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Short title: Reinstatement of *Pedicularis delavayi*

Reinstatement of *Pedicularis delavayi* (Orobanchaceae): a species separating from *P. siphonantha* revealed by phylogenetic analyses

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1 **ABSTRACT**

2 **Background.** Morphological identification of *Pedicularis* depends on floral characters because
3 interspecific variations these characters is very large. However, some important characters may be lost
4 during the process of pressing the specimen. *Pedicularis delavayi* was described from Lijiang, northwestern
5 Yunnan, and it was widely adopted as a variety of *P. siphonantha*. Unfortunately, the name “*P. siphonantha*
6 var. *delavayi*” incorrectly referred to *P. milliana*/*P. tenuituba* in some identified specimens and publications.
7 Moreover, phylogenetic relationships between *P. delavayi* and *P. siphonantha* and its allies (*P. milliana* and
8 *P. tenuituba*) were not fully resolved.

9 **Methods.** In total, we sampled 75 individuals representing 56 taxa. Of them, 10 taxa were from *P.*
10 *siphonantha* group, and 11 individuals of *P. delavayi* represented 9 populations. One nuclear gene (nrITS)
11 and four chloroplast genes/regions (*matK*, *rbcL*, *trnH-psbA*, and *trnL-F*) were sequenced for phylogenetic
12 analyses. The nrITS and plastid datasets were combined to analyze. Bayesian Inference (BI) and Maximum
13 Likelihood (ML) methods were used to reconstruct phylogenetic trees. Species identification, morphological
14 comparison and line drawing were based on field observation, dried herbarium specimens and FFA-fixed
15 samples.

16 **Results.** Phylogenetic analyses showed that the *P. siphonantha* group was polyphyletic: monophyletic *P.*
17 *delavayi*, sister to *P. obliquigaleata*, fell into clade A; and the remaining species of *P. siphonantha* group
18 was in clade B as monophyletic (i.e. *P. siphonantha* lineage). In the *P. siphonantha* lineage, *P. milliana*, *P.*
19 *siphonantha*, and *P. tenuituba* (= *P. siphonantha* var. *stictochila*) were well supported as monophyletic, and
20 *P. dolichosiphon* (= *P. siphonantha* var. *dolichosiphon*) was sister to *P. leptosiphon*. Morphologically, *P.*
21 *delavayi* differs from species of the *P. siphonantha* lineage in having a long petiole (~ 50 mm) and pedicel
22 (~ 40 mm), a ridged corolla tube, and a folded lower-lip of the corolla.

23 **Discussion.** Phylogenetic analyses showed evolution of *P. delavayi* was independent from the *P.*
24 *siphonantha* lineage. The long-tubular corollas in *P. delavayi* and *P. siphonantha* lineage might be a
25 convergent character. Both morphological and phylogenetic evidence strongly supported to reinstate *P.*
26 *delavayi* as an independent species. In addition, *P. neolatituba* was proposed to reduce as a new synonymy
27 of *P. delavayi*.

28

29 **Keywords:** *Pedicularis*, *Pedicularis delavayi*, *Pedicularis milliana*, *Pedicularis siphonantha*, species
30 delimitation, the Hengduan Mountains

1 INTRODUCTION

2 Flowers of *Pedicularis* L. (Orobanchaceae) show striking interspecific variations (Li 1951; Yu et al. 2008),
3 so morphological identification of these species depends much on floral characters (Liu, Yu & Wang 2013).
4 Generally, one species is easily distinguished from another morphologically similar species using fresh
5 flowers in the field. However, floral shape and structure may be changed during the process of pressing and
6 drying the specimen and, in practice, herbarium specimens of closely related species are very difficult to
7 discriminate. DNA barcodes have been widely applied to assist species identification (Hebert et al. 2003;
8 Kress et al. 2005; China Plant BOL Group 2011), particularly when morphological identification is
9 uncertain. In *Pedicularis*, the nuclear ribosomal internal transcribed spacer (nrITS) or nrITS+*rbcL* can
10 discriminate at least 78% of species in the genus (Yu et al. 2011; Liu, Yu & Wang 2013). However, there is
11 little consensus between the phylogenetic tree and traditional classification in *Pedicularis* (Ree 2005; Yang
12 & Wang 2007; Tkach et al. 2014; Robart et al. 2015; Yu et al. 2015), and morphologically similar species
13 may not be sister to each other in phylogenetic analyses. Therefore, DNA sequences are very useful to
14 delimit species and to confirm phylogenetic relationship among species.

15 *Pedicularis delavayi* was firstly named by Franchet after J. M. Delavay, who collected the type
16 material (Fig. S1) at Yulong Mountain in Lijiang, northwestern Yunnan, China in 1886, while it was validly
17 published by Maximowicz (1888). This species was treated as an independent species (Prain 1890; Bonati
18 1910; Limpricht 1924; Li 1949) until Tsoong (1963), who downgraded it to a variety in *P. siphonantha* D.
19 Don. According to illustrations in Chinese Floras (Tsoong 1963; Yang, Holmgren & Mill 1998), the lower
20 lip of *P. siphonantha* var. *delavayi* (Franch. ex Maxim.) P. C. Tsoong should be similar to *P. siphonantha* D.
21 Don var. *siphonantha* as spreading (see Fig. 1A). From illustrated publications, the name “*P. siphonantha*
22 var. *delavayi*” was used for a “long-tubed and purple-red species” (Fig. 1B), which is a common species in
23 alpine meadow at altitudes from 3000 m to 4000 m a.s.l. (above sea level, hereafter) in northwestern
24 Yunnan (e.g., Guan 1998; Yu, Zhang & Wang 2008; Xu, Li & Sun 2013). In addition, some publications
25 used the name “*P. siphonantha*” for this “long-tubed and purple-red species” (e.g., Yang et al. 2002; Yang,
26 Sun & Guo 2005; Huang & Fenster 2007; Yu et al. 2013a; Huang, Wang & Sun 2016).

27 During field expeditions for *Pedicularis* in the Hengduan Mountains region from 2006 to 2010, we
28 collected an unknown long-tubed species with a purple-red corolla in Shangri-La, northwestern Yunnan,
29 and Jiulong and Kangding, Sichuan, at altitudes around 4000 m (Figs. 1C-F). This species differs from
30 infraspecific taxa on *P. siphonantha* and other long-tubed and purple-red species in series *Longiflorae* Prain
31 by having an incurved middle lobe of the lower lip and a ridged corolla tube (Figs. 1G, H). DNA barcoding
32 showed that samples of this species were separated from *P. siphonantha* (Yu et al. 2011). We considered
33 that this species may be new until we checked the type materials of *P. delavayi* conserved at the herbaria of
34 the V. L. Komarov Botanical Institute in St. Petersburg (LE) (Fig. S1) and the Muséum National d’Histoire
35 Naturelle in Paris (P). Based on morphological comparisons of specimens, we found that our specimens
36 were very similar to the type of *P. delavayi*. In order to clarify the taxonomical confusion, we examined
37 herbarium specimens of *P. siphonantha* collected from Yulong Mountain (type location of *P. delavayi*)
38 conserved at the herbaria of CAS Kunming Institute of Botany (KUN) and CAS Institute of Botany (PE).

1 We found that specimens labeled as “*P. siphonantha* var. *delavayi*” included two taxa: one is similar to the
2 type of *P. delavayi*, and another is the “long-tubed and purple-red species” (Fig. 1B), a common species in
3 northwestern Yunnan. Indeed, it is very difficult to discriminate the herbarium specimens as two taxa.
4 Based on the field investigations, we found that *P. delavayi* differed from the “long-tubed and purple-red
5 species” by having a long petiole and pedicel, inflated calyx tube in the middle upper parts, and folded
6 lower lip of the corolla, as well as occurring at altitudes over 3600 m a.s.l. During recent field expeditions,
7 specimens of *P. delavayi* were collected from the Yulong Mountain at over 4000 m a.s.l (Fig. 1F), and those
8 of the “long-tubed and purple-red species” between 3600 m and 4000 m a.s.l. (Fig. 1B). Therefore, we
9 confirmed that *P. delavayi* and the “long-tubed and purple-red species” were two separated species, and the
10 “long-tubed and purple-red species” should be an undescribed species. To reduce descriptive confusion, we
11 proposed a name “*P. millina* W. B. Yu & H. Wang” for this taxon in following statements and discussion.

12 Recently, a comprehensive phylogeny of Chinese *Pedicularis* shows that *P. siphonantha* is a
13 polyphyletic group, var. *delavayi* (\equiv *P. delavayi*) and other varieties of *P. siphonantha* falling into two
14 subclades in clade 3 (Yu et al. 2015). *Pedicularis delavayi* was sister to *P. obliquigeleata* in subclade A. In
15 the subclade 3B, var. *siphonantha* and var. *stictochila* H. Wang & W.B. Yu (= *P. tenuituba* H.L. Li), and
16 five species from series *Longiflorae* with purple/red/pink corollas with twisted beaks formed a strongly
17 supported lineage, i.e. the *P. siphonantha* lineage (that is molecular delimitation). In the present study, we
18 made extensive sampling of *P. delavayi* from 9 populations (10 new samples), and two additional samples
19 of *P. millina* from Yulong Mountains in Lijiang, one additional new samples of *P. tenuituba*, and all
20 recognized taxa in clade 3 and the sister *P. axillaris* Franch. ex Maxim. (Yu et al. 2015). DNA sequences
21 from nrITS and four chloroplast regions (*matK*, *rbcL*, *trnH-psbA* and *trnL-F*) were generated and analyzed.
22 Our main goal was to evaluate the monophyly of *P. delavayi*, and its phylogenetic relationship to the *P.*
23 *siphonantha* lineage, in particular to *P. milliana* and *P. tenuituba*. If monophyletic *P. delavayi* was excluded
24 from the *P. siphonantha* lineage, *P. delavayi* should be reinstated as an independent species.

25

26 MATERIAL AND METHODS

27 **Plant samplings.** In total, we sampled 75 individuals representing 56 taxa, including all taxa were
28 identified in clade 3 and its sister *P. axillaris* (Yu et al. 2015). *Pedicularis siphonantha* group, based on
29 morphological delimitation, consisted of 11 species (Table S1). Of them, four species *P. delavayi*, *P.*
30 *milliana* (new species), *P. siphonantha*, and *P. tenuituba* (= *P. siphonantha* var. *stictochila*) have a wide
31 distribution range. The remaining seven species only collected once or few gatherings around the type
32 locality: 1) *P. sigmoidea* Franch. ex Maxim. were found in around Eryuan and Lijiang, northwestern
33 Yunnan; 2) *P. dolichosiphon* (Hand.-Mazz.) H.L.Li (\equiv *P. siphonantha* var. *dolichosiphon* Hand.-Mazz.), *P.*
34 *dolichantha* Bonati, *P. leptosiphon* H. L. Li, *P. variegata* H. L. Li and *P. humilis* Bonati were recollected
35 from the type locality; and 3) *P. fastigiata* Franch. only had the type, which did not include in this study. In
36 this study, we chose 11 samples of *P. delavayi* (three samples from the type locality Yulong Mountain,
37 Lijiang), and three samples of *P. milliana* and *P. tenuituba* (Table S2). Natural population of *P. humilis* was
38 just rediscovered in 2015 (Li et al. 2016). It is the first time to include this species for phylogenetic

1 analyses.

2 Fresh leaf tissues were collected in the field and preserved in silica gel. All DNA samples and voucher
3 specimens are stored at the Germplasm Bank of Wild Species and the herbarium of CAS Kunming Institute
4 of Botany (KUN), respectively. There are 284 sequences from 64 individuals which have been published in
5 other studies (China Plant BOL Group 2011; Yu et al. 2011; Liu & Yu 2015; Yu et al. 2015). In this study,
6 we generated 62 new sequences from 23 individuals (with 11 new individuals). A conspectus of voucher
7 information is presented in Table S2.

8
9 **Specimen examination and identification.** Fresh specimens were observed in the field. Fresh flowers
10 were collected and fixed in FAA solution. Herbarium specimens from the herbaria CDBI, KUN, LE, and
11 PE were examined and identified, and digital images of types from the herbaria E, K and P were accessed
12 online. Flower and fruits characters in the line drawings of *P. delavayi* were based on field photos and
13 FAA-preserved flowers.

14
15 **Molecular methods.** For the 11 new samples, total genomic DNA was extracted from silica gel-dried
16 tissue using a modified 2× CTAB method. Five DNA loci, one nuclear gene (nrITS) and four chloroplast
17 genes/regions (*matK*, *rbcL*, *trnH-psbA*, and *trnL-F*), were sequenced in this study. Primer information for
18 the five loci were presented in previous studies (Yu et al. 2011; Yu et al. 2013b). Protocols for polymerase
19 chain reaction (PCR) amplification and sequencing followed the study of (Yu et al. 2011).

20
21 **Sequence assembly and alignment.** The newly obtained raw sequences were assembled and edited using
22 Geneious version 7.1 (Kearse et al. 2012). The nrITS is a multiple copy region. These copies showed
23 evolutionary consistent in the sequenced 85 samples, only three samples had one ambiguous basecall (i.e.
24 multiple superimposed peaks in chromatograms). Two samples, LID1199 and HW10244, belonging to *P.*
25 *tenuituba*, and sample HW10163 is *P. milliana*. The ambiguous site was assigned using IUPAC ambiguity
26 characters.

27 Preliminary alignments were automatically aligned using MAFFT version 7.2 (Kato & Toh 2010),
28 then adjusted manually in Geneious. The aligned matrix was concatenated to a combined matrix using
29 SequenceMatrix version 1.73 (Vaidya, Lohman & Meier 2011). Sequence characteristics were calculated
30 using MEGA version 6.0 (Tamura et al. 2013).

31
32 **Phylogenetic analyses.** Bayesian Inference (BI) and Maximum Likelihood (ML) methods were used to
33 reconstruct phylogenetic trees. The nrITS and plastid datasets were combined to analyze. No nucleotide
34 positions were excluded from analyses. Partitioned BI analyses were performed using MrBayes (Ronquist &
35 Huelsenbeck 2003), with DNA substitution models selected for each gene partition by the Bayesian
36 information criterion (BIC) using jModeltest (Guindon & Gascuel 2003; Darriba et al. 2012). Markov Chain
37 Monte Carlo (MCMC) analyses were run in MrBayes for 10,000,000 generations for each dataset, with two
38 simultaneous runs, and each run comprising four incrementally heated chains. The BI analyses were started

1 with a random tree and sampled every 1000 generations. Number of generations for the three datasets were
2 sufficient, because the average standard deviation of split frequencies for the datasets was lower than 0.005
3 (0.002900), and Potential Scale Reduction Factor of Convergence Diagnostic (Gelman & Rubin 1992) for
4 the datasets was 1.00. The first 25% of the trees was discarded as burn-in, and the remaining trees were used
5 to generate a majority-rule consensus tree. Posterior probability values (PP) ≥ 0.95 were considered as well
6 supported (Alfaro, Zoller & Lutzoni 2003; Erixon et al. 2003; Kolaczowski & Thornton 2007). The ML
7 tree searches and bootstrap estimation of clade support were conducted with RAxML (Stamatakis, Hoover &
8 Rougemont 2008). These analyses used the GTR substitution model with gamma-distributed rate
9 heterogeneity among sites and the proportion of invariable sites estimated from the data. The dataset was
10 partitioned by genes. Support values for the node and clade were estimated from 1000 bootstrap replicates.
11 Bootstrap support (BS) ≥ 70 are considered well supported (Hillis & Bull 1993). Both BI and ML analyses,
12 as well as jModeltest, were performed at the CIPRES Science Gateway (<http://www.phylo.org>).
13

14

14 RESULTS

15 **Information of DNA sequences.** Sequence characteristics of five DNA regions and the concatenated
16 datasets are summarized in Table 1. In the total dataset, the numbers of variable and parsimony informative
17 sites were highest for nrITS, followed by *trnH-psbA*, *trnL-F*, *matK* and *rbcL*. For three selected groups,
18 three spacers (nrITS, *trnH-psbA* and *trnL-F*) were more variable and informative than two coding genes
19 (*matK* and *rbcL*), then *matK* was more than *rbcL*. One exception for *P. delavayi*, alignment of *matK* had
20 only one variable site in the 11 individuals, whereas alignment of *rbcL* had three variable and two
21 informative sites, respectively.
22

23

23 **Phylogenetic analyses.** The BI tree using the total dataset was presented in Figure 2. The topology was
24 similar to that in previous study (Yu et al. 2015). Two major clades were recovered, named as A and B
25 following Yu et al. (2015). *Pedicularis delavayi* fell into clade A, and *P. siphonantha* lineage was in clade B.
26 Both *P. delavayi* (BS/PP = 100/1.00) and *P. siphonantha* lineage (BS/PP = 96/1.00) were strongly as
27 monophyletic, respectively. In the clade of *P. delavayi*, three Lijiang samples (type locality) formed a group
28 (BS/PP = 98/1.00), which was weakly supported sister to the remaining eight samples (PP = 0.62); three
29 Sichuan samples were strongly supported as monophyletic (BS/PP = 92/1.00), and two Yunnan samples
30 (HW10130 and HW10172) as sister. The *P. siphonantha* lineage split in two groups. One group included
31 clade *P. dolichosiphon* + *P. leptosiphon* (BS/PP = 100/1.00), and monophyletic *P. siphonantha* (BS/PP =
32 100/1.00) and *P. tenuituba* (= *P. siphonantha* var. *stictochila*) (BS/PP = 100/1.00). Another group comprised
33 of the remaining five sampled species (including *P. humilis*) and sample LIDZ1518. Three samples of *P.*
34 *millina* from Lijiang were monophyletic by moderate supporting (BS/PP = 55/0.88), then the Lijiang
35 sample (LIDZ1584) of *P. sigmoidea* was resolved as sister (BS/PP = 99/1.00), followed by the Eryuan
36 sample (YWB2015059) of *P. sigmoidea* (BS/PP = 100/1.00). *Pedicularis humilis* nested with sample
37 LIDZ1518 (BS/PP = 84/0.79), with long branch length, and *P. variegata* was sister to them (BS/PP =
38 90/1.00).

1 **Morphological comparisons.** Morphologically, *P. delavayi* is similar to *P. siphonantha* by in having
2 large and bi-lobed middle lobe of lower-lip, and semi-circle and crestless beak. However, the middle lobe
3 of *P. delavayi* was significantly incurved (Figs. 1C-G; vs. spreading in *P. siphonantha*, Fig. 1A), which was
4 crushed in herbarium specimens (e.g. Fig. S1). Based on comparisons of flowering specimens, we found
5 that *P. delavayi* also differed from *P. siphonantha* by having a long petiole (~ 50 mm) and pedicel (~
6 40mm), a furfuraceous surface on the abaxial leaf blade, a ridged corolla tube, a folded lower-lip of the
7 corolla, and four pubescent filaments. In addition, we found that the type of *P. neolatituba* was very close
8 to specimens of *P. delavayi* and should be reduced to a synonym of *P. delavayi*.

9 *Pedicularis milliana* (Fig. 1C) is very similar to *P. siphonantha* by having smooth corolla tube,
10 spreading corolla lower-lip, large and bi-lobed middle lobe, and semi-circle and crestless beak. Because the
11 distribution of *P. delavayi* overlaps with *P. milliana* in northwestern Yunnan, Tsoong (1963) might have
12 misidentified *P. milliana* as *P. delavayi*. Therefore, he downgraded *P. delavayi* to a variety under *P.*
13 *siphonantha*. Clearly, *P. milliana* was separated from *P. siphonantha*, which is strongly supported by
14 phylogenetic analyses. In addition, sample LIDZ1518 was similar to *P. milliana* in having spreading corolla
15 lower-lip, large and bi-lobed middle lobe, and semi-circle beak, and to *P. sigmoidea* in having spreading
16 corolla lower-lip, large and bi-lobed middle lobe, and crested beak. However, phylogenetic analyses
17 indicating it was a separated lineage, close *P. humilis* and *P. variegata*.

18

19 DISCUSSION

20 **Phylogenetic delimitation of *P. siphonantha* group.** *Pedicularis siphonantha* was firstly described from
21 Nepal (Don, Hamilton & Wallich 1825), which has been recognized as endemic to the Himalayan region
22 (Pennell 1935; Li 1949). According to current taxonomic treatments (Tsoong 1963; Yang, Holmgren & Mill
23 1998), *P. siphonantha* var. *delavayi* and var. *stictochila* occur in the Hengduan Mountains region, i.e.
24 northwestern Yunnan, western Sichuan, and southeastern Qinghai. *Pedicularis siphonantha* var.
25 *dolichosiphon* was discovered in Muli region of southern Sichuan (Handel-Mazzetti 1923), then upgraded
26 to an independent species by Li (1949). In the Chinese edition of *Flora Reipublicae Popularis Sinicae*,
27 Tsoong (1963) did not mention *P. dolichosiphon*, or he might have overlooked this species. According to
28 current phylogenetic analyses, *P. siphonantha* was polyphyletic, delimitation of *P. siphonantha* group
29 needed to revise. Firstly, *P. siphonantha* var. *delavayi* was close to *P. obliquigaleata* in clade A, whereas the
30 other taxa of *P. siphonantha* were included in the *P. siphonantha* lineage. Therefore, *P. siphonantha* var.
31 *delavayi* should be reinstated as an independent species. Then, the remaining three infraspecific taxa of *P.*
32 *siphonantha* (var. *dolichosiphon*, var. *siphonantha* and var. *stictochila*) and *P. leptosiphon* formed a clade,
33 and var. *dolichosiphon* was strongly supported as sister to *P. leptosiphon*. Of them, *P. siphonantha* var.
34 *siphonantha* has a semicircle beak, and the other three taxa have S-shaped beak. Integrating geographical
35 distribution, we agree with the treatment by Li (1949) to adopt var. *dolichosiphon* and var. *stictochila* as
36 independent species as *P. dolichosiphon* and *P. tenuituba*, respectively.

37 Infraspecific delimitation of *P. siphonantha* was not fully resolved. In a taxonomical revision, Prain
38 (1890) included *P. hookeriana* Wall. ex Benth. as a synonym of *P. siphonantha* var. *siphonantha*, and *P.*

1 *elephas* Boiss. and *P. punctata* Decne. as synonyms of var. *brevituba* Prain. Nevertheless, some
2 taxonomists treated *P. hookeriana* and *P. punctata* as independent species (Pennell 1943; Yamazaki 1988;
3 Husain, Garg & Agnihotri 2010), and have placed *P. elephas* close to *P. rhinanthoides* Schrenk
4 (Maximowicz 1888; Pennell 1943). A comprehensive phylogeny of *Pedicularis* showed that both *P.*
5 *hookeriana* and *P. punctata* fell into the clade of *P. siphonantha* from the Himalayas (R. Ree, Personal
6 Communication). In the early of 1900s, Bonati added two varieties under *P. siphonantha*, var. *prostrata*
7 Bonati (1904) from Sikkim and var. *birmanica* Bonati (1921) from upper Burma. In a revision of
8 *Pedicularis* from Bhutan, Mill (2001) pointed out that *P. siphonantha* var. *prostrata* was easily confused
9 with *P. hookeriana*, whereas this variety had broader and ovate leaves and shorter corolla tubes. For *P.*
10 *siphonantha* var. *birmanica*, we found its type materials were close to that of *P. humilis*.

11

12 **Parallel evolution of long-tubular corollas in *Pedicularis*.** During revision of *Pedicularis*, Li (1948,
13 1949, 1951) and Tsoong (1955, 1963) hypothesized that long-tubular corollas were independently evolved
14 at least six and ten times, respectively. Phylogenetic inferences supported their hypotheses that long-tubular
15 corollas were independently derived from short-tubular corollas at least eight times (Ree 2005), or up to 21
16 times (Yu et al. 2015). Long-tubular species occurred in seven of 13 clades, plus two unresolved species *P.*
17 *batangensis* Franch. & Bur. and *P. flexuosa* Hook. f. (Yu et al. 2015). Series *Longiflorae* Prain included
18 more than 20 long-tubular species from the Himalaya-Hengduan Mountains region (Li 1949; Tsoong 1963;
19 Yamazaki 1988; Mill 2001). Species of series *Longiflorae* fell into clade 3, however, this series was
20 supported as monophyletic (Yu et al. 2015; this study). Phylogenetic analyses tended to split series
21 *Longiflorae* into four groups: a) *P. siphonantha* lineage, b) *P. delavayi*, c) *P. longiflora*, and 4) *P. armata* – *P.*
22 *cranolopha* group (including a short-tubular species, *P. fletcherii*). From morphological similarity and
23 geographical distribution, *P. delavayi* and *P. longiflora* were close to *P. siphonantha* lineage and *P. armata*
24 – *P. cranolopha* group, respectively. However, phylogenetic evidence indicated that the four groups may
25 evolve independently.

26 Evolution of long-tubular corollas in *Pedicularis* were hypothesized to adopt long-tongued pollinators
27 (Li 1951). However, pollination observations showed that long-tubular species were exclusively pollinated
28 by bumblebees (Macior & Sood 1991; Macior & Tang 1997; Macior, Tang & Zhang 2001; Wang & Li 2005;
29 Huang & Fenster 2007; Huang, Wang & Sun 2016). Long-tubular corollas are associated with beaked galea,
30 and beaked species rewards pollinators for pollen alone (Macior & Sood 1991; Yu et al. 2008). Due to
31 anthers are tightly enclosed by the beaked galea, long-tongued Lepidoptera are impossible to dislodge
32 pollen from the tightly enclosed anthers. Only bumblebees can open concealed anthers from the beaked
33 galea using forelegs, and release pollen by vibrating wings in high speed, i.e. buzz-pollination (Yu, Li &
34 Wang 2012). When long-tongued pollinators driving evolution of long-tubular corollas was rejected, an
35 alternative hypothesis for enhancing pollination attractiveness was proposed (Macior & Sood 1991; Macior,
36 Tang & Zhang 2001). However, pollinator attraction hypothesis was not supported by experiments on *P.*
37 *siphonantha* (corrected as *P. milliana* herein) and *P. tricolor* Hand.-Mazz. (Huang, Wang & Sun 2016).
38 Pollination treatments indicated that elongation of corolla tube (and pistil length) may put more selective

1 pressure for male-to-male competition during the pollen germination (Yang & Wang 2015). Moreover,
2 plants growing in more fertilized conditions can produce longer corolla tube (Huang, Wang & Sun 2016).
3 We suggested that evolution of long-tubular corollas may have some advantages in high altitudes, because
4 most of long-tubular species occur in alpine meadow over 3000 m a.s.l. in the Himalya-Hengduan
5 Mountains region (Tsoong 1956, 1961). Such ecological factors may independently drive elongation of
6 corolla tube in different lineages. Subsequent diversification of lineage may be mainly induced by
7 geographical isolation. *Pedicularis siphonantha* lineage is one good example to illustrate geographical
8 isolation facilitating species divergence in the Himalya-Hengduan Mountains region (Yu et al. 2015).

9
10 **Reinstatement of *Pedicularis delavayi*.** Phylogenetic analyses strongly support *P. delavayi* as a
11 separated species, which is sister to *P. obliquigaleata* in clade A, not included in *P. siphonantha* lineage in
12 clade B. From floral color and beak shape, *P. delavayi* was easy to misplace into the *P. siphonantha* group.
13 In the revision of Chinese *Pedicularis*, Li (1949) cited dozens of specimens for *P. delavayi*; however, some
14 Sichuan specimens were *P. tenuituba*, and some Yunnan specimens were *P. milliana*. Subsequently, Tsoong
15 (1963) might be failed to check diagnostic characters of *P. delvayi*, or might misidentify *P. milliana* or *P.*
16 *tenuituba* as *P. delavayi*, thus he downgraded *P. delavayi* as a variety in *P. siphonantha*. Unfortunately,
17 Tsoong's incorrect treatment has been widely adopted by current Chinese Floras (Yang, Holmgren & Mill
18 1998; Wang 2006), checklists (Wang & Wu 1994; Guan 1998; Xu, Li & Sun 2013) and other publications
19 (Cai et al. 2004; Yu, Zhang & Wang 2008). Moreover, illustrations and/or voucher specimens of "*P.*
20 *siphonantha* var. *delvayi*" from northwestern Yunnan were *P. milliana*, or mixed with *P. milliana* (e.g. Wang
21 & Wu 1994; Guan 1998; Cai et al. 2004; Yu, Zhang & Wang 2008; Xu, Li & Sun 2013). Some herbarium
22 specimens of *P. tenuituba* from Sichuan were misidentified as "*P. siphonantha* var. *delvayi*". Phylogenetic
23 analyses supported *P. tenuituba* sister to *P. siphonantha*, and *P. milliana* sister to *P. sigmoidea*. To further
24 clarify phylogenetic relationship between *P. milliana* and *P. sigmoidea* needs to extensively sample more
25 populations of them in northwestern Yunnan. According to morphological and phylogenetic evidence, we
26 propose to reinstate *P. delavayi* as an independent species. Full description and line drawing (Fig. 3) were
27 provided.

28 *Pedicularis neolatituba* P. C. Tsoong was described from Songpan, northern Sichuan, which had short
29 plant (less than 10 cm), long pedicel (up to 4 cm) and basal circinate-incurved galea (Tsoong 1963). In
30 protologue, Tsoong proposed this species similar to three long-pedicelled species, *P. franchetiana*, *P.*
31 *mussotii*, and *P. mychophila*, then established series *Neolatitubae* P. C. Tsoong. After checking the type
32 specimen of *P. neolatituba* (Fig. S2), we found that it was difficult to distinguished from specimens of *P.*
33 *delavayi*. *Pedicularis delavayi* also has long pedicel, anterior cleft and mid-upper part inflated calyx, basal
34 twisted galea, semi-circle beak, ciliate corolla lobes and pubescent filaments. The plant height is variable in
35 different specimens. Therefore, we proposed to reduce *P. neolatituba* as a new synonymy of *P. delavayi*.

37 Taxonomic treatments

38 *Pedicularis delavayi* Franch. ex Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 32: 531, pl. 1, fig. 7. 1888

1 ≡ *Pedicularis siphonantha* var. *delavayi* (Franch. ex Maxim.) P. C. Tsoong, Fl. Reipubl. Popularis Sin.
2 68: 374. 1963 — **Type:** CHINA. Yunnan: Lijiang (Li-kiang), Yulong Snow Mountain (Suee Shan), alt.
3 4,000m, 14 Aug. 1886, *J. M. Delavay s.n.* (holotype: LE!, barcode 01010308; isotypes: K!, barcode
4 000708729, MPU!, barcode 020765, P!, barcode 02987194).

5 *Synonymy:* *Pedicularis neolatituba* P. C. Tsoong, in Fl. Reipubl. Popularis Sin. 68: 418–419, pl. 72, f. 1–3.
6 1963. *Syn. nov.* — **Type:** CHINA. Sichuan: Songpan (Dongrergo), alt. 4,700m, 9 Aug 1922, *H. Smith*
7 *3162* (holotype: PE!, barcode 00033070; isotype: PE!, barcode 00119661).

8 Perennial herb, barely 10 cm tall, drying black or not. Roots fleshy, fusiform. Stems 1 to several,
9 unbranched and erect or ± ascending, 2–10 cm, with lines of hairs. Basal leaves numerous, mostly
10 membranous and no leaf blade when beginning to flowering, blades development delayed; petiole up to 5
11 cm, winged, glabrescent; leaf blades lanceolate-oblong, 10–30 mm, sparsely pubescent on both surfaces,
12 abaxially furfuraceous, pinnatipartite; leaf segments 5–10 pairs, triangular-ovate to oblong-ovate, margin
13 dentate; leaf veins sparsely pubescent. Cauline leaves alternate or pseudo-opposite; petiole 0.5–5 cm,
14 sparsely pubescent; leaf blades and segments similar to basal ones. Flowers alternate and axillary, dense,
15 flowering ± synchronous; pedicel 0.5–4 cm, sparsely pubescent. Calyx tube 0.8–1 cm, 1/3–2/5 cleft
16 anteriorly, mid-upper part inflated in flowering, sparsely long-pubescent; calyx lobes 3 or 5, rarely 2, lateral
17 lobes leaflike, and posterior lobe ± entire or absent. Corolla purple-red, base whitish, and white spots on the
18 base of galea and the center of lower lip; corolla tube 3–6.5 cm, slender, glabrescent, ridged; galea strongly
19 twisted apically; beak slender, semicircular or slightly S-shaped, bent upward, to 1.2 cm; lower lip ciliate,
20 1.5–2.0 × 1.5–1.8 cm, lobes emarginate, middle lobe smaller and involute; filaments attached near tube
21 throats, pubescent. Capsule obliquely oblong, apiculate, 1.4–1.7 × 0.4–0.6 cm; seed black, linear-ovate.

22 *Distribution and Habitat.* — *Pedicularis delavayi* is endemic to the Hengduan Mountains regions.
23 After re-examination of the herbarium specimens and extensive field expeditions, we confirmed that this
24 species occurs in Northwest Yunnan (Deqin, Lijiang, and Shangri-La counties), and West and North
25 Sichuan (Daocheng, Jiulong, Kangding, Luding, Miangning, Muli, Songpan, and Xiangcheng counties).
26 This species mainly grows in alpine meadows or at the margin of alpine shrub, at the altitude over 3600 m
27 a.s.l.

28 *Phenology.* — According to field collection and herbarium records, flowering individuals were
29 collected from early June to early August. Fruiting specimens conserved at the herbaria were difficult to
30 identify. In August, 2007 and 2008, we collected fruiting individuals with mature seeds at Daxueshan
31 Mountain of Shangri-Lain, Northwest Yunnan.

32 *Conservation status.* — *Pedicularis delavayi* is not common, and it is restricted to alpine meadows.
33 Its habitats may be threatened by human activities in pasture and tourism. This species can be considered
34 Least Concern (LC) according to IUCN Red List criteria.

35 *Selected specimens examined.* — CHINA. Yunnan: Deqin, *L.-M. Gao et al.*, 25794 (KUN); Lijiang,
36 Yulong Mt. *H.-D. Li & H. Tang LHD2014-01* (KUN), *LHD201-20* (KUN), *LHD201340* (KUN);
37 Shangri-La, *W.-B. Yu 015* (KUN), *W.-B. Yu et al. HW10130* (KUN), *HW10172* (KUN), *HW10200* (KUN),
38 *LIDZ1258* (KUN). Sichuan: Daocheng, Bowa Mt., *Sichuan Vegetation Exped. 1923* (CDBI); Jiulong,

1 *Qing-Quan Wang 20508* (CDBI), *W.-B. Yu et al., LIDZ1116* (KUN), *YWB201507224* (KUN),
2 *YWB201507260* (KUN); Kangding, Zheduo Mt., *Ru Jiang & Cun-Li Jin 02086* (KUN, PE), W.B. Yu et al.,
3 *HW10316* (KUN); Xiangcheng, Wuming Mt., *Fu-Sheng Yang Y0071* (PE).

4

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