

# Karyotypes of thirteen species of *Pedicularis* (Orobanchaceae) from the Hengduan Mountains Region, NW Yunnan, China

CAI JIE<sup>1</sup>, WANG HONG<sup>1\*</sup>, GU ZHIJIAN<sup>1</sup>, ROBERT R. MILL<sup>2</sup> and LI DEZHU<sup>1</sup>

<sup>1</sup> Laboratory of Plant Biodiversity and Biogeography, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan 650204, P. R. China

<sup>2</sup> Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, Scotland, UK

**Abstract** — Karyotypes of thirteen species (including 3 subspecies, 2 varieties) of *Pedicularis* L. (Orobanchaceae) from the Hengduan Mountains Region, NW Yunnan, China were investigated. Twelve species of them were reported for the first time. The species examined all had one or other of two basic chromosome numbers:  $2n=14$  and  $2n=16$ . All species investigated are diploid and share the same type of chromocenters in prophase nuclei, but differed in their interphase nuclei. The species with  $2n=14$  have the simple chromocenter type of interphase nuclei, while those with  $2n=16$  have the complex chromocenter type of interphase nuclei. These results confirm former reports, which have shown that  $2n=16$  is by far the most common number in this genus. Based on the karyomorphological evidence as well as morphological characters, relationships between the species studied are discussed.

**Key words:** China, Chromosome, Hengduan Mountains Region, Karyotypes, *Pedicularis*

## INTRODUCTION

The genus *Pedicularis*, with about 500 species (HONG 1983), belongs to Scrophulariaceae traditionally. However, OLMSTEAD *et al.* (2001) transferred it and the other hemiparasitic and parasitic 'scrophs' to Orobanchaceae on the basis of molecular evidence. Whether it is placed in "traditional Scrophulariaceae" or in Orobanchaceae, it is by far the largest genus in its family, and distributes primarily in the Arctic-alpine regions of the northern hemisphere (HONG 1983; MILL 2001). At least 352 species and probably closer to 400 occur in China (TSOONG 1963; YANG *et al.* 1998), mainly in the southwest China, especially in the Hengduan Mountains region, where 268 species occur (WANG 1993). The Hengduan Mountains lie to the southeast of the Qinghai-Xizang Plateau, and comprise the northwest part of Yunnan, southwest part of Sichuan and southeast part of Tibet, extending between latitudes 25-32°N and longitudes 96-102°E. Many *Pedicularis* species from this region exhibit endemism and geo-

graphic disjunctions, it was regarded as one of the original and divergent centers of this genus. (LI 1951; TSOONG 1955; LI *et al.* 2002).

The species of *Pedicularis* are hemiparasitic, generally perennial or annual (rarely biennial) herbs. The personate flower has a corolla tube of very variable length, which extends distally into a trilobate lower lip and an upper lip (galea) with occasional basal echinations or distal teeth. The galea encloses four introrse anthers and in some species it is extended into a rostra that is variable in length and form. Previous classifications of *Pedicularis* were mainly based on a combination of phyllotaxy and floral morphology (PRAIN 1890; BONATI 1918; LIMPRICHT 1924). LI (1948, 1949) followed in the steps of earlier workers and divided the genus into three major groups. Subsequently, LI (1951) proposed four major evolutionary corolla types, and pointed out that leaves are more stable characters than flowers in the evolutionary history of *Pedicularis*, so that species supposedly related by common descent show very close foliar resemblance. Tsoong's system (TSOONG 1955) suggested two basic types of corolla named the "*capitata*" and "*flammea*" types (see DISCUSSION), and divided the genus into 136 series. Additional series have been described by later workers (and others reduced to synonymy). In our paper, TSOONG's classification is followed since it also formed the basis of the classification of the genus in

\* Corresponding author: Laboratory of Plant Biodiversity and Biogeography, Kunming Institute of Botany, Chinese Academy of Sciences, Heilongtan, Kunming, Yunnan 650204, People's Republic of China. tel. +86-871-5223534; fax +86-871-5217791. e-mail: wanghong@mail.kib.ac.cn.

*Flora of China* (YANG *et al.* 1998). In that treatment, 112 series were recognized.

Previous cytological studies of *Pedicularis* have mainly investigated the chromosome numbers of species in North America, Europe and the western Himalayas (e.g. LÖVE and LÖVE 1961; ZHUKOVA 1966; GILL 1972; ROOSE 1973; AMANO 1999). Prior to the present study, the chromosome numbers of 123 taxa belonging to 104 species of *Pedicularis* had been reported. Three chromosome numbers have so far been recorded in the genus:  $x=8$  (98 species prior to the present paper),  $x=7$  (four taxa: *P. anserantha* var. *elevatogaleata* and *P. longiflora* var. *tubiformis*: AMANO 1999; *P. ludwigii*: ZAKHARJEVA 1993; *P. bicornuta*: VASUDEVAN 1975),  $x=6$  (only *P. verticillata*; ZHUKOVA and PETROVSKY 1987 and *P. bifida*; VERMA and DHILLON 1967 as *P. carnosus* Wall.). Tetraploids are known from 12 species; 11 have  $2n=32$ , based on  $x=8$  (ZHUKOVA 1966; CARR 1971; ZHUKOVA and TIKHONOVA 1971; ZHUKOVA *et al.*, 1977; STRID and FRANZÉN 1981; AMANO 1999), while the remaining one has  $2n=28$ , based on  $x=7$  (AMANO 1999). In six species (*P. hirsuta*, *P. hoffmeisteri*, *P. pauciflora*, *P. sudetica*, *P. sylvatica*, *P. villosa*), both diploids and tetraploids are known.

HUANG *et al.* (1996a, b) reported the chromosome counts of ten species of *Pedicularis* from north-west China and the Tibet-Qinghai plateau, all of which had  $2n=16$ ; their papers were the first studies to deal with Chinese species. Their first paper (HUANG *et al.* 1996a) analysed the karyotypes of six species from NW China, but no such details were given for the other four (HUANG *et al.* 1996b). The chromosome numbers and karyotypes of 13 species from the Hengduan Mountains Region are reported here, 12 being counted for the first time, bringing

the total number of cytologically known Chinese species of the genus to 23 and the world total to 116.

## MATERIALS AND METHODS

Thirteen species of *Pedicularis* representing all corolla types were investigated. All seed samples were collected from the Hengduan Mountains Region, NW Yunnan (Table 1); all were collected at Shangri-La (Zhongdian) County, except for *P. rhodotricha* at Deqin County. The voucher specimens are deposited in the Herbarium of Kunming Institute of Botany (KUN), Chinese Academy of Sciences.

For the chromosome number and karyotype observations, the source of the seeds was several capsules from different individual plants in the same population. Seeds germination on filter paper in Petri dishes took 10-14 days. The seedlings were grown in a 20°C growth chamber, while root tips of germinating young seedlings were harvested and pre-treated in 0.1% colchicines at room temperature for 2 hours. Root tips were fixed in Carnoy's solution (glacial acetic acid: 95% ethanol = 1: 3) at 4°C for 30 min, soaked in 70% ethanol overnight. After hydrolysis for 40 seconds in a 1: 1 solution of 1N hydrochloric acid and 45% acetic acid at 60°C, the roots were stained in 1% aceto-orcin for 1 hour.

Observations were made on nuclei at somatic mitotic prophase, metaphase and interphase. The karyomorphological classification follows the system of TANAKA (1971, 1977). Descriptive karyomorphological terminology follows LEVAN *et al.* (1964). Karyotype formulas are based on the measured data of somatic chromosomes at mid-metaphase. Chro-

Table 1 — Species of *Pedicularis* investigated nomenclature and numbering of series follow YANG *et al.* (1998).

| Taxon  | Series                              | Voucher number | Corolla type         | Phyllotaxy type |
|--|-------------------------------------|----------------|----------------------|-----------------|
| <i>P. dunniana</i> Bonati  | 6. <i>Rudes</i> Prain               | 0080           | Rostrate, Short tube | Alternate       |
| <i>P. rhodotricha</i> Maxim.   | 10. <i>Trichoglossae</i> H.L. Li    | 0090           | Rostrate, Short tube | Alternate       |
| <i>P. dichotoma</i> Bonati   | 39. <i>Dichotomae</i> H.L. Li       | 0066           | Rostrate, Short tube | Opposite        |
| <i>P. rex</i> C. B. Clarke ex Maxim.   | 40. <i>Reges</i> H.L. Li            | 0072           | Erostrate, Toothed   | Verticillate    |
| <i>P. densispica</i> Franch. ssp. <i>densispica</i>                                      | 60. <i>Abrotanifoliae</i> Limpr.    | 0024           | Erostrate, Toothless | Opposite        |
| <i>P. strobilacea</i> Franch. ex Forbes & Hemsl.   | 67. <i>Strobilaceae</i> P.C. Tsoong | 0071           | Rostrate, Short tube | Alternate       |
| <i>P. oxycarpa</i> Franch. ex Maxim.   | 69. <i>Oxycarpae</i> Prain          | 0057           | Rostrate, Short tube | Alternate       |
| <i>P. lutescens</i> Franch. ssp. <i>lutescens</i>  | 76. <i>Lyratae</i> Maxim.           | 0081           | Erostrate, Toothed   | Verticillate    |
| <i>P. integrifolia</i> Hook.f. ssp. <i>integerrima</i> (Pennell & H. L. Li) P. C. Tsoong | 80. <i>Integrifoliae</i> Prain      | 0063           | Rostrate, Short tube | Opposite        |
| <i>P. umbelliformis</i> H. L. Li   | 95. <i>Paucifoliae</i> Prain        | 0059           | Rostrate, Short tube | Alternate       |
| <i>P. longiflora</i> Rudolph var. <i>tubiformis</i> (Klotzsch) P. C. Tsoong              | 111. <i>Longiflorae</i> Prain       | 0076           | Rostrate, Long tube  | Alternate       |
| <i>P. tricolor</i> Hand.-Mazz.   | 111. <i>Longiflorae</i> Prain       | 0062           | Rostrate, Long tube  | Alternate       |
| <i>P. siphonantha</i> D. Don var. <i>delavayi</i> (Franch. ex Maxim.) P. C. Tsoong       | 111. <i>Longiflorae</i> Prain       | 0077           | Rostrate, Long tube  | Alternate       |

mosome counts are based on 20 cells and measurements were made on at least 10 chromosome complements at metaphase and interphase.

## RESULTS

The karyotypes of 13 species of *Pedicularis* observed are listed in Table 2. These species represent 11 series; 3 species belong to series *Longiflorae*, while the other 10 species belong to 10 different series. All taxa except *P. longiflora* var. *tubiformis* were previously uncategorized. Eleven species had a chromosome number  $2n=16$  while the other two taxa (*P. siphonantha* var. *delavayi*, *P. integrifolia* ssp. *integerrima*) had  $2n=14$ . The species with  $2n=16$  have the complex chromocenter types of interphase nuclei (Fig. 1: a), while the species with  $2n=14$  belong to the simple chromocenter types of interphase nuclei (TANAKA 1971, 1977) (Fig. 2: c). All species examined share the same type of chromocenter in prophase nuclei (Fig. 1, 2: b, d). The karyological variation at metaphase reveals distinct differences between samples, but there are some similarities at individual taxon level. The results for somatic metaphase nuclei are described below.

*Capitata* corolla type: *Pedicularis dunniana* Bonati  $2n=16=2m+12sm+2st(1sat)$  (Fig. 1: D; Fig. 3: D) - This species is endemic to China and distributes in the Hengduan Mountains region of NW Yunnan and W Sichuan. It was characterised by a diploid complement of  $2n=16$ . The metaphase karyotype comprised 2 metacentric chromosomes (nos. 15, 16), 2 subtelocentric (nos. 13, 14) and 12 submetacentric chromosomes, in which chromosome 13 showed a satellite. Chromosomes are gradual from  $3\mu m$  to  $7\mu m$ .

*Pedicularis rex* C. B. Clarke ex Maxim.  $2n=16=2m+10sm+4st$  (Fig. 1: B; Fig. 2: B) - This species is distributed in SW Sichuan, C, NE and NW Yunnan, N India and N Myanmar. The investigated material had a basic complement of  $2n=16$ . The metaphase karyotype consisted of 2 metacentric chromosomes (nos. 5 and 6), 4 subtelocentric chromosomes (nos. 11-14) and 10 submetacentric chromosomes. No chromosomes showed satellites. Chromosomes are gradual from  $3\mu m$  to  $5\mu m$ .

*Pedicularis rhodotricha* Maxim.  $2n=16=10sm+6st(4sat)$  (Fig. 1: C; Fig. 2: C) - This species is endemic to China and distributes in the Hengduan Mountains region of NW Yunnan and W Sichuan. It showed a complement of  $2n=16$ . The metaphase karyotype consisted of 6 subtelocentric chromo-

somes (nos. 9-14) and 10 submetacentric chromosomes; chromosomes 9, 10, 11 and 12 showed satellites. Chromosomes are gradual from  $3\mu m$  to  $6\mu m$ .

*Flammea* corolla type: *Pedicularis densispica* Franch. ssp. *densispica*  $2n=16=12sm+4st(2sat)$  (Fig. 1: H; Fig. 3: H) - This species is endemic to China, distributed in the Hengduan Mountains region from NW Yunnan, SW and W Sichuan to SE Tibet, and is diploid with  $2n=16$ . The metaphase complement comprised 4 subtelocentric chromosomes (nos. 11-14) while the remaining 12 were submetacentric. Chromosomes 13 and 14 each showed a satellite. Chromosomes are gradual from  $3\mu m$  to  $6\mu m$ .

*Pedicularis dichotoma* Bonati  $2n=16=1m+8sm+7st(1sat)$  (Fig. 1: F; Fig. 3: F) - This species is endemic to China and distributes in the Hengduan Mountains region from NW Yunnan to SW Sichuan. It was characterised by a diploid complement of  $2n=16$ . The metaphase complement consisted of 1 metacentric chromosome (chromosome 7), 8 submetacentric chromosomes (chromosomes 1-6, 15 and 16) and 7 subtelocentric chromosomes (nos. 8-13 and 14), in which chromosome 10 showed a satellite. Chromosomes 7 and 8 were heterologous, although characterised as m and sm respectively; the arm of chromosome 7 appears probably to show inversion or translocation positions. Chromosomes are gradual from  $3\mu m$  to  $6\mu m$ .

*Pedicularis integrifolia* Hook. f. ssp. *integerrima* (Pennell & Li) P. C. Tsoong  $2n=14=2m+6sm+6st$  (Fig. 2: M; Fig. 3: M) - This species is endemic to China and distributes in the Hengduan Mountains region from NW Yunnan and SW and W Sichuan to SE Tibet; it showed  $2n=14$ . The metaphase complement was made up of 2 metacentric chromosomes (nos. 1 and 2), 6 subtelocentric chromosomes (nos. 9-14) and 6 submetacentric chromosomes. No satellite was observed. Chromosomes are gradual from  $3\mu m$  to  $6\mu m$ .

*Pedicularis longiflora* Don var. *tubiformis* (Klotzsch) Tsoong  $2n=16=14sm(2sat)+2st(2sat)$  (Fig. 1: G; Fig. 3: G) - This species is distributed in NW Yunnan, W Sichuan, SE Tibet, Nepal, Pakistan, and Sikkim. It was diploid with  $2n=16$ . The metaphase complement comprised 2 subtelocentric chromosomes (nos. 13 and 14, both with satellites) and 14 submetacentric chromosomes. Submetacentric chromosomes 11 and 12, and subtelocentric chromosomes 13 and 14, all showed satellites. Chromosomes are gradual from  $3\mu m$  to  $5\mu m$ .

*Pedicularis lutescens* Franch. ssp. *lutescens*  $2n=16=12sm+4st(2sat)$  (Fig. 2: J, Fig. 3: J) - This

Table 2 — The parameters of karyotypes in the 13 investigated species of *Pedicularis*

| <i>P. strobilacea</i><br>K=2n=2x=16=2m + 12sm (1sat) + 2st                         |                  |     |      | <i>P. rex</i><br>K=2n=2x=16=2m + 10sm + 4st                                 |     |      | <i>P. rhodotricha</i><br>K=2n=2x=16=10sm + 6st (4sat)   |     |      |
|--|------------------|-----|------|---|-----|------|---|-----|------|
| No   | RL               | AR  | Type | RL  | AR  | Type | RL  | AR  | Type |
| 1  | 5.46+2.16 = 7.62 | 2.5 | sm   | 5.01+2.79 = 7.80  | 1.8 | sm   | 5.96+2.10 = 8.06  | 2.8 | sm   |
| 2  | 5.29+2.08 = 7.37 | 2.5 | sm   | 4.94+2.80 = 7.74  | 1.8 | sm   | 5.69+2.19 = 7.88  | 2.6 | sm   |
| 3  | 4.64+2.50 = 7.14 | 1.9 | sm   | 4.84+2.49 = 7.33  | 1.9 | sm   | 5.42+2.38 = 7.80  | 2.3 | sm   |
| 4  | 4.69+2.31 = 7.00 | 2.0 | sm   | 4.82+2.29 = 7.10  | 2.1 | sm   | 5.33+2.29 = 7.62  | 2.3 | sm   |
| 5  | 4.63+2.28 = 6.91 | 2.0 | sm   | 4.23+2.75 = 6.98  | 1.5 | m    | 5.22+2.28 = 7.50  | 2.3 | sm   |
| 6  | 4.48+2.25 = 6.73 | 2.0 | sm   | 4.18+2.58 = 6.76  | 1.6 | m    | 5.01+2.40 = 7.41  | 2.1 | sm   |
| 7  | 4.41+2.19 = 6.60 | 2.0 | sm   | 4.32+2.37 = 6.69  | 1.8 | sm   | 5.16+1.94 = 7.10  | 2.7 | sm   |
| 8  | 4.54+2.01 = 6.55 | 2.3 | sm   | 4.27+2.22 = 6.49  | 1.9 | sm   | 5.17+1.76 = 6.93  | 2.9 | sm   |
| 9  | 4.90+1.65 = 6.55 | 3.0 | sm   | 4.45+1.93 = 6.38  | 2.3 | sm   | 5.14+1.31 = 6.44  | 3.9 | st*  |
| 10   | 4.74+1.65 = 6.39 | 2.9 | sm   | 4.20+1.92 = 6.12  | 2.2 | sm   | 4.86+1.34 = 6.20  | 3.6 | st*  |
| 11   | 4.72+1.31 = 6.03 | 3.6 | st   | 4.17+1.35 = 5.52  | 3.1 | st   | 4.04+1.25 = 5.29  | 3.2 | st*  |
| 12   | 4.66+1.27 = 5.93 | 3.7 | st   | 4.02+1.28 = 5.30  | 3.1 | st   | 3.82+1.18 = 5.00  | 3.2 | st*  |
| 13   | 3.81+1.75 = 5.56 | 2.2 | sm   | 3.99+1.27 = 5.26  | 3.1 | st   | 3.78+0.89 = 4.67  | 4.3 | st   |
| 14   | 3.54+1.60 = 5.14 | 2.2 | sm*  | 3.97+1.28 = 5.25  | 3.1 | st   | 3.61+0.78 = 4.39  | 4.6 | st   |
| 15   | 2.75+1.74 = 4.49 | 1.6 | m    | 2.81+1.59 = 4.40  | 1.8 | sm   | 2.55+1.38 = 3.93  | 1.9 | sm   |
| 16   | 2.55+1.67 = 4.22 | 1.5 | m    | 2.66+1.45 = 4.11  | 1.8 | sm   | 2.40+1.35 = 3.75  | 1.8 | sm   |
| <i>P. dunniana</i><br>K=2n=2x=16= 2m + 12sm + 2st (1sat)                           |                  |     |      | <i>P. tricolor</i><br>K=2n=2x=16=2m + 10sm (1sat)+ 4st (2sat)               |     |      | <i>P. dichotoma</i><br>K=2n=2x=16=1m + 8sm + 7st (1sat) |     |      |
| 1  | 5.47+3.04 = 8.51 | 1.8 | sm   | 5.46+2.32 = 7.78  | 2.4 | sm   | 5.04+2.51 = 7.55  | 2.0 | sm   |
| 2  | 5.27+2.92 = 8.19 | 1.8 | sm   | 5.19+2.43 = 7.62  | 2.1 | sm   | 4.97+2.52 = 7.49  | 2.0 | sm   |
| 3  | 5.37+2.28 = 7.65 | 2.4 | sm   | 5.13+2.43 = 7.56  | 2.1 | sm   | 5.22+2.05 = 7.47  | 2.6 | sm   |
| 4  | 4.92+2.73 = 7.65 | 1.8 | sm   | 4.92+2.16 = 7.08  | 2.3 | sm   | 5.36+2.01 = 7.37  | 2.7 | sm   |
| 5  | 4.63+2.63 = 7.26 | 1.8 | sm   | 4.86+2.16 = 7.02  | 2.3 | sm   | 5.24+1.94 = 7.18  | 2.7 | sm   |
| 6  | 4.59+2.59 = 7.18 | 1.8 | sm   | 4.48+2.49 = 6.97  | 1.8 | sm   | 4.75+2.17 = 6.92  | 2.2 | sm   |
| 7  | 4.56+2.45 = 7.01 | 1.9 | sm   | 4.35+2.57 = 6.92  | 1.7 | m    | 4.10+2.44 = 6.54  | 1.7 | m    |
| 8  | 4.77+2.10 = 6.87 | 2.3 | sm   | 3.78+2.70 = 6.48  | 1.4 | m    | 5.07+1.19 = 6.26  | 4.3 | st   |
| 9  | 3.80+2.16 = 5.96 | 1.8 | sm   | 5.10+1.29 = 6.39  | 4.0 | st   | 5.01+0.93 = 5.94  | 5.4 | st   |
| 10   | 3.64+2.07 = 5.71 | 1.8 | sm   | 4.92+1.37 = 6.29  | 3.6 | st   | 4.90+0.98 = 5.88  | 5.0 | st*  |
| 11   | 3.79+1.76 = 5.55 | 2.2 | sm   | 4.44+1.68 = 6.12  | 2.6 | sm*  | 4.26+1.21 = 5.47  | 3.5 | st   |
| 12   | 3.83+1.56 = 5.40 | 2.5 | sm   | 4.11+1.40 = 5.51  | 2.9 | sm   | 4.29+1.09 = 5.38  | 3.9 | st   |
| 13   | 4.27+1.02 = 5.29 | 4.2 | st*  | 4.32+1.13 = 5.46  | 3.8 | st*  | 3.99+0.99 = 4.98  | 4.0 | st   |
| 14   | 3.47+0.96 = 4.43 | 3.6 | st   | 4.05+1.08 = 5.13  | 3.8 | st*  | 3.96+0.94 = 4.90  | 4.2 | st   |
| 15   | 2.11+1.58 = 3.69 | 1.3 | m    | 3.40+1.40 = 4.81  | 2.4 | sm   | 2.91+1.44 = 4.35  | 2.0 | sm   |
| 16   | 2.01+1.45 = 3.46 | 1.4 | m    | 3.13+1.51 = 4.65  | 2.1 | sm   | 2.94+1.29 = 4.23  | 2.3 | sm   |
| <i>P. longiflora</i> var. <i>tubiformis</i><br>K=2n=2x=16=14sm (2sat) + 2st (2sat) |                  |     |      | <i>P. densispica</i> ssp. <i>densispica</i><br>K=2n=2x=16=12sm + 4st (2sat) |     |      | <i>P. umbelliformis</i><br>K=2n=2x=16= 2m + 12sm + 2st  |     |      |
| 1  | 5.79+2.67 = 8.46 | 2.2 | sm   | 4.93+2.53 = 7.46  | 2.0 | sm   | 5.65+2.73 = 8.38  | 2.1 | sm   |
| 2  | 5.55+2.37 = 7.92 | 2.3 | sm   | 4.45+2.48 = 7.33  | 1.8 | sm   | 5.60+2.38 = 7.98  | 2.4 | sm   |
| 3  | 5.28+2.64 = 7.92 | 2.0 | sm   | 4.89+2.27 = 7.16  | 2.2 | sm   | 5.80+1.85 = 7.65  | 3.1 | st   |
| 4  | 5.02+2.54 = 7.56 | 2.0 | sm   | 4.70+2.40 = 7.10  | 2.0 | sm   | 5.74+1.90 = 7.64  | 3.0 | st   |
| 5  | 5.16+2.34 = 7.50 | 2.2 | sm   | 5.23+1.87 = 6.80  | 2.8 | sm   | 4.70+2.83 = 7.53  | 1.7 | m    |
| 6  | 5.12+2.37 = 7.49 | 2.2 | sm   | 5.01+1.77 = 6.78  | 2.8 | sm   | 4.65+2.76 = 7.41  | 1.7 | m    |
| 7  | 4.68+2.43 = 7.11 | 1.9 | sm   | 4.97+1.77 = 6.74  | 2.8 | sm   | 4.66+2.64 = 7.30  | 1.8 | sm   |
| 8  | 4.45+2.39 = 6.84 | 1.9 | sm   | 4.70+1.83 = 6.53  | 2.6 | sm   | 4.55+2.58 = 7.13  | 1.8 | sm   |
| 9  | 4.80+1.97 = 6.77 | 2.4 | sm   | 4.39+1.71 = 6.10  | 2.6 | sm   | 4.39+1.82 = 6.21  | 2.4 | sm   |
| 10   | 4.39+2.12 = 6.51 | 2.1 | sm   | 4.38+1.57 = 5.95  | 2.8 | sm   | 4.04+1.95 = 5.98  | 2.1 | sm   |
| 11   | 4.41+1.63 = 6.04 | 2.7 | sm*  | 4.72+1.04 = 5.76  | 4.5 | st   | 3.70+1.99 = 5.69  | 1.9 | sm   |
| 12   | 4.04+1.73 = 5.67 | 2.3 | sm*  | 4.41+1.15 = 5.66  | 3.8 | st   | 3.63+1.75 = 5.38  | 2.1 | sm   |
| 13   | 3.84+1.25 = 5.09 | 3.1 | st*  | 4.28+1.27 = 5.57  | 3.4 | st*  | 3.27+1.80 = 5.07  | 1.8 | sm   |
| 14   | 3.58+1.15 = 4.73 | 3.1 | st*  | 4.36+1.16 = 5.52  | 3.8 | st*  | 3.10+1.61 = 4.71  | 1.9 | sm   |
| 15   | 2.96+1.48 = 4.44 | 2.0 | sm   | 3.43+1.86 = 5.29  | 1.8 | sm   | 2.74+1.56 = 4.30  | 1.8 | sm   |
| 16   | 2.92+1.41 = 4.33 | 2.1 | sm   | 3.15+1.46 = 4.61  | 2.1 | sm   | 2.61+1.48 = 4.09  | 1.8 | sm   |

(to be continued)

(Table 2, continued)

| <i>P. lutescens</i> ssp. <i>lutescens</i><br>K=2n=2x=16=12sm + 4st (2sat) |                  |     |      | <i>P. oxycarpa</i><br>K=2n=2x=16=4m + 6sm + 6st (1sat)                      |     |      |
|---|------------------|-----|------|---|-----|------|
| No  | RL               | AR  | Type | RL  | AR  | Type |
| 1   | 5.15+2.35 = 7.68 | 2.0 | sm   | 4.57+4.24 = 8.81  | 1.1 | m    |
| 2   | 4.88+2.43 = 7.31 | 2.0 | sm   | 4.00+4.02 = 8.02  | 1.0 | m    |
| 3   | 5.34+1.96 = 7.30 | 2.7 | sm   | 4.08+3.35 = 7.43  | 1.2 | m    |
| 4   | 5.08+2.13 = 7.21 | 2.4 | sm   | 4.08+3.34 = 7.42  | 1.2 | m    |
| 5   | 4.79+2.35 = 7.14 | 2.0 | sm   | 5.34+2.00 = 7.34  | 2.7 | sm   |
| 6   | 4.77+2.23 = 7.10 | 2.1 | sm   | 4.63+2.51 = 7.14  | 1.8 | sm   |
| 7   | 4.32+2.41 = 6.73 | 1.8 | sm   | 4.88+1.97 = 6.85  | 2.5 | sm   |
| 8   | 4.51+2.07 = 6.58 | 2.2 | sm   | 4.21+2.08 = 6.29  | 2.0 | sm   |
| 9   | 4.90+1.57 = 6.47 | 3.1 | st*  | 4.97+0.89 = 5.86  | 5.6 | st   |
| 10  | 4.74+1.50 = 6.24 | 3.2 | st*  | 4.93+0.72 = 5.65  | 6.9 | st   |
| 11  | 4.45+1.58 = 6.03 | 2.8 | sm   | 4.64+1.10 = 5.74  | 4.2 | st   |
| 12  | 3.68+1.78 = 5.46 | 2.2 | sm   | 4.37+1.37 = 5.64  | 3.2 | st   |
| 13  | 4.08+1.07 = 5.15 | 3.8 | st   | 4.42+1.07 = 5.49  | 4.1 | st*  |
| 14  | 4.00+1.00 = 5.00 | 4.0 | st   | 4.37+0.94 = 5.31  | 4.7 | st   |
| 15  | 3.18+1.75 = 4.93 | 1.8 | sm   | 2.59+1.14 = 3.73  | 2.3 | sm   |
| 16  | 3.05+1.72 = 4.77 | 1.8 | sm   | 2.43+1.16 = 3.59  | 2.1 | sm   |
| <i>P. siphonantha</i> var. <i>delavayi</i><br>K=2n=2x=14=14sm (2sat)      |                  |     |      | <i>P. integrifolia</i> ssp. <i>integerrima</i><br>K=2n=2x=14=2m + 6sm + 6st |     |      |
| 1   | 5.72+2.58 = 8.30 | 2.2 | sm   | 5.40+4.24 = 9.64  | 1.3 | m    |
| 2   | 5.60+2.69 = 8.29 | 2.1 | sm   | 4.98+4.21 = 9.19  | 1.2 | m    |
| 3   | 5.66+2.58 = 8.24 | 2.2 | sm   | 5.73+2.64 = 8.37  | 2.2 | sm   |
| 4   | 5.23+2.88 = 8.11 | 1.8 | sm   | 5.55+2.38 = 7.93  | 2.3 | sm   |
| 5   | 5.41+2.56 = 7.97 | 2.1 | sm   | 4.92+2.52 = 7.44  | 2.0 | sm   |
| 6   | 5.22+2.64 = 7.86 | 2.0 | sm   | 4.81+2.63 = 7.44  | 1.8 | sm   |
| 7   | 4.81+2.63 = 7.44 | 1.8 | sm*  | 5.08+2.20 = 7.28  | 2.3 | sm   |
| 8   | 4.84+2.57 = 7.41 | 1.9 | sm   | 4.90+2.38 = 7.28  | 2.1 | sm   |
| 9   | 4.63+2.25 = 6.88 | 2.1 | sm   | 5.00+1.64 = 6.64  | 3.1 | st   |
| 10  | 4.45+2.25 = 6.70 | 2.0 | sm   | 4.88+1.58 = 6.46  | 3.1 | st   |
| 11  | 4.68+1.84 = 6.53 | 2.5 | sm   | 4.80+1.19 = 5.99  | 4.0 | st   |
| 12  | 4.36+2.02 = 6.38 | 2.2 | sm   | 4.42+1.16 = 5.58  | 3.8 | st   |
| 13  | 4.13+1.88 = 6.01 | 2.2 | sm*  | 4.19+1.29 = 5.48  | 3.3 | st   |
| 14  | 3.92+1.84 = 5.76 | 2.1 | sm   | 4.17+1.08 = 5.26  | 3.9 | st   |

species is endemic to China and distributes in the Hengduan Mountains region of NW Yunnan and SW Sichuan. It showed diploidy with  $2n=16$ . The metaphase complement comprised 12 submetacentric and 4 (nos. 9, 10, 13 and 14) subtelocentric chromosomes. Two of the subtelocentric chromosomes (nos. 9 and 10) showed satellites. Chromosomes are gradual from  $3\mu\text{m}$  to  $6\mu\text{m}$ .

*Pedicularis oxycarpa* Franch.  $2n=16=4m+6sm+6st$  (1sat) (Fig. 2: K; Fig. 3: K) - This species, endemic to China and distributed in the Hengduan Mountains region of NW Yunnan and SW Sichuan, is diploid with  $2n=16$ . The metaphase karyotype consisted of 4 metacentric chromosomes (nos. 1-4), 6 subtelocentric chromosomes (nos. 9-14) and 6 submetacentric chromosomes (nos. 5-8, 15 and 16). Chromosome 13 showed a satellite. The arm lengths of both the first and second pairs were unequal, indicating heterozygosity. Chromosomes are gradual from  $3\mu\text{m}$  to  $7\mu\text{m}$ .

*Pedicularis siphonantha* D. Don var. *delavayi* (Franch.) P. C. Tsoong  $2n=14=14sm$  (2sat) (Fig. 2: c.

d. L; Fig. 3: L) - This species is endemic to the Hengduan Mountains region of NW Yunnan and W Sichuan; it showed  $2n=14$ . The metaphase complement was made up of 14 submetacentric chromosomes, in which chromosomes 7 and 13 each showed a satellite. Chromosomes are gradual from  $3\mu\text{m}$  to  $4\mu\text{m}$ .

*Pedicularis strobilacea* Franch.  $2n=16=2m+12sm$  (1sat)+2st (Fig. 1: a, b, A; Fig. 2: A) - This species is distributed in the Hengduan Mountains region of NW Yunnan, and in adjacent NE Myanmar. It had a diploid number of  $2n=16$ . The metaphase complement comprised 2 metacentric chromosomes (nos. 15 and 16), 2 subtelocentric chromosomes (nos. 11, 12) and 12 submetacentric chromosomes, in which chromosome 14 showed a satellite. Chromosomes are gradual from  $3\mu\text{m}$  to  $5\mu\text{m}$ .

*Pedicularis tricolor* Hand. -Mazz.  $2n=16=2m+10sm$  (1sat)+4st(2sat) (Fig. 1: E; Fig. 3: E) - This species, endemic to China and distributed in the Hengduan

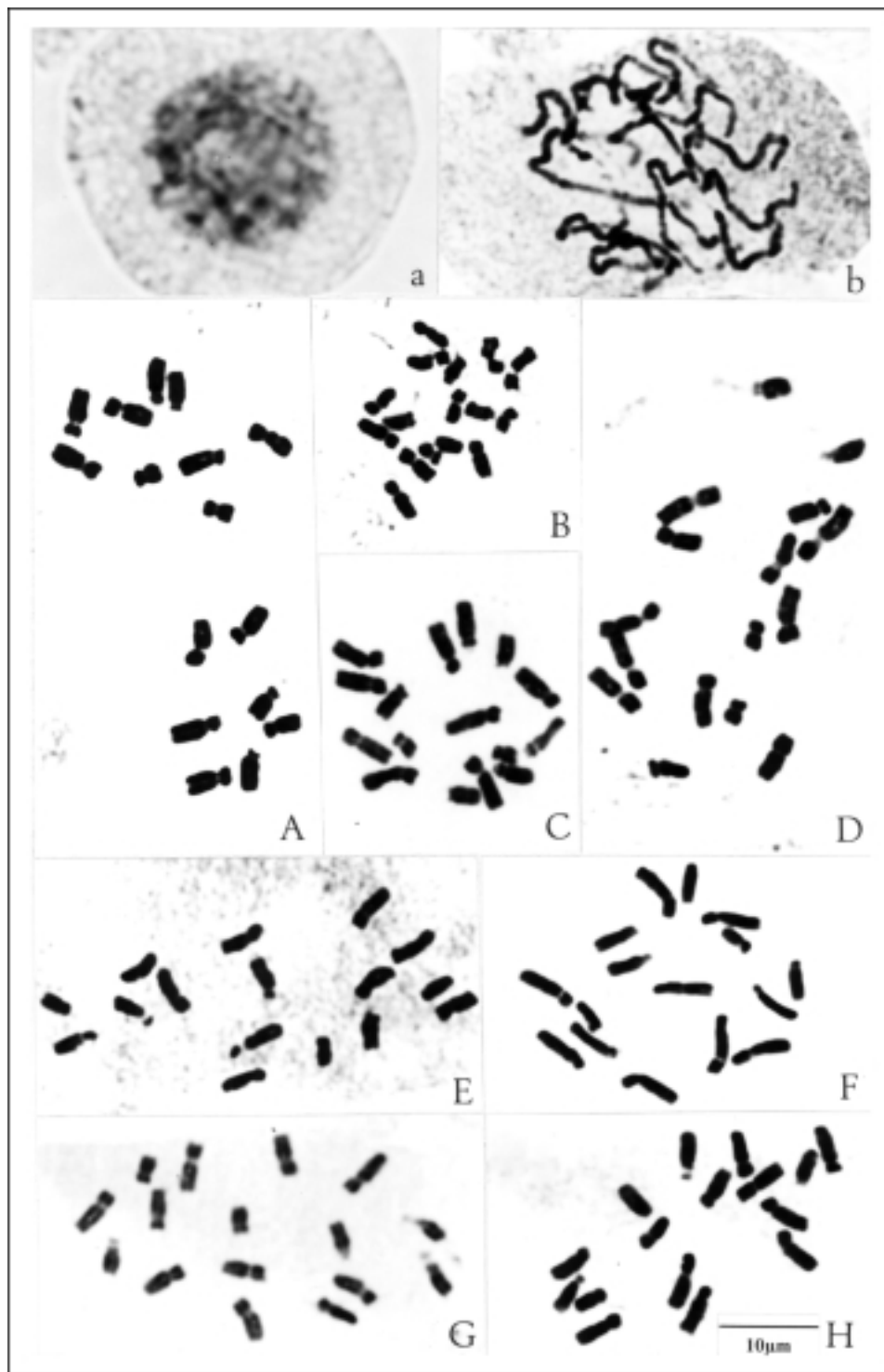


Fig. 1 a-b) — The interphase nuclei and the prophase chromosomes of *P. strobilacea*; A-H) The metaphase chromosomes of *Pedicularis*: A) *P. strobilacea*; B) *P. rex*; C) *P. rhodotricha*; D) *P. dunniana*; E) *P. tricolor*; F) *P. dichotoma*; G) *P. longiflora* var. *tubiformis*; H) *P. densispica* ssp. *densispica*; Bar = 10 µm.

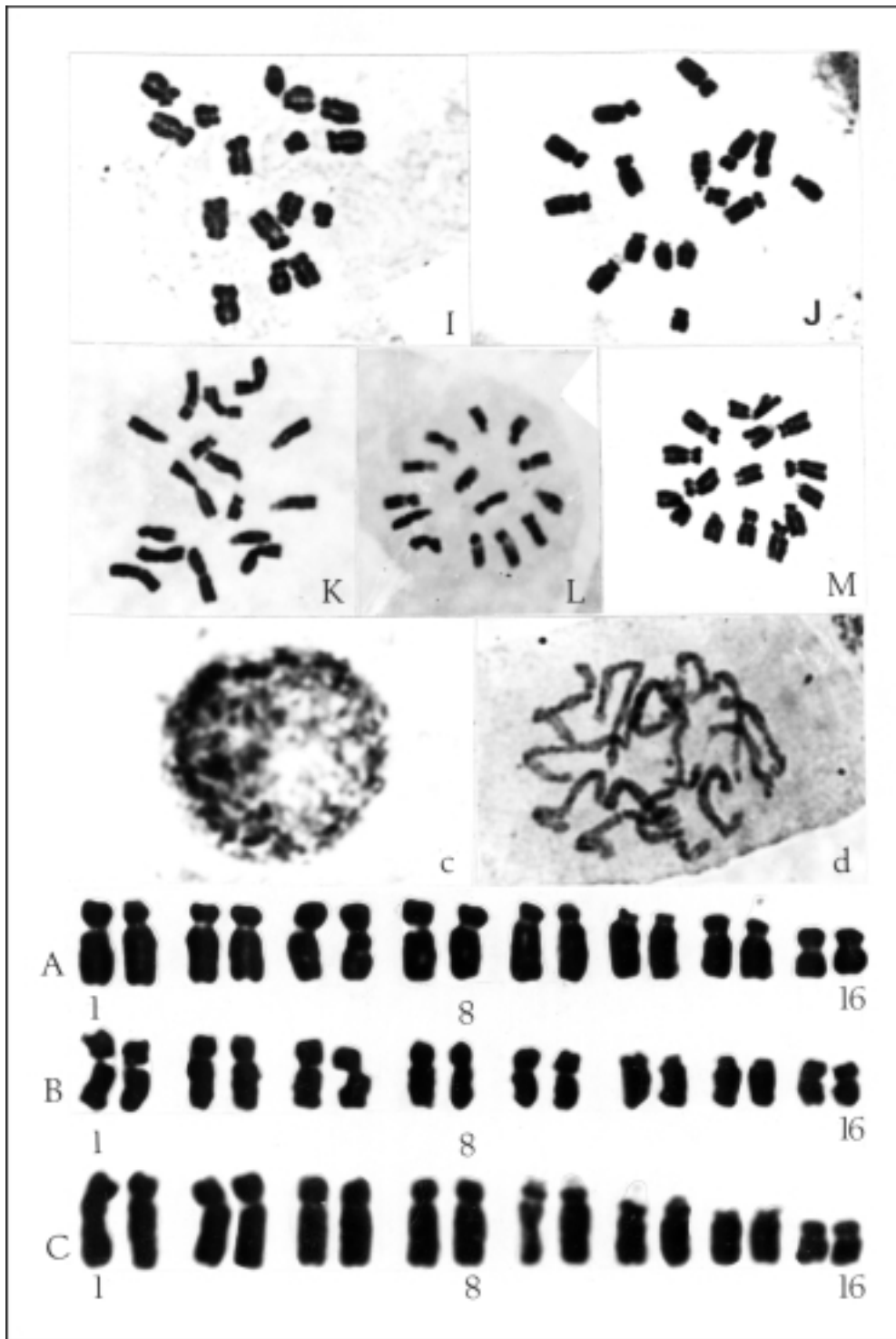


Fig. 2 I-M) — The metaphase chromosomes of *Pedicularis*: I) *P. umbelliformis*; J) *P. lutescens* ssp. *lutescens*; K) *P. oxycarpa*; L) *P. siphonantha* var. *delavayi*; M) *P. integrifolia* ssp. *integerrima*; c-d) The interphase nuclei and the prophase chromosomes of *P. siphonantha* var. *delavayi*; A-C) The karyogram of *Pedicularis*: A) *P. strobilacea*; B) *P. rex*; C) *P. rhodotricha*; Bar in I-M, c-d apply to Fig. 1; Bar in A-C also apply to Fig. 3.



Fig. 3 D-M) — The karyogram of *Pedicularis*: D) *P. dunniiana*; E) *P. tricolor*; F) *P. dichotoma*; G) *P. longiflora* var. *tubiformis*; H) *P. densispica* ssp. *densispica*; I) *P. umbelliformis*; J) *P. lutescens* ssp. *lutescens*; K) *P. oxycarpa*; L) *P. siphanantha* var. *delavayi*; M) *P. integrifolia* ssp. *integerrima*; Bar = 10  $\mu\text{m}$ .



Mountains region of NW Yunnan and SE Tibet, consistently showed  $2n=16$ . The metaphase complement comprised 2 metacentric chromosomes (nos. 7 and 8), 4 subtelocentric chromosomes (nos. 9, 10, 13, 14), and 10 submetacentric chromosomes. One submetacentric chromosome (nos. 11) and two subtelocentric chromosomes (nos. 13 and 14) showed satellites. Chromosomes are gradual from  $3\mu\text{m}$  to  $5\mu\text{m}$ .

*Pedicularis umbelliformis* Li  $2n=16=2m+12sm+2st$  (Fig. 2: I; Fig. 3: I) - This species is endemic to the Hengduan Mountains region of NW Yunnan. It had a basic diploid number of  $2n=16$ . The metaphase complement consisted of 2 metacentric chromosomes (nos. 5 and 6), 2 subtelocentric (nos. 3, 4) and 12 submetacentric chromosomes. No chromosomes showed satellites. Chromosomes are gradual from  $3\mu\text{m}$  to  $5\mu\text{m}$ .

## DISCUSSION

Several systems of classification for *Pedicularis* have been proposed. STEVEN's (1823) grouping was mainly based on floral morphology. MAXIMOWICZ (1888) proposed a system of *Pedicularis* on the basis of four basic corolla types which he first recognized: 1) beakless, toothed and short-tubed; 2) beakless, toothless and short-tubed; 3) beaked, toothless and short-tubed and 4) beaked, toothless and long-tubed. His system followed by subsequent authors (e.g. PRAIN 1890; BONATI 1918; LIMPRICHT 1924). LI (1948, 1949) established a system notably different from previous systems. He divided *Pedicularis* into three groups (greges) in recognising the importance of phyllotaxy: 1) *Cyclophyllum*, with verticillate or opposite leaves; 2) *Allophyllum*, with spiral leaves, erect stems and terminal inflorescences and 3) *Poecilophyllum*, with spiral or subopposite leaves, spreading stems and axillary inflorescences. LI emphasized that parallel evolution had occurred in corolla morphology by clearly defining the series according to the four corolla types proposed by MAXIMOWICZ. He assumed that toothed corollas were derived from toothless, beaked from non-beaked and long-tubed from short tubed based on his evolutionary theory of flowers in *Pedicularis* under the pressure of pollination and adaptation to pollinator insects.

TSOONG (1955, 1956) proposed another important classification system for the genus, which was similar to Li's in that all the species in each primary group had the same phyllotaxy. However, TSOONG did not place as much importance on phyllotaxy as Li did. Instead, he suggested that the primary group-

ing in *Pedicularis* could be inferred from two basic corolla types, the "capitata" type, which is characterised by having a straight corolla tube and erect lower lip; and the "flammea" type, in which the corolla has a tube bending abruptly toward the apex and a lower lip spreading more or less at right angles to the tube and the galea. These corolla types were not used strictly in his system, however. He attributed this pattern to a possible biphyletic origin of *Pedicularis*, with subsequent hybridization between the ancestral lineages leading to the speciation of the intermediate species and groups.

These results confirm many earlier reports, which have shown that  $2n=16$  is by far the most common number in this genus. Within the "capitata" type, 3 species were investigated in this study. Of the three species, both *P. dunniana* and *P. rhodotricha* have spirally arranged leaves and beaked corollas, while *P. rex* is verticillate-leaved and toothed corolla. Representing three different series, these three species are distinguished in their karyotypes. *P. dunniana* had 2 metacentric chromosomes (15 and 16) and 2 st chromosomes (13, 14), while *P. rhodotricha* had no metacentric chromosomes but 6 subtelocentric chromosomes of which four (9, 10, 11 and 12) had satellites. Karyotype of *P. rex* was similar to *P. dunniana*, but with more satellites (nos. 11-14). There may be some correlations between the differences of karyomorphology and floral morphology and phyllotaxy although our sampling is too low to be sure of this. It is assumed that karyotype evolution is from symmetry to asymmetry (STEBBINS 1971). In this regard, the evolutionary trends in the "capitata" type may be from *P. dunniana* to *P. rex*, to *P. rhodotricha*. However, a better understanding of karyotype evolution will only be gained when a larger sample of species has been studied and when more than one species has been sampled in those series (such as *Reges*) that are not monotypic.

In the "flammea" corolla type, 10 species of eight series were studied. Four species (*P. integrifolia* ssp. *integerrima*, *P. densispica* ssp. *densispica*, *P. lutescens* ssp. *lutescens* and *P. dichotoma*) are verticillate or opposite leaves, the rest had spirally arranged leaves, and beaked corollas. Between different series, the karyotypes were not very variable. However, within Ser. *Longiflorae*, three species were sampled and two basic chromosome numbers,  $2n=16$  and 14, were recorded. The chromosome number of *P. siphonantha* var. *delavayi* was  $2n=14$ , while *P. longiflora* var. *tubiformis* and *P. tricolor* shared the same chromosome number  $2n=16$ , and the karyotypes of the latter two are similar. The count for *P. longiflora* var. *tubiformis* obtained by us differs from that from Nepalese material, which had  $2n=14$  (AMANO 1999).

However, it agrees with the only other previous count for *P. longiflora* s.l. (KRASNIKOVA *et al.* 1983), which, since the origin of the material was southern Siberia, would have belonged to var. *longiflora*, the only variety that occurs there. The karyotypes of the Nepalese and Chinese *P. longiflora* var. *tubiformis* also differed: the plants from Hengduan Mountains had 14 submetacentric and 2 subtelocentric chromosomes, while the complement of the Nepalese material had 12 metacentric and 2 submetacentric chromosomes (AMANO 1999). Our count of  $2n=14$  for *P. siphonantha* var. *delavayi* differs from the previous count for *P. siphonantha*,  $n=8$  (VERMA and DHILLON 1967). Another counts allegedly of *P. siphonantha* (also  $n=8$ ; GILL 1972) are disregarded because they were published under the name "*P. siphonantha* Hook. f.", which is a synonym of *P. rbinanthoides* Schrenk ssp. *labellata* (Jacquem.) Pennell, a species unrelated to D. Don's *P. siphonantha*. The material for the accepted count came from the western Himalayas and thus belonged to var. *siphonantha*, the only variety present there. The two varieties are disjunct and because of the difference in chromosome number it may be that var. *delavayi* deserves to be reinstated as a full species (*P. delavayi* Franch. ex Maxim.). It would be interesting to find out if the western Himalayan material of *P. siphonantha* (with  $2n=16$ ) has a simple chromocenter type (as in the Chinese var. *delavayi* and *P. integrifolia*) or the complex type, as in all the Chinese species with  $2n=16$ .

Until now, in this genus, three chromosome numbers have been reported:  $2n=12$ , 14 and 16. No species among the 13 studied by us had a base number of  $2n=12$ , which has only been reported in *P. bifida* (VERMA and DHILLON 1967, as *P. carnosus* Wall.) and *P. verticillata* (at least 14 separate publications, e.g. JOHNSON and PACKER 1968). *P. verticillata* was raised to generic rank as *Pediculariopsis* Á. and D. by LÖVE and LÖVE (1976). HUANG *et al.* (1996b), however, recorded  $2n=16$  for *P. verticillata* but their report, which disagrees with all the others, should be treated with caution in case it is based on a misidentification.

Other than *P. verticillata*, the only species that apparently have intraspecific variation in chromosome base number (assuming all material is correctly identified) are *P. siphonantha* (VERMA and DHILLON 1967; present study) and *P. longiflora* var. *tubiformis* (AMANO 1999; present study) which both belong to series *Longiflorae* and for which both  $2n=14$  and  $2n=16$  have now been found. The chromosome number  $2n=14$  had previously been reported for *P. ludwigii*, *P. bicornuta*, *P. anserantha* var. *elevatogaleata* and *P. longiflora* var. *tubiformis*, we found this base number in two additional species (*P. in-*

*tegrifolia* var. *integerrima* and *P. siphonantha* var. *delavayi*). Except for *P. longiflora* and *P. siphonantha*, both of which belong to series *Longiflorae* and have variable chromosome numbers (14 or 16), none of these five species is placed close to any of the other in existing classifications and both of *P. integrifolia* and *P. bicornuta* are particularly distinctive in the genus.

For a genus with a minimum of some 500 species arranged in at least 136 series, the chromosome counting of 13 species belonging to 11 series is still far from adequate. World-widely, 115 species belonging to at least 56 series (a few species are currently unplaced) have so far been counted. By far the majority (108) have the chromosome number of  $2n=16$ . It is most parsimonious, therefore, to propose that 8 may be the ancestral base number, as did HUANG *et al.* (1996a), since only four, disjunct and unrelated, species have so far been found to have  $2n=14$ . However, among the 71 species of 43 series in 20 sections in a molecular phylogenetic study (REE 2001), only 20 species were studied cytologically. A preliminary mapping of the chromosome numbers of the studied species on the molecular tree revealed that species with  $2n=12$  and  $2n=14$  were scatteredly distributed in the tree, implying their likely parallel evolution and possible aneuploid origin. However, both the molecular and cytological data are insufficient at the present time. It is therefore difficult to make a sound conclusion concerning chromosome evolution on the basis of the present study alone.

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