus far carried out has not satisfactorily explained the relationship between highly diverse *Pedicularis* species and pollinators. In the present study, the same pollinator species pollinated all the studied species and the same nectariferous *Pedicularis* species were pollinated by different pollinator species. The present study strengthens the conclusions of the previous studies that there is no obligatory relationship between *Pedicularis* and bumblebees. Bumblebees are the primary pollinators of *Pedicularis*. Therefore, the geographical distribution of *Pedicularis* might be closely related to the geographical distribution of bumblebees. A comparative study on the biogeography of *Pedicularis* and bumblebees might provide useful information for studies of pollination adaptation of *Pedicularis* in subalpine and alpine areas.

Li's (1948) suggestion that the corolla structure varied in the direction of increased pollination efficiency appears reasonable. Flowers of *Pedicularis* are symmetric. Style and stigma of nectarless flowers of *Pedicularis* are not in the middle of the flower; such flowers are mainly buzz-pollinated (Endress, 2001). But the upper floral lip or galea of the nectarless species of the present study is distorted anticlockwise, not clockwise as reported by Endress (2001). The flowers with enclosed pollination organs are ergonomically more difficult to work by pollinators than those with unenclosed pollination organs. But for the nectarless species, pollinators worked mostly from only one side (either right or left). One-side distorted flowers may facilitate bee's consistent work from the same side for a given species, which may reduce the ergonomic disadvantage. Pollination takes less time (Endress, 2001). Corolla structure of *P. cyathophylla* and field pollination observations on this and other nectarless species confirmed this hypothesis. The corolla structure of this species facilitates only visitation by bumblebees from the right side (Figs. 25–27). Bumblebee's visitation to other nectarless species was also from one side only. Visitation time to nectarless species was also shorter than to nectariferous species.

Since many *Pedicularis* species occurred together, a high rate of hybridization might be expected. Among around 600 species of this genus, however, only a few hybrids have been confirmed. This implies that effective barrier mechanisms are present. Pollination mechanism was thought to play a role in propagation barrier. The present study does not support such a barrier among *Pedicularis* species because the same pollinator species visited up to the six *Pedicularis* species studied in this paper. Moreover, there are few pure *Pedicularis corbicular* pollen loads in many studied species (e.g., this study; Macior, 1968a, 1969, 1970, 1982, 1986b, Macior et al., 2001). These results imply that pollen of more than one species would be deposited on stigma of a *Pedicularis* species. Further study is needed to investigate whether the stigma is selective and pollination as propagation barrier mechanism might need reevaluation in speciation of this genus. Studies of inter-relationships between stigma and pollen would provide useful information. During our field studies in the past 9 yr, we have noticed that diversity and occurrence of species of *Pedicularis* was closely related to microhabitats and that species composition varied when microhabitats changed, implying that microhabitats might play an important role in determining occurrence of species and might also be one of the separation mechanisms. Studies on relationships between *Pedicularis* species and microhabitats would provide useful data to evaluate high diversification of *Pedicularis* in mountains of southwestern China.

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