Taxonomy and Distribution of Desmodium and Related Genera (Leguminosae) in Malesia (II)

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This second part of my revision of Malesian Desmodium and its relatives includes taxonomic treatments of the following eight genera - Hanslia (including two new combinations), Hegnera, Hylodesmum, Monarthrocarpus, Ohwia, Phyllodium, Tadehagi, and Trifidacanthus, and phytogeographic considerations for the taxa of Desmodium and its relatives in Malesia. Thirteen genera and 64 species are recognized as Desmodium and its relatives in Malesia. Their distribution patterns are diverse. Of 64 species recognized in this study 56 are native to Malesia and are divided by their distribution patterns into the following four groups: Malesia (including 8 species), Asia (29 spp.), Australia (11 spp.), and Asia-Australia (8 spp.) groups. All species of the genera native to Jawa and New Guinea and the Philippines are discussed. Each area has almost equal numbers of native species, 31, 32, and 29, respectively. This fact suggest insufficient collections in New Guinea and the Philippines. The present-day composition and distribution of taxa in Desmodium and related genera in Malesia are considered to be derived from various spatially and temporally diverse ancestors.

Key words: Desmodium relatives, distribution patterns, Hanslia, Jawa, New Guinea.

Hanslia Schindl. in Repert. Spec. Nov. Regni Veg. 20: 276 (1924) [Type: Hanslia adhaerens Schindl. (= Hedysarum adhaerens Poir., non Vahl.)].


Hanslia is similar to Ohwia in having a scarcely developed rim-aril around the hilum of seeds, uncinate hairs on the loments, long articles, and a coarser, reticulate sculpture on pollen grains. They are considered to be related to each other. Ohwia and Hanslia ormocarpoides have white to creamy flowers, but H. hentyi has purple to pink flowers. The genus comprises two species and both are found in Malesia.

Key to the species of Hanslia
1. Leaves 3-foliolate, rarely mixed with 1-foliolate; leaflets acute at base...H. hentyi
2. Leaves 1-foliolate; leaflets round at base..............................H. ormocarpoides

Hanslia hentyi (Verdc.) H. Ohashi, comb. nov. (Fig. 5)


Leaves of this species have three leaflets or rarely with single leaflets on the same plant. This species occurs under forest and such habitat is supposed to be similar with that of Hylodesmum laxum and H. leptopus.

Hanslia ormocarpoides (DC.) H. Ohashi, comb. nov.

Hedysarum adhaerens Poir. in Lam., Encycl. Suppl. 5: 15 (1817), non Vahl. (1791). [Type: Java. Labillardiére (P. n. v.)]. [Hedysarum ormocarpum Desv. ex Poir.
in Lam., Encycl. Suppl. 5: 15 (1817), pro syn.]


D. pendulum F. Muell. in Campbell, A Year New Hebrides: 9 (1873) [Type: Tana. Campbell (?)]; F. Muell., Fragm. 8: 225 (1874).


The genus is monotypic.


Distr.: Myanmar, Thailand, Indo-China, and Malesia.


Uraria obcordata Miq. was recognized first by Bentham (1865a) as belonging to Desmodium. He classified the species as a member of subsect. Nephromeria Bentham in Desmodium sect. Heteroloma Bentham., but did not publish a new combination.

HYLODESMUM

Key to the species of *Hylodesmum* in Malesia

1. Calyx-lobes not shorter than the tube; primary bracts ovate to broadly ovate; pedicels 15–30(–40) mm long; flowers longer than 8 mm; stipules patent or reflexed, 10–25 mm long, 2–3 mm wide; leaflets slightly undulate along the margin; corolla orange to red............ *H. repandum*

2. Principal lateral nerves reaching the margin; fruit stipes usually less than 7(–10) mm long .................. *H. podocarpum*

2. Principal lateral nerves looped within the margin; fruit stipes usually more than 10 mm long .......................... 3

3. Articles 12–18 mm long; leaflets with white spots and indistinct nerves............. ............................... *H. leptopus*

3. Articles 9–10 mm long; leaflets pale green and with distinct nerves beneath ............ ............................... *H. laxum*

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(Fig. 6)


*D. elongatum* Zoll. & Moritzi in Nat. en


Distr.: Sri Lanka, India, Nepal, Thailand, Indo-China, _Malesia_, Solomon Is. (Guadalcanal), China, and Japan.


_Maluku_. Buru: Wae Kose, primary forest, on a riverside, 0-50 m alt. Moege & Ismail JPM-5203 (BO, K).


_Hylodesmum laxum_ shows a much variation in the shape of leaflets in the _Philippines_. Elmer 10029 (A) and others have a narrowly elliptic terminal leaflet, and Elmer 13820 (A) has an ovate one, but Elmer 22372 (A) has a narrowly elliptic one in the lower leaves and an ovate one in the upper leaves.

The specimens from the _Philippines_, Elmer 11216 (CAL) and 13820 (CAL), were cited by Ohashi (1973) as _Desmodium laxum_ subsp. _leptopus_, but they were erroneous for _Hylodesmum laxum_.


Distr.: Indo-China, _Malesia_, S. China, Taiwan, and S. Japan.


**Hylodesmum laxum** and **H. leptopus** are found in New Guinea, but the latter appears to be rare.


**Key to the subspecies of *Hylodesmum podocarpum***

1. Terminal leaflets broadly obovate to orbicular, broadest at or above the middle, apex rounded with an acute tip.................

1. Terminal leaflets elliptic-ovate, broadest below the middle, apex acute to acuminate

.................subsp. *podocarpum*


Distr. (subsp. *podocarpum*): India, Nepal, Malesia (Philippines: Luzon, rare), China, Taiwan (rare), Japan and Korea.


Distribution of *Hylodesmum podocarpum* (DC.) H. Ohashi & R. R. Mill subsp. *podocarpum* is confined to Luzon. Occurrence of the species was, however, uncertain in the Philippines. Specimens kept as *D. podocarpum* DC. from the Philippines so far as I have examined are all referable to *H. repandum* (Vahl) H. Ohashi & R. R. Mill, i. e., Mt. Santo Tomas in Benguet Ramos & Edano Bur. Sci. 45098 (K, NY, SING, US), and loc. cit. Merrill 11655 (SING, US). Merrill (1910) reported *Desmodium podocarpum* DC. from Luzon based on two specimens, i. e., Williams 1398 and Merrill 4356, although Merrill 4356 in K and NY (Fig. 8) was erroneously determined by him as *D. scalpe* DC., a synonym of *H. repandum*. These two specimens are without doubt *H. podocarpum* subsp. *podocarpum*. The occurrence of the species was confirmed in the Philippines by our recent collection, Nemoto & al. 10750 (TUS).

Meeuwen (1962) recorded *Desmodium racemosum* (Thunb.) DC. from the Philippines based on Saran & Party 30147. I could not find this specimen in L and other herbaria. A specimen, Dr. Cinklin & del Rosario Phil. Nat. Herb. 72413 (L), was determined by Meeuwen as *D. racemosum*. This specimen (as *D. podocarpum*) is kept in several herbaria, but all are *Hylodesmum laxum* (DC.) H. Ohashi & R. R. Mill subsp. *laxum* (Fig. 6). Meeuwen (1962) included *D. podocarpum* DC., *D. gardneri* Benth. and *D. fallax* Schidl. in her *D. racemosum* as synonyms. She circumscribed *D. racemosum* most broadly. Excepting *Desmodium gardneri*, other three species she regarded as conspecific are distinguished as subspecies of *Hylodesmum podocarpum* (DC.) H. Ohashi & R. R. Mill, i. e., subsp. *fallax* (Schidl.) H. Ohashi & R. R. Mill, subsp. *oxyphyllum* (DC.) H. Ohashi & R. R. Mill (= typical *D. racemosum*), and subsp. *podocarpum*. *Desmodium gardneri* comprises *H. laxum* and *H. leptopus* (A. Gray ex Benth.) H. Ohashi & R. R. Mill.


Fig. 7. *Hylodesmum leptopus* (A.Gray ex Benth.) H. Ohashi & R. R. Mill. a: Philippines. Luzon. Lectotype (K). b: Part of the lectotype with label (enlarged from fig. a). c: Loment (enlarged from fig. a).


(1998), nom. illegit.


The specimen, Zollinger 1905 cited above, is labeled as “planta Javanica a cl. Zollingero lecta”, but is composed of two plants; *Ohwia caudata* (Thunb.) H. Ohashi and *Hylodesmus podocarpum* subsp. *oxyphyllum* (DC.) H. Ohashi & R. R. Mill. The two taxa are mounted on the same herbarium sheet in A. A duplicate specimen of Zollinger 1905 is kept in BM, but this composes purely *O. caudata*. *Hylodesmus podocarpum* subsp. *oxyphyllum* mounted on the sheet in A may be erroneously mixed in Zollinger 1905. This specimen must be brought from outside of Jawa, because *H. podocarpum* subsp. *oxyphyllum* has not been known in Jawa.

A specimen, Lörzing 11737 (BO) from...
North Sumatera, is named *Desmodium oxyphyllum* (= *Hylodesmum podocarpum* subsp. *oxyphyllum*), but is *D. elegans* DC. This specimen was collected from a cultivated plant and *D. elegans* is not indigenous in Malesia.


**Hedysarum repandum** Vahl, Symb. Bot. 2: 82 (1791) [Type: Yemen. 1763. Forsskål (holo. C-Vahl)].

**Aeschinomene remota** Poir. in lam., Encyc. 4: 452 (1798).


**D. strangulatum** Wight & Arn., Prodr. Fl. Ind. Orient.: 228 (1834) [Type: Peninsula Ind. orientalis. Wight 774 (K lecto.; isolecto. E)].


**Papilionopsis stylioides** Steenis in Nova Guinea, Bot. 3: 17 (1960) [Type: The apical part of an inflorescence of *Hylodesmum repandum* (Fabaceae), D. Bergman 287 (S), which also comprises foliage, roots and a young scape of *Burmannia disticha* L. (Burmanniaceae)].


Distr.: Africa and Asia. Asia: North Yemen, Sri Lanka, India, Myanmar, Thailand, Indo-China, **Malesia**, and China (Yunnan). No records from Australia.


*Hylodesmum repandum* is often very similar to *H. podocarpus* subsp. *podocarpus* especially in leaflets and loments. Sometimes both were misidentified each other as noted under the latter.

Verdcourt (1979) doubted the indigenous status of *Hylodesmum repandum* (as *Desmodium repandum*) in New Guinea. Distribution pattern of this species differs entirely from those of other members of the genus.

**MONARTHROCARPUS**


**Desmofischera** Holthuis in Blumea 5: 188 (1942) [Type: *Desmofischera monosperma* Holthuis].


**Monarthrocarpus** Merr. is distinct from
Desmodium in having falcate, 1-seeded loments, scarcely rim-arillate, flat seeds, and diadelphous stamens, although it was included in Desmodium subgenus Podocarpium (Ohashi 1973).

The genus is monotypic.

Monarthrocarpus securiforme (Benth.) Merr. in Philipp. J. Sci., C. 5: 88 (1910) & Enum. Philipp. Flow. Pl. 2: 291 (1923). (Fig. 9).


Desmofischera monosperma Holthuis in Blumea 5: 189, fig. 5 (1942) [Type: Taland isl., Karakelong, O. v. Beo. 26 Apr. 1926. H. J. Lam 2637 (L holo.; iso. BO)].


Specimens examined: Maluku: Mt. Permatang 500
m. Kostermans 958 (A, BO, K, L) Mt. Permatang, along Sabgawi river, alt. 200 m. Kostermans 908 (L) Mt. Totodohoe 30 m. Kostermans 761 & 1455 (L); Morotai. Kostermans 7856 (L); Morotai. H. J. Lam 3645 (L); Mortai. Lam 3681 (K); Halmahera Island. Taylor P-319 (A); Maluku. Yoshida 2429 (L); Obi Isl. Anggai, alt. 200 m. E.F. de Vogel 4195 (L). New Guinea: Misool near Waima. Shrub, 1 m high, fls white. D. R. Pleyta 1046 (A, K, L); Mori River, Abau sub-district, Papua, alt. 50 m. Sayers NGF19660 (L); Usino, alt. 400 ft. Henty NGF28020 (L); Sorong, alt. 20 m. Plezte 629 (L). Philippines: Luzon. Cuming 576 along Sabgawi river white. D. Calamangan-Mariano. M.S. Clemens 16729 (L); weg Oedjoeng Lamoero-Takalala. C. Salebabae Poir.)

**New Guinea**: Misool near Waima. Shrub, 1 m high, fls white. D. R. Pleyta 1046 (A, K, L); Mori River, Abau sub-district, Papua, alt. 50 m. Sayers NGF19660 (L); Usino, alt. 400 ft. Henty NGF28020 (L); Sorong, alt. 20 m. Plezte 629 (L). **Philippines**: Luzon. Cuming 576 (K holo.; iso. BM, K), Irosin. Elmer 15907 (NY, TI), Isabela, Calamangan–Mariano. M.S. Clemens 16729 (UC); Isabela Prov., rather open forest trail above Calamangan, Mt. Moises. Aug. 1926. M. S. Clemens 16730 (UC). **Sulawesi**: Taland isl., Karakelong. Cleaed old folest, rather frequent, alt. 90 m. Small undershrub, partly prostrate, cololla and filaments white, fr. green. Lam 2637 (L, BO types); Taland isl. Salebabae, top G. Ajambana. 20 May 1926. H. J. Lam 3057 (L); weg Oedjoeng Lamoero–Takalala. C. Monod de Froideville 421 (L).

**OHWIA**


*Ohwia* H. Ohashi is named instead of *Catenaria* (Ohashi 1999). *Catenaria* was created by Bentham (1852) and maintained by Schindler (1924b) and Hutchinson (1964), but it has been widely recognized as a member of *Desmodium*. Although *O. caudata* has remarkable characters in common with *Desmodium*, i.e., jointed pods with hooked hairs, the differences between *Ohwia* and *Desmodium* are described by Ohashi (1973) for *D. caudatum* in morphological and palynological characters. It is revived to a genus *Ohwia*, because it is distinct from *Desmodium* in having a disk around the base of the pistil and seeds with a scarcely developed hilum lacking a rim-aril. Moreover, *Ohwia* differs from most of *Desmodium* in having distinctly veined chartaceous petals (against slightly veined membranaceous petals in most of *Desmodium*), equally indented linear pods and coarsely reticulate pollen grains (Ohashi 1999).

The genus comprises two species of which one is found in Malesia.


*Hedysarum caudatum* Thunb. in Murray, Syst. Veg. ed. 14, 675 (1784); Thunb., Fl. Jap.: 286 (1784) [Type: Japan. Thunberg (UPS)].

*H. laburnifolium* Poir. in Lam., Encycl. 6: 422 (1805) [Type: from Java. (P), n. v.].


*D. laburnifolium* (Poir.) DC., Prodr. 2: 337 (1825); Ridl., Fl. Malay Penins. 1: 608 (1922).


*D. excelsa* var. *excelsa* (F. Yang & P. H. Huang in F. Yang & P. H. Huang in Fl. Malay Penins. 1: 608 (1922).) 1. Lateral leaflets smaller (ca. 2 times) than the terminal one and similar to primary bracts; flowers less than 7 mm long .......2 2. Pods usually 2-jointed, sparsely pubescent on lateral surfaces, reticulate-veined; stipules narrowly triangular, 6–8 mm long. Lowest calyx-lobe almost equal to the lateral one. Bracteal leaflets uniformly appressed pubescent on nerves on adaxial surfaces............................*P. pulchellum* 2. Pods usually 3–4-jointed; stipules broadly triangular, 3–5 mm long. Lowest calyx-lobe longer than the lateral one. Bracteal leaflets densely hairy on nerves on adaxial surface .....................*P. elegans*


**Key to the species of Phyllodium in Malesia**

1. Lateral leaflets similar to the terminal one and distinct from primary bracts; flowers more than 10 mm long ..........*P. vestitum*

1. Lateral leaflets smaller (ca. 2 times) than the terminal one and similar to primary bracts; flowers less than 7 mm long ......2

2. Pods usually 2-jointed, sparsely pubescent on lateral surfaces, reticulate-veined; stipules narrowly triangular, 6–8 mm long. Lowest calyx-lobe almost equal to the lateral one. Bracteal leaflets uniformly appressed pubescent on nerves on adaxial surfaces............................*P. pulchellum* 2. Pods usually 3–4-jointed; stipules broadly triangular, 3–5 mm long. Lowest calyx-lobe longer than the lateral one. Bracteal leaflets densely hairy on nerves on adaxial surface .....................*P. elegans*
Specimens examined: **Jawa.** Teyjesmann 1868 (K, NY), Backer s. n. July 1904 (K, L), Miquel s. n. (K), Horsfield 60 (BM) & Horsfield 81 (GH, K, L), Horsfield 585 (K), Junghuhin 117 (K), Winterbottom s. n. July 1846 (K), Waitz s. n. (L); Tjisara. Möler on 17/4 1897 (A).

**Phyllodium elegans** var. **javanicum** is distinguished from var. **elegans** by its grayish hairy leaves, broadly ovate terminal leaflet with rounded base and distinct lateral and third (between lateral nerves) nerves, wrinkled primary leafy bracts with conspicuous third nerves and 4–5 mm long fruiting pedicels.

**Phyllodium elegans** var. **elegans** is not found in Malesia, and is confined to Thailand, Indo-China and S. China (Ohashi 1997c).


**Hedysarum pulchellum** L., Sp. Pl.: 747 (1753) [Type: Herb. Linn. No. 921.24 (LNN decto., see Pedley in Turland & Jarvis 1997)].


Distr.: Asia, Australia and Pacific (Solomon Is.). Asia: Sri Lanka, India, Myanmar, Thailand, Indo-China, **Malesia** (throughout), China, Taiwan, and S. Japan (Ryukyus).


**Desmodium vestitum** (Benth.) Benth. ex Baker in Hook. f., Fl. Birt. Ind. 2: 162 (1876); Ridl., Fl. Malay Penins. 1: 607 (1922).

Distr.: Myanmar, Thailand, Indo-China, and **Malesia**.


**TADEHAGI**


The genus comprises six species of which one is found in Malesia. Merrill (1923) recorded **Tadehagi auriculatum** (DC.) H. Ohashi (as **Desmodium auriculatum** DC.) from Luzon, but it was misidentification of **T. triquetrum** (L.) H. Ohashi nothosubsp. **philippinense** H. Ohashi var. **philippinense** H. Ohashi.


**Key to the subspecies and their hybrids of** **Tadehagi triquetrum**

1. Loments densely to sparsely pubescent on lateral surfaces ........................................ 2
2. Loments glabrous on lateral surfaces ....... 3
3. Leaf-blade usually more than 3 times longer than broad, linear to narrowly ob-
long-ovate or narrowly ovate

2. Leaf-blade less than 3 times longer than broad, usually ovate or narrowly ovate......

3. Leaf-blade less than 3 times longer than broad, usually ovate or narrowly ovate......

3. Leaf-blade usually more than 3 times longer than broad, linear to narrowly ob-long-ovate or narrowly ovate..............


*Pteroloma tiquetrum* (L.) Desv. ex Benth. in Miq., Pl. Jungh.: 220 (1852).


= **Tadesahi tiquetrum** subsp. *tiquetrum* × **Tadesahi tiquetrum** subsp. *pseudotiquetrum* (DC.) H. Ohashi

var. *philippinensis* H. Ohashi in J. Jpn. Bot. 78: 293, figs. 11–12 (2003), as “philippinensis”.


This hybrid has loments glabrous on the lateral surface as subsp. pseudotriquetrum. Merrill (1923) determined this hybrid as *Desmodium auriculatum* based on “Ramos B. S. 1036, Ramos B. S. 22685 and Merrill 7394”, although I have not examine the last one. See the differences between Tadehagi *auriculatum* and *T. triquetrum* (nothosubsp. *philippines* var. *philippines*) in Ohashi in J. Jpn. Bot. 78: 279 (2003).

var. *palawanense* H. Ohashi in J. Jpn. Bot. 78: 293, fig. 13 (2003), as “*palawanensis*”


This hybrid has loments pubescent on the lateral surface.

**TRIFIDACANTHUS**


*Trifidacanthus* Merr. was first established and placed, by Merrill (1917), close to *Arthroclianthus* Baill. endemic to New Caledonia, but was included in *Desmodium* by Steenis (1982). It was again recognized as distinct from *Desmodium* and was considered one of the genera nearest to *Desmodium* (Ohashi et al. 1996). *Trifidacanthus* is characterized in having lignified trifid spines (derived from an inflorescence axis and two lateral pedicels), the marginal venation pattern of the leaflets, sympodial terminal inflorescences, and loments without hooked hairs.

The genus is monotypic.


Distr.: **Malesia** (Lesser Sunda Is: Lombok and Flores and the Philippines: Luzon), S. Vietnam and S. China (Hainan).


**Phytogeographic considerations**

1. **Distribution of genera in Malesia**

The boundary between Malesia and Indo-China floristic regions lies slightly to the north of the political border of Malaysia (Johns 1995). Continental Asia in this paper means an area excluding the southern half of Malay Peninsula. Malesia has much diversity in distribution of organisms. In current phytogeographical studies, Malesia is divided into three floristic regions: Western Malesia (Sunda Shelf) including Borneo, Jawa, southern half of Malay Peninsula, Palawan, and Sumatera, Central Malesia including the Lesser Sunda Islands, Maluku, the Philippines (excluding Palawan), and Sulawesi, and Eastern Malesia or Papuasia including New Guinea and the Bismarck Archipelago (Johns 1995). The boundary between these floristic regions seems to correspond to a line previously proposed on the basis of distribution of remarkable animals or plants in Malesia. Various faunal or floristic lines have been proposed in Malesia: Haxley’s or Merrill’s line, Lydekker’s line,
Wallace's line, Weber's line, Zollinger's line, etc. Some of the lines agree entirely or partly with the eastern or western boundaries of the Central floristic region and others run within the floristic region. The Lydekker's faunal line seems to correspond with the floristic boundary between the Eastern and Central floristic regions.

The distribution patterns of the 13 genera of Desmodium and relatives are diverse in Malesia. The monotypic Monarthrocarpus is endemic to Malesia and is apparently confined to the Central and Eastern Malesia floristic regions. It is known in New Guinea, Luzon in the Philippines and Sulawesi. Hanslia is also found in the Central and Eastern Malesia floristic regions and Australia but not in continental Asia.

Five genera are distributed in continental Asia and Malesia: Desmodiastum, Hegnera, Hylodesmus, Ohwia, and Trifidacanthus, but their distribution patterns differ from each other within these regions. With the exception of Hylodesmus these genera are represented by only a single species each in Malesia. All species of Desmodiastum (4 spp.) are confined to India except Desmodiastum parviflorum, which extends to East Jawa in the Western Malesia floristic region, but is not found elsewhere in Indo-China. Hegnera is distributed in Myanmar, Thailand, Indo-China, and in Jawa, Malay Peninsula, and Sumatera in the Western Malesia floristic region. Ohwia is widely distributed in India, Sri Lanka, Nepal, Sikkim, Bhutan, Myanmar, Vietnam, Laos, and E. Asia, but in Malesia is confined to the Western Malesia floristic region. Hegnera and Ohwia are considered to be derived in Malesia from Indo-China, but it is possible that Desmodiastum migrated to Malesia directly, rather than through Indo-China. Trifidacanthus is monotypic and rare, being found sporadically in Hainan, south Vietnam, Luzon and Lombok. This suggests a connection between the Central Malesia floristic region and southern China.

Hylodesmus has four species in Malesia: H. laxum, H. leptopus and H. repandum are common and widely distributed in Malesia, but H. podocarpum is rare and known only in Luzon, the Philippines.

The remaining six genera (Aphyllodium, Codariocalyx, Dendrolobium, Desmodium, Pylodium, and Tadehagi) contain species distributed widely in continental Asia through Malesia to Australia, but their distribution patterns are individually characteristic. Aphyllodium comprises eight species including four endemic to Australia (Pedley 1999), one each endemic to New Guinea (A. novoguineense) and Myanmar (A. hispidum (Schindl.) H. Ohashi; Ohashi 1997b), one confined to New Guinea and Australia (A. schindleri), and only A. biarticulatum distributed widely in Sri Lanka, India, Myanmar, Indo-China, Hainan, Western and Central Malesia and Australia. Thus there are three species in Malesia, but there is a distant gap in the distribution of A. biarticulatum between Jawa/Sulawesi and Australia. This disjunction straddles the range of the two East Malesian species, A. novoguineense (New Guinea) and A. schindleri (New Guinea/northern Australia).

Dendrolobium comprises 19 species and is abundant in Indo-China (9 spp.) and Malesia to Australia (7 spp.) (Ohashi in Lewis et al. in prep.). It includes four species endemic to Malesia of which three are from the Philippines. Dendrolobium papuacola is endemic to New Guinea and close to D. arbuscula which is distributed in New Guinea, northern Australia and Fiji. Dendrolobium rugosum is apparently part of the Indo-Chinese floristic element and is confined to Malay Peninsula in Malesia. It seems to be derived from continental Asia. Dendrolobium triangulare and D. umbellatum are widespread species, but the former occurs on hills or low altitude montane sides, while the latter is coastal.
Desmodium includes one species (*D. bolsteri*) endemic to the Philippines, 15 species common in Asia, eight in Australia and only three covering both continents. Of the 15 species distributed in continental Asia only five are found in New Guinea while all the eight of the Australian species are distributed in New Guinea. This pattern of distribution shows that *Desmodium* of New Guinea and Australia appears to be closely related than that between New Guinea and the regions west of New Guinea treated in this paper (Central and Western Malesia floristic regions and continental Asia).

Phyllodium appears to have undergone a major radiation in Indo-China where six of eight species of the genus occur. Four of these six species are almost endemic to the region. In Malesia, *Phyllodium pulchellum* is widely distributed, but *P. vestitum* is confined to the Malay Peninsula and *P. elegans* var. *javanicum* to Java (var. *elegans* is confined to Indo-China and southern China). Tadehagi is represented by *T. triquetrum* in Malesia. It shows unique variation in the Philippines, Lesser Sunda islands and New Guinea (Ohashi 2003). The genus is rare in Australia: *T. triquetrum* is uncertain in Australia and only one endemic *T. robustum* is known in north Western Australia (Pedley 1999).

2. Distribution of species in Malesia

Species of *Desmodium* and its related genera may be considered difficult to interpret in terms of distribution due to their weedy nature and remarkable ability for dispersal of seeds. However, many species have definite distribution patterns. Those represented by introduced and widespread species are exceptional. Of the sixty-four species I recognize in the group in Malesia, eight species of *Desmodium* are introductions from tropical or subtropical America. Fifty-six are native species of which 27 belong to *Desmodium*, eight to *Dendrolobium*, four to *Hylodesmus*, three to each of *Aphyllodium*, *Codariocalyx* and *Phyllodium*, two to *Hanslia*, and one each in *Desmodiastrium*, *Hegnera*, *Monarthrocarpus*, *Ohwia*, *Tadehagi*, and *Trifidacanthus*. The native Malesian species are diverse in distribution pattern, and are primarily divided into four groups: 1) species endemic to Malesia, 2) species distributed in Malesia and continental Asia, 3) species distributed in Malesia and Australia, and 4) species distributed in the whole area from continental Asia through Malesia to Australia. These groups are referred to here as Malesia group, Asia group, Australia group and Asia-Australia group, respectively (Table 1).

(i) Malesia group

The eight following species (14% of the 56 native Malesian species) are distributed as indicated in parentheses after each name: *Aphyllodium novoguineense* (New Guinea), *Dendrolobium cumingianum* (Luzon), *Dendrolobium geesinkii* (Luzon), *Dendrolobium papuacola* (New Guinea), *Dendrolobium quinquepetalum* (Luzon and rarely in Mindoro), *Desmodium bolsteri* (Luzon), *Hanslia hentyi* (New Guinea and newly in Borneo) and *Monarthrocarpus securiforme* (Luzon and Isabela islands in the Philippines, Maluku, and New Guinea).

The following two subspecies are also endemic to Malesia: *Desmodium nemorosum* subsp. *whitfordii* is endemic to Luzon and *Desmodium strigillosum* subsp. *celebicum* is confined to Sulawesi. Tadehagi *triquetrum* produces hybrids (nothosubsp. *philippinense*) between subsp. *triquetrum* and subsp. *pseudotriquefurum* in Luzon, Palawan, and New Guinea. The hybrid is divided into two varieties: var. *philippinense* in Luzon and var. *palawanense* in Palawan and New Guinea. These subspecies and notho-subspecies belong actually to the Malesia group, but they are not treated in this phytogeographical consideration as separate
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<tr>
<th>Malesia group</th>
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<th>Australia group</th>
<th>Asia-Australia group</th>
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<td>D. rhytidophyllum</td>
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<td>D. diffusum</td>
<td>D. tenax</td>
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<td>P. vestitum</td>
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<td>[9 gen. 29 spp.]</td>
<td>[9 gen. 29 spp.]</td>
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from its mother species.

Among the Malesia group, five species (and one subspecies and one nothovariety) are found in Luzon island in the Philippines, and four species (and one nothovariety) are found in New Guinea. In addition, one subspecies of an Asian group is endemic to Sulawesi, Desmodium strigillosum subsp. celebicum. With the exception of Monarthrocþrus securiforme, which is found widely in Malesia (Maluku, New Guinea, Philippines and Sulawesi), other endemic species occur in locally limited habitats.

A disjunction between the Western and Eastern Malesia floristic regions is apparent in the distribution pattern of Hanslia hentyi and Tadehagi triquetrum nothovariety. palawanense.

(ii) Asia group

Twenty-nine species (52% of the 56 native species) are distributed in Malesia and continental Asia (excluding southern half of Malay Peninsula), but not in Australia. They belong to nine genera as shown in Table 1. Desmodium heterophyllum was recorded from Australia by Whele & Frances [in Bot. Bull. Queensland 22: 14 (1920)] but the species is said to be recent introduction to Australia (Pedley 1999). Desmodium strigillosum and D. velutinum were also regarded as recent introductions (Pedley 1999). Desmodium renifolium was recorded from Australia (Meeuwen 1962, Ohashi 1973), but is not included in Pedley’s work (1999). I have not examine specimens of the species from Australia.

The Asian group is divided into two subgroups according to their distribution patterns; a general subgroup and a West Malesia subgroup. Species of the general subgroup include 18 species and are found in two or three floristic regions in Malesia, but the others include 11 species and are distributed only in the West Malesia floristic region. The latter subgroup contains Dendrolobium rugosum, Desmodiastrium parviflorum, Desmodium auricomum, D. renifolium, D. rubrum, D. teres, Hegnera obcordata, Hylodesmus podocarpum, Ohwia caudata, Phyllodium elegans, and P. vestitum.

Dendrolobium rugosum, Desmodium rubrum, and Phyllodium vestitum are noteworthy as they are confined only to the Malay Peninsula. Infraspecific taxa of D. heterocarpon (i.e., subsp. angustifolium and subsp. ovalifolium) and D. strigillosum (i.e., subsp. strigillosum) are also limited to the region. Desmodium heterocarpon subsp. angustifolium is confined to the Malay Peninsula, but subsp. heterocarpon is widely distributed, belonging to the Asia-Australia group. Hylodesmus podocarpum and its infraspecific taxa are common in continental Asia, but is very rare in Malesia: subsp. podocarpum is known rarely from Luzon in the Philippines (Fig. 8) and subsp. oxyphyllum is probably not found in Malesia. The taxa of the West Malesia subgroup are considered to have come into the area from continental Asia.

Of the 29 species belonging to the Asia group, Desmodiastrium parviflorum is the only example that is disjunctively distributed in India and Jawa. Desmodium dichotomum has a similar distribution pattern, occurring in India, China (Yunnan) and Malesia (Jawa, Lesser Sunda Islands, and Sulawesi). They are not in Indo-China or Thailand.

Trifidacanthus unifoliolatus shows a unique distribution pattern in the Asia group. It is a rare species and is found only in one or a few localities in Hainan, southern Vietnam (Phu Khanh), Luzon, Lombok and Flores. Its principal areas of distribution are around the South China Sea, and disjunctively Lesser Sunda Islands. The species is not known from Indo-China except for the one locality in southern Vietnam and the West Malesia floristic region in Malesia.

Desmodium sequax is widely distributed
in montane areas in Northern India, Nepal, Sikkim, Bhutan, Myanmar, Thailand, Malesia, Laos, Vietnam, China, and Taiwan. It usually occurs above 600 m altitude, although it has been collected between 200 m (in Vietnam) and 2850 m (in China) above sea level. It is distributed sporadically in Malesia (Maluku—New Guinea—Philippines—Sulawesi, and Sumatera), where it is apparently confined to high altitudes. This distribution pattern suggests that the species may spread by birds and may be imported from continental Asia. The distribution pattern is similar to that of Ohwia caudata.

(iii) Australia group

The following eleven species (20% of the 56 native Malesian species) are found in Malesia and Australia (areas in Malesia are shown in parentheses): Aphylodium schindleri (New Guinea), Dendrolobium arbucula (New Guinea), Desmodium brachypodium (New Guinea), D. filiforme (Jawa and New Guinea), D. gunnii (New Guinea), D. nemorosum subsp. nemorosum (New Guinea; subsp. whitfordii belongs to the Malesia group), D. pullenii (Alor in the Lesser Sunda Islands and New Guinea), D. rhytidophyllum (New Guinea), D. tenax (New Guinea), D. trichostachyum (Maluku and New Guinea), and Hanslia ormocarpoides (many places in Malesia and New Hebrides) (Table 1). As can be seen, in Malesia, these species are mainly distributed in or even confined to New Guinea. All except Hanslia ormocarpoides occur more frequently in Australia where they are often widely distributed. Desmodium filiforme is disjunctively distributed in Jawa from New Guinea and northern Australia. It is close to D. pullenii, which is found in Alor in Malesia and northern Australia. Direct dispersals from northern Australia to Jawa or Alor, rather than via New Guinea, are supposed from their distribution patterns.

(iv) Asia-Australia group

Eight species (14% of the native Malesian species) occur across Malesia, continental Asia, and Australia (Table 1). Tadehagi triquetrum was first recorded from Australia by Holtze in 1892 (Chapman 1991), Desmodium renifolium by Bailey in 1900 (Chapman 1991) and D. repandum by Meeuwen (1962), but Pedley (1996, 1999) denied their occurrence in Australia. I have not found specimens of these species from Australia and therefore include them in the Asia group in this study.

Codariocalyx microphyllus, Desmodium heterocarpon, D. velutinum and Tadehagi triquetrum are included in this group, but their infraspecific taxa show different patterns of distribution from the type taxa. Codariocalyx microphyllus occurs widely in Malesia and continental Asia and less frequently in northeastern Australia, but it has a variety endemic to Assam and a form to Nepal (Ohashi 1984). Desmodium heterocarpon subsp. heterocarpon belongs to the Asia-Australia group, while subsp. angustifolium and subsp. ovalifolium are not found in Australia, so the latter two subspecies belong to the Asia group. Desmodium velutinum is divided into subsp. velutinum and subsp. longibracteatum; the latter subspecies belongs to the Asia group. Tadehagi triquetrum, though its distribution in Australia is dubious, includes subsp. pseudotriquetrum of the Asia group. Subsp. pseudotriquetrum is frequent in continental Asia but rare in Malesia where it is only found sporadically in New Guinea and the Philippines. From their distribution patterns and infraspecific differentiation patterns Codariocalyx microphyllus, Desmodium heterocarpon, D. velutinum, and Tadehagi...
triquetrum may be regarded mainly as members of the Asia group.

Among other members of the Asia-Australia group, Aphyllodium biarticulatum, Desmodium gangeticum, D. triflorum, and Phyllodium pulchellum may also be regarded as members of the Asia group on the basis of their distribution patterns. Only Dendrolobium umbellatum is different from the other members of the Asia group. It is a coastal plant and disperses the seeds enclosed in corky pericarp by an ocean current. With the exception of the last species, all members of the Asia-Australia group are considered as originally distributed in Asia.

3. Comparisons of Desmodium and related genera between Jawa, New Guinea and the Philippines

Comprehensive works for Leguminosae were provided by Merrill (1923) for the Philippines, Backer and Bakhuizen van den Brink Jr. (1963) for Jawa, and Verdcourt (1979) for New Guinea. Desmodium and related genera in these regions appear to be better known than in other regions in Malesia. However, Jawa is estimated as having been botanized more than 2–4 times more intensively than the Philippines and Papua New Guinea based on comparisons of previous collections in each regions (Campbell and Hammond 1989, Johns 1995). The relatively recent discoveries of such distinct species as Desmodium hentyi Verdc. from near Lae in Papua New Guinea, Dendrolobium papuacola from Loloki River in Papua New Guinea and Dendrolobium geesinkii from Luzon may reflect a paucity of collections of Desmodium and related genera from New Guinea and the Philippines. In spite of the disparity in the inventories among these regions, I have attempted a preliminary comparison of species and distribution patterns for the genera in the areas:

(i) **Jawa**: Thirty-one species of Desmodium and related genera were recorded from Jawa (Backer and Bakhuizen van den Brink Jr. 1963), of which 28 were considered to be native. The three excluded species are naturalized from America, Desmodium adscendens (var. trifoliastriatum), D. tortuosum, and D. uncinatum. Thirty-one species are recognized as native to Jawa in this paper and are classified into the following 10 genera: Aphyllodium biarticulatum (not included in Backer and Bakh. f.), Codariocalyx 3 spp. (as Desmodium gyroides, D. microphyllum, and D. motorium in Backer and Bakh. f.), Dendrolobium 2 spp. (as Desmodium triangulare and D. umbellatum in Backer and Bakh. f.), Desmodiastrum parvi flora (as Desmodium alysicarpoides in Backer and Bakh. f.), Desmodium 16 spp. (15 species in Backer and Bakh. f., of which D. lasiocarpum is synonymous; and D. diffusum and D. teres are added), Hegnera obcordata (as Desmodium obcordatum in Backer and Bakh. f.), Hylodesmum 3 spp. (as Desmodium laxum and D. repandum in Backer and Bakh. f.; and Hylodesmum leptopus is added but H. podocarpum is dubious and excluded), Ohwia 1 sp. (as Desmodium caudatum in Backer and Bakh. f.), Phyllodium 2 spp. (as Desmodium blandum and D. pulchellum in Backer and Bakh. f.), and Tadehagi triquetrum (as Desmodium triquetrum in Backer and Bakh. f.) (Table 2).

Distribution patterns of these species are as follows: 22 species belong to the Asia group (71% of the 31 native species in Jawa), one (Desmodium filiforme) to the Australia group (3% of species in Jawa), and eight belong to the Asia-Australia group (26% of Javanese natives). All species except Desmodium filiforme relate to continental Asia in distribution.

(ii) **New Guinea**: Verdcourt (1979) recorded 33 species including one unknown from New Guinea, of which seven were in-
Table 2. Distribution of *Desmodium* and related species in Jawa, the Philippines and New Guinea with those in Indo-China and Australia

<table>
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<th>Species common in Jawa, the Philippines and New Guinea</th>
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<th>New Guinea</th>
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¹ Dy Phon, Ohashi and Vidal (1994), ² Pedley (1999), ³ subsp. whitfordii, ⁴ subsp. nemorosum, ⁵ var. elegans, ⁶ var. javanicum.
troduced from America. Thirty-two indigenous species are recognized in this study including Verdcourt’s unknown (= Desmodium sequax) (Table 2). They are Aphyllodium 2 spp. (as Desmodium biarticulatum in Verdcourt, but is Aphyllodium novoguineense; and A. schindleri is added), Codariocalyx 2 spp. (as Desmodium gyroides and D. microphyllum in Verdcourt), Dendrolobium 3 spp. (as Desmodium umbellatum in Verdcourt, but Dendrolobium arbuscula and D. papuacola are added), Desmodium 17 spp. (14 species in Verdcourt; and Desmodium diffusum, D. pullenii and D. tenax are added), Hanslia 2 spp. (as Desmodium henteyi and D. ornocarpoides in Verdcourt), Hylodesmum 3 spp. (as Desmodium laxum and D. repandum in Verdcourt; Hylodesmum leptopus is added), Monarthrocarpus 1 sp. (as Desmodium securiforme in Verdcourt), Phyllodium 1 sp. (as Desmodium pulchellum in Verdcourt), and Tadehagi 1 sp. (as Desmodium triquetrum in Verdcourt). Additions to Verdcourt (1979) are seven species, i.e., Aphyllodium schindleri (as D. biarticulatum var. australiense in Verdcourt), Dendrolobium arbuscula, D. papuacola, Desmodium diffusum, D. pullenii, D. tenax (as D. rhytidophyllum subsp. acutifoliolum in Verdcourt), and Hylodesmum leptopus (as D. laxum subsp. leptopus in Verdcourt).

Thirty-two species of Desmodium and relatives in New Guinea comprise four species of the Malesia group including two endemic species (Aphyllodium novoguineense and Dendrolobium papuacola), 10 from the Asia group, 11 from the Australia group, and seven from the Asia-Australia group. All species of the Australia group (i.e. 100 %) are found in New Guinea, whilst 10 of the 29 species of the Asia group known in Malesia (34 %) are found in New Guinea. It is apparent that the members of Desmodium and relatives in New Guinea have stronger ties to Australian taxa than continental Asian ones. The distribution boundary between the Asia and Australia groups in these genera seems to agree with that of Malesia and Papuasia.

Among the Asia-Australia group only Aphyllodium biarticulatum is not found in New Guinea, although this species is widely but sporadically distributed in Asia, Malesia and Australia. However, in New Guinea, there is one endemic species of Aphyllodium as well as a member of the Australia group. Differentiation of the genus in New Guinea and Australia needs to be studied.

(iii) The Philippines: Merrill (1923) enumerated 32 species of Desmodium and one species of each of Monarthrocarpus and Trifidacanthus in the Philippines of which 30 species are native to the region (Table 2). Desmodium malacophyllum, D. procumbens, D. scoriarius and D. trifoliatum are excluded from his list as species introduced from America. Twenty-nine species are recognized in this paper and are reclassified as follows: Codariocalyx 3 spp. (as Desmodium gyrans, D. gyroides and D. microphyllum in Merrill), Dendrolobium 4 spp. (as Desmodium cunningianum, D. quinquepetalum and D. umbellatum in Merrill; and Dendrolobium geesinkii), Desmodium 13 spp. (14 species in Merrill in which D. buergeri, D. lasiocarpum and D. ovalifolium are synonymous; and D. diffusum and D. nemorosum (subsp. whitfordii) are added); Hanslia ornocarpoides (as Desmodium ornocarpoides in Merrill), Hylodesmum 4 spp. (as Desmodium laxum, D. podocarpum, and D. scalpe in Merrill; and Hylodesmum leptopus is added), Monarthrocarpus securiforme (as in Merrill), Phyllodium pulchellum (as Desmodium pulchellum in Merrill), Tadehagi triquetrum (as Desmodium auriculatum, D. pseudotriquetrum and D. triquetrum in Merrill) and Trifidacanthus unifoliolatus (as in Merrill).

The distribution patterns of these species fit with the Malesia, Asia, Australia, and Asia-Australia groups. The Malesia group comprises five species (17 % of native spe-
cies in the Philippines), i. e., *Dendrolobium cumingianum*, *D. geesinkii*, *D. quinquepeta-
lum*, *Desmodium bolsteri*, and *Monarthro-
carpus securiforme*. The Asia group includes
the following 15 species (52 % of species in the
Philippines): *Codariocalyx gyroides*, *C.
motorius*, *Desmodium capitatum*, *D.
diffusum*, *D. heterophyllum*, *D. laxiflorum*,
*D. sequax*, *D. styracifolium*, *D. velutinum*, *D.
zonatum*, *Hylodesmum laxum*, *H. leptopus*,
*H. podocarpum*, *H. repandum*, and *Trifida-
canthus unifoliolatus*. The Australia group
comprises two species (7 % of species in the
Philippines), *Desmodium nemorosum* (subsp.
whitfordii) and *Hanslia ormocarpoides*. The
Asia-Australia group has seven representa-
tives in the Philippines (24 % of the area’s
species), i. e., *Codariocalyx microphyllus*,
*Dendrolobium umbellatum*, *Desmodium
gangeticum*, *D. heterocarpon*, *D. triflorum*,
*Phyllodium pulchellum* and *Tadehagi
triquetrum*.

Geographically, the Philippines lies close
to south China and Taiwan. Most of the spe-
cies belonging to the Asia and Asia-Australia
groups are also found in China and/or
Taiwan, while the two species of the
Australia groups found in the Philippines do
not occur in China and Taiwan. This indi-
cates a close distributional relationship in
*Desmodium* and related genera between the
Philippines and south China and Taiwan.

(iv) Comparison between Jawa and New
Guinea: Thirty-one species of *Desmodium*
and relatives are recorded from Jawa and 32
from New Guinea. Such similarity in numbers of species may suggest
those in New Guinea are poorly known in
the light of its larger areas, richness of envi-
ronmental conditions and remaining unde-
veloped natural areas. It seems probable that
more new species will be found in New
Guinea in future.

Of the 31 Javanese species, 18 are in com-
mon with New Guinea (58 % of all species
in Jawa), and 13 are not found in New
Guinea (Table 2). With the exception of
*Codariocalyx motorius* and *Desmodium
capitatum* the remaining 11 Jawanese spe-
cies not found in New Guinea are also not
distributed in the Philippines.

Fourteen species from New Guinea (44 %
of New Guinea species) are not found in
Jawa (Table 2). Other than the four species
belonging to the Malesia group, the remain-
ing species (10 spp.) all belong to the
Australia group (Table 1). This indicates that
the species of Desmodium and its relatives in
New Guinea are very close to those of
Australia but those in Jawa are not.

(v) Comparison between Jawa and the
Philippines: Jawa and the Philippines have
nearly equal number of species in the genera
treated in this paper. Nineteen species of
Jawa (61 % of the island’s species) are also
found in the Philippines (Table 2), but 12
species (the remaining 39 %) are indigenous
to Jawa (Table 2). The Jawanese species ab-
sent in the Philippines suggest a close con-
nection between Jawa and Indo-China and
India in distribution, because they are found
in Indo-China and/or India, but not (or only
rarely) in China. *Desmodiastrum parviflo-
rum*, *Desmodium auricomum*, *D. teres*,
*Hegnera obcordata*, and *Phyllodium elegans*
var. *javanicum* are not distributed in China,
*Aphyllodium biarticulatum* is only known in
Hainan and *Desmodium dichotomum* and *D.
megaphyllum* are found in Yunnan in China.

Apart from four species endemic to the
Philippines, the following six species of the
Asia and Asia-Australia groups are not found
in Jawa: *Desmodium nemorosum*, *D. styraci-
folium*, *Hanslia ormocarpoides*, *Hylodes-
rum podocarpum*, *Monarthrocarpus securi-
forme*, and *Trifidacanthus unifoliolatus*. *Hylodesmum podocarpum* is very rare in
Luzon and is not found in Indo-China but is
common in continental China and Japan. Its
ranges from NW India, through Nepal, China,
Taiwan, Korea and into Japan. *Trifidacanthus
unifoliolatus* is a very rare
species not only in Malesia but also in China and Vietnam. These facts may indicate that species in *Desmodium* and related genera in the Philippines are remote from Jawa. Three endemic *Dendrolobium* species are characteristic of these genera in the Philippines.

(vi) **Comparison between New Guinea and the Philippines:** Twenty species from New Guinea are also found in the Philippines (Table 2). Twelve New Guinean species, all of which belong to the Australia group, are absent from the Philippines (Table 3). *Desmodium nemorosum* is distributed in both regions, but separated into subsp. *nemorosum* in New Guinea and subsp. *whitfordii* endemic to the Philippines. *Codariocalyx motorius, Dendrolobium cumingianum, D. geesinkii, D. quinquemertum, Desmodium bolsteri, D. capitatum, D. styracifolium, Hylostemum podocarpum* and *Trifidacanthus unifoliolatus* are not found in New Guinea. With the exception of four endemics, the remaining Philippine species all belong to the Asia group and show a close distributional association to Indo-China and China, not to New Guinea.

4. **Diversity and distribution in *Desmodium* and related genera in Malesia**

The origin of diversity in genera and species as well as distribution patterns of *Desmodium* and its related genera in Malesia is considered here. These genera are most diverse in the Sino-Indian region and are considered to have primarily originated and differentiated in this region (Ohashi et al. 1981). They are included in the subtribe Desmodiinae. Fossil woods of *Ougeinia (= Desmodium* in Ohashi 1973 but is recognized as distinct, cf. Nemoto and Ohashi 2003) were found from the Miocene of Assam, India (cf. Wheeler and Baas 1992), leaves of *Codariocalyx* (as *Desmodium* cf. *microphyllum*), *Desmodium* and *Phyllodium* (as *D. pulchellum*) from the Miocene of China (Guo and Zhou 1992) and leaflet im-
like to thank F. Adima (L), D. E. Boufford and E. W. Wood (Harvard University Herbaria), B. Verdcourt, R. M. Polhill, G. Lewis, B. Schrire, and Lulu Rico-Arce (K), and H. Wiriadinata and B. Sunarno (BO) for their help when I had worked in their herbaria. I am also very grateful to Y. Endo (Ibaragi University), Y. Iokawa (Jyotsubo Kyoiku University), T. Kajita and J. Murata (The University of Tokyo), T. Nemoto (Ishinomaki Senshu University), and Y. Tateishi (Ryukyu University) for their collaboration in field and herbarium works and for providing necessary references. I sincerely thank to Y. Kadota (TNS), J. Murata, H. Nakai (Sapporo International University), L. Rico-Arce and E. W. Wood for their help in bibliography; to Gregory Kenicer (Edinburgh University) for reading the manuscript; and to Ihsan A. Al-Shehbaz (MO), D. E. Boufford, Alice Grabovskaya (LE), L. Rico-Arce, and H. Walter Lack (B) for their help searching the type of *Hedysarum malacophyllum* Link and/or Chamisso collections.

**References**


Guo S. X. and Zhou Z. K. 1992. The Megafossil leg-


大橋広好： Malesia のマメ科シバハギ属と近縁属の分類と分布（II）

本研究では Malesia のシバハギ属とその近縁属は13属65種よりなることを明らかにした。前編（本誌79巻2号）の Aphyllum から Desmodium までに続いて、この後編では Hanslia から Trifidacanthus までの8属14種について分類学的な整理を行った。また Malesia におけるシバハギ属と近縁属について分布を整理し、系統進化的な考察を試みた。

Hanslia は Malesia に固有の属で、形態および花粉形質においてシバハギ属に類似するが、柱頭が花柱の側面につく点で異なる。Hanslia hentyi は1977年にニュージニアから1点だけの果期の標本に基づいて記載された種であった。その後やはりニュージニアからの標本が2点見つかかったが、も果実もない標本であった。今回の標本は Kew から未同定のまま Leiden に貸し出されていたので、断片的な花と数個の花蕾とをつけている（Fig. 5）。これが4枚の目的標本であり、Borneo からの初発見である。本種については完全な状態の花は未発見であり、この種の正体はまだ分からない点がある。

ヌスビトハギ属は Malesia に4種が分布する。Hyloidesmum repanum はこの属で唯一アフリカに分布する種であるが、形態的にはマルバヌスビトハギに類似し、しばしば誤ってそれと同定されている。Verdourt (1979) によれば、New Guinea の H. repanum は帰化であろうという。オオバヌスビトハギ Hyloidesmum laxum (DC.) H. Ohashi & R. R. Mill とトキワブプハギ H. leptopus (A. Gray ex Benth.) H. Ohashi & R. R. Mill は Malesia に広く分布し、New Guinea まで見られる。一方マルバヌスビトハギ H. podocarpum (DC.) H. Ohashi & R. R. Mill subsp. podocarpum は Malesia ではルソン島にだけ生育し（Fig. 8）、ここが分布の南限である。マルバヌスビトハギは日本と中国にはいつでもあるが、台湾中部南投県と嘉義県に稀であり、台湾北部と沖縄を飛んで九州やアジア大陸に分布する。

Malesia のヌスビトハギ H. podocarpum subsp. oxyphylum (DC.) H. Ohashi & R. R. Mill としてはハーバード大学標本館に所蔵されるジャワ島産シバハギの標本に貼り付けられている断片的な個体があるので、この標本はジャワで1905年に採集されたものである。しかし、この標本によってジャワ島にヌスビトハギがあるとするには疑問が残る。このシバハギ標本の重複品がロンドンの自然史博物館にもあるが、それはミソナオシだけが貼り付けられた標本である。また、これまでジャワ島からヌスビトハギが記録されたことはなく、一方、シバハギはジャワに一つである。ハーバード大学標本館他の地域で採集されたヌスビトハギが混入したものである可能性がある。多く Malesia 地域にはヌスビトハギは分布しないと思われる。現在のところヌスビトハギは台湾北部が南限である。日本では沖縄本島及び沖縄県南部地方であったが、かつては山前に稀でなかったともあったようで、開発などによって生育地が破壊されたという（沖縄県1996沖縄県の絶滅の恐れのある野生生物）。

Malesia 地域における13属の分布についてみると、固有属は Monarthrocarpus のみ、Malesia とアジア大陸に分布するのは Desmodiastrea, Hegnera, ヌスビトハギ属 Hyloidesmum, シバハギ属, および Trifidacanthus の5属であり、Malesia とオーストラリアに限られるのは Hanslia のみである。残りの6属 (Aphyllum, マイハギ属, ナハッハギ属, Desmodiastrea, ウチワナギ属, タデハギ属) は Malesia, ジャワ, オーストラリアに分布する。なお、マレー半島のほぼ南半分は、植物地理学上の Malesia に含まれるため、本論文でアジア大陸とよぶ地域からはここを除いている。

次に、Malesia に自生する57種を対象として種の分布について調べてみた。ここではアメリカからの帰化種である8種を除いて考察する。Malesia
固有種、Malesia とアジア大陸に分布する種、Malesia とオーストラリアに分布する種、アジア大陸・Malesia・オーストラリアに分布する種をまとめ、それぞれを Malesia, Asia, Australia, Asia-Australia group と名付ける。種数をみると Malesia group は 5 属 8 種（全体の 14 %）、Asia group は 9 属 29 種（全体の 52 %）、Australia group は 4 属 11 種（全体の 20 %）、Asia-Australia group は 6 属 8 種（全体の 14 %）であった（Table 1）。種数の比較からみると、Malesia におけるシバハギ属と近縁属はアジア大陸の種との関連が顕著である。

Asia group の種の中では Western Malesia floristic region（マレー半島南部、スマトラ、ボルネオ、ジャワ、バラワン島を含む）にみ分布する種が11種あり、アジア大陸との結びつきを強く示す。さらに Asia-Australia group の 8 種の中のナハキハギ Dendrolobium umbellatum を除く他の 7 種もアジア大陸との結びつきを示す種であると思われる。

なお、Malesia に分布するヌスピトハギ属 4 種は全て Asia group に属する。

一方、Malesia とオーストラリアとの共通種の中にはシバハギ属 8 種が含まれるが、これらは高度に分化したと考えられる種である。また、固有種の多くは狭い分布域をもつ。Dendrolobium cunningianum, Dendrolobium geesinkii, Desmodium bolsteri などはルソン島、Dendrolobium quinquepetalum はルソン島、バリ島とチルマンド島、Aphylodium novoguineense, Dendrolobium papaucola はニューギニア。Hanslia hentyi はニューギニアと新しくボルネオ島で発見された。ただ 1 種 Monarthrocarpus securifolium はルソン、バラワン、バリ島、シバハギ属に知られているが、広い分布域をもっている。8 種のうち 5 種がルソン島で、4 種がニューギニアでみられる。亜種としては Desmodium nemorosum subsp. whitfordii がルソン島に、D. strigillosum subsp. celebicum がスラウェシに固有である。種種タイデハギ triquetrum nothosubsp. philippinense はフィリピン、バリワン、ニューギニアでみられる。固有種の多くはアジア大陸の種に形態的に最も近く、また固有種がルソン島とニューギニアに集中することは Malesia におけるシバハギ属と近縁属の進化に関して問題を解く鍵となる現象であると思われる。

Malesia の中ではジャワ、ニューギニア、フィリピンがマメ科について他の地域よりもまとまった研究が発表されている。したがって標本も多く、シバハギ属と近縁属の自生種について他の地域よりもよく調べることができた。3 地域を比較してみると、ジャワには10属31種、ニューギニアには 9 属32種、フィリピンには 9 属29種が認められた（Table 2）。この結果から、3 地域がほぼ同数の種をもつことが示された。しかし、3 地域の間には面積、生育地環境の多様性、開発程度の多様な条件に近い差のあることから推定するに、ニューギニアとフィリピンにはジャワよりも多くの種が生育すると予想される。この結果はニューギニアとフィリピンの研究がジャワのそれに比べて不足していることに起因するためであろうと考えられる。

次に、3 地域と共通する種および 2 地域間ごとの共通種と非共通種をまとめてみた（Table 2）。ジャワにはインドシナあるいはインドとの共通種が含まれ、オーストラリアとの共通種は少ない。ニューギニアは Malesia 固有種とオーストラリアとの共通種が特色であり、フィリピンには Malesia 固有種と中国との共通種がみられることがある。

ルソン島に分布する種はインドと中国からは発見されていない。Malesia においてシバハギ属と近縁属の種類と分布型の多様性とがどのように生まれてきただろうかに興味を持つ。シバハギ属と近縁属はインドから中国に至るアジア大陸で属レベルの分化が見られ、ここで第一次的に分化したと考えられている（Ohashi et al. 1981）。Desmodiinae 亜属に属するシバハギ属、Ougeinia, Codariocalyx, Phyllodium の中新世からの化石はインドと中国から発見されている。Malesia においてシバハギ属と近縁属の化石は記録されていないが、Asia group と Asia-Australia group の種は基本的にアジア大陸の種に由来して今日 Malesia に分布するに至った種であると考えられる。さらに Malesia を経てオーストラリアに分布を広げたと予測される。

この過程で地元の種分化が起こり、Malesia 固有種である Malesia group の種が生まれ、オーストラリアでも種レベルでの分化が起こり、今日 Malesia にみられる Australia group の種はオーストラリアから Malesia に侵入したと考えられる。

Malesia におけるシバハギ属と近縁属の多様性は歴史を通じて発展を広げてきた進化の結果であると考えられる。

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