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Indigofera pseudonigrescens (Fabaceae: Papilionoideae): A new species from Sichuan, China

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Abstract

Indigofera pseudonigrescens (Fabaceae), a new species from Sichuan, China, is described and illustrated based on morphological and molecular evidence. The new species is morphologically similar to *I. nigrescens*, but differs from the latter in having shorter bracts, smaller leaflet size, and fewer leaflets whose abaxial surfaces do not become dark or black or do not have black spots when dry. Molecular analysis based on nuclear (nrITS) and plastid (*ndhJ-trnF*, *atpF-atpH*) data indicated that *I. pseudonigrescens* is clearly distant from *I. nigrescens*. The results also revealed that *I. pseudonigrescens* is phylogenetically close to *I. delavayi* which is morphologically remarkably different from *I. pseudonigrescens*.

Key Words: Indigofereae, ITS, Leguminosae, new species, Sichuan

Introduction

Indigofera Linnaeus (1753: 751) is the third largest genus in Fabaceae comprising about 750 species (Schrire *et al.* 2005, 2009). The species of the genus occur mostly in tropical and subtropical regions worldwide with four major diversity centers: Africa (ca. 550 spp.), the Sino-Himalayan region (ca. 105 spp.), Australia (ca. 50 spp.), and the New World (ca. 45 spp.) (Schrire *et al*. 2009).

In China, there are 79 species and nine varieties of *Indigofera*, of which 45 species are endemic (Gao & Schrire 2010). Southwest China has the highest species diversity of *Indigofera* in China (Yin *et al*. 1992). During extensive fieldwork conducted in this region for the systematic studies of the genus *Indigofera*, a new species was discovered from Mianning County in southwestern Sichuan, China. This species was initially identified as *I. nigrescens* Kurz ex King & Prain (1898: 286) based on morphology. *Indigofera nigrescens* is widely distributed in Asia, and one of its diagnostic characters is that the abaxial surface of its leaflets can become dark or black or have black spots when dry, which is not the case in the new species. Subsequent observations of related specimens revealed a number of differences between the new species and *I. nigrescens*. In this study, we combined morphological and molecular data to test whether the relevant specimens represent a species new to science.

Materials and methods

Morphological Study:—We collected specimens of two populations including 40 individuals from Mianning, Sichuan, China. The specimens were deposited in Herbarium of Chengdu Institute of Biology, Chinese Academy of Sciences (CDBI). Comparison of morphological characters was conducted between the putative new species and its morphologically or phylogenetically close species.

Taxon Sampling for Molecular Analysis:—To assess the phylogenetic placement of the putative new species, we conducted phylogenetic analysis based on DNA sequences of nuclear ribosomal internal transcribed spacer (nrITS)

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and plastid regions (*ndhJ-trnF* and *atpF-atpH*). Taxon sampling was chosen according to our unpublished study which built a large phylogenetic framework of *Indigofera*.

For the phylogenetic analysis based on nrITS, *Cyamopsis serrata* Schinz (1888: 161) was chosen as the outgroup following the previous study (Schrire *et al*. 2009), and one sequence of *C*. *serrata* was obtained from GenBank. Thirty-nine sequences of 34 species of *Indigofera* were uesd in this analysis. Two ITS sequences of the putative new species and one ITS sequence of *I. linnaei* Ali (1958: 549) were newly generated in this study, and the other ITS sequences of *Indigofera* species were obtained from our unpublished phylogenetic study of *Indigofera*. We selected eleven species for the phylogenetic analysis of chloroplast markers, and all the sequences used were newly generated. Voucher information and GenBank accession numbers were provided in Table 1.

TABLE 1. Vouchers and GenBank accession numbers of specimens used in this study. A dash (-) indicates missing data, an asterisk (*) denotes sequences obtained in this study. CDBI=Herbarium of Chengdu Institute of Biology, Chinese Academy of Sciences, K=Herbarium of the Royal Botanic Gardens, Kew.

Taxon	Voucher	ITS	*ndhJ-trnF*	*atpF-atpH*
Indigofera argutidens Craib	X.F. Gao *et al*. 11143 (CDBI)	KM983119	KP829979*	KP829993*
Indigofera atropurpurea Buchanan-Hamilton ex Horne-mann	X.F. Gao *et al*. 9772-3 (CDBI)	KM983123	KP829980*	KP829994*
Indigofera calcicola Craib	X.F. Gao *et al*. 9577-12 (CDBI)	KM983155	-	-
Indigofera cassioides Rottler ex Candolle	X.F. Gao & B. Xu 10033 (CDBI)	KM983156	KP829981*	KP829995*
Indigofera chaetodonta Franchet	X.F. Gao *et al*. 9616-1 (CDBI)	KM983158	-	-
Indigofera delavayi Franchet 1	X.F. Gao *et al*. 9689-19 (CDBI)	KM983168	KP829982*	KP829996*
Indigofera delavayi Franchet 2	X.F. Gao *et al*. 9689-22 (CDBI)	KM983169	-	-
Indigofera dichroa Craib	X.F. Gao *et al*. 9797 (CDBI)	KM983170	-	-
Indigofera dosua Buchanan-Hamilton ex D. Don	X.F. Gao & B. Xu 10080 (CDBI)	KM983171	KP829983*	KP829997*
Indigofera esquirolii H. Léveillé	Z.M. Zhu & W.B. Ju 396-2 (CDBI)	KM983172	-	-
Indigofera franchetii X. F. Gao & Schrire	X.F. Gao *et al*. 9380 (CDBI)	KM983178	-	-
Indigofera hancockii Craib	X.F. Gao 206 (CDBI)	KM983175	-	-
Indigofera hendecaphylla Jacquin	X.F. Gao & B. Xu 10125 (CDBI)	KM983180	-	-
Indigofera henryi Craib	X.F. Gao *et al*.9814 (CDBI)	KM983187	-	-
Indigofera heterantha Wallich ex Brandis	X.F. Gao *et al*. 9579-1 (CDBI)	KM983189	-	-
Indigofera jindongensis Y. Y. Fang & C. Z. Zheng	X.F. Gao *et al*. 11061 (CDBI)	KM983192	-	-
Indigofera kirilowii Maximowicz ex Palibin	X.F. Gao *et al*. 9831-9 (CDBI)	KM983193	KP829984*	KP829998*
Indigofera lenticellata Craib	X.F. Gao *et al*. 9564 (CDBI)	KM983201	-	-
Indigofera linnaei Ali	X.L. Zhao 219-1 (CDBI)	KP844603*	KP829985*	KP829999*
Indigofera megaphylla X. F. Gao	X.F. Gao & B. Xu 10057 (CDBI)	KM983209	-	-
Indigofera muliensis Y. Y. Fang & C. Z. Zheng	X.F. Gao *et al*. 9719-1 (CDBI)	KM983210	-	-
Indigofera myosurus Craib	X.F. Gao *et al*. 9362-1 (CDBI)	KM983183	-	-
Indigofera nigrescens Kurz ex King & Prain 1	X.F. Gao *et al*. 11433 (CDBI)	KM983214	KP829986*	KP830000*
Indigofera nigrescens Kurz ex King & Prain 2	X.F. Gao *et al*. 9759 (CDBI)	KM983217	KP829987*	KP830001*
Indigofera nigrescens Kurz ex King & Prain 3	X.F. Gao *et al*. 9780 (CDBI)	KM983218	KP829988*	KP830002*
Indigofera nigrescens Kurz ex King & Prain 4	Kingdom Ward 8517 (K)	EU729572	-	-
Indigofera pampaniniana Craib	X.F. Gao & B. Xu 10082-3 (CDBI)	KM983219	-	-
Indigofera parkesii Craib	B. Xu & X. Sun 258-1 (CDBI)	KM983222	-	-
Indigofera pendula Franchet	X.F. Gao *et al*. 9763 (CDBI)	KM983230	-	-
Indigofera pseudonigrescens 1	X.F. Gao *et al*. 9796-4 (CDBI)	KP830007*	KP829989*	KP830003*
Indigofera pseudonigrescens 2	X.F. Gao *et al*. 9738 (CDBI)	KP830008*	KP829990*	KP830004*
Indigofera reticulata Franchet	X.F. Gao *et al*. 9591-2 (CDBI)	KM983232	KP829991*	KP830005*
Indigofera rigioclada Craib	X.F. Gao *et al*. 11005 (CDBI)	KM983234	-	-
Indigofera scabrida Dunn	X.F. Gao *et al*. 9677 (CDBI)	KM983237	-	-
Indigofera sensitiva Franchet	X.F. Gao *et al*. 9363-16 (CDBI)	KM983238	-	-
Indigofera stachyodes Lindley	X.F. Gao & B. Xu 10079-1 (CDBI)	KM983248	-	-
Indigofera sticta Craib	X.F. Gao *et al*. 9680-2 (CDBI)	KM983251	KP829992*	KP830006*
Indigofera szechuensis Craib	X.F. Gao & X.L. Zhao 15912-1 (CDBI)	KM983268	-	-
Indigofera wilsonii Craib	X.F. Gao & X.M. Wei 6-6 (CDBI)	KM983281	-	-
Cyamopsis serrata Schinz	Gernishuizen 2618 (K)	EU729487	-	-

Molecular Study:—Total genomic DNA was extracted from silica-gel-dried leaves with TIANGEN plant genomic DNA extraction kit (TIANGEN Biotech., Beijing, China), following the manufacturer's protocol. We used two chloroplast markers (*ndhJ-trnF* and *atpF-atpH*) and nrITS in this study. Primer information is listed in Table 2.

TABLE 2. Primers used in this study.

Region	Primer	Sequence (5'→3')	Origin
ITS	ITS4	TCCTCCGCTTATTGATATGC	White *et al*. (1990)
	ITSA	GGAAGGAGAAGTCGTAACAAGG	White *et al*. (1990)
ndhJ-trnF	ndhJ	ATGCCYGAAAGTTGGATAGG	Shaw *et al*. (2007)
	TabE	GGTTCAAGTCCCTCTATCCC	Taberlet *et al.* (1991)
atpF-atpH	atpF	ACTCGCACACACTCCCTTTCC	Lahaye *et al*. (2008)
	atpH	GCTTTTATGGAAGCTTTAACAAT	Lahaye *et al*. (2008)

All amplifications were performed in 50µl reactions containing 34µl deionized sterile water, 3µl of 25mmol/L $MgCl_2$, 5µl Taq reaction buffer, 4µl of 2.5mmol/L dNTP, 1µl of each primer at 10 pmol/mL, 1µl (2.5 unit) Taq DNA polymerase (TIANGEN), and 1µl genomic DNA (20-100ng). The PCR program was as follows: denaturation at 94 °C for 5 min; 33 cycles of 94 °C for 45s, 54 °C for 30s and extension at 72 °C for 1 min; final extension at 72 °C for 7 min prior to holding at 12 °C forever.

The amplified products were purified using an E.Z.N.A gel extraction kit (OMEGA, Biotech., USA). The purified PCR products were sequenced by Life Technologies™ (Shanghai, China).

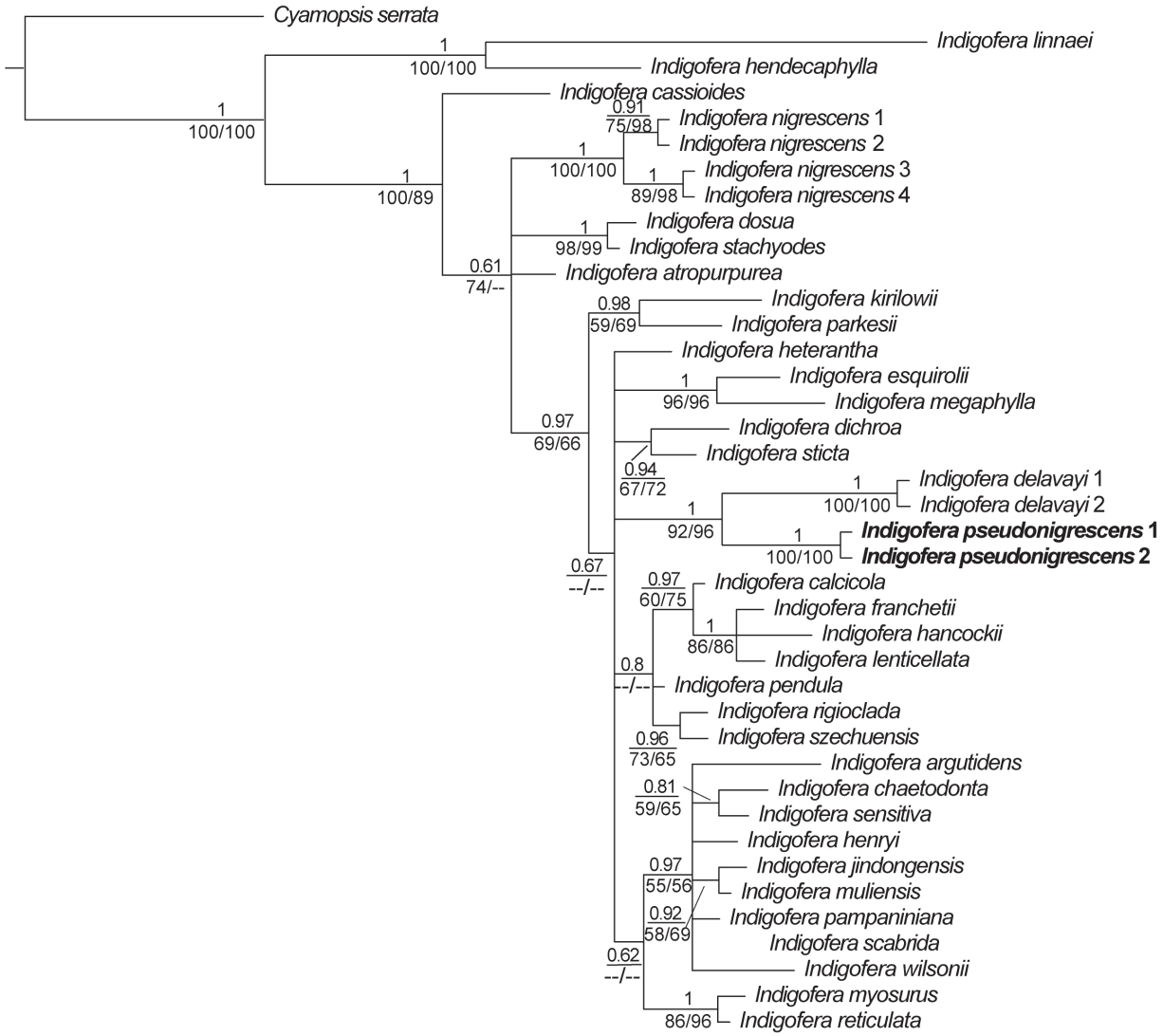

FIGURE 1. Bayesian consensus tree based on nrITS sequences. The numbers above the branches indicate the Bayesian posterior probabilities. The numbers below the branches represent the ML bootstrap supports (before the slashes) and the MP jackknife supports (after the slashes). Double dashes indicate bootstrap values and jackknife values below 50%.

The sequences were assembled and edited with the Sequencher 4.14 program (Gene Codes, Ann Arbor, MI), aligned using Clustal X 1.81 software (Thompson *et al*. 1997) and subsequently manually adjusted. The gap characters were treated as missing data. Phylogenetic trees were constructed using the maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) methods.

Unweighted maximum parsimony (MP) analysis was performed using PAUP 4.0b10 (Swofford 2002), using the heuristic search options with 1000 random replications of stepwise data addition, holding one tree for each step, TBR (tree-bisection-reconnection) swapping and saved as the optimal trees. The maximum number of trees was set to 10000, and automatically increased by 100. Parsimony jackknife (JK) analysis was performed with 1000 replicates and ca. 37% deletion. Bayesian inference was implemented in MrBayes 3.1 (Ronquist & Huelsenbeck 2003) under the GTR + I (nrITS) and HKY + I (cpDNA) model, which is found to be the best model using jModeltest 2.1.2 (Darriba *et al*. 2012). Four Markov chain Monte Carlo were run for 10,000,000 generations, starting from random trees and sampling one tree every 1000 generations. The first 2,000,000 generations (20%) were discarded as ‘‘burn-in” after using the software Tracer 1.5 (Rambaut & Drummond 2009) to check the parameter convergence and effective sample size. A 50% majority-rule consensus tree was summarized with posterior probabilities as nodal support. Maximum likelihood tree searches and ML bootstrapping were performed in RAxML v. 7.0.4 (Stamatakis *et al*. 2008) via CIPRES (http://phylobench.vital-it.ch/raxml-bb/) with 1000 rapid bootstrap analyses followed by a search for the best-scoring tree in one single run.

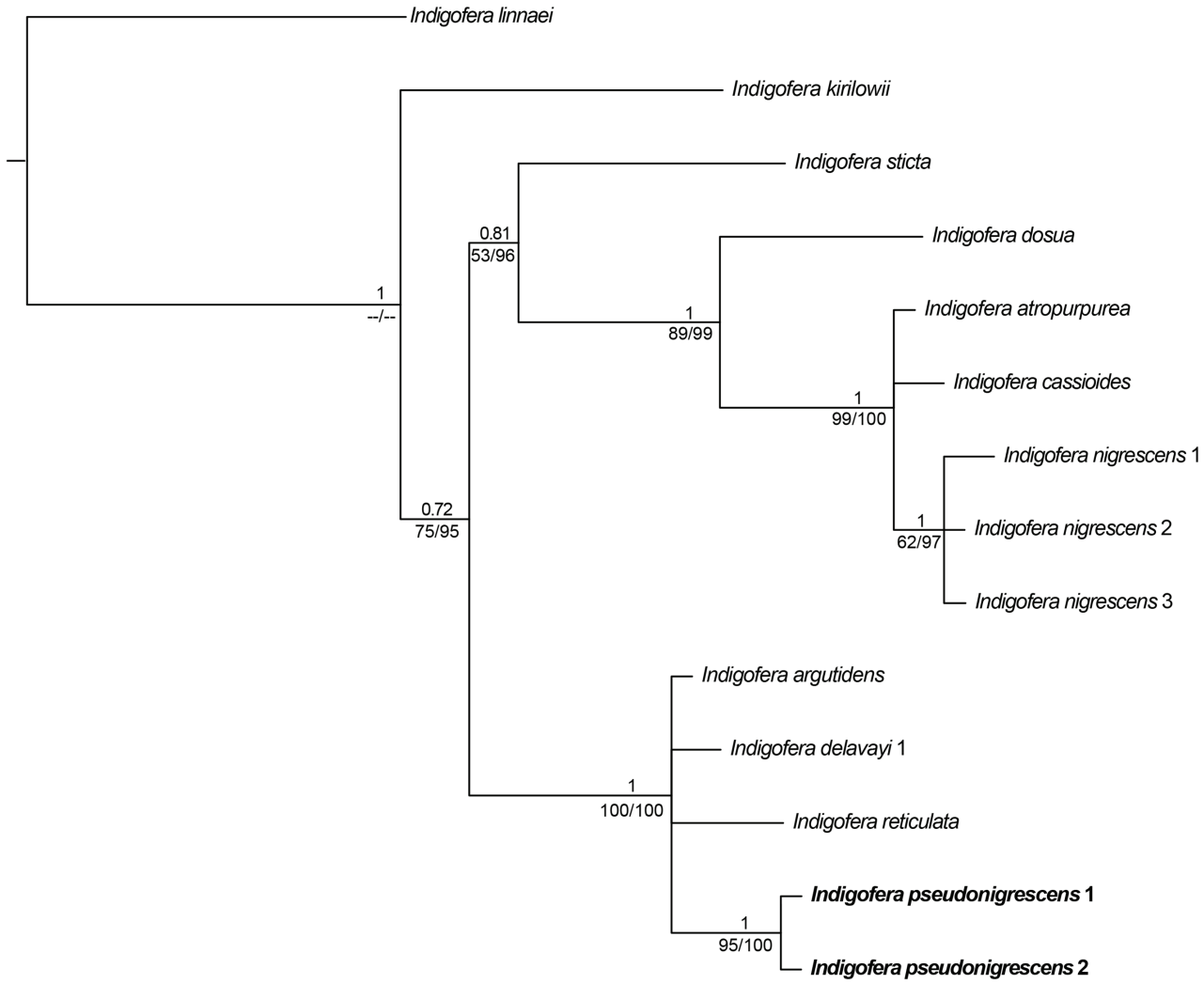

FIGURE 2. Bayesian consensus tree based on the sequences of plastid *ndhJ-trnF* and *atpF-atpH*. The numbers above the branches indicate the Bayesian posterior probabilities. The numbers below the branches represent the ML bootstrap supports (before the slashes) and the MP jackknife supports (after the slashes). Double dashes indicate bootstrap values and jackknife values below 50%.

Results

Morphological study:—*Indigofera pseudonigrescens* is similar to *I. nigrescens*, but the new species can be distinguished by the shorter bracts, smaller leaflet size, fewer number of leaflets, moreover, the abaxial surface of leaflets do not become dark or black or do not have black spots when dry. *Indigofera pseudonigrescens* is morphologically remarkably different from *I. delavayi* Franchet (1889: 154). The plants of *I. pseudonigrescens* are 0.5–1m tall, leaflets 5–13, leave 2–10 cm, petiole 4–15 mm, corolla red to purple, hair of standard brown, bract 1–1.5 mm, standard 4–6mm long × 2–3 mm wide, stamen 3–4 mm. In contrast, the plants of *I. delavayi* are 1–2 m tall, leaflets (13–)15–19, leave 8–18 cm, petiole 30–40 mm, corolla white, hair of standard white, bract 5 mm, standard 12–15(–18)mm long × 7–8 mm wide, stamen 13–17 mm. Morphological comparsions of the new species with *I. nigrescens* (morphologically close) and *I. delavayi* (phylogenetically close) are shown in Table 3.

TABLE 3. Comparision of morphological characters of *I. pseudonigrescens* with *I. nigrescens* and *I. delavayi.*

Characters	*I. nigrescens*	*I. pseudonigrescens*	*I. delavayi*
Plant height	1–2 m	0.5–1 m	1–2 m
No. of leaflets	11–23	5–13	(13–) 15–19
Leave length	8–18 cm	2–10 cm	8–18 cm
Petiole length	20–25 mm	4–15 mm	30–40 mm
Color of corolla	Red to purple	Red to purple	White or pink
Hair of standard	Brown	Brown	White
Bract length	5–7 (–9) mm	1–1.5 mm	5 mm
Standard size	6.5–7 × 4 mm	4–6 × 2–3 mm	12–15 (–18) × 7–8 mm
Stamen length	4–5 mm	3–4 mm	13–17 mm

Molecular study:—The length of the aligned matrix of nrITS was 662 bp, of which 179 were variable, and 92 were parsimony-informative. For the two plastid regions, the length of the alignment was 2250 bp, of which 108 were variable, and 23 were parsimony-informative. Molecular analysis of nrITS and plastid sequences are shown in Figs. 1 and 2. The results of nrITS revealed a sister relationship between *I. pseudonigrescens* and *I. delavayi* with a strong support. In the phylogenetic tree of plastid sequences, *I. pseudonigrescens* exhibited a close relationship to *I. delavayi*, *I. argutidens* Craib (1913: 65) and *I. reticulata* Franchet (1889: 153). Both the results of nuclear and plastid sequences support that *I. pseudonigrescens* is a species new to science.

FIGURE 3. *Indigofera pseudonigrescens*.—A. Branch.—B. Habit.—C. Inflorescens.—D and E. Magnified flower, showing standard, wings, keel, stamen, and pistil.

Description

Indigofera pseudonigrescens X.F. Gao & Xue Li Zhao, *sp. nov.* (Figs. 3, 4).

Type:—CHINA. Sichuan: Miansha Town, Mianning County, 1400 m, 28°26’57”N, 101°52’20”E, 2 August 2007, *X.F. Gao et al. 9796* (holotype CDBI!, isotypes CDBI!).

FIGURE 4. *Indigofera pseudonigrescens*.—A. Habit.—B. Leaflet blade above, showing detail of pilosity.—C. 2-branched trichomes.—D. Flower.—E. Standard.—F. Wing.—G. Keel.—H. Stamens and pistil.—I. Anther.—J. Calyx. Illustration drawn by Jian Li based on the holotype, *X.F. Gao et al. 9796-10*.

Shrubs, erect, 50–100 cm tall. Stems reddish brown; young braches green, striate, with appressed white and brown medifixed symmetrically 2-branched trichomes. Stipules linear, ca. 3mm. Leaves 2–10 cm, 5–13-foliolate; petiole and rachis with dense appressed medifixed trichomes; petiole 0.4–1.5 cm; rachis adaxially grooved; stipels narrowly triangular, ca. 1 mm; leaflet blades opposite or subopposite, elliptic to obovate-elliptic, (0.7–)1–2.5 × 0.4–1.2 cm, papery, abaxially with short appressed medifixed trichomes, adaxially with dense longer appressed medifixed trichomes, base broadly cuneate to rounded, apex obtuse and mucronate. Racemes (3–)5–19(–26) cm; peduncle ca. 0.5–2.3 cm; bracts linear, 1–1.5 mm, abaxially with brown medifixed trichomes, caducous. Pedicel ca. 1 mm, with brown medifixed trichomes. Calyx 2–2.5 mm, with appressed brown and white medifixed trichomes; tube ca. 1 mm; teeth narrowly triangular, 1–1.5 mm. Corolla red to purple; standard ovate, 4–6 × 2–3 mm, outside with appressed brown and white medifixed trichomes, apex acute, inside apex hairy; wings ca. 4 mm, margin ciliate; keel slightly longer than wings, outside apically with appressed brown and white trichomes, spur ca. 1 mm. Stamens 4–5 mm; anthers ovoid-globose, base with a few trichomes. Ovary glabrous. Legume cylindric, with dense appressed brown and white trichomes when young. Fl. Jun.–Sep., fr. unknown.

Distribution and habitat:—*Indigofera pseudonigrescens* is known from Mianning and Yanbian County in southwestern Sichuan, growing on roadside, hill slopes, forest margins at elevation of 1400–2000 m.

Etymology:—The epithet refers to its resemblance to *Indigofera nigrescens*.

Additional specimens examined:—CHINA. Sichuan Province: Mianning County, Maidigou Town, 28° 19’14’’N, 101°54’26’’E, 1500 m, 4 July 2014, X.L. Zhao 2014-1 (CDBI); Yanbian County, Gesala Town, 27°04’14’’N, 101°20’27’’E, 1760 m, 29 July 2007, *X.F. Gao et al. 9738* (CDBI).

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