

## Phylogenetic Analyses for a New Classification of the *Desmodium* Group of *Leguminosae* Tribe *Desmodieae*

Kazuaki OHASHI<sup>a</sup>, Hiroyoshi OHASHI<sup>b,\*</sup>, Tomoyuki NEMOTO<sup>c</sup>,  
Tatsuki IKEDA<sup>a</sup>, Haruna IZUMI<sup>a</sup>, Haruna KOBAYASHI<sup>a</sup>,  
Hirokazu MURAGAKI<sup>a</sup>, Koji NATA<sup>a</sup>, Natsumi SATO<sup>a</sup> and Maika SUZUKI<sup>a</sup>

<sup>a</sup>School of Pharmacy, Iwate Medical University, Yahaba, Iwate, 028-3694 JAPAN ;

<sup>b</sup>Herbarium TUS, Botanical Garden, Tohoku University, Sendai, 980-0862 JAPAN;

<sup>c</sup>Department of Biological Sciences, Faculty of Science and Engineering,

Ishinomaki Senshu University, Ishinomaki, 986-8580 JAPAN

\*Corresponding author: ohashi@m.tohoku.ac.jp

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The tribe *Desmodieae* (*Leguminosae*/*Fabaceae*), comprising 33 genera, is subdivided into the *Desmodium* group, *Phyllodium* group and *Lespedeza* group. The *Desmodium* group consists of 20 genera, but includes a polyphyletic genus *Desmodium*. We used molecular phylogenetic analyses to resolve the polyphyly of *Desmodium*. Both nuclear ITS (ITS1, 5.8S and ITS2) and nine chloroplast regions (*5'trnK* intron, *ndhJ-trnL-trnF*, *trnT-trnL*, *trnG-trnS*, *trnQ-rps16*, *trnL-rpl32*, *rpl16* intron, *trnC-rpoB* and *ndhA* intron) of DNA were examined for this study. New phylogenetic trees deduced from the results of our analyses are provided. Based on the phylogenetic results with morphological and palynological characters, new taxonomic treatments are proposed for *Desmodium campylocaulon*, *D. concinnum*, *D. dichotomum*, *D. pycnostachyum*, *D. renifolium*, *D. gangeticum*, *D. oblongum* and *Codariocalyx microphyllus*. Of these eight species, each of the first five is proposed as representative of a new genus, *Desmodiopsis*, *Tateishia*, *Bouffordia*, *Oxytes* and *Huangtcia*, respectively. The sixth species is recognized as *Pleurolobus gangeticus* (L.) J. St.-Hil. and the last two are transferred to *Uraria* and *Leptodesmia*, respectively. Consequently, 26 genera are recognized in the *Desmodium* group in this paper.

**Key words:** *Bouffordia*, *Desmodiopsis*, *Desmodium*, *Huangtcia*, *Oxytes*, phylogenetic analyses, *Pleurolobus*, *Tateishia*, tribe *Desmodieae*, *Uraria*.

*Desmodium* was distinguished by Desvoux (1813, 1826) from the genus *Hedysarum* in Linnaeus' (1753) *Species Plantarum*. *Lourea* and *Uraria* were also separated from *Hedysarum*. Natural classification systems of *Desmodium* and its related genera had been proposed by Candolle (1825), Bentham (1852, 1865), who circumscribed these genera as *Hedysareae* subtribe *Desmodieae*, Schindler (1924a, 1924b,

1928), Hutchinson (1964), who recognized *Desmodieae* at tribal rank, Ohashi (1971, 1973, 2004a, 2004b, 2005), Ohashi, Polhill and Schubert (1981), Pedley (1999), and Ohashi and Ohashi (2018a, 2018b). The tribe is currently divided into the *Desmodium* group, *Phyllodium* group and *Lespedeza* group (Ohashi 2005) and comprises 33 genera (Ohashi and Ohashi 2018a). Each of the groups has been considered

to be monophyletic (Nemoto et al. 2010, Han et al. 2010, Xu et al. 2012, Ohashi and Nemoto 2014, Jabbour et al. 2018).

The *Desmodium* group was established to include 16 genera: *Alysicarpus*, *Christia*, *Codariocalyx*, *Desmodiastrum*, *Desmodium*, *Eleiotis*, *Hegnera*, *Hylodesmum*, *Leptodesmia*, *Mecopus*, *Meliniella*, *Monarthrocarpus*, *Pseudarthria*, *Pycnospora*, *Trifidacanthus* and *Uraria* (Ohashi 2005). Four genera later added to the group were *Ototropis* (Ohashi and Ohashi 2012a, 2013b), *Verdesmum* (Ohashi and Ohashi 2012b, 2013a), *Grona* (Ohashi and Ohashi 2018a) and *Sohmaea* (Ohashi and Ohashi 2018b). Of these 20 genera *Alysicarpus*, *Christia*, *Desmodiastrum*, *Eleiotis*, *Mecopus*, *Meliniella*, *Pseudarthria*, *Pycnospora*, and *Uraria* have independently been recognized apart from *Desmodium* since their foundation, whereas nine genera, *Codariocalyx*, *Grona*, *Hegnera*, *Hylodesmum*, *Monarthrocarpus*, *Ototropis*, *Sohmaea*, *Trifidacanthus* and *Verdesmum*, were separated from *Desmodium*. The number of species in these genera are at present as follows: *Desmodium* ca. 200, *Grona* 41, *Alysicarpus* 25–30, *Uraria* ca. 20, *Hylodesmum* 14, *Ototropis* 13, *Christia* ca. 10, *Sohmaea* 7, *Pseudarthria* 3 or 4, *Codariocalyx* 3, *Desmodiastrum* 3, *Leptodesmia* 3, *Eleiotis* 2, *Monarthrocarpus* 2, *Verdesmum* 2, *Hegnera* 1, *Mecopus* 1, *Meliniella* 1, *Pycnospora* 1, and *Trifidacanthus* 1 (Ohashi 2005, Ohashi and Ohashi 2018a, 2018b). *Desmodium* is the largest and core genus of the group.

Recently, however, polyphyly of *Desmodium* has been suggested by molecular analyses of the tribe *Desmodieae* (Kajita et al. 1996, [2010 unpublished], Jabbour et al. 2018). The *Desmodium* group forms a single clade in the phylogenetic tree by Jabbour et al. (2018, ‘clade C’ in fig. 4). Jabbour et al. examined five species of *Desmodium*: *D. adscendens*, *D. heterocarpon*, *D. heterophyllum*, *D. intortum* and *D. velutinum*. Except for *D. intortum* of subgenus *Desmodium*, the other species belong to subgenus *Sagotia* in

Ohashi’s (1973) system. The first two species belong to sections *Nicolsonia*, the third to section *Sagotia* and the last to section *Heteroloma*. These were divided into three clades comprising *D. adscendens* and *D. intortum*, *D. heterocarpon* and *D. heterophyllum*, and *D. velutinum*. *Alysicarpus*, *Codariocalyx*, *Hegnera*, *Leptodesmia*, *Meliniella* and *Uraria crinita* were placed between the three clades in the phylogenetic trees of Jabbour et al. (2018, figs. 2 and 4). These trees clearly indicate the paraphyly of *Desmodium*.

In comparison, ‘clade C’ of Jabbour et al. (2018) may be interpreted as suggesting a single monophyletic genus, *Desmodium*, including *Alysicarpus*, *Christia*, *Codariocalyx*, *Hegnera*, *Leptodesmia*, *Mecopus*, *Meliniella* and *Uraria*. However, as was discussed in “how to circumscribe *Desmodium*” by Ohashi et al. (1981), we follow the basic concept for classifying the tribe *Desmodieae* by “maintaining most familiar generic names and adding relatively few additional segregates that are, for the most part, fairly readily recognisable” as being the most advantageous course (Ohashi et al. 1981). Morphological similarities or differences among the species or infrageneric taxa of *Desmodium* are, however, not always supported by results of recent phylogenetic molecular analyses (e.g., Ohashi and Ohashi 2018b). A new classification of the *Desmodium* group of *Desmodieae* proposed here is based on results of our phylogenetic molecular analyses in case that the results show discrepancy for the present system.

*Desmodium* is now composed of subgenera *Desmodium*, *Sagotia* and *Acanthocladum* in the sense of Ohashi (1973) and Pedley (1999). Subgenus *Desmodium* was treated as being composed of two sections: *Desmodium* and *Angustistipulosa* (Ohashi 1973), but section *Angustistipulosa* is now separated as the independent genus *Sohmaea* (Ohashi and Ohashi 2018b). The remaining section *Desmodium* includes *D. scorpiurus* (Sw.) Desv.

and almost all the species native to the Americas, which were regarded by Schindler (1924a) as *Meibomia* Möhring (= *Meibomia* Heist. ex Fabr.) and distinct from *Desmodium* based on morphological evidence. Schubert (1950) recognized five series for the North American species of *Desmodium* in the sense of Bentham (1865) and suggested a further classification system for Schindler's *Meibomia* as a subgenus (Schubert 1963), but her system was not published. The American taxa of subgenus *Desmodium* diversified into numerous species, but an infrageneric system is incomplete as reviewed by Lima et al. (2014).

In contrast, subgenus *Sagotia*, distributed in Asia and Oceania, was classified into infrageneric taxa in the systems of Ohashi (1973) and Pedley (1999). The subgenus was divided into six sections, of which sections *Nicolsonia* and *Sagotia* were separated as the distinct genus *Grona* (Ohashi and Ohashi 2018a). The remaining sections *Chararioides*, *Heteroloma*, *Oxytes*, and *Renifolia* were adopted by Ohashi (1973) and section *Desmodiopsis* was added by Pedley (1999). Of the seven sections, no samples of *Chararioides*, *Oxytes*, *Renifolia* and *Desmodiopsis* were examined by Jabbour et al. (2018), but representatives of all of these sections were analyzed in our study.

The genus *Desmodium* is still problematic, because it was suggested to be polyphyletic on the basis of the results from the molecular analyses by Kajita et al. (1996, [2010 unpublished]) and Jabbour et al. (2018). The intent of this paper, therefore, is to clarify the phylogenetic relationships among the genera and infrageneric taxa in the *Desmodium* group in detail. Three new phylogenetic trees deduced from the results of our analyses are provided. Eight new taxonomic treatments are proposed for phylogenetically independent species and their relatives. They include 1) *Desmodiopsis* based on *Desmodium campylocaulon*, 2) *Tateishia* on *D. concinnum*, 3) *Bouffordia* on *D. dichotomum*, 4) *Oxytes* on *D. pycnostachyum*, 6)

*Huangtcia* on *D. renifolium*, 6) *Pleurolobus* on *D. gangeticum*, 7) *D. oblongum* on *Uraria* and 8) *Codariocalyx microphyllus* on *Leptodesmia*. As a result, the *Desmodium* group includes 26 genera.

This paper was prepared through the collaboration of three research groups. The molecular analyses were performed by K. Ohashi with members of Iwate Medical University since 2015; taxonomic considerations were worked out by H. Ohashi and K. Ohashi; and the manuscript was prepared through discussions between H. Ohashi, K. Ohashi and Nemoto.

## Materials and Methods

### Materials

Plant materials are listed in Table 1. Samples were basically collected from herbarium specimens kept in A, NOU, TUS. The samples of *Pseudarthria hookeri* and *Christia vespertilionis* were collected from fresh leaves of cultivated plants in Iwate Medical University. Voucher specimens of these plants are deposited in TUS.

### DNA extraction, amplification and sequencing

Genomic DNA was extracted from the leaf tissue using Cica genus DNA Prep Kit (for Plant) (KANTO KAGAKU, Japan). PCR amplification of the markers was performed on the ITS (internal transcribed spacer) and nine chloroplast regions: 5'*trnK* intron (upstream sequence of *matK*), *ndhJ-trnL-trnF* (*trnL* intron and *trnF-trnL* spacer), *trnT-trnL* spacer, *trnG-trnS* (*trnG* intron and *trnG-trnS* spacer), *trnQ-rps16* (*trnQ-rps16* spacer and *rps16* intron), *trnL-rpl32* spacer, *rpl16* intron, *trnC-rpoB* spacer and *ndhA* intron. The PCR primers used for these markers are as follows: *trnK1L* (Hu et al. 2000) and *trnK810R* (5'-AAA GTG GGT ATA GGA TGT CCT G-3') for *trnK*, *ndhJ2* (5'-CCC GAA AGT TGG ATA GGA TGG CC-3') and primer 'c' (Taberlet et al. 1991) for *ndhJ*-

Table 1. List of voucher specimens for this paper

Taxon	Locality and date	Collector no. (Herbarium)
<i>Alysicarpus bupleurifolius</i>	Taiwan. Pingtung Co., Hsiao-chien-shih-shan. 6 Oct. 1990.	T. C. Huang & M. J. Wu 14826 (TUS)
<i>Alysicarpus monilifer</i>	Myanmar. Magway Division. 30 Nov. 2002.	J. Murata & al. 024801 (TUS)
<i>Alysicarpus ovalifolius</i>	USA. Florida, Leon Co., downtown Tallahassee. 8 Oct. 1997.	H. Ohashi & al. 61095 (TUS)
<i>Alysicarpus rugosus</i>	Myanmar. Magway Division. 20 Nov. 2011.	L. S. Man 087879 (TUS)
<i>Alysicarpus vaginalis</i>	Japan. Okinawa Pref. Yaeyama-gun, Taketomi-cho. 16 Apr. 1998.	K. Yonekura & al. 98078 (TUS)
<i>Christia obcordata</i>	Japan. Okinawa Pref., Isl. Iriote. 15 Nov. 2004.	K. Yonekura 12047 (TUS)
<i>Christia vespertilionis</i>	Japan. Iwate Pref. Cult. in Iwate Medical Univ. 4 Aug. 2017.	K. Ohashi 2981 (TUS)
<i>Codariocalyx gyroides</i>	Nepal. Chitwan Distr., Sayraga (alt. 160m) – Padampur. 17 Jan. 1996.	K. Yoda & al. 9614111 (TUS)
<i>Codariocalyx microphyllus</i>	China. Hunan Prov., Mt. Mangshan. 1 Jul. 2005.	Xiao Bai-Zhong 4362 (TUS)
<i>Codariocalyx motorius</i>	Taiwan. Taitung Co., Hungyeh. 21 Oct. 1992.	J. M. Hu & K. H. Wang 849 (TUS)
<i>Desmodium acanthocladum</i>	Australia. New South Wales. Wilsons River, ca. 2 km S of Wyrallah. 7 Feb. 1987.	R. Pullen 11140 (TUS)
<i>Desmodium campylocaulon</i>	Australia. Northern Territory. North from “Creswell Downs”. 16 June 1974.	R. Pullen 9274 (TUS)
<i>Desmodium canadense</i>	USA. Massachusetts, Hampden Co., Holyoke. 13 Aug. 2008.	D. E. Boufford & Mehrhoff 40526 (TUS)
<i>Desmodium concinnum</i>	Nepal. Seti Zone, Bajhang Distr., Roshidanda – Aagar. 22 Aug. 1991.	M. Suzuki & al. 9160908 (TUS)
<i>Desmodium cuspidatum</i>	USA. Iowa. Van Buren Co., Lacey-Keosauqua State Park. 24 Aug. 1995.	T. Nemoto & J. Yokoyama 95824002 (TUS).
<i>Desmodium dichotomum</i>	Myanmar. Magway Division. 20 Nov. 2011.	L. S. Man 087882 (TUS)
<i>Desmodium floridanum</i>	USA. Florida, Leon Co., north of Elinor Klapp Phipps Park. 8 Oct. 1997.	H. Ohashi & al. 61075 (TUS)
<i>Desmodium gangeticum</i>	Japan. Miyagi Pref., Sendai. Cult. in Tohoku Univ. (Origin: Nepal). 1 Feb. 1998.	N. Sasamoto 80201 (TUS)
<i>Desmodium gangeticum 2</i>	Taiwan. Changhua Hsien, Lukang Town. 18 Apr. 1999.	K. F. Chung 1148 (TUS)
<i>Desmodium incanum</i>	Japan. Okinawa Pref., Yaeyama-gun. Isl. Iriote. 10 Dec. 2002.	K. Yonekura 9667 (TUS)
<i>Desmodium laevigatum</i>	USA. Florida, Leon Co., North of Elinor Klapp Phipps Park. 8 Oct. 1997.	H. Ohashi & al. 61073 (TUS).
<i>Desmodium marilandicum</i> (var. <i>marilandicum</i> )	USA. Missouri. Barry Co., Roaring River State Park. 16 Aug. 1995.	T. Nemoto & J. Yokoyama 95816016 (TUS).
<i>Desmodium oblongum</i>	Japan. Miyagi Pref., Sendai. Cult. in Tohoku Univ. (Origin: Thailand). 13 Feb. 1997.	H. Ohashi 97214 (TUS)
<i>Desmodium pycnostachyum</i>	New Caledonia. Koutio. 9 Sep. 1992.	H. S. McKee 45980 (NOU)
<i>Desmodium renifolium</i>	Japan. Miyagi Pref., Sendai. Cult. in Tohoku Univ. (Origin: Thailand). 8 Feb. 1999.	N. Sasamoto 902081 (TUS)
<i>Desmodium rotundifolium</i>	USA. Alabama. Barbour Co., Eufala. 10 Jun. 1998.	MacDonald 11424 (TUS).
<i>Desmodium scorpiurus</i>	Taiwan. Kaohsiung Co., Chia-hsien, Tai-yang-ku. 3 Nov. 1989.	T. C. Huang & W. T. Huang 14490 (TUS).
<i>Desmodium tenuifolium</i>	USA. North Carolina. Scotland Co., Sandhills Game land. 4 Aug. 1995.	H. Ohashi & al. 95804107 (TUS).
<i>Desmodium tortuosum</i>	USA. Georgia. Effingham Co., Savannah River. 6 Aug. 1995.	H. Ohashi & al. 9580602-1 (TUS)
<i>Desmodium viridiflorum</i>	USA. Kentucky. Lyon Co., Confederate. 5 Oct. 1996.	H. Ohashi & al. 60110 (TUS).
<i>Eleiotis sororia</i>	Myanmar. Magwe Division, between Irrawaddy Riber and Saw Town. 30 Nov. 2002.	J. Murata & al. 24817 (TUS)
<i>Grona adscendens</i> (var. <i>adscendens</i> )	Mexico. Mupio. Atoyac de Alvarez. 19 Aug. 1985.	J. C. Soto Munez 10102 (TUS)
<i>Grona barbata</i>	Brazil. Para. Belem, in the premises of EMBRAPA/CPATU. 10 Nov. 1992.	H. Iketani 2849 (TUS)
<i>Grona filiformis</i>	Australia. Queensland. Upper Clifdale Creek area. 28 Jul. 1998.	R. Pullen 9131 (TUS)
<i>Grona glareosa</i>	Australia. Northern Territory. CSIRO Kapalga Research Station. 20 Mar. 1990.	R. Pullen 11276 (TUS)
<i>Grona griffithiana</i>	China. Yunnan. Dali Baizu Zizhishou. 30 Aug. 1984.	K. Iwatsuki & al. 1634 (TUS)
<i>Grona heterocarpa</i>	Japan. Kochi Pref., Kami Co., Kagami town, Masamitsu. 21 Sep. 2002.	N. Yamashita FOK605319 (TUS)
<i>Grona heterophylla</i>	Taiwan. Taipei Co., Tsaolingkutoa. 17 Sep. 2000.	Huan-Yu Chen 1544 (TUS)
<i>Grona trichostachya</i>	Australia. Northern Territory., Narramoor Lagoon. 20 Mar. 1990.	R. Pullen 11279 (TUS)
<i>Grona triflora</i>	Japan. Okinawa Pref., Yaeyama-gun, Taketomi-cho, Isl. Iriote. 2 Apr. 2004.	K. Yonekura & K. Yasuda 11200 (TUS)
<i>Hegnara obcordata</i>	Cambodia. Kamchay, Kampot Liane. 16 Nov. 1933.	Poilane 22850 (TUS)
<i>Hylodesmum podocarpum</i> (subsp. <i>podocarpum</i> )	Japan. Miyagi Pref., Sendai. Cult. at Nijinooka. 10 Sep. 2004.	H. Ohashi 68914 (1 of 2) (TUS)
<i>Leptodesmia congesta</i>	India. Travancore High Ranges. 18 Dec. 1937.	E. Barnes No. 5 (A)
<i>Lespedeza cyrtobotrya</i>	Japan. Nagano Pref., Suzaka-shi. Garyu Koen, Suda-jyo site. 29 Sep. 2014.	H. Ohashi 780934 (TUS)
<i>Mecopus nidulans</i>	China. Hainan, Sanya. 25 Oct. 1983.	Y. Tateishi & al. 1025001 (TUS)
<i>Ohwia caudata</i>	Japan. Shiga Pref., Higashioomi-shi. 22 Sep. 2008.	Murata & Mori 88083 (TUS)
<i>Ototropis elegans</i>	Japan. Miyagi Pref., Sendai. Cult. at Nijinooka. 15 Oct. 2008.	H. Ohashi 721015 (TUS)
<i>Pseudarthria hookeri</i>	Japan. Iwate Pref., Cult. in Iwate Medical Univ. (Origin: South Africa).	K. Ohashi (TUS)
<i>Pycnospora lutescens</i>	Taiwan. Taitung Co., Yenping Hsiang. 11 Jan. 1996.	T. Y. Liu 1202 (TUS)
<i>Sohmaea diffusa</i>	Taiwan. Kaohsiung Co., Liu-kuei, Tsai-tieh-ku. 16 Oct. 1989.	T. C. Huang & al. 14456 (TUS)
<i>Sohmaea gracillima</i>	Japan. Miyagi Pref., Sendai. Cult. in Tohoku Univ. (Origin: Taiwan). 7 Nov. 1983.	Y. Tateishi 10292 (TUS)
<i>Sohmaea hispida</i>	Myanmar. Chin State, Natma Taung National Park. 4 Sep. 2012.	L. S. Man 091650 (TUS)
<i>Sohmaea laxiflora</i>	Japan. Miyagi Pref., Sendai. Cult. in Tohoku Univ. (Origin: Nepal). 25 Sep. 1998.	N. Sasamoto 809254 (TUS)
<i>Sohmaea teres</i>	Myanmar. Chin State, Natma Taung National Park. 3 Sep. 2013.	K. Fujisawa & al. 094972 (TUS)
<i>Sohmaea zonata</i>	Taiwan. Taitung Co., Hungyeh. 21 Oct. 1992.	J. M. Hu & K. H. Wang 853 (TUS)
<i>Trifidacanthum unifoliatum</i>	China. Hainan, Dongfang Co., Datian District, Datian. 20 Oct. 1993.	Y. Tateishi & al. 1020113 (TUS)
<i>Uraria crinita</i>	Japan. Miyagi Pref., Sendai. Cult. in Tohoku Univ. (Origin: Nepal). 25 Sep. 1998	N. Sasamoto 809254 (TUS)
<i>Uraria lagopodioides</i>	Taiwan. Pingtung, Chingshuiyen. 5 Oct. 1990.	T. C. Huang & M. J. Wu 14812 (TUS)
<i>Uraria picta</i>	Nepal. Seti Zone., Bajura Distr., Tolebhir (1700 m) – Berma (1170 m). 9 Aug. 1991.	M. Suzuki & al. 9191248 (TUS)
<i>Uraria poilanei</i>	Myanmar. Magway Division. 10 Dec. 2002.	J. Murata & al. 25276 (TUS)
<i>Uraria rufescens</i>	Myanmar. Mt. Popa, Kyaaukpadaung Township. 11 Dec. 2002.	J. Murata & al. 25314 (TUS)



Table 2. Taxon, GenBank accession number for 5'*trnK* intron, *ndhJ-trnF-trnL*, *trnT-trnL*, *trnG-trnS*, *trnQ-rps16*, *trnL-rpl32*, *rpl16* intron, *trnC-rpoB*, *ndhA* intron and ITS

*Alysicarpus bupleurifolius*: LC378020, LC378320, LC378200, LC377960, LC378260, LC378080, LC377656, LC378140, LC377716, LC377381; *Alysicarpus monilifer*: LC378022, LC378322, LC378202, LC377962, LC378262, LC378082, LC377658, LC378142, LC377718, LC377383; *Alysicarpus ovalifolius*: LC378023, LC378323, LC378203, LC377963, LC378263, LC378083, LC377659, LC378143, LC377719, LC377384; *Alysicarpus rugosus*: LC378024, LC378324, LC378204, LC377964, LC378264, LC378084, LC377660, LC378144, LC377661, LC378145, LC377721, LC377386; *Codariocalyx vaginalis*: LC378021, LC378321, LC378201, LC377961, LC378261, LC378081, LC377657, LC378141, LC377717, LC377382; *Christia obcordata*: LC378028, LC378328, LC378208, LC377968, LC378268, LC378088, LC377664, LC378148, LC377724, LC377389; *Christia vespertilionis*: LC378026, LC378326, LC378206, LC377966, LC378266, LC378086, LC377662, LC378146, LC377722, LC377387; *Codariocalyx gyroides*: LC378025, LC378325, LC378205, LC377965, LC378265, LC378085, LC377661, LC378145, LC377721, LC377386; *Codariocalyx microphyllus*: LC378043, LC378343, LC378223, LC377983, LC378283, LC378103, LC377679, LC378163, LC377739, LC377404; *Codariocalyx motorius*: LC378027, LC378327, LC378207, LC377967, LC378267, LC378087, LC377663, LC378147, LC377723, LC377388; *Desmodium campylocaulon*: LC378055, LC378355, LC378235, LC377995, LC378295, LC378115, LC377691, LC378175, LC377751, LC377416; *Desmodium canadense*: LC378031, LC378331, LC378211, LC377971, LC377871, LC378091, LC377667, LC378151, LC377727, LC377392; *Desmodium concinnum*: LC378017, LC378317, LC378197, LC377957, LC378257, LC378077, LC377653, LC378137, LC377713, LC377378; *Desmodium cuspidatum*: LC378032, LC378332, LC378212, LC377972, LC378272, LC378092, LC377668, LC378152, LC377728, LC377393; *Desmodium dichotomum*: LC378033, LC378333, LC378213, LC377973, LC378273, LC378093, LC377669, LC378153, LC377729, LC377394; *Desmodium floridanum*: LC378035, LC378335, LC378215, LC377975, LC378275, LC378095, LC377671, LC378155, LC377731, LC377396; *Desmodium gangeticum*: LC378036, LC378336, LC378216, LC377976, LC378276, LC378096, LC377672, LC378156, LC377732, LC377397; *Desmodium gangeticum* 2: LC378014, LC378314, LC378194, LC377954, LC378254, LC378074, LC377650, LC378134, LC377710, LC377375; *Desmodium incanum*: LC378039, LC378339, LC378219, LC377979, LC378279, LC378099, LC377675, LC378159, LC377735, LC377400; *Desmodium laevigatum*: LC378040, LC378340, LC378220, LC377980, LC378280, LC378100, LC377676, LC378160, LC377736, LC377401; *Desmodium marilandicum*: LC378042, LC378342, LC378222, LC377982, LC378282, LC378102, LC377678, LC378162, LC377738, LC377403; *Desmodium oblongum*: LC378044, LC378344, LC378224, LC377984, LC378284, LC378104, LC377680, LC378164, LC377740, LC377405; *Desmodium pycnostachyum*: LC378045, LC378345, LC378225, LC377985, LC378285, LC378105, LC377681, LC378165, LC377741, LC377406; *Desmodium renifolium*: LC378046, LC378346, LC378226, LC377986, LC378286, LC378106, LC377682, LC378166, LC377742, LC377407; *Desmodium rotundifolium*: LC378047, LC378347, LC378227, LC377987, LC378287, LC378107, LC377683, LC378167, LC377743, LC377408; *Desmodium scorpiurus*: LC378048, LC378348, LC378228, LC377988, LC378288, LC378108, LC377684, LC377744, LC377409; *Desmodium tenuifolium*: LC378050, LC378350, LC378230, LC377990, LC378290, LC378110, LC377686, LC378170, LC377746, LC377411; *Desmodium tortuosum*: LC378049, LC378349, LC378229, LC377989, LC378289, LC378109, LC377685, LC378169, LC377745, LC377410; *Desmodium viridiflorum*: LC378052, LC378352, LC378232, LC377992, LC378292, LC378112, LC377688, LC378172, LC377748, LC377413; *Eliotis sororia*: LC378054, LC378354, LC378234, LC378294, LC377994, LC378114, LC377690, LC378174, LC377750, LC377415; *Grona adscendens*: LC378029, LC378329, LC378209, LC377969, LC378269, LC378089, LC377665, LC378149, LC377725, LC377390; *Grona barbata*: LC378030, LC378330, LC378210, LC377970, LC378270, LC378090, LC377666, LC378150, LC377726, LC377391; *Grona filiformis*: LC378013, LC378313, LC378193, LC377953, LC378253, LC378073, LC377649, LC378133, LC377709, LC377374; *Grona glareosa*: LC378019, LC378319, LC378199, LC377959, LC378259, LC378079, LC377655, LC378139, LC377715, LC377380; *Grona griffithiana*: LC378018, LC378318, LC378198, LC377958, LC378258, LC378078, LC377654, LC378138, LC377714, LC377379; *Grona heterocarpa*: LC378037, LC378337, LC378217, LC377977, LC378277, LC378097, LC377673, LC378157, LC377733, LC377398; *Grona heterophylla*: LC378038, LC378338, LC378218, LC377978, LC378278, LC378098, LC377674, LC378158, LC377734, LC377399; *Grona trichostachya*: LC378015, LC378315, LC378195, LC377955, LC378255, LC378075, LC377651, LC378135, LC377711, LC377376; *Grona triflora*: LC378051, LC378351, LC378231, LC377991, LC378291, LC378111, LC377687, LC378171, LC377747, LC377412; *Hegnerea obcordata*: LC378056, LC378356, LC378236, LC377996, LC378296, LC378116, LC377692, LC378176, LC377752, LC377417; *Hylodesmum podocarpum*: LC378058, LC378358, LC378238, LC377998, LC378298, LC378118, LC377694, LC378178, LC377754, LC377419; *Leptodesmia congesta*: LC378060, LC378360, LC378240, LC378080, LC378300, LC378120, LC377696, LC378180, LC377756, LC377421; *Lespedeza cyrtobotrya*: LC378059, LC378359, LC378239, LC377999, LC378299, LC378119, LC377695, LC378179, LC377755, LC377420; *Mecopus nidulans*: LC378061, LC378361, LC378241, LC378001, LC378301, LC378121, LC377697, LC378181, LC377757, LC377422; *Ohwia caudata*: LC378062, LC378362, LC378242, LC378002, LC378302, LC378122, LC377698, LC378182, LC377758, LC377423; *Ototropis elegans*: LC378063, LC378363, LC378243, LC378003, LC378303, LC378123, LC377699, LC378183, LC377759, LC377424; *Pseudarthria hookeri*: LC378065, LC378365, LC378245, LC378005, LC378305, LC378125, LC377701, LC378185, LC377761, LC377426; *Pycnospora lutescens*: LC378064, LC378364, LC378244, LC378004, LC378304, LC378124, LC377700, LC378184, LC377760, LC377425; *Sohmaea diffusa*: LC378034, LC378334, LC378214, LC377974, LC378274, LC378094, LC377670, LC378154, LC377730, LC377395; *Sohmaea gracillima*: LC378016, LC378316, LC378196, LC377956, LC378256, LC378076, LC377652, LC378136, LC377712, LC377377; *Sohmaea hispida*: LC378057, LC378357, LC378237, LC377997, LC378297, LC378117, LC377693, LC378177, LC377753, LC377418; *Sohmaea laxiflora*: LC378041, LC378341, LC378221, LC377981, LC378281, LC378101, LC377677, LC378161, LC377737, LC377402; *Sohmaea teres*: LC378066, LC378366, LC378246, LC378006, LC378306, LC378126, LC377702, LC378186, LC377762, LC377427; *Sohmaea zonata*: LC378053, LC378353, LC378233, LC377993, LC378293, LC378113, LC377689, LC378173, LC377749, LC377414; *Trifidacanthus unifolilatus*: LC378067, LC378367, LC378247, LC378007, LC378307, LC378127, LC377703, LC378187, LC377763, LC377428; *Uraria crinita*: LC378068, LC378368, LC378248, LC378008, LC378308, LC378128, LC377704, LC378188, LC377764, LC377429; *Uraria lagopodioides*: LC378069, LC378369, LC378249, LC378009, LC378309, LC378129, LC377705, LC378189, LC377765, LC377430; *Uraria picta*: LC378070, LC378370, LC378250, LC378010, LC378310, LC378130, LC377706, LC378190, LC377766, LC377431; *Uraria poilanei*: LC378071, LC378371, LC378251, LC378011, LC378311, LC378131, LC377707, LC378191, LC377767, LC377432; *Uraria rufescens*: LC378072, LC378372, LC378252, LC378012, LC378312, LC378132, LC377708, LC378192, LC377768, LC377433.

*trnL-trnF*, *trnTLA3* (5'-ATT ACA AAT GCG ATG CTC TAA CCT-3') and *trnTLB2* (5'-CGT CTA CCA ATT TCG CCA TAT CC-3') for *trnT-trnL*, *trnG<sup>(UUC)\*</sup>* and *trnS<sup>(GCU)\*</sup>* (Shaw et al. 2007) for *trnG-trnS*, *trnQ<sup>(UUG)</sup>* (Shaw et al. 2007) and *rps16-1B* (5'-CTG TAG GTT GAG CNC CTC GTT CAA G-3') for *trnQ-rps16*, *trnL<sup>(UAG)2</sup>* (5'-CTG CTT CCT AAG AGC AGC GTG TC-3') and *rpl32-F2* (5'-CAG TTC CAA AAA AAC GTA CTT CTA TAT C-3') for *trnL-rpl32*, F71 and R1516 (Jordan et al. 1996) for *rpl16* intron, *trnC<sup>GCA</sup>R* (Shaw et al. 2005) and *rpoB3* (5'-GAA CCT ACA AAA CCC TTC AAA TTG TAT CTG-3') for *trnC-rpoB*, *ndhAx1A* (5'-AGC TGC TCA ATC GAT TAG TTA TGA AAT ACC-3') and *ndhAx2A* (5'-CCA TAG GTT GAC GCC ACA AAT TCCA-3') for *ndhA* intron and ITS4 and ITS5 (White et al. 1990) for ITS. The PCR condition and DNA sequencing analyses basically followed Ohashi et al. (2017). The accession numbers of newly sequenced material in this analysis are shown in Table 2. For the DNA sequences of *Apios americana* used for the analysis, corresponding portions were obtained from the whole chloroplast genome sequence deposited in GenBank (KF856618) with reference to the annotation. ITS sequence of *A. americana* used is also obtained from GenBank (KF272878).

### Phylogenetic analyses

Sequence alignment was initially performed using MUSCLE (Edgar 2004) in Mega version 7.0 (Kumar et al. 2016) and manually adjusted. Phylogenetic analyses were carried out basically as previously described (Ohashi et al. 2017), using Bayesian inference (BI) and maximum likelihood (ML) approaches.

An appropriate model of sequence evolution for the combined dataset was estimated using the program Kakusan4 (Tanabe 2007). The dataset was divided into data partitions (5'*trnK* intron, *ndhJ-trnF-trnL*, *trnT-trnL*, *trnG-trnS*, *trnQ-rps16*, *trnL-rpl32*, *rpl16* intron, *trnC-rpoB*, *ndhA* intron and ITS). Models of sequence evolution

for each of the partitions and for all combined datasets were determined.

Bayesian inference (BI) analyses were conducted using MrBayes version 3.2 (Ronquist et al. 2012). The Proportional model was selected based on BIC. The models applied with each partition were as follow: F81+G for *trnK* and *trnGS*, HKY85+G for ITS, and GTR+G for all the other partitions. Markov Chain Monte Carlo (MCMC) analysis was executed for 20 million generations with four chains, and sampled every 500th generation. The average standard deviation of split frequencies was checked below 0.01. Tracer v.1.6.0 (Rambaut et al. 2014) was used to examine the convergence of model parameters and to check whether the values of effective sample size (ESS) were over 200. The first 10% of the trees from each run were discarded as burn-in from the final tree set that was used to determine the posterior probability distribution.

Maximum likelihood (ML; Felsenstein 1981) and ML bootstrap (Felsenstein 1985) analyses were performed using RAxML v.8 (Stamatakis 2014), with the partitioned dataset. Equal rate model was selected based on BIC. One thousand replicates for bootstrap test were performed for ML. All positions containing gaps and missing data were eliminated for BI and ML analysis.

### Results and Discussion

To clarify phylogenetic relationships among the genera in the *Desmodium* group, especially to explore the phylogenetic relationships between the species of *Desmodium*, molecular phylogenetic analyses were performed using nine cpDNA regions (5'*trnK* intron, *ndhJ-trnF-trnL*, *trnT-trnL*, *trnG-trnS*, *trnQ-rps16*, *trnL-rpl32*, *rpl16* intron, *trnC-rpoB* and *ndhA* intron) and a nuclear ITS (ITS1, 5.8S and ITS2) region. The aligned cpDNA dataset contained 12898 positions, the ITS dataset 711 positions and the cpDNA+ITS dataset 13609 positions. The Bayesian 50% majority rule consensus trees of cpDNA (Fig. 1), of ITS (Fig. 2) and of the

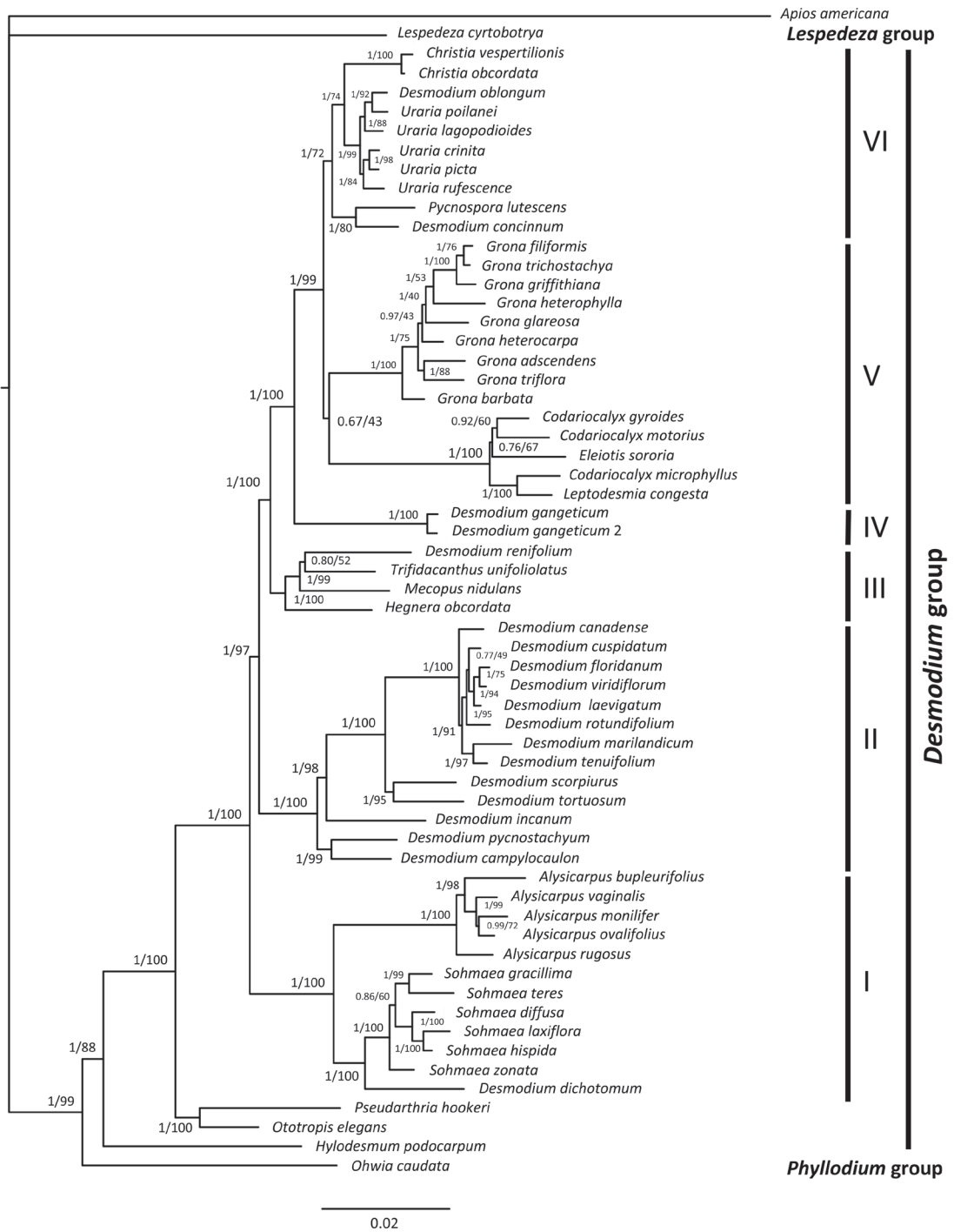


Fig. 1. The 50% majority-rule consensus tree (Bayesian analysis) of *Desmodium* and related species based on the cpDNA dataset (*5'trnK* intron, *ndhJ-trnF-trnL*, *trnT-trnL*, *trnG-trnS*, *trnQ-rps16*, *trnL-rpl32*, *rpl16* intron, *trnC-rpoB* and *ndhA* intron). Support values on the branches are presented as follows: BI-PP/ML-BS. Scale bar shows the expected number of substitutions per site in Bayesian analysis.

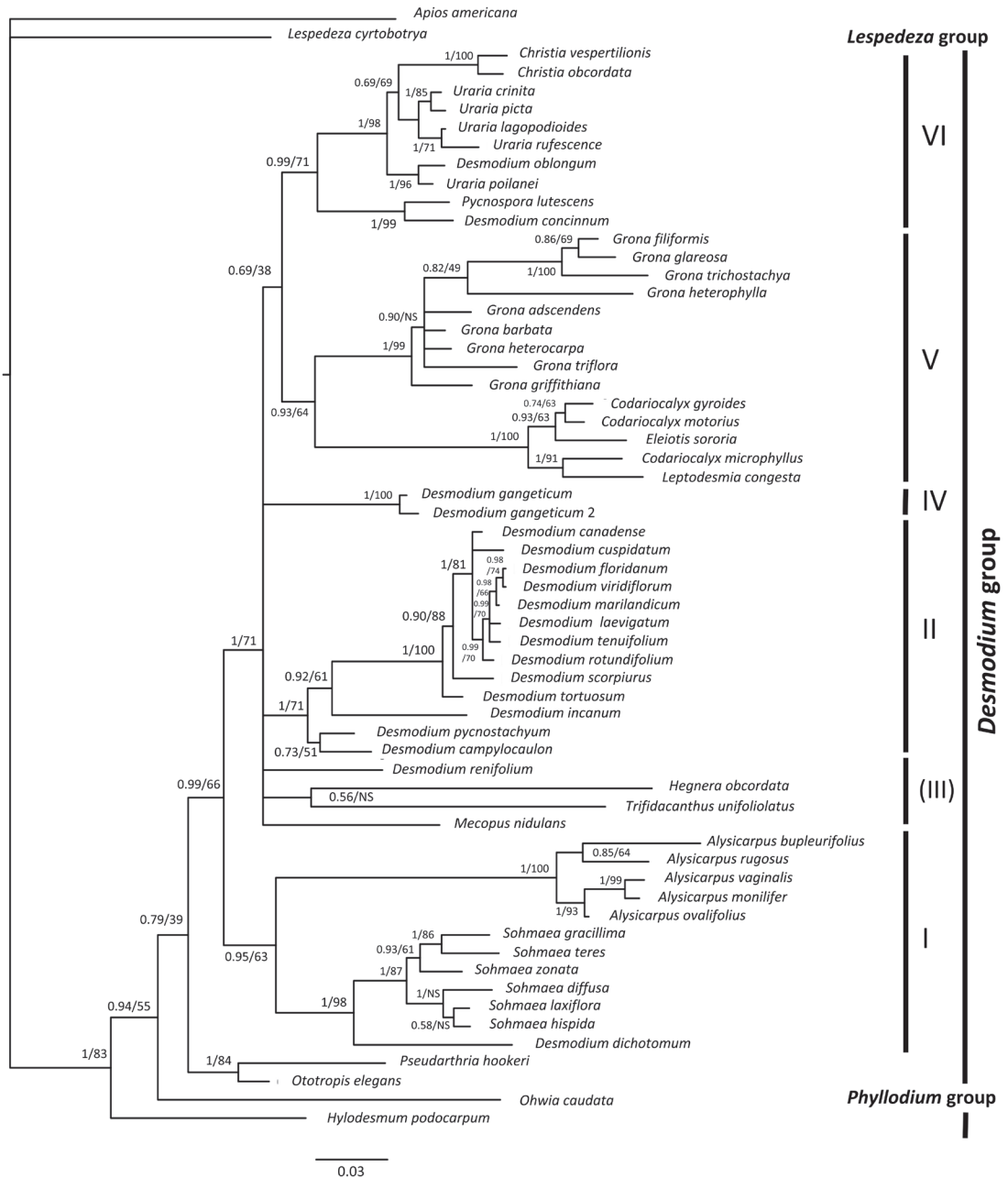


Fig. 2. The 50% majority-rule consensus tree (Bayesian analysis) of *Desmodium* and related species based on nuclear DNA (ITS). Support values on the branches are presented as follows: BI-PP/ML-BS. Scale bar shows the expected number of substitutions per site in Bayesian analysis.



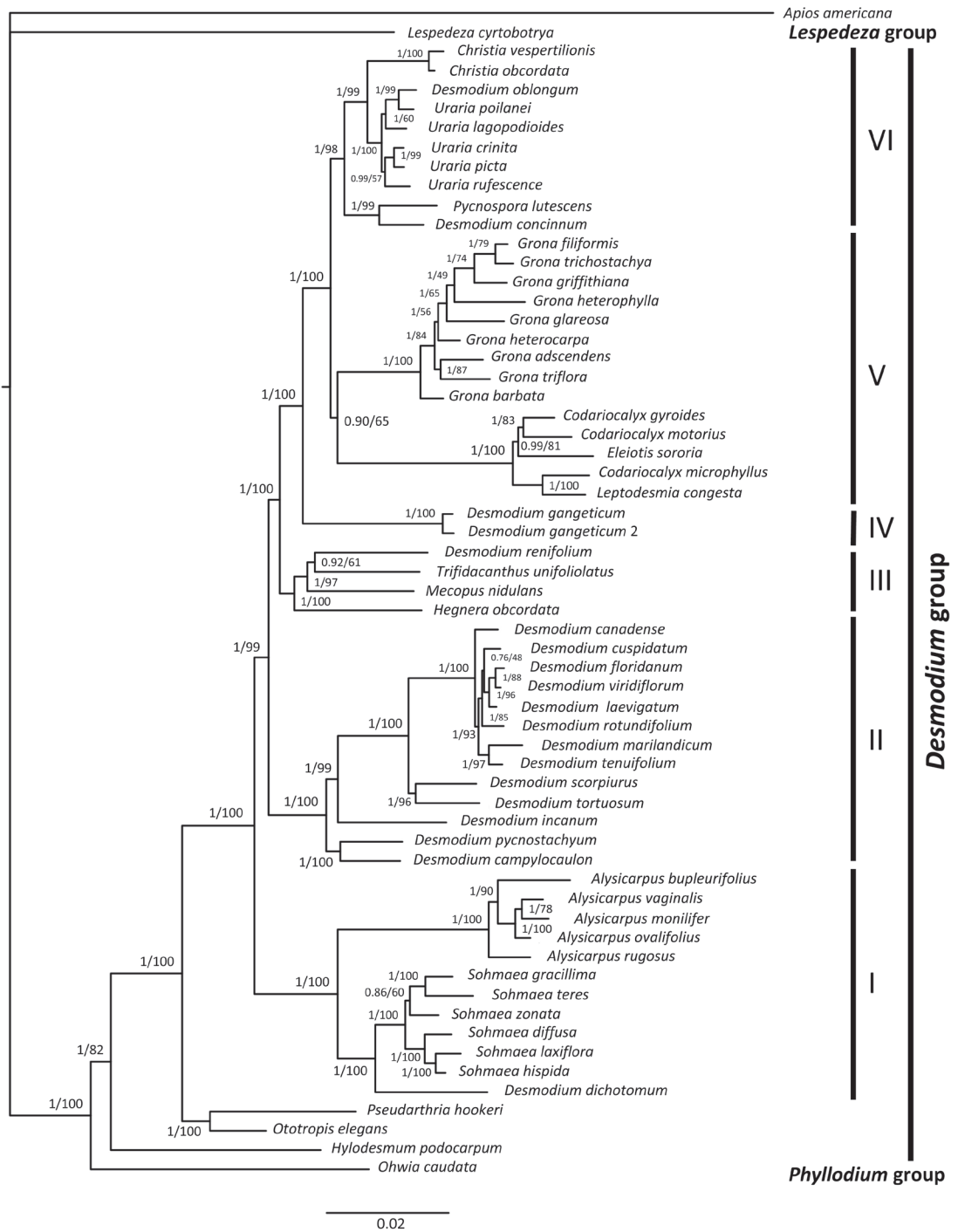


Fig. 3. The 50% majority-rule consensus tree (Bayesian analysis) of *Desmodium* and related species based on combined dataset of ITS and the cpDNA (5'*trnK* intron, *ndhJ-trnF-trnL*, *trnT-trnL*, *trnG-trnS*, *trnQ-rps16*, *trnL-rpl32*, *rpl16* intron, *trnC-rpoB* and *ndhA* intron). Support values on the branches are presented as follows: BI-PP/ML-BS. Scale bar shows the expected number of substitutions per site in Bayesian analysis.

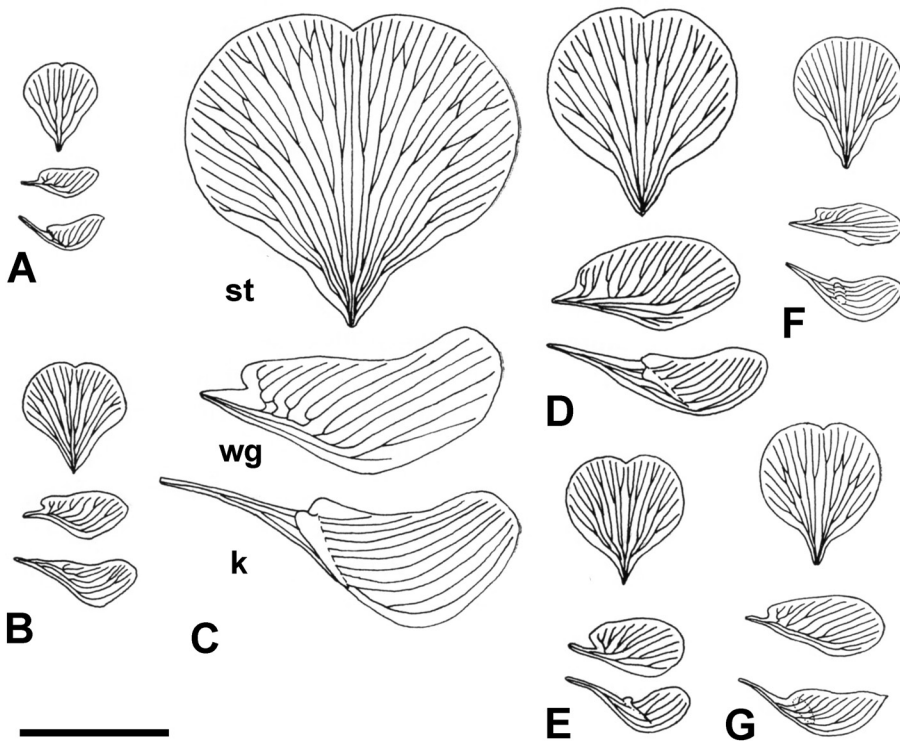


Fig. 4. Petals (st: standard, wg: wing, k: keel petals). A. *Bouffordia dichotoma* (China. Henry 9234. CAL). B. *Pleurolobus gangeticus* (India. Ohashi 26186. TI). C. *Uraria oblonga* (Thailand. Iwatsuki & Fukuoka T.3211. TI). D. *Tateishia concinna* (Nepal. Stainton & al. 8863. TI). E. *Leptodesmia microphylla* (Nepal. Stainton & al. 4728. TI). F. *Huangtcia renifolia* (Thailand. Hayata s.n. anno 1921. TI). G. *Oxytes brachypoda* (Australia. McKee 9726. NSW). Scale bar: 5 mm. Reproduced from fig. 55 in H. Ohashi, *Ginkgoana* 1 (1973) [©H. Ohashi].

combined cpDNA and ITS dataset (Fig. 3) are shown with posterior probability and bootstrap support values from the ML analysis.

The resulting phylogenetic trees showed the polyphyly of *Desmodium* as currently circumscribed (Figs. 1–3). The trees derived from the cpDNA (Fig. 1) and ITS (Fig. 2) were partially incongruent with each other in the material of *Desmodium* examined. The species of *Desmodium* were distributed sporadically in many similar clades. In the cpDNA and ITS trees such species as *D. concinnum*, *D. dichotomum*, *D. oblongum* formed monophyletic groups with *Pycnospora*, *Sohmaea* and *Uraria*, respectively, whereas three groups of *D. campylocaulon*–*D. pycnostachyum*, *D. gangeticum* and 11 species of American *Desmodium* including *D. scorpiurus*

formed exclusive *Desmodium* clades (Figs. 1, 2). In contrast, *D. renifolium* formed a clade with *Trifidacanthus* in the cpDNA tree (Fig. 1), but the two species were placed in different clades in the ITS tree (Fig. 2). Another incongruence between the cpDNA tree and the ITS tree was the position of *Ohwia* and *Hylodesmum*. In the ITS tree, *Hylodesmum* separated before the separation of *Ohwia*.

The tree obtained from the combined cpDNA and ITS dataset (Fig. 3) showed almost similar topology to the cpDNA tree (Fig. 1). In addition, support values were improved especially at the branching of the clade composed of *Grona* and that composed of *Codariocalyx*, *Eleiotis* and *Leptodesmia* (BI-PP/ML-BS = 0.67/43 in Fig. 1 whereas 0.90/65 in Fig. 3).

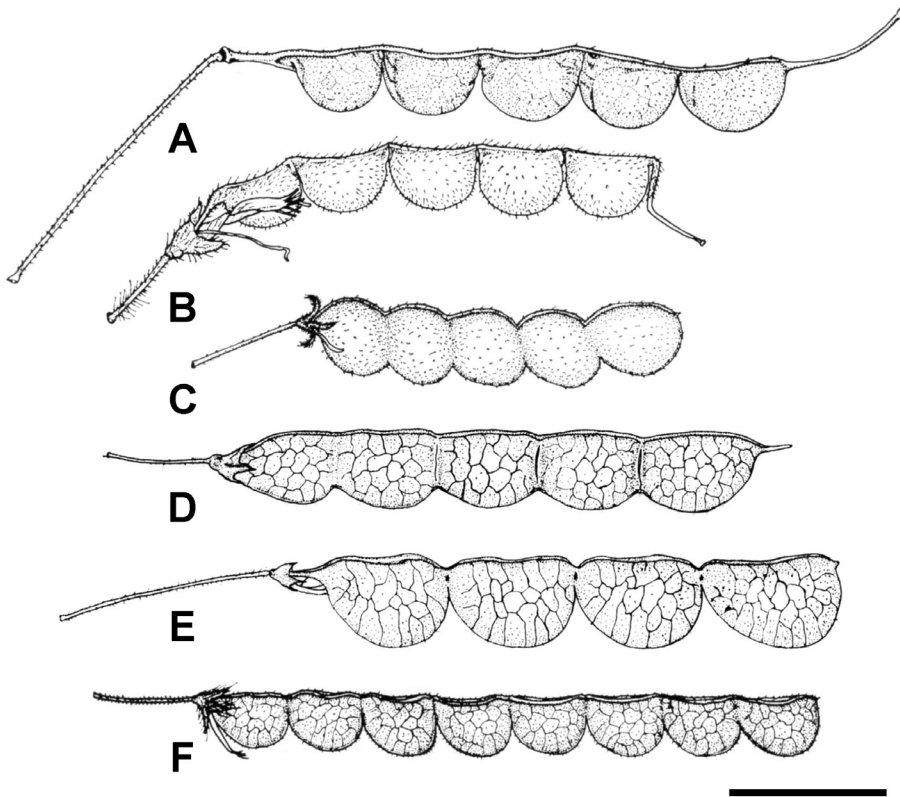


Fig. 5. Loments. A. *Tateishia concinna* (Nepal. Hara & al. 6301383. TI). B. *T. retusa* (Nepal. Hara & al. 6301400. TI). C. *Bouffordia dichotoma* (India. Wight 717. CAL). D. *Huangtcia renifolia* (Nepal. Stainton & al. 8875. TI). E. *H. oblata* (Thailand. Tagawa & al. T.361. TI). F. *Pleurolobus gangeticus* (Laos. Hayata s.n. anno 1921. TI). Scale bar: 5 mm. Reproduced from figs. 56 and 67 in H. Ohashi, *Ginkgoana* 1 (1973) [©H. Ohashi].

In the *Desmodium* group, *Hylodesmum* separated first. After separation of the clade of *Ototropis* and *Pseudarthria*, the remainder of the *Desmodium* group comprised six clades with high support values (BI-PP/ML-BS  $\geq 1/96$  in Figs. 1 and 3). These clades were named arbitrarily Clade-I to Clade-VI.

Clade-I contained two genera *Alysicarpus* and *Sohmaea* and a single species *Desmodium dichotomum*. *Sohmaea* and *D. dichotomum* constitute a subclade, in which *D. dichotomum* is sister to *Sohmaea*. *Sohmaea* was composed of *Desmodium* section *Angustistipulosa* and *D. hispidum* (Ohashi and Ohashi 2018b). *Desmodium dichotomum* is considered to be a natural monotypic independent genus, because

it differs from *Sohmaea* conspicuously in stipules, flowers (Fig. 4) and loments (Fig. 5). Clade-II comprised two subclades: American or Oceanic species of *Desmodium*. The Oceanic subclade was separated into *D. campylocaulon* and *D. pycnostachyum*. Each of them should be treated as a monotypic independent genus, because the treatment is supported by morphological differences in leaf, flower and loments between them. Clade-III included three monotypic genera, *Hegnara*, *Mecopus* and *Trifidacanthus*, and *D. renifolium*. *Desmodium renifolium* will be treated here as a monotypic independent genus, because the species stands separately from the *Desmodium* clade in Clade-II and shares no synapomorphic characters

with *Trifidacanthus unifoliolatus*. Clade-IV constituted a single species *Desmodium gangeticum*. *Desmodium gangeticum* must, therefore, be treated as a monotypic independent genus. Clade-V comprised two subclades: *Grona* subclade and *Codariocalyx*, *Eleiotis* and *Leptodesmia* subclade. *Grona* included members of *Desmodium* sections *Nicolsonia* and *Sagotia* (Ohashi 1973), but was recently separated from *Desmodium* (Ohashi and Ohashi 2018a). *Grona* is sister to the *Codariocalyx-Eleiotis-Leptodesmia* subclade. *Codariocalyx microphyllus* forms a clade with *Leptodesmia*. Clade-VI involved three genera *Pycnospora*, *Christia* and *Uraria*, and two species of *Desmodium*, *D. concinnum* and *D. oblongum*. *Desmodium concinnum* is sister to the monotypic genus *Pycnospora* and *D. oblongum* is included within *Uraria* clade as an ingroup. Clade-VI suggests that *D. concinnum* represents a distinct, undescribed genus and *D. oblongum* belongs to *Uraria*.

Our phylogenetic trees indicate diverse distribution of the seven sections of subgenus *Sagotia* of Ohashi (1973) and Pedley (1999), which appear sporadically in different clades (Fig. 3). Section *Chalarioides* was included in Clade-I, sections *Oxytes* and *Desmodiopsis* in Clade-II, section *Renifolia* in Clade-III, sections *Nicolsonia* and *Sagotia* in Clade-V, but section *Heteroloma* did not form a single clade. The results of the phylogenetic trees support previously recognized sections as distinct taxa except *Heteroloma*. We examined *D. concinnum*, *D. gangeticum* and *D. oblongum* of section *Heteroloma*, but they were placed in two separate clades rather than being in the clade consisting of other section(s) in the subgenus *Sagotia*. *Desmodium gangeticum* formed an independent Clade-IV, while *D. concinnum* and *D. oblongum* were contained in Clade-VI, although separated into a different subclade.

Based on the results of our phylogenetic analyses and in comparison with morphological and/or palynological studies, we propose here

new taxonomic treatments for the following taxa of subgenus *Sagotia*: 1) *Desmodium campylocaulon* of section *Desmodiopsis*, 2) *D. concinnum* of section *Heteroloma*, 3) *D. dichotomum* of section *Chalarioides*, 4) *D. gangetirum* of section *Heteroloma*, 5) *D. pycnostachyum* of section *Oxytes*, and 6) *D. renifolium* of section *Renifolia*. Each of these taxa constitutes a distinct clade separated from the subgenus *Desmodium* clade. Each of these six clades is considered as representing a distinct genus. 7) *Desmodium oblongum* of section *Heteroloma* is transferred to *Uraria* and 8) *Codariocalyx microphyllus* to *Leptodesmia*.

### Taxonomic treatment

#### 1) *Desmodiopsis*, a new genus based on *Desmodium campylocaulon*

*Desmodiopsis* was created by Schindler (1925) as a section of *Alysicarpus* on the basis of *Desmodium campylocaulon* F. Muell. ex Benth. (Figs. 6, 7). Pedley (1999) transferred the section to *Desmodium* and discussed the taxonomic position of *D. campylocaulon* within *Desmodium*. Our phylogenetic trees clearly support Pedley's treatment, since *Desmodium campylocaulon* formed a monotypic clade. The phylogenetic position of *Desmodium campylocaulon* is in Clade-II and distinctly distinguished from the *Alysicarpus*-clade in Clade-I (Figs. 1–3). *Desmodium campylocaulon*, endemic to Australia, is sister to the New Caledonian *Desmodium pycnostachyum*. The *D. pycnostachyum-campylocaulon* clade is sister to the American *Desmodium* species clade. Each of these clades is a distinct lineage. *Desmodium* sect. *Desmodiopsis* is recognized morphologically here as a distinct monotypic genus based on its inflated loment.

*Desmodiopsis* (Schindl.) H. Ohashi & K. Ohashi, **stat. nov.**

*Alysicarpus* sect. *Desmodiopsis* Schindl. in Rep. Sp. Nov. Reg. Veg. **21**: 14 (1925). – *Desmodium* sect. *Desmodiopsis* (Schindl.)



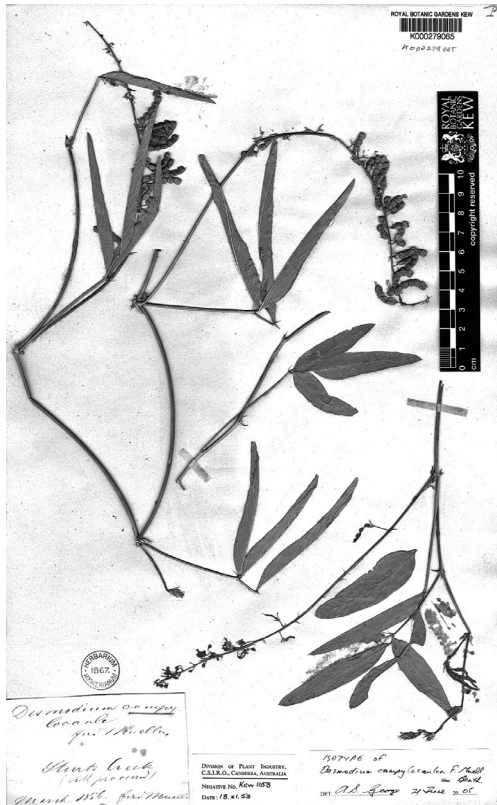


Fig. 6. *Desmodium campylocaulon* F. Muell. ex Benth. Holotype K000279065 (©The Board of Trustees of the Royal Botanic Gardens, Kew).



Fig. 7. Loments of *Desmodiopsis campylocaulon* (F. Muell. ex Benth.) H. Ohashi & K. Ohashi. Australia. Northern Territory. North from "Creswell Downs". 16 June 1974. R. Pullen 9274 (TUS).

Pedley in *Austrobaileya* 5(2): 226 (1999).

**Type:** *Desmodiopsis campylocaulon* (F. Muell. ex Benth.) H. Ohashi & K. Ohashi (= *Desmodium campylocaulon* F. Muell. ex Benth.).

**Diagnosis:** *Desmodiopsis* is similar to *Grona muelleri* (Benth.) H. Ohashi & K. Ohashi in habit, general appearance and ecology (Pedley 1999), but *Desmodiopsis* was in Clade-II, whereas *Grona* in Clade-V. *Desmodiopsis* is distinct from the other members of the tribe *Desmodieae* except *Pycnospora*, in the inflated articles of the loments (Fig. 7). The inflated pods of *Pycnospora* are 7–10-seeded and not segmented. *Pycnospora* was in Clade-VI and formed a subclade with *Desmodium concinnum* (= *Tateishia concinna*) in our phylogenetic trees (Figs. 1–3).

**Description:** Perennial herbs, prostrate or somewhat ascending. Leaves 3-foliolate, leaflets narrowly ovate, apex acute or obtuse and mucronulate, base attenuate; terminal leaflet distinctly petiolulate; lateral leaflets similar to terminal one but slightly smaller. Inflorescences terminal, rarely leaf-opposed, peduncle and rachis with spreading uncinuate hairs; 2-flowered at node. Primary bracts ovate, acuminate, deciduous. Bracteoles absent. Calyx 4-lobed, adaxial lobes connate, bifid. Corolla pink or pale purple; standard obovate, wings shorter than keel petals. Stamens diadelphous. Disk absent. Loments straight, with 5–7 articles, with spreading uncinuate hairs, adaxial (upper) suture thickened, abaxial (lower) suture deeply indented; articles inflated, indehiscent, (2.5–)3–4 mm long, 2.2–3.3 mm wide. Seeds oblongioid,



thickened, rim-arillate. Detailed description provided by Pedley (1999).

***Desmodiopsis campylocaulon*** (F. Muell. ex Benth.) H. Ohashi & K. Ohashi, **comb. nov.**

*Desmodium campylocaulon* F. Muell. ex Benth., Fl. Austr. 2: 233 (1864) [Type: Australia. Northern Territory. Northern Territory Sturts Creek. March 1856. F. Mueller s.n. 1856 Mar. (K000279065 holotype) (Fig. 6)]; Pedley in *Austrobaileya* 5(2): 233 (1999). – *Meibomia campylocaulis* (F. Muell. ex Benth.) Kuntze, Revis. Gen. Pl. 1: 197 (1891). – *Alysicarpus campylocaulis* (F. Muell. ex Benth.) Schindl. in Rep. Sp. Nov. Reg. Veg. 21: 14 (1925).

Distribution: Australia (Western Australia, Northern Territory, Queensland).

## 2) *Tateishia*, a new genus based on *Desmodium concinnum*

*Desmodium concinnum* DC. belongs to the section *Heteroloma* of subgenus *Sagotia* (Ohashi 1973). The species comprises an independent clade with *Pycnospora lutescens* within Clade-VI (Figs. 1–3). However, *D. concinnum* differs greatly from *P. lutescens* Schindl. in having compressed loments (Fig. 5) and diadelphous stamens (whereas turgid legumes and nearly monadelphous stamens in *P. lutescens*) and in anatomical structure of the pericarp and the joint (Nemoto and Ohashi 2003). Moreover, the lack of sclerenchyma in the pericarp of *D. concinnum* shows a unique pattern among the *Desmodium* and *Phyllodium* groups (Nemoto and Ohashi 2003). We consider that *Desmodium concinnum* to be better treated as an independent genus distinct from *Pycnospora*.

***Tateishia*** H. Ohashi & K. Ohashi, **gen. nov.**

**Type:** *Tateishia concinna* (DC.) H. Ohashi & K. Ohashi.

*Tateishia* includes two species and is similar in morphology and palynology to the species of *Desmodium* section *Heteroloma* in the sense of Ohashi (1973), but differs from them by the

combination of the following characteristics: as 3-foliolate leaves, pseudoracemes, rachis with straight glandular hairs and uncinete hairs, narrowly ovate, long acuminate primary bracts without secondary bracts, larger flowers more than 5 mm long, and stalked loments with a deeply incised lower (abaxial) margin (Fig. 5).

Description: Shrubs with slender branches and long inflorescences, usually 80–150 cm tall; branches terete, glabrescent; leaves 3-foliolate, stipulate, petiolate; terminal leaflet elliptic or obovate, principal lateral nerves conspicuous, not reaching margin. Inflorescences terminal, pseudoracemes, terminal one 20–35 cm long; rachis with straight glandular hairs (1 mm long) and uncinete hairs (0.5 mm long). Primary bracts closely imbricate, narrowly ovate, long acuminate; secondary bracts absent. Flowers 7–7.5 mm long, 2–4 per node; pedicels and inflorescence rachis hairy; bracteoles absent. Calyx broadly campanulate, 4-lobed, adaxial lobes deltoid, apex obscurely bifid, lateral lobes broadly triangular. Corolla purple, violet or rose; standard broadly obovate or orbicular, 6–7 mm long, 4–6 mm wide, wings broadly obovate, shorter than keel petals. Stamens 6.5–8 mm long, diadelphous. Pistil linear, 8–9 mm long, style incurved. Loments narrowly oblong, short stipitate, with 4–6 articles, densely puberulent with uncinete and straight hairs, adaxial suture usually slightly undulate, abaxial suture deeply incised, isthmus ca. 1/5 as broad as loment; articles nearly semicircular, ca. 4 mm long, ca. 2.5 mm wide. Seeds transversely elliptic, ca. 2.3 mm × 1.8 mm.

Distribution: Pakistan, Kashmir, India, Nepal, Sikkim, Bhutan, Myanmar, Thailand, Laos, Vietnam and China.

Etymology: *Tateishia* honors Dr. Yoichi Tateishi, Professor Emeritus of Ryukyuu University, who worked on *Leguminosae* with H. Ohashi and Nemoto at the University of Tokyo and Tohoku University and made key contributions to the flora and to conservation of the Ryukyus at Ryukyuu University.

### Key to the species

1. Fruiting pedicels 11–18 mm long; articles 4–4.5 mm × 2.5–3 mm, with sparse minutely uncinuate hairs; inflorescences laxly flowered, rachides often zigzag in the upper part .....  
 ..... *T. concinna*
1. Fruiting pedicels 2–5 mm long; articles 3–3.4 mm × 2–2.2 mm, with continuous minutely uncinuate and straight hairs; inflorescences rather densely flowered, rachides straight ....  
 ..... *T. retusa*

*Tateishia concinna* (DC.) H. Ohashi & K. Ohashi, **comb. nov.**

*Desmodium concinnum* DC. in Ann. Sci. Nat. 4: 101 (Jan. 1825) et Prodr. 2: 335 (Nov. 1825) [**Type:** Napaulia. Wallich (G–holotype)]; Baker in Hook. f., Fl. Brit. India 2: 170 (1876), p.p.; H. Ohashi in Ginkgoana 1: 179 (1973), p.p., excl. var. *retusum* (D. Don) H. Ohashi; Ali, Fl. W. Pakistan 100, Pap. 354 (1977); Grierson & Long, Fl. Bhutan 1: 676 (1987); H. Ohashi in Dy Phon & al., Fl. Cambodge, Laos & Vietnam 27: 116 (1994); P. H. Huang & H. Ohashi in Fl. China 10: 271 (2010); Saisorn & al. in Phytotaxa 263(2): 159 (2016). – *Meibomia concinna* (DC.) Kuntze, Revis. Gen. Pl. 1: 197 (1891).

*Desmodium pendulum* Wall., Pl. Asiat. Rar. 1: 81, t. 94 (1830) [**Type:** “In montibus Sillet confinibus legit F. De Silva”].

*Desmodium amoenum* Wall. [Numer. List n. 5726 (1831–32), nom. nud.] ex Benth. in Miq., Pl. Jungh. 224 (1852), in adnota. [**Type:** India. Cat. no. 5726. (K–holotype 2 sheets [K000639655, K000639656])]. – *Desmodium concinum* var. *amoenum* (Wall. ex Benth.) Baker in Hook. f., Fl. Brit. Ind. 2: 170 (1876). – *Desmodium retusum* var. *amoenum* (Wall. ex Benth.) Schindl. in Repert. Spec. Nov. Regni Veg. 23: 354 (1927).

Distribution: Pakistan, Kashmir, India, Nepal, Sikkim, Bhutan, Myanmar, Thailand, Laos, Vietnam, China.

*Tateishia retusa* (D. Don) H. Ohashi & K. Ohashi, **comb. nov.**

*Hedysarum retusum* D. Don, Prodr. Fl. Nepal. 243 (Feb. 1825) [**Type:** Nepalia ad Narainhetty. Hamilton (BM–holotype)]. – *Desmodium retusum* (D. Don) G. Don, Gen. Hist. 2: 297 (1832); Schindl. in Repert. Spec. Nov. Regni Veg. 23: 354 (1927); H. Ohashi in H. Hara, Fl. E. Himal. 54 (1966). – *D. concinnum* var. *retusum* (D. Don) H. Ohashi in Ginkgoana 1: 182 (1973).

Distribution: NE. India, Nepal.

### 3) *Bouffordia*, a new genus based on *Desmodium dichotomum*

Bentham (1852) treated *Desmodium diffusum* (Willd.) DC. in the monotypic section *Chalarioides* of *Desmodium*, as it is similar to the tropical American section *Chalarium* in having spreading persistent stipules, which are amplexicaul with an auriculate base, but distinguished it from *Chalarium* by the sessile legumes and diadelphous stamens. Ohashi (1973) adopted *D. dichotomum* (Willd.) DC. as the correct name instead of *D. diffusum*, which was a later homonym of *D. diffusum* DC. (Ohashi 2004a), and classified the species into the section *Chalarioides* of the subgenus *Sagotia*, although it differs from other members of section *Heteroloma* of subgenus *Sagotia* (*D. concinnum* and *D. gangeticum* examined in this study) in the anatomical structure of the pericarp (Nemoto and Ohashi 2003). In our molecular analyses, *D. dichotomum* forms an independent clade in Clade I (Figs. 1–3). The clade is placed in a position different from that represented by *D. scorpiurus* (Sw.) Desv., the type species of the genus *Desmodium*.

*Bouffordia* H. Ohashi & K. Ohashi, **gen. nov.**

*Desmodium* sect. *Chalarioides* Benth. in Miq., Pl. Jungh. 225 (1852), in adnota [**Type:** *Desmodium diffusum* (Willd.) DC., nom. illeg. = *Desmodium dichotomum* (Willd.) DC.]; H.

Ohashi in *Ginkgoana* **1**: 173 (1973), sub subgen. *Sagotia* (Duchass. & Walp.) Baker.

**Type:** *Bouffordia dichotoma* (Willd.) H. Ohashi & K. Ohashi.

Diagnosis: The genus is monotypic. It is similar to *Desmodium*, but differs from it in a combination of the following characteristics: the angular and deeply sulcate stems, amplexicaul and auricled stipules, (1–)3-foliolate leaves, acute keel petals (Fig. 4), diadelphous stamens with free vexillary stamen, sessile ovary, and slightly moniliform, sessile loments with obliquely quadrate articles (Fig. 5).

Description: See the description of *Desmodium dichotomum* in Ohashi (1973).

***Bouffordia dichotoma*** (Willd.) H. Ohashi & K. Ohashi, **comb. nov.**

*Hedysarum dichotomum* Willd., Sp. Pl. **3**(2): 1180 (1802) [**Type:** India. Madras, Tranquebaria, Kumbagonam. Klein? in Herb. Willdenow 13785 (B-W 13785-01 0–holotype)]. – *Desmodium dichotomum* (Willd.) DC., Prodr. **2**: 336 (1825); Meeuwen in Reinwardtia **6**: 248 (1962); B. G. Schub. in Fl. Trop. E. Afr. Legum. **3**, Papil. **1**: 471 (1971); H. Ohashi in *Ginkgoana* **1**: 173, t. 21a (1973), excl. syn. *Hedysarum diffusum* Willd., *D. diffusum* (Willd.) DC., *Meibomia diffusa* (Willd.) Kuntze; Y. C. Yang & P. H. Huang, Fl. Reipubl. Pop. Sin. **41**: 25 (1995); Ohashi in J. Jpn. Bot. **79**: 121 (2004); P. H. Huang & H. Ohashi in Fl. China **10**: 271 (2010).

*Hedysarum diffusum* Willd., Sp. Pl. **3**(2): 1180 (1802) [**Type:** India. Madras, Tranquebaria. Herb. Willdenow 13781 (B–holotype, n.v.)]. – *Desmodium diffusum* (Willd.) DC., Prodr. **2**: 336, no. 88 (Nov. 1825), nom. illeg., non DC. in Ann. Sci. Nat. **4**: 100 (Jan. 1825); Benth. in Miq., Pl. Jungh. 225 (1852), in adnota; Baker in Hook. f., Fl. Brit. India **2**: 169 (1876); Schindl. in Repert. Spec. Nov. Regni Veg. Beih. **49**: 272 (1928).

*Hedysarum quinquangulatum* Roxb., [Hort. Beng. 57 (1814), n.n.] Fl. Ind. ed. 2, **3**:

355 (1832). – *Desmodium quinquangulatum* (Roxb.) Wight, Icon. **1**: No. 15: 293 as ‘*quinqueangulatum*’, t. 293 as ‘*quinqueangulare*’ (1840).

*Desmodium amplexicaule* Zoll. & Moritzi in Nat. en Geneesk. Arch. Neêrl. Ind. **3**: 58, 77 (1846) [**Type:** Java. Besoeki. Zollinger 2789 (L–holotype, n.v.; A, BM, BO–isotypes)].

Distribution: Africa (Uganda, Nigeria, Sudan, Ethiopia) and Asia: India, Myanmar, China (S. Yunnan) and Indonesia (Java, Lesser Sunda Is. and Sulawesi).

Etymology: *Bouffordia* honors Dr. David E. Boufford of the Harvard University Herbaria, who has contributed to the development of floristic studies of East Asia since his initial interest in the floristic relationships between eastern Asia and eastern North America in 1980 and who alone has joined all floristic projects of four countries in eastern Asia; Flora of Japan, Flora of Taiwan and Flora of Korea as an editor, and Flora of China as a member of the Editorial Committee.

#### **4) *Oxytes*, a new genus for *Desmodium pycnostachyum***

Schindler (1926) accommodated *Desmodium pycnostachyum* Benth. in subgenus *Oxytes* Schindl. together with *D. brachypodum* A. Gray and *D. deplanchei* Harms based on their imparipinnate leaves and flowers. He named the subgenus for the acute apex of the keel petals (Fig. 4).

***Oxytes*** (Schindl.) H. Ohashi & K. Ohashi, **stat. nov.**

*Desmodium* subgen. *Oxytes* Schindl. in Repert. Spec. Nov. Regni Veg. **22**: 257 (1926). – *Desmodium* subgen. *Sagotia* sect. *Oxytes* (Schindl.) H. Ohashi in *Ginkgoana* **1**: 227 (1973); Pedley in *Austrobaileya* **5**: 226 (1999).

**Type:** *Oxytes brachypoda* (A. Gray) H. Ohashi & K. Ohashi (designated in Ohashi 1973 as the type of *Desmodium* sect. *Oxytes*).

Diagnosis: Leaves imparipinnate, (1–)3–7-foliolate, often drying bluish black;

inflorescences racemes, 1- or 2-flowered, nodose at nodes; keel petals acute at apex. Except for the three species of *Oxytes*, 5- or 7-foliolate leaves are only found in five species in the tribe *Desmodieae*. *Hylodesmum oldhamii* of which the development of 5- or 7-foliolate leaves was described in Ohashi (1973, p. 12 as *Desmodium oldhamii*), and four species in *Uraria*, i.e., *U. acuminata*, *U. candida*, *U. crinita* and *U. picta*. The three genera are distributed sporadically in remote clades in our phylogenetic trees (Figs. 1–3). The 5- or 7-foliolate leaves are considered to be derived from a 3-foliolate character state and are advanced as a result of parallel evolution in the tribe.

**Description:** Shrubs, copiously branched. Leaves pinnate, (1–)3–7-foliolate, chartaceous texture often bluish black when dry; terminal leaflet more or less larger than the lateral ones, apex emarginate to truncate. Inflorescences terminal, racemes, 1- or 2-flowered, nodose at nodes; preliminary bract deciduous, secondary bracts minute. Flowers explosive; calyx broadly campanulate, 4-lobed, lobes broadly deltate, adaxial lobe minutely bifid, apex of lateral lobes acute, abaxial lobe slightly longer than others; standard broadly obovate to orbicular; wings shortly clawed, apex obtuse; keel petals long clawed, apex acute. Stamens diadelphous. Loments linear, sessile or shortly stalked, 3–8-jointed, reticulate veined, both sutures thickened, adaxial suture straight, abaxial suture incised between seeds, isthmi 1/2 to 2/3 as broad as articles.

**Distribution:** Australia, New Caledonia, New Guinea.

### Key to the species

1. Stipules very broadly ovate, 4–8 mm long, apex long acuminate to caudate, base auriculate; leaves (1- or)3- or 5-foliolate .....  
..... *O. brachypoda*
1. Stipules narrowly ovate to ovate, 2–4 mm long, apex acute to acuminate, base not auriculate; leaves (3- or)5- or 7-foliolate ... 2
2. Leaflets chartaceous, oblong, 7–25 mm wide, veins and veinlets inconspicuous, not raised on both surfaces; lateral leaflets pulvinate hence seemingly short petiolulate .....  
..... *O. pycnostachya*
2. Leaflets subcoriaceous, linear to narrowly oblong, 1–4 mm wide, veins and veinlets conspicuous, raised on both surfaces, lateral leaflets minutely pulvinate hence seemingly sessile ..... *O. deplanchei*

***Oxytes brachypoda*** (A. Gray) H. Ohashi & K. Ohashi, **comb. nov.**

*Desmodium brachypodum* A. Gray in U.S. Expl. Exped. Phan. **1**: 434 (1854) [**Type:** Australia. New South Wales, Sydney and Hunter's River. 1838. Wilkes Expedition (GH 00053836)]; Benth., Fl. Austral. **2**: 232 (1864); H. Ohashi in Ginkgoana **1**: 227 (1973); Pedley in Austrobaileya **5**: 233 (1999). – *Meibomia brachypoda* (A. Gray) Kuntze, Revis. Gen. **1**: 197 (1891), ut '*brachypodia*'.

*Desmodium indigotinum* Harms & K. Schum. in Nachtr. Fl. Schutzgeb. Südsee [Schumann & Lauterbach] 276 (1905) [**Type:** Kaiser Wilhelmsland. Finschhafen. Wieland s.n. (herb. unknown)].

**Distribution:** Australia, New Caledonia, New Guinea.

***Oxytes deplanchei*** (Harms) H. Ohashi & K. Ohashi, **comb. nov.**

*Desmodium stenophyllum* Harms in Repert. Spec. Nov. Regni Veg. **10**: 132 (1911), non Pamp. (1910) [**Type:** New Caledonia. Kap Devert. Deplanche 332 (B, n.v.)]. – *Desmodium deplanchei* Harms in Repert. Spec. Nov. Regni Veg. **10**: 176 (1911).

**Distribution:** New Caledonia.

***Oxytes pycnostachya*** (Benth.) H. Ohashi & K. Ohashi, **comb. nov.**

*Desmodium pycnostachyum* Benth. in Trans. Linn. Soc. **25**: 299 (1866) [**Type:** New Caledonia. Isle of Pines. MacGillivray (herb.



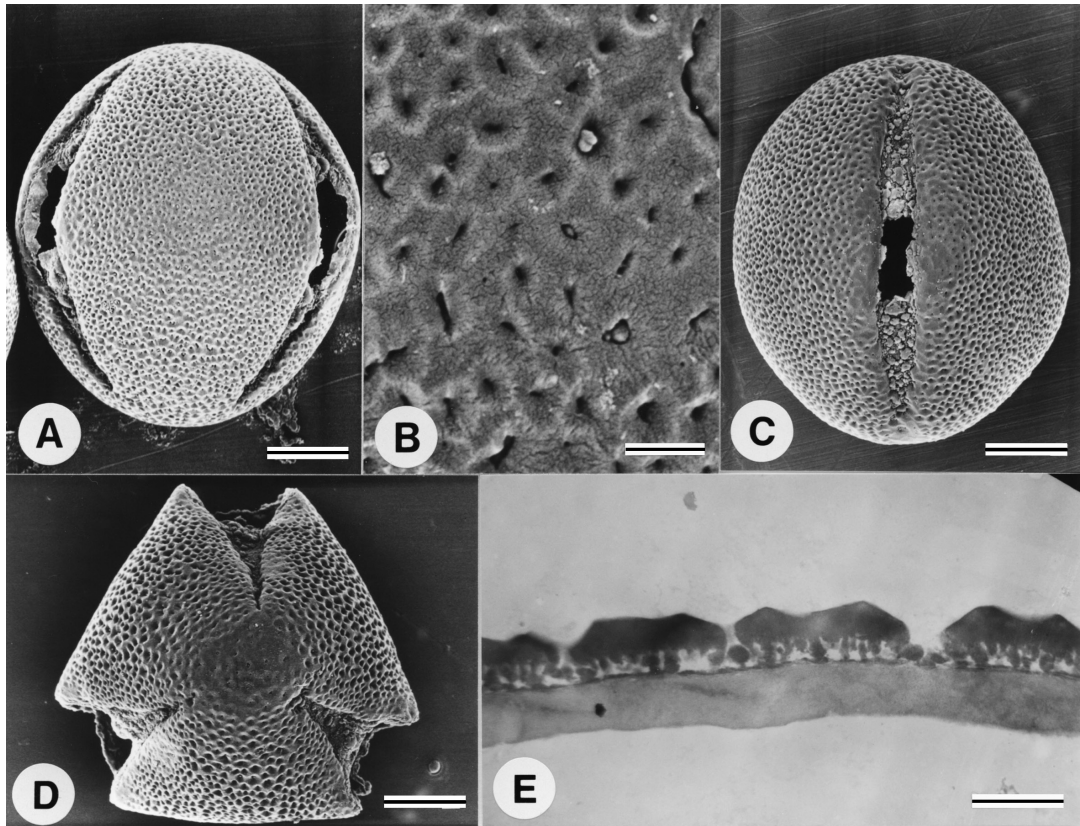


Fig. 8. Pollen grains of *Huangtcia oblata* (Baker ex Kurz) H. Ohashi & K. Ohashi. A. Equatorial view at mesocolpium. B. Tectum at mesocolpium. C. Equatorial view at aperture. D. Polar view. E. Radial section across mesocolpium. Scale bar = 1  $\mu\text{m}$  (B, E), 5  $\mu\text{m}$  (A, C, D). Voucher specimen: Thailand. Chiang Mai. N. Murakami & al. 1187 (TUS). Courtesy of Dr. B. Ye (Tohoku University).

unknown)]; Harms in Repert. Spec. Nov. Regni Veg. **10**: 132 (1911).

*Desmodium pentaphyllum* Harms in Repert. Spec. Nov. Regni Veg. **10**: 131 (1911) [Type: New Caledonia. 'Südbezirk, Base du Mont Mou. Apr. 1904. Le Rat 2006' (B, n.v.)].

Distribution: New Caledonia.

##### 5) *Huangtcia*, a new genus for *Desmodium renifolium* and *D. oblata*

*Desmodium renifolium* (L.) Schindl. was regarded by Ohashi (1973) as representing an independent section *Renifolia* of subgenus *Sagotia* in *Desmodium*, because it has reniform or depressed obovate leaflets, calyx lobes not longer than the tube, monadelphous stamens,

and loments with dense glandular dots on the lateral surfaces. The distinction of the species in morphology is strongly supported by our molecular analyses. We distinguish *D. renifolium* as a new genus *Huangtcia* from *Desmodium* based on this evidence.

##### *Huangtcia* H. Ohashi & K. Ohashi, gen. nov.

*Desmodium* subgen. *Sagotia* sect. *Renifolia* H. Ohashi in Ginkgoana **1**: 229 (1973) [Type: *Desmodium renifolium* (L.) Schindl.].

**Type:** *Huangtcia renifolia* (L.) H. Ohashi & K. Ohashi.

**Description:** Much branched shrubs or subshrubs, branches terete, glabrous. Leaves



1-foliolate, almost glabrous; leaflets chartaceous, reniform or depressed obovate or occasionally very broadly ovate, lower surface with small glands, lateral nerves 4 pairs, prominent. Inflorescences terminal and axillary, racemes or panicles; rachides with minute hooked hairs. Flowers in fascicles of 2–5 at nodes. Primary bracts narrowly ovate, secondary bracts very small, ovate, glabrous. Bracteoles absent. Calyx 4-lobed, lobes not longer than the tube; abaxial lobe broadly triangular, not longer than others. Standard broadly obovate, short clawed; keel petals slightly longer than wings, obtuse. Stamens monadelphous, vexillary stamen shorter than others and connate at base. Ovary short stalked, 4–6-ovuled, style incurved, not thickened. Loments (Fig. 4) narrowly oblong, 4–6-jointed, glabrous or with sparse uncinulate hairs, lateral surfaces densely gland dotted, adaxial suture nearly straight; articles reticulate veined. Seeds transversely elliptic. Pollen grains have fine reticulate sculpturing, the exine less than 1.5  $\mu\text{m}$  thick and a thin but continuous foot layer (Fig. 8).

Distribution: India, Nepal, Bhutan, Myanmar, Thailand, Cambodia, Vietnam, Indonesia (W. Java), China and Taiwan.

Etymology: *Huangtcia* honors Dr. Tseng-Chiang Huang, Professor Emeritus of National Taiwan University, who contributed greatly to our knowledge of the vascular plant flora and pollen flora of Taiwan and taught many students of taxonomy in Taiwan. We cooperated on taxonomic studies of Taiwanese *Leguminosae* and the compilation of the Flora of Taiwan, 2nd edition, from 1981 through 2003.

### Key to the species of *Huangtcia*

1. Loments 3.5–4 mm wide, stalked (stipes 1–1.5 mm long), abaxial suture deeply incised, isthmus 1/5–1/4 as broad as loment, articles semicircular, ca. 5 mm long. Seeds broadly oblong, 2.5–3 mm  $\times$  3.3–4 mm. Flowers blue or purple. Pedicels 6–15 mm long. Erect shrubs ..... *H. oblata*

1. Loments 2.5–3 mm wide, minutely stalked (stipes ca. 0.5 mm long), abaxial suture undulate, isthmus 4/5–5/6 as broad as loment; articles oblong, 4–5 mm long. Seeds elliptic, 1.2–1.5  $\times$  2–2.3 mm in size. Flowers white or pale yellow. Pedicels 2–6 mm long. Usually prostrate subshrubs ..... *H. renifolia*

*Huangtcia oblata* (Baker ex Kurz) H. Ohashi & K. Ohashi, **comb. nov.**

*Desmodium oblatum* Baker ex Kurz in J. Asiat. Soc. Beng. **42**(2): 230 (1874) [**Lectotype** (selected by H. Ohashi 1994): Myanmar. Pegu (S. Kurz 1628, K)]; Baker in Hook. f., Fl. Brit. India **2**: 166 (1876); Prain in J. Asiat. Soc. Beng. **66**(2): 394 (1897); Gagnep., Fl. Gén. Indoch. **2**: 599 (1920); Ohashi in Dy Phon & al., Fl. Cambodge, Laos & Vietnam **27**: 101, t. 14 (1994). – *Meibomia oblata* (Baker ex Kurz) Kuntze, Revis. Gen. Pl. **1**: 198 (1891). – *D. renifolium* var. *oblatum* (Baker ex Kurz) H. Ohashi in Ginkgoana **1**: 233, pl. 34b (1973).

Distribution: Burma, Thailand, Laos.

*Huangtcia renifolia* (L.) H. Ohashi & K. Ohashi, **comb. nov.**

*Hedysarum renifolium* L., Syst. Nat., ed. 10. **2**: 1169 (1759) [**Lectotype** (designated by H. Ohashi in Dy Phon & al., Fl. Cambodge, Laos & Vietnam **27**: 104, 1994; Pedley in Turland & Jarvis in Taxon **46**: 472, 1997; Jarvis, Ord. Chaos 561, 2007): [“Habitat in India.”] Herb. Linnaeus No. 921.8 (LINN)]. – *Desmodium renifolium* (L.) Schindl. in Repert. Spec. Nov. Regni Veg. **22**: 262 (1926); Meeuwen in Reinwardtia **6**: 257 (1962); H. Ohashi in Ginkgoana **1**: 230 (1973), p.p., excl. var. *oblatum*; Huang & H. Ohashi, Fl. Taiwan **3**: 266 (1977); H. Ohashi in Dy Phon & al., Fl. Cambodge, Laos & Vietnam **27**: 102, pl. 103 (1994); H. Ohashi in J. Jpn. Bot. **79**(2): 128 (2004); P. H. Huang & H. Ohashi in Fl. China **10**: 275 (2010).

*Hedysarum reniforme* L., Sp. Pl. ed. 2, **2**: 1051 (1763), nom. illeg. superfl. [**Lectotype** (designated by H. Ohashi in Dy Phon & al., Fl.

Cambodge, Laos & Vietnam **27**: 104, 1994; Jarvis, Ord. Chaos: 562, 2007): Herb. Linnaeus No. 921.8 (LINN). – *Desmodium reniforme* (L.) DC., Prodr. **2**: 327 (1825); Baker in Hook. f., Fl. Brit. India **2**: 173 (1876); Prain in J. Asiat. Soc. Beng. **66**(2): 401 (1897); Gagnep. in Fl. Gén. Indoch. **2**: 604 (1920). – *Meibomia renifolmis* (L.) Kuntze, Revis. Gen. Pl. **1**: 198 (1891).

Distribution: India, Myanmar, Thailand, Indo-China, Indonesia (W. Java), China (Yunnan), Taiwan.

### 6) Resurrection of the genus *Pleurolobus*

*Desmodium gangeticum* (L.) DC. is similar to members of *Desmodium* subgenus *Sagotia* section *Heteroloma* in gross morphology and pollen morphology (Ohashi 1973), and is characterized by flowers less than 5 mm long, sessile loment with a shallowly incised abaxial margin about 1/3–1/2 as broad as the loment (Fig. 5). However, the species forms a distinct lineage different from all genera of the tribe *Desmodieae* as suggested in the results of our molecular phylogenetic analyses (Figs. 1–3). We therefore treat *D. gangeticum* as a representing a separate genus from *Desmodium*. The oldest available generic name for the species is *Pleurolobus* J. St.-Hil. published in 1812, which was rejected against the conserved name *Desmodium* Desv., published in 1813. *Pleurolobus* is resurrected here for the species under ICN Art. 14.6. (McNeill et al. 2012).

*Pleurolobus* J. St.-Hil. in Nouv. Bull. Sci. Soc. Philom. Paris **3**: 192 (1812) & J. Bot. Agric. **1**(2): 61 (1813).

[Type: *Pleurolobus gangeticus* (L.) J. St.-Hil.].

*Desmodium* sect. *Heteroloma* Benth. [unranked] *Latifolia* Benth. in Miq., Pl. Jungh. 224 (1852), in adnot., p.p., incl. ‘3. *D. gangeticum* DC.’, cet excl.; H. Ohashi in Ginkgoana **1**: 178 (1973), ut ‘ser. *Latifolia*.’ [Lectotype (designated here): *D. gangeticum* (L.) DC.].

Diagnosis: Leaves 1-foliolate; leaflets usually narrowly to ordinarily elliptic-ovate, apex acute or acuminate; inflorescences pseudoracemes or often panicles, to 30 cm long, flowers less than 5 mm long; loment usually 6–8-jointed; articles broadly oblong.

Description: Subshrubs or shrubs, 20–200 cm tall. Leaves stipulate, petiolate. Leaflets chartaceous, entire, principal lateral nerves directly reaching the margin, reticulate veins inconspicuous. Inflorescences terminal and axillary, pseudoracemes or often panicles, to 30 cm long; rachis with long straight hairs and minute hooked hairs. Secondary bracts narrowly triangular, acuminate. Bracteoles usually absent. Flowers 2–4 per node; pedicels with dense retrorse minute hooked hairs. Calyx rather broadly campanulate, 4-lobed; adaxial lobes connate, shallowly triangular, minutely bifid. Corolla white, pale yellow, rose or violet; vexillum obovate or broadly obovate, rounded or emarginate; wings shorter than keel petal. Loment linear, 12–25 mm long, with (4–)6–8 articles, with dense minute hooked hairs, abaxial suture deeply undulate; articles broadly oblong, more or less reticulate veined, 2–3 mm long, 2–2.5 mm wide. Seeds depressed obovate or transversely elliptic, 1.5–1.8 mm × 2–2.5 mm.

*Pleurolobus gangeticus* (L.) J. St.-Hil. in Nouv. Bull. Soc. Philom. **3**: 192 (1812) et in J. Bot. Agric. **1**: 61 (1813).

*Hedysarum gangeticum* L., Sp. Pl. **2**: 746 (1753) [Lectotype (designated by Fawcett & Rendle, Fl. Jamaica **4**: 35, 1920: Herb. Linn. No. 921.13 (LINN); Jarvis, Ord. Chaos: 560 (2007)]. – *Aeschynomene gangetica* (L.) Poir. in J. Lamarck et al., Encyc. Meth. Bot. **4**(2): 453 (1798). – *Desmodium gangeticum* (L.) DC., Prodr. **2**: 327 (1825); Benth. in Miq., Pl. Jungh. 228 (1852); B. G. Schub. in Fl. Trop. E. Afr. Legum. **3**, Papil. **1**: 467 (1971); H. Ohashi, Ginkgoana **1**: 184 (1973); Ali, Fl. W. Pakistan 100, Pap. 348 (1977); Verdc., Man. New Guinea Leg. 397 (1979); T. C. Huang & Ohashi, Fl.

Taiwan ed. 2, **3**: 253, pl. 121 (1993); H. Ohashi in Dy Phon & al., Fl. Cambodge, Laos & Vietnam **27**: 121 (1994); H. Ohashi in J. Jpn. Bot. **70**: 113 (1995); Pedley in Rev. Handb. Fl. Ceylon **10**: 182 (1996) & in *Austrobaileya* **5**: 249 (1999); H. Ohashi in J. Jpn. Bot. **79**: 122 (2004); P. H. Huang & H. Ohashi in Fl. China **10**: 272 (2010). – *Meibomia gangetica* (L.) Kuntze, Revis. Gen. Pl. **1**: 196 (1891).

*Hedysarum maculatum* L., Sp. Pl. **2**: 746 (1753) [Lectotype (designated by B. G. Schub. in J. Arnold Arbor. **44**: 294, 1963; Jarvis, Ord. Chaos: 560, 2007): Herb. Linn. No. 921.14 (LINN)]. – *Aeschynomene maculata* (L.) Poir. in J. Lamarck & al., Encycl. **4**(2): 452 (1798). – *Pleurolobus maculatus* (L.) J. St.-Hil. in Nouv. Bull. Soc. Philom. **3**: 192 (1812), & in J. Bot. Agric. **1**: 61 (1813). – *Desmodium maculatum* (L.) DC., Prodr. **2**: 327 (1825).

*Desmodium gangeticum* var. *maculatum* (L.) Baker in Hook. f., Fl. Brit. India **2**: 168 (1876).

Distribution: Africa, Australia and Asia, naturalized in the West Indies. Asia: W. Asia (Yemen, Oman, Saudi Arabia), Pakistan, Sri Lanka, India, Nepal, Sikkim, Bhutan, Myanmar, Thailand, Cambodia, Laos, Vietnam, China, Taiwan, Japan (S. Ryukyus), Philippines, Indonesia, New Guinea, Solomon Islands.

## 7) Taxonomic position of *Desmodium oblongum*

*Desmodium oblongum* Wall. ex Benth. was placed in *Desmodium* subgenus *Sagotia* section *Heteroloma* by Ohashi (1973). The species is characteristic in the section in having oblong 1-foliolate leaves, laxly flowered panicles, large bluish flowers with long pedicels and stipitate loment. These features as well as general features of *D. oblongum* are distinct from *Uraria*, although their close relationship was observed in the phylogenetic analysis (Figs. 1–3). We could not find synapomorphic morphological characters between *Uraria* and *D. oblongum*. The pollen morphology is also different between them. Pollen grains of *Uraria*

have psilate or finely rugulate sculpture with fine microperforations and the foot layer is reduced to a thin discontinuous layer; *D. oblongum* has microreticulate sculpturing and a thick foot-layer (Ye 1999, Ye and Ohashi 2002). In spite of the differences in general appearance, *D. oblongum* belongs to *Uraria* as an ingroup as shown in our phylogenetic trees (Figs. 1–3). Clade-VI shows no relationships to *D. scorpiurus* (Sw.) Desv., the type of the genus, in our molecular analyses. We propose to transfer the species to *Uraria* as follows.

*Uraria oblonga* (Wall. ex Benth.) H. Ohashi & K. Ohashi, **comb. nov.**

*Desmodium oblongum* Wall. ex Benth. in Miq., Pl. Jungh. 224 in adnota (1852) [Type: Myanmar: in monte Taong Dong. Wallich 5714 (K-holotype K000858865; N. Wallich, Cat. no. 5714. K-Wall. K001121836, CAL-isotype)]; Baker in Hook. f., Fl. Brit. India **2**: 166 (1876); H. Ohashi in Ginkgoana **1**: 188 (1973), & in Dy Phon, H. Ohashi & J. E. Vidal in Fl. Cambodge, Laos & Vietnam **27**: 114 (1994); Y. C. Yang & P. H. Huang in Fl. Reipub. Pop. Sin. **41**: 27 (1995); P. H. Huang & H. Ohashi in Fl. China **10**: 272 (2010). – *Meibomia oblonga* (Wall. ex Benth.) Kuntze, Revis. Gen. Pl. **1**: 198 (1891).

*Desmodium oblongum* var. *acutifolium* Prain in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. **66**: 394 (1897) [Type: Myanmar. Nattoung Mts. Cross s.n. (K-syntype, n.v.), Mogouk. Cooper (K-syntype, n.v.)].

Distribution: India (Assam), Bhutan, Myanmar, Thailand, Cambodia, Laos, Vietnam, SW. China (Yunnan, Guangxi).

## 8) Taxonomic position of *Codariocalyx microphyllus*

This species is characteristic especially in having arillate seeds. It was a member of *Desmodium* sect. *Sagotia* (Ohashi 1973, Pedley 1999), but then transferred to *Codariocalyx* (Ohashi 2004a) based on additional morphological and palynological

evidence. In our recent molecular analyses, the species forms an independent clade with *Leptodesmia congesta* (Benth.) Benth., which is distinct from the *Codariocalyx* clade (Figs. 1–3). Morphologically, *Codariocalyx* and *Leptodesmia* share arillate seeds (Kirkbride et al. 2003), dehiscent legumes and 1- or 3-foliolate leaves with rather small leaflets.

***Leptodesmia microphylla*** (Thunb.) H. Ohashi & K. Ohashi, **comb. nov.**

*Hedysarum microphyllum* Thunb. in Murray, Syst. Veg. ed. 14. 675 (1784), & Fl. Jap. 284 (1784) [Type: Japonia. Thunberg (UPS–holotype UPS–Thunb no. 17237)]. – *Desmodium microphyllum* (Thunb.) DC., Prodr. 2: 337 (1825); Miq., Fl. Ned. Ind. 1(1): 239 (1855); H. Ohashi in Ginkgoana 1: 241 (1973); Verdc., Man. New Guinea Leg.: 402 (1979); H. Ohashi in J. Jap. Bot. 59: 45 (1984); Grierson & Long, Fl. Bhutan 1(3): 673 (1987); H. Ohashi in Dy Phon & al., Fl. Cambodge, Laos & Vietnam 27: 105 (1994); Pedley in Austrobaileya 5: 235 (1999); P. H. Huang & H. Ohashi in Fl. China 10: 275 (2010). – *Codariocalyx microphyllus* (Thunb.) H. Ohashi in J. Jpn. Bot. 79(2): 109 (2004). Huang and Ohashi (2010) adopted *Codariocalyx* but ‘Hasskarl (in Flora 25 (Beibl. 2): 48. 7 Aug. 1842) corrected “*Codariocalyx*” to “*Codariocalyx*” (Ethymology: Codarium (an Afn. legume) + calyx)’ (IPNI on 16 Dec. 2017).

*Desmodium parvifolium* DC. in Ann. Sci. Nat. 4: 100 (1825) [Type: ‘In Napaulia. *Affinis D. trifloro*. (v.s. comm. a cl. Wallich)’ (G–holotype)] & Prodr. 2: 234 (1825); Benth. in Miq., Pl. Jungh. 223 (1852).

Distribution: Sri Lanka, India, Nepal, Sikkim, Bhutan, Myanmar, Thailand, Malaysia, Cambodia, Laos, Vietnam, China, Taiwan, S. Japan, Philippines, Indonesia, New Guinea, Australia (Queensland and Arnhem Land).

***Leptodesmia microphylla* var. *macrocarpa*** (Baker) H. Ohashi & K. Ohashi, **comb. nov.**

*Desmodium parvifolium* DC. var. *macro-*

*carpum* Baker in Hook. f., Fl. Brit. Ind. 2: 174 (1876) [Lectotype (designated by Ohashi 1984): India. Assam, Khasia. Griffith 355 (K)]. – *Desmodium microphyllum* var. *macrocarpum* (Baker) H. Ohashi in J. Jap. Bot. 59: 45 (1984). – *Codariocalyx microphyllus* var. *macrocarpus* (Baker) H. Ohashi in J. Jpn. Bot. 79(6): 371 (2004).

Distribution: E. Nepal, E. India (Khasi Hill).

***Leptodesmia microphylla* f. *glaber*** (H. Ohashi & T. T. Chen) H. Ohashi & K. Ohashi, **comb. nov.**

*Desmodium microphyllum* (Thunb.) DC. f. *glabrum* H. Ohashi & T. T. Chen in J. Jap. Bot. 59(1): 45 (1984) [Type: Nepal. Arun Valley. Y. Tateishi 8038 (TUS–holotype)].

Distribution: E. Nepal.

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大橋一晶<sup>a</sup>, 大橋広好<sup>b</sup>, 根本智行<sup>c</sup>, 池田樹生<sup>a</sup>, 泉春奈<sup>a</sup>, 小林春菜<sup>a</sup>, 村垣宏和<sup>a</sup>, 那谷耕司<sup>a</sup>, 佐藤夏美<sup>a</sup>, 鈴木舞香<sup>a</sup>: マメ科アコウマイハギ連アコウマイハギ群の分子系統学的解析

マメ科 Tribe *Desmodieae* は 33 属を含み, *Desmodium* 群, *Phyllodium* 群, *Lespedeza* 群に分けられている (Ohashi 2005). *Desmodieae* は *Desmodium* に基づく学名で, その和名は *Desmodium* をヌスビトハギ属と呼んだままにヌスビトハギ連として残されていたが (大橋

広好 マメ科. 大橋広好ほか「改訂新版日本の野生植物」第2巻 p. 243, 平凡社, 2016), 学名と和名とが一致しなくなったため, 今回, アコウマイハギ連と改称したい. ヌスビトハギが *Hylodesmum* に移されて *Hylodesmum* がヌスビトハギ属となり, *Desmodium* の和名はシバハ

ギ属と改称されたが、本誌前号でシバハギを *Grona* に移し、*Grona* をシバハギ属と呼ぶことにしたため、再び *Desmodium* には和名がなくなった。日本にはシバハギのほかにもカワリバマキエハギ、ハイマキエハギ、タマツナギが自生していたが（改訂新版日本の野生植物 第2巻 pp. 264–265）、カワリバマキエハギとハイマキエハギもシバハギ属となり、タマツナギは後述のようにタマツナギ属として独立した。その結果、日本には *Desmodium* の自生種はなくなり、アメリカ大陸からの帰化種であるアレチヌスビトハギ *D. paniculatum* (L.) DC. ほか数種が見られることとなった。このために新たな *Desmodium* の和名が必要であり、属のタイプ種であるアコウマイハギ *D. scorpiurus* (Sw.) Desv. に基づいてアコウマイハギ属とした（本誌 93(2): 120 参照）。アコウマイハギ連 Tribe *Desmodieae* はアコウマイハギ属に基づく。

*Desmodium* 群（アコウマイハギ群）、*Phylloidium* 群（ウチワツナギ群）、*Lepedeza* 群（ハギ群）はそれぞれ単系統であるが、アコウマイハギ群に含まれているアコウマイハギ属 *Desmodium* は多系統であった。われわれはアコウマイハギ群を中心に分子系統学的解析をおこなった結果、アコウマイハギ属内にいくつかの単系統群を認めることができた。これらの単系統群について形態形質、花粉形質などに基づいてまとめてきた分類学上の結果とも併せて、それぞれを独立属と認めることとした。先に発表した論文で *Grona* はタイプである *G. heterocarpa* に基づいてシバハギ属 (Ohashi and Ohashi 2018a)、*Sohmaea* はタイプである *S. laxiflora* に基づいてホソミハギ属とした (Ohashi and Ohashi 2018a)。さらに本論文では、次の6属を提案した。1)

オーストラリア固有種 *Desmodium campylocaulon* に基づく *Desmodiopsis* 節を独立属としての *Desmodiopsis*, 2) *Desmodium concinnum* をタイプとする新属を琉球大学名誉教授立石庸一博士に献名して *Tateishia*, 3) *Desmodium dichotomum* をタイプとする新属は Harvard University Herbaria の David E. Boufford 博士を記念して *Bouffordia*, 4) 先島諸島に自生し、旧世界の熱帯・亜熱帯に分布するタマツナギ *Desmodium gangeticum* (L.) DC. は1種で単系統の単型属となった。タマツナギには保存名 *Desmodium* に対して廃棄されていた先行属名 *Pleurolobus* があったので、これを復活させ、タマツナギ属とし、種名は新組み合わせ *Pleurolobus gangeticus* (L.) J. St.-Hil. とした。5) オセアニアの *Desmodium pycnostachyum* は(3-)5-7小葉をもち、竜骨弁が鋭頭であることなどの形態的特徴をもつ。単系統であり、独立属 *Oxytes* とした。6) *Desmodium renifolium* をタイプとする新属は台湾大学名誉教授黄増泉博士に献名し、*Huangtia* とした。*D. renifolium* には台湾で命名されたジンヨウマキエハギなる和名があるので、ジンヨウマキエハギ属の和名を用意した。また、7) *Desmodium oblongum* Wall. ex Benth. はフジボハギ属 *Uraria* の内群となったため、同属に移し、8) ヒメノハギ *Codariocalyx microphyllus* (Thunb.) H. Ohashi は *Leptodesmia* と単系統となり、分類学上の位置を変更して、新学名を *Leptodesmia microphylla* (Thunb.) H. Ohashi & K. Ohashi とした。紀伊半島以西に分布する。属名 *Leptodesmia* (Benth.) Benth. をヒメノハギ属と呼ぶこととする。

<sup>a</sup>岩手医科大学薬学部、

<sup>b</sup>東北大学植物園津田記念館、

<sup>c</sup>石巻専修大学理工学部生物科学科)