

A synopsis of *Coelostegia* (Bombacaceae/Malvaceae: Helicteroideae: Durioneae) and new records from Borneo

I. Nadiah¹ and E. Soepadmo

Forest Research Institute Malaysia, 52109 Kepong, Selangor, Malaysia

¹nadiyahidris@frim.gov.my

ABSTRACT. A synoptic revision of *Coelostegia* Benth. (Bombacaceae/Malvaceae subfam. Helicteroideae–Durioneae) in Borneo is given. Six species are recognised, of which four (*C. chartacea*, *C. kostermansii*, *C. montana* and *C. neesiocarpa*) are endemic to Borneo. *Coelostegia griffithii*, previously recorded only from Peninsular Malaysia, Singapore, Java and Sumatra, is now also found in Borneo, while *C. montana* previously known only from Sarawak and Kalimantan also occurs in Sabah. Gross morphological and micromorphological characters show that the genus *Coelostegia* can be readily distinguished from other genera in the Durioneae-group by the epicalyx being much shorter than the calyx, the induplicate-saccate calyx character and the ovary being partly enclosed by the receptacle. The distinction is also supported by micromorphological characters derived from trichomes, stomata, and pollen. Nomenclatural (typification and synonymy) and taxonomic notes, ecology and geographical distribution of the recognised species are provided.

Keywords. Borneo, *Coelostegia*, Durioneae, Helicteroideae, Malvaceae, taxonomy

Introduction

Bentham (1862) first described *Coelostegia* with one species, *C. griffithii*, from Peninsular Malaysia. Beccari (1886) described two more species, from Sumatra (*C. sumatrana*) and Borneo (*C. borneensis*), and was the first to describe the fruit and seed of *Coelostegia*. Soegeng (1960) revised the genus and added three more species from Borneo, and provided full descriptions, an identification key and illustrations of all five species known to him. Sidiyasa (2001) described a new species, *C. montana*, from East Kalimantan and Sarawak.

Prior to 1998, taxonomic and systematic studies based mainly on morphological and anatomy characters carried out by various authors (e.g., Hutchinson 1959; Cronquist 1968, 1981; Keng 1969; Takhtajan 1969) included *Boschia*, *Coelostegia*, *Cullenia*, *Durio*, *Kostermansia* and *Neesia* in the tribe/section Durioneae of the family Bombacaceae. From the late 1990's, however, phylogenetic studies based on chloroplast and nuclear ribosomal DNA (e.g., Alverson et al. 1998, 1999; Baum et al. 1998; Bayer et al. 1999; Nyffeler & Baum 2000; Bayer & Kubitzki 2003) strongly suggested that the core Malvales families (Bombacaceae, Malvaceae, Sterculiaceae and Tiliaceae) should be merged into an expanded family Malvaceae, and that nine

subfamilies should be recognised, with the genera of the Durioneae-group to be included in subfam. Helicteroideae-Durioneae. Cheek (2006, 2007), however, disagreed and proposed placing the Durioneae genera in a separate family, the Durionaceae.

Synopsis of recognised taxa

Coelostegia Benth., Gen. Pl. 1 (1862) 213; Hooker f., Fl. Brit. India 1 (1875) 352; Beccari, Malesia 3 (1889) 269; King, J. As. Soc. Beng. 60, 1 (1891) 56; Schumann in Engler & Prantl., Nat. Pflanzenfam. 3, 6 (1895) 68; Ridley, Fl. Malay Penins. 1 (1922) 266; Bakhuizen f., Bull. Jard. Bot. Buitenz. 6, 3 (1924) 223; Soegeng, Reinwardtia 5, 3 (1960) 270; Hutchinson, Gen. Flow. Pl. 2 (1967) 526; Kochummen, Tree Fl. Malaya 1 (1972) 104; Cockburn, Trees of Sabah 1 (1976) 22; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 53; Salma et al., Pl. Resources of South-East Asia 5, 2 (1995) 140; Coode et al. (eds), Checkl. Flow. Pl. Gymno. Brunei (1996) 41; Argent et al. (eds), Man. Non-Dipt. Trees Centr. Kalimantan 1 (1997) 96; Beaman et al., Pl. Mount Kinabalu 4 (2001) 164; Bayer & Kubitzki, Fam. Gen. Vasc. Pl. 5 (2003) 261. TYPE SPECIES: *Coelostegia griffithii* Benth.

Distribution. Six species distributed in Sumatra (including Riau Archipelago), Peninsular Malaysia, Java, Singapore and Borneo. In Borneo, four species are endemics; Sarawak has five species (non endemic); Sabah three species (non endemic); Brunei two species (non endemic) and Kalimantan five species (one endemic) (Fig 1).

Ecology. Lowland mixed dipterocarp and lower montane forest on clay-rich soils, to c. 1450 m.

Notes. Soegeng (1959, 1960) pointed out that based on their overall vegetative and reproductive characters, *Coelostegia*, *Durio*, *Kostermansia* and *Neesia* are distinct genera but closely related to one another. Basing his conclusion on the anatomy of vegetative parts, Baas (1972) fully supported Soegeng's suggestion. Appendix A summarises the macromorphological and micromorphological characters which can be used to distinguish *Coelostegia* from the other genera.

1. ***Coelostegia borneensis*** Becc., Malesia 3 (1889) 272, Nelle Foreste Di Borneo (1902) 572; Merrill, J. Str. Br. Roy. As. Soc., Spec. No. (1921) 377; Bakhuizen f., Bull. Jard. Bot. Buitenz. 6, 3 (1924) 224; Masamune, En. Phan. Born. (1942) 454; Soegeng, Reinwardtia 5, 3 (1960) 272; Kochummen, Tree Fl. Malaya 1 (1972) 106; Anderson, Checkl. Trees Sarawak (1980) 153; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 54; Turner, Gard. Bull. Sing. 47, 1 (1995) 151; Salma et al., Pl. Resources of South-East Asia 5, 2 (1995) 143; Argent et al. (eds), Man. Non-Dipt. Trees Centr. Kalimantan 1 (1997) 97. TYPE: Beccari PB 2688, Borneo, Sarawak, Kuching district (holo FI, iso BO! K!).

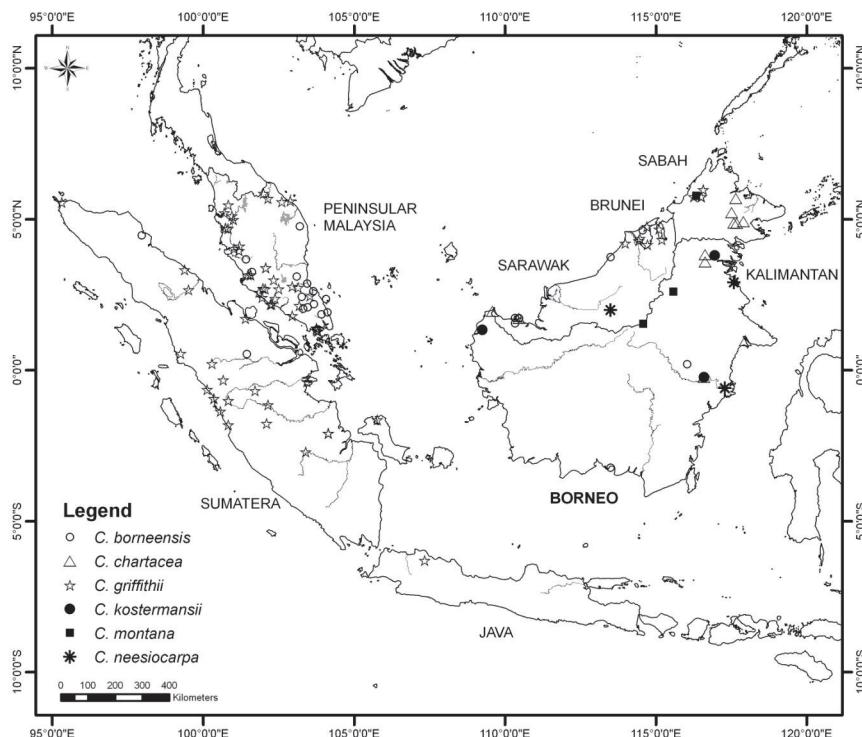


Fig. 1. Distribution of six *Coelostegia* species in Peninsular Malaysia, Singapore, Borneo, Sumatra and Java.

Distribution. Sumatra, Peninsular Malaysia and Borneo (Sarawak, Kalimantan, Brunei).

Ecology. Lowland mixed dipterocarp, *kerangas* and swampy forest on slopes, river banks, hillsides, low undulating country, on waterlogged soils and deep yellow sands overlying tertiary clays at altitude 20–303 m.

Notes. In leaf surface, size, number of lateral veins, twig and types of fruit spines, *C. borneensis* is closely related to *C. chartacea* but differs in the leaf texture (coriaceous vs. chartaceous), leaf apex (short-acuminate, acumen 0.6 cm vs. long-acuminate, acumen up to 1.5 cm), and fruit shape (globular vs. ellipsoid).

Specimens examined: PENINSULAR MALAYSIA. **Johor:** Lenggor FR, *Whitmore FRI* 8651 (KEP); Gunung Sumalayang, *Everett FRI* 13875 (K, KEP, L, SAN, SING); Panti FR, *Pilus KEP* 104507 (KEP); Labis FR, *Yaacob KEP* 104744 (KEP); Kluang FR, *Heaslett s.n.* (KEP); *ibid.*, *Samsuri SA* 391 (SING); Kg. Hubong, *Kadim KN* 284 (BO, L, SING). **Pahang:** Aur FR, *Whitmore FRI* 3626 (KEP, L); Kuala Kemapan, *Saw FRI* 34187 (KEP); Menchali FR, *Meijer KEP* 94890 (K, KEP, L, SING). **Selangor:** Bukit Lagong FR, *Hamid KEP* 81089 (KEP); Bukit Belata FR, *Kochummen KEP* 99372 (KEP); **Terengganu:** Dungun, *Abdullah KEP* 53363 (BO, KEP). – SUMATRA. North

Sumatra: Langsa, *Boschbouwproefstation bb.* 2578 (BO, BZF, L). **East Sumatra:** Pakan Baru, Tenajan River, *Soepadmo* 252 (BO). – **BORNEO.** **Sarawak:** Bako NP, *Yap* 527 (KEP); ibid., *Ashton S* 24320 (A, BO, K, L, SAN, SAR, SING); ibid., *Kuswata* 401 (BO, K, L, SING); Similajau FR, *Brunig S* 8631 (BO, L, SAN); Telok Belian, *Ilias Paie S* 35997 (KEP, L); Kuching, *Beccari PB* 2688 (BO, K) (type). **Brunei:** Andulau FR, *Ashton BRUN* 586 (KEP, L, SING). **Kalimantan:** East Kalimantan, Ulu Mahakam, *Sidiyasa* 1653 (BO, KEP, L, SAN, WAN). Central Kalimantan, Sampit River, near Kuala Kuajan, *Kostermans* 8070 (BO).

2. *Coelostegia chartacea* Soegeng, Reinwardtia 5, 3 (1960) 273; Argent et al. (eds), Man. Non-Dipt. Trees Centr. Kalimantan 1 (1997) 97. TYPE: *Kostermans* 5262, Indonesia, East Kalimantan, East Kutei, Sangkulirang, Menubar R. (holo BO! iso A, K, L! LAE, P, PNH, SING!).

Distribution. Endemic in Borneo (Sabah, Sarawak, Kalimantan).

Ecology. In primary forest, on hill and riversides at 25–606 m altitude.

Notes. A very distinct species that can be distinguished from the other species of *Coelostegia* by its chartaceous leaves. Morphologically, *C. chartacea* is closely related to *C. borneensis* but differs in its longer leaf acumen and the ellipsoid fruit (see note on *C. borneensis*).

Specimens examined: BORNEO. **Sabah:** Lung Manis FR, *Charington SAN* 24731 (K, SAN); Tankong, *Lassan SAN* 72805 (SAN); Sungai Beatrice, *Cockburn SAN* 84979 (K, SAN); Sungai Bole, *Lee SAN* 96767 (SAN); Ulu Segama, *Tamin SAN* 98872 (SAN).

Sarawak: Samunsam Wildlife Sanctuary, *Abang Mohtar S* 52657 (KEP, SAR); Bako NP, *Nadiyah et al. S* 100582 (KEP). **Kalimantan:** East Kalimantan, Desa Gong Solok, *Arifin AA* 3010 (BO, WAN); Sungai Menubar, *Kostermans* 5262 (BO, L, SING) (type); Belajan River near Tabang, *Kostermans* 10679 (K); Tidoengsche Landen, *bb.* 17958 (BO, BZF, L).

3. *Coelostegia griffithii* Benth., Gen. Pl. 1 (1862) 213; Hooker f., Fl. Brit. India 1 (1875) 353; Masters, J. Linn. Soc. Bot. 14 (1875) 505; Beccari, Malesia 3 (1889) 270; King, J. As. Soc. Beng. 60, 1 (1891) 57; Schumann in Engler & Prantl., Nat. Pflanzenfam. 3, 6 (1895) 68; Ridley, Fl. Malay Penins. 1 (1922) 266; Bakhuizen f., Bull. Jard. Bot. Buitenz. 6, 3 (1924) 224; Soegeng, Reinwardtia 5, 3 (1960) 274; Kochummen, Tree Fl. Malaya 1 (1972) 106; Cockburn, Trees of Sabah 1 (1976) 23; Anderson, Checkl. Trees Sarawak (1980) 153; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 54; Turner, Gard. Bull. Sing. 47, 1 (1995) 151; Coode et al. (eds), Checkl. Flow. Pl. Gymno. Brunei (1996) 41; Beaman et al., Pl. Mount Kinabalu 4 (2001) 164. TYPE: *Griffith* 547, Malaya, Malacca (holo K! iso A, L! P).

Coelostegia sumatrana Becc., Malesia 3 (1889) 271; Bakhuizen f., Bull. Jard. Bot. Buitenz. 6, 3 (1924) 224; *Coelostegia griffithii* Benth. forma *sumatrana* (Becc.) Bakhuizen f., Bull. Jard. Bot. Buitenz. 6, 3 (1924) 248. TYPE: Beccari PS 738, West Sumatra, Padang Prov., Air Manchur (holo FI, iso BO! K! L!).

Distribution. Sumatra (including Riau Archipelago), Peninsular Malaysia, Singapore, Java and Borneo (Sabah, Sarawak, Brunei) (Fig. 1).

Ecology. In mixed dipterocarp, *kerangas* and lower montane forests at 15–1393 m.

Notes. Soegeng (1960) cited *C. griffithii* as occurring only in Peninsular Malaysia, Sumatra and Bangka. Detailed comparative study of specimens currently available at BO, K, L, SAN and SAR herbaria show that the species also occurs in Borneo.

In Borneo, sterile specimens of *C. griffithii* can be easily confused with those of *C. kostermansii*, *C. neesiocarpa* and *C. montana*. However, the fruit surface of *C. griffithii* is typically covered with sharp conical spines compared to that of the other three species which have a smooth or submuricate or muricate surface.

Specimens examined (* denotes new records in Borneo; ** denotes additional localities in Peninsular Malaysia): PENINSULAR MALAYSIA. **Johor:** Bukit Paloh Estate, *Mohd Shah MS 395* (BO, SAR, SING); Labis FR, *Whitmore FRI 3847* (KEP); Banang FR, *Suleiman KEP 70172* (KEP). ****Kedah:** Gunung Inas FR, *Whitmore FRI 4694* (KEP). **Kelantan:** Kemahang FR, *Chelliah FRI 6502* (K, KEP, L); Kuala Balak, *Suppiah FRI 28017* (K, KEP, L); Temangan, *Baki KEP 68766* (KEP). **Malacca:** loc. not. indicated, *Derry 123* (SING); ibid., *Griffith 547* (K, L) (type); Bukit China, *Derry 95* (SING); Selandar, *Alvins s.n.* (SING). **Negeri Sembilan:** Senawang FR, *Yakim FMS 518* (K, KEP, SING); Sendayan FR, *FG Din 536* (BO, SING); Pasir Panjang, *Yusop FMS 4222* (KEP, SING); Gunung Angsi, *Zainuddin FRI 14591* (K, KEP, L, SING); Pasoh FR, *Nadiyah et al. FRI 53951* (A, K, KEP, L, SAN, SAR, SING). ****Penang:** Lesong FR, *Whitmore FRI 15851* (KEP); Rompin, *Ng FRI 22992* (KEP), *Ng FRI 22921* (KEP). **Perak:** loc. not. indicated, *Scortechini 1862* (SING); ibid., *Scortechini 1863* (SING); Selama, *Mat Said FMS 1250* (KEP); Chikus FR, *Speldenwinde 5366* (KEP); Changkat Jong FR, *Ng FRI 5644* (KEP); ibid., *Ng FRI 5878* (KEP, L); Babu FR, *Selvaraj FRI 11154* (KEP, L); ibid., *Suppiah FRI 11675* (KEP); ibid., *Abdul Rahim KEP 86060* (KEP); Trong, *Everett FRI 13987* (K, KEP, L, SAN, SING); Teluk Intan, *Mohd Haniff SFN 14315* (SING); Bintang Hijau FR, *Kamarudin FRI 34556* (K, KEP, SAN, SAR). **Selangor:** Sungai Buloh FR, *Hamid FMS 1183* (KEP); ibid., *Strugnell FMS 7068* (KEP, SING); ibid., *Kiai FMS 8387* (KEP); ibid., *Foxworthy FMS 10213* (KEP); ibid., *Jamaat FMS 15311* (KEP); ibid., *DFO Klang FMS 18715* (KEP); ibid., *Strugnell 23931* (KEP); ibid., *Symington FMS 24445* (KEP); ibid., *Strugnell FMS 27880* (KEP); ibid., *Jamaat FMS 44944* (KEP); ibid., *Jamaat FMS 45002* (KEP); Bukit Cherakah FR, *Abu Amin FMS 18721* (KEP); Forest Research Institute Malaysia, *Ng FRI 33540* (KEP); ibid., *Motan KEP 94744* (K, KEP, L, SING). ****Terengganu:** Gunung Tebu FR, *Zainuddin FRI 17922* (K, KEP). SINGAPORE. Botanic Gardens,

Ridley 3887 (K, SING); *ibid.*, *Mat s.n.* (SING); *Bukit Mandai, Corner s.n.* (SING), *Bukit Timah, Ridley* 4738 (SING); *Mandai Rd., Kiah SFN 37112* (BO, KEP, SING). **JAVA**. Jakarta, cultivated in garden, *van Steenis* 3105 (BO). – **SUMATRA**. **North Sumatra**: Atjeh, *Boschbouwproefstation bb.* 8873 (BO). **South Sumatra**: Belinju, *Grashoff* 48 (BO, L); Bajunglentjir, *Endert* 276 (BO, L); *ibid.*, *Grashoff* 812 (BO, L); *ibid.*, *Endert* 85E. *IP.* 754 (BO, BZF, K, L); *ibid.*, *Boschbouwproefstation 1. PT.* 788 (BO, L); Rawas, *Grashoff* 1110 (BO, L). **East Sumatra**: Indrapura, *Volke* 5 (BO, L); Jambi, *Roos TFB* 2055 (L); Bandar Poelau, *Yates* 2586 (K, L); Bajalinggi, *Lorzing* 7397 (BO); Muarapantai, *Mol* 23859 (BO, BZF, L); Indragiri, *Buwalda bb.* 30081 (BO, BZF, L); Sungai Missingit, *Beguin* 556 (BO, L). **West Sumatra**: Balaiselasa, *Boschbouwproefstation bb.* 5969 (BO, L); Pariaman, *Boschbouwproefstation bb.* 6736 (BO, L); Ophir, *Neth. Ind. For. Service bb.* 19481 (BO, BZF, L, SING); *ibid.*, *Djabar bb.* 19629 (BO, BZF, L); Pengkalan Tapus, *de Haan bb.* 29537 (BO, BZF, L); Malintang, *Korthals s.n.* (L); Between Bondjol-Lubuk Sikapang, *Teijsmann s.n.* (BO); Painan, *Boschbouwproefstation S.W.K./I-32* (BO, BZF, L); Air Manchur, *Beccari PS* 620 (L); *ibid.*, *Beccari PS* 738 (BO, K, L) (type of *C. sumatrana* Becc.). – ***BORNEO**. **Sabah**: Kundasang, *Singh SAN* 27495 (L, SAN); *ibid.*, *Meijer SAN* 37996 (SAN); *ibid.*, *Fosberg SAN* 44135 (L); Sosopodon, *Lajangah SAN* 33145 (SAN); *ibid.*, *Mikil SAN* 38516 (K, L, SAN); *ibid.*, *Mikil SAN* 46782 (K, SAN); *ibid.*, *Sinanggul SAN* 47979 (SAN); Sunsuron, *Phillips SAN* 89353 (SAN). **Sarawak**: Tg. Long Amok, *Rena George S* 43060 (K, L, SAR); Lambir Hills NP, *Nadiah et al. S* 100573 (KEP, SAR, SING). **Brunei**: River Ingei, *Wong WKM* 607 (K, KEP, L, SAN); Labi Hills FR, *Coode et al.* 6826 (K); Bukit Teraja, *Niga BRUN* 15094 (SING); Pendayan FR, *Wyatt-Smith KEP* 80130 (KEP); Bukit Biang, *Ashton BRUN* 5584A (BO, K, KEP, L, SAR, SING).

4. *Coelostegia kostermansii* Soegeng, Reinwardtia 5, 3 (1960) 277; Argent et al. (eds), Man. Non-Dipt. Trees Centr. Kalimantan 1 (1997) 97. TYPE: *Kostermans* 12548, Indonesia, East Kalimantan, West Kutei, Tudjung Plateau, Mt. Maranga (holo BO! iso A, CANB, K! KEP! L! NY, P).

Distribution. Endemic in Borneo (confined to Kalimantan).

Ecology. Primary forest on sandy loam soil, at 100–250 m.

Notes. *C. kostermansii* is morphologically very similar to *C. neesiocarpa* but consistently differs in having a rough-surface and distinctly 5-angled fruit (vs. smooth and rounded), elongate-ovoid seed with a caruncle up to 0.7 cm long (vs. ovoid with a caruncle up to 1.2 cm long), and slender slightly kneeled petiole (vs. thick and strongly kneeled petiole).

Specimens examined: BORNEO. **Kalimantan**: West Kalimantan, Mt. Maranga, *Kostermans* 12548 (BO, K, KEP, L) (type); Mt. Damus, *Hallier* 776 (BO). East

Kalimantan, Belajan River near Tabang, *Kostermans 10583* (L); Tabang, *Kostermans 10659* (L).

5. *Coelostegia montana* Sidiyasa, Blumea 46 (2001) 165. TYPE: *Sidiyasa & Arifin 1529*, Indonesia, East Kalimantan, Bulungan District, Kayan Mentarang National Park, Gunung Lunjut (holo WAN, iso BO!, K, L!).

Distribution. Endemic in Borneo (confined to Sabah, Sarawak and Kalimantan) (Fig. 1).

Ecology. In dipterocarp and submontane forests on well-drained ridges, on igneous (andesitic) derived soils, at 884–1450 m altitude.

Notes. Sidiyasa (2001) described *C. montana* based on fruiting specimens from Sarawak (*Anderson S 28461*) and fruiting specimens with young flower buds from Kalimantan (*Sidiyasa & Arifin 1529*). The recently collected specimens from Sabah (*Nadiah et al. SAN 149577*) bearing matured fruits and fully develop flowers represent a new record of this species for the state, thus extending its distribution in Borneo.

Coelostegia montana is closely related to *C. kostermansii* but can be distinguished by its c. 7–8 pairs of leaf lateral veins (vs. c. 9–13 pairs), narrowly obovate stipules, c. 6 mm long (vs. lanceolate stipules, c. 4 mm long), depressed conical and apically lobed flower buds c. 3 mm in diameter (vs. apiculate flower buds, up to 2 mm), and dark blue, subglobose fruits with rounded base (vs. yellowish green, ovoid fruits that are distinctly 5-angled at base).

Specimens examined: BORNEO. **Sabah:** Tambunan district, Rafflesia trail, *Nadiah et al. SAN 149577* (KEP, SAN). **Sarawak:** Kapit, Sungai Balleh, *Anderson S 28461* (BO, K, KEP, KLU, L, SAR). **Kalimantan:** East Kalimantan, Kayan Mentarang NP, Gunung Lunjut, *Sidiyasa & Arifin 1529* (BO, K, L, WAN) (type).

6. *Coelostegia neesiocarpa* Soegeng, Reinwardtia 5, 3 (1960) 279; Anderson, Checkl. Trees Sarawak (1980) 153; Ashton, Man. Non-Dipt. Trees Sarawak 2 (1988) 56; Argent et al. (eds), Man. Non-Dipt. Trees Centr. Kalimantan 1 (1997) 97. TYPE: *de Zwaan bb. II288*, Indonesia, East Kalimantan, Bulungan, Rumah R. (holo BO! iso BZF!).

Distribution. Endemic in Borneo (confined to Sarawak and Kalimantan).

Ecology. In lowland forest at 100–300 m altitude, growing on dacite-derived alluvial fans in damp sandy valleys.

Notes. *Coelostegia neesiocarpa* differs from the other species in the genus in having an elliptic-ovate, coriaceous, concolorous leaves with rounded base; thick and strongly

kneed petiole; subglobose fruits up to 14 cm long, 11 cm diameter, with a smooth surface and rounded base; and ovoid seeds with a caruncle c. 1.2 cm long.

Specimens examined: BORNEO. Sarawak: Hose Mountain, Mujong, Batu Kapal, Ashton S 21242 (BO, K, L, SAR, SING). Kalimantan: East Kalimantan, Salimbata, Rumah R., de Zwaan bb. 11288 (BO, BZF) (type); Upper Mahakam, Henar bb. 20696 (BO, BZF).

ACKNOWLEDGEMENTS. We acknowledge the generosity of the directors, keepers and curators of herbaria (BO, BZF, K, KEP, L, SAN, SAR, SING and the Kinabalu National Park) for the loan of specimens and facilities rendered. This project was financially supported by RM-9 grants (Vote. no. 20300202023).

References

- Alverson, W.S., Karol, K.G., Baum, D.A., Chase, M.W., Swensen, S.M., McCourt, R. & Systema, K.J. (1998) Circumscription of the Malvales and relationships to other Rosidae: evidence from *rbcL* sequence data. *Amer. J. Bot.* 85(6): 876–887.
- Alverson, W.S., Whitlock, B.A., Nyffeler, R., Bayer, C. & Baum, D.A. (1999) Phylogeny of the core Malvales: evidence from *ndhF* sequence data. *Amer. J. Bot.* 86(10): 1474–1486.
- Baas, P. (1972) The vegetative anatomy of *Kostermansia malayana* Soegeng. *Reinwardtia* 8(2): 335–344.
- Baum, D.A., Alverson, W.S. & Nyffeler, R. (1998) A durian by any other name: taxonomy and nomenclature of the core Malvales. *Harvard Pap. Bot.* 3(2): 315–330.
- Bayer, C. & Kubitzki, K. (2003) Malvaceae. In: Kubitzki, K. (ed) *The Families and Genera of Vascular Plants* 5: 225–311.
- Bayer, C., Fay, M.F., Bruijn, A.Y. de, Savolainen, V., Morton, C.M., Kubitzki, K., Alverson, W.S. & Chase, M.W. (1999) Support for an expanded family concept of Malvaceae within a recircumscribed order Malvales: a combined analysis of plastid *atpB* and *rbcL* DNA sequences. *Bot. J. Linn. Soc.* 129: 267–303.
- Beccari, O. (1886) Le Bombacaceae Malesi descritte ed illustrate. *Malesia* 3(4): 202–280, Tavola XII–XXXVI.
- Bentham, G. & Hooker, J.D. (1862) Bombacaceae (Malvaceae Tribe Bombaceae). *Genera Plantarum* 1: 195–213.
- Cheek, M. (2006) The validation of two new family names in Malvales: Durionaceae and Brownlowiaceae. *Kew Bull.* 61: 443.
- Cheek, M. (2007) Durionaceae. In: Heywood, V.H. et al. (eds) *Flowering Plants Families of the World*, p. 134.
- Cronquist, A. (1968) *The Evolution and Classification of Flowering Plants*. London and Edinburgh: Thomas Nelson & Sons Ltd.

- Cronquist, A. (1981) *An Integrated System of Classification of Flowering Plants*. New York: Columbia University Press.
- Hutchinson, J. (1959) *The Families of Flowering Plants Volume 1–Dicotyledons*. London: Oxford University Press.
- Keng, H. (1969) *Orders and Families of Malayan Seed Plants*. Singapore: Singapore University Press.
- Kostermans, A.J.G.H. (1958) The genus *Durio* Adans. (Bombac.). *Reinwardtia* 4(3): 47–153.
- Masliya, M. (2008) *Kajian Epidermis Daun ke Atas Beberapa Spesies Bombax, Durio dan Kostermansia (Bombacaceae)*. B.Sc. Thesis, Universiti Kebangsaan Malaysia.
- Nilsson, S. & Robyns, A. (1986) Bombacaceae. *World Pollen and Spore Flora* 14. Stockholm: The Almqvist & Wiksell Periodical Company.
- Nyffeler, R. & Baum, D.A. (2000) Phylogenetic relationships of the durians (Bombacaceae-Durioneae or /Malvaceae/Helicteroidae/Durioneae) based on chloroplast nuclear ribosomal DNA sequences. *Plant Syst. Evol.* 224: 55–82.
- Salma, I. (1999) The taxonomic significance of trichome morphology in the genus *Durio* (Bombacaceae). *Gard. Bull. Singapore* 51: 55–70.
- Salma, I. (2000) The significance of pollen morphology in the taxonomy of the genus *Durio* (Bombacaceae). *Gard. Bull. Singapore* 52: 261–271.
- Salmizawati, M.S. (2008) *Kajian Anatomi dan Mikromorfologi Epidermis Daun Terhadap Beberapa Spesies Neesia Bl. (Bombacaceae)*. B.Sc. Thesis, Universiti Kebangsaan Malaysia.
- Sidiyasa, K. (2001) *Coelostegia montana*, a new species of Bombacaceae from Borneo. *Blumea* 46: 165–168.
- Siti Fatimah, S. (2008) *Kajian Morfologi Polen ke Atas Beberapa Spesies Daripada Genus Durio dan Neesia (Bombacaceae)*. B.Sc. Thesis, Universiti Kebangsaan Malaysia.
- Soegeng, R.W. (1959) *Kostermansia Soegeng*, a new genus in Bombacaceae (Durioneae). *Reinwardtia* 5(1): 1–9.
- Soegeng, R.W. (1960) The genus *Coelostegia* Benth. (Bombac.). *Reinwardtia* 5(3): 269–291.
- Soepadmo, E. (1961) A monograph of the genus *Neesia* Blume (Bombacaceae). *Reinwardtia* 5(4): 481–508.
- Takhtajan, A. (1969) *Flowering Plants—Origin and Dispersal*. Edinburgh: Oliver & Boyd Ltd.
- Tan, L.H. (2008) *Kajian Epidermis Daun ke Atas Beberapa Spesies Daripada Genus Coelostegia dan Ceiba (Bombacaceae)*. B.Sc. Thesis, Universiti Kebangsaan Malaysia.
- Webster, G.L., Del-Arco-Aguilar, M.J. & Smith, B.A. (1996) Systematic distribution of foliar trichome types in *Croton* (Euphorbiaceae). *Bot. J. Linn. Soc.* 121: 41–57.

Appendix A. Morphological characters distinguishing the genera of the Durioneae-group in Borneo: *Coelostegia*, *Durio*, *Kostermansia* and *Neesia*. Sources: Kostermans 1958; Soegeng 1959, 1960; Soepadmo 1961; Baas 1972; Nilsson & Robyns 1986; Webster et al. 1996; Salma 1999, 2000; Sidiyasa 2001; Salmizawati 2008; Siti Fatimah 2008; Tan 2008.

Characters	<i>Coelostegia</i>	<i>Durio</i>	<i>Kostermansia</i>	<i>Neesia</i>
Buttresses	large, thin, convex, spreading	rounded, straight to concave, not spreading	up to 7 m high, plank-like, spreading	large, thin, convex, spreading
Leaf size (cm)	(4.5–)6–12(–14.8) × (1.1–)2–5(–6)	3–42.5 × 3–15	(6–)9–13(–19) × (2–)4–6(–9.5)	6–60 × 3–25
Lower leaf surface: pubescence	scales only	simple & stellate hairs, also scales	scales only	stellate hairs; rarely sparse minute long-fimbriate scales
Tertiary/ inter-costal veins	indistinct, reticulate	generally not prominent, reticulate	prominent, reticulate	distinct, reticulate
Midrib	evident, flat or raised above	sunken or channelled above	strongly prominent above	obscure, depressed above
Epicalyx	reduced in size, subtending calyx, 3-lobed at anthesis	completely enveloping flower bud, splitting into 2 lobes	partly enveloping flower bud, splitting into 2 lobes	completely enveloping flower bud, splitting into 2–5 lobes
Calyx-lobes/ sepals	induplicate-saccate	not induplicate-saccate	not induplicate-saccate	not induplicate-saccate
Corolla/ petals	shorter than calyx, calyptrate, perigynous	mostly showy, longer than calyx, free, long-persistent, hypogynous	shorter than calyx, not showy, free, caducous, hypogynous	shorter than calyx, hypogynous, calyptrate
Stamens (filament & anther)	longer than ovary; topped by three 1-celled anthers	longer than ovary; each filament with 1–many unilocular anthers	shorter than ovary; topped by two bean-shaped, basifixed, 2-celled anthers	longer than ovary; topped by one 2-celled anther
Ovary	partly embedded in receptacle, covered by peltate scales	superior, covered by peltate scales & stellate hairs	superior, covered by peltate scales	superior, covered by hirsute, stellate hairs
Style	conspicuous, filiform	well developed	reduced, or very short, thick	short, conical or filiform
Stigma	discoid, peltate, conspicuous	small, capitellate	large, convex, discoid, peltate	small, capitellate, round or subpentagonal

Fruit surface	spiny to muricate or smooth	covered with slender or stout spines	densely spiny	muricate or short-spiny
Fruit-valves inside	glabrous	glabrous	glabrous	with dense brownish, hirsute, pruriens hairs
Fruit dehiscence	dehiscing to c. 1/2–1/3 of its length (valves split while fruit is still attached to tree, becoming erect or reflexed)	some fruits do not dehisc, or dehisc to the very base (generally dehiscent only after falling to the ground)	dehiscing to the base (valves split while fruit is still attached to tree, becoming erect or reflexed)	dehiscing to c. 1/2–1/3 of its length to ± completely (valves split while fruit is still attached to tree, becoming erect or reflexed)
Aril or caruncle	basal caruncle present	aril absent or present and covering half to whole seed	no aril / caruncle	basal caruncle present
Seeds	smooth, in 2 rows in each locule	ellipsoid, in 2 rows in each locule; large, pale brown to reddish / black	few, large, glossy, dark brown (white when fresh)	ellipsoid, smooth
Cotyledons	thin, foliaceous, covered by 2 flat-convex lobes of the endosperm	thick, flat-convex, fleshy; endosperm absent	foliaceous, flat, covered by 2 partite endosperm	foliaceous, enveloped by 2 flat-convex lobes of the endosperm
Pollen type	<i>Durio</i> -type	<i>Durio</i> -type	<i>Kostermansia</i> -type	<i>Durio</i> -type
Type of apertures	3-colporate, short narrow colpus	3-colporate, short broad colpus	3-colporate, long narrow colpus	3-colporate, short narrow colpus
Pollen shape	prolate-spheroidal	oblance-spheroidal	oblance-spheroidal	prolate-spheroidal
Ornamentation of exine	microreticulate to smooth	smooth	microreticulate	microreticulate
Trichomes (on lower leaf surface)	dentate-peltate scales & glandular hairs	stellate & dentate peltate scales; appressed stellate & simple hairs; glandular hairs	subentire peltate scales & glandular hairs	appressed stellate, dendritic, simple & glandular hairs
Stomata type	anisocytic, tetracytic	paracytic	amfiparacytic	anisocytic, tetracytic
Stomata on lower leaf surface	randomly arranged	randomly arranged	in circles around trichome bases	randomly arranged

