Notes on South-East Asian Diospyros L. (Ebenaceae, Ericales): commonly misidentified species in mainland South-East Asia

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Research article

Notes on South-East Asian *Diospyros* L. (Ebenaceae, Ericales): commonly misidentified species in mainland South-East Asia

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Abstract. *Diospyros* L. is a large genus of flowering plants predominantly distributed in the tropics. It comprises over 700 species globally and around 300 are believed to occur in South-East Asia. Many species are economically important and exploited for the production of ebony wood and persimmons, yet taxonomic information on the genus is incomplete and inconsistent due to its morphological and nomenclatural complexity. Revisions of *Diospyros* in continental and insular South-East Asia were conducted independently by different authors, occasionally with different names used for the same species, or different species being given the same name in different countries. During our ongoing study of the genus *Diospyros* in Indochina (Cambodia, Laos, Thailand and Vietnam), we identified several such instances. Here, we clarify the most commonly misidentified species, including 1) *D. apiculata* Hiern, *D. strigosa* Hemsl. and *D. tamiriensis* Lecomte; 2) *D. bejaudii* Lecomte and *D. retrofracta* Bakh.; 3) *D. dictyoneura* Hiern and *D. hasseltii* Zoll.; 4) *D. borneensis* Hiern and *D. fecunda* H.R.Fletcher. Lectotypifications are also made for *D. brachiata* King & Gamble var. *lanceolata* H.R.Fletcher, *D. fecunda*, *D. similis* Craib and *D. strigosa*.

Keywords. Ebony, flora, Indochina, lectotypification, nomenclature, taxonomy.

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Introduction

South-East Asia is one of the centres of diversity of *Diospyros* L. as around 300 species are found there (40% out of around 730 species worldwide) (POWO 2022). Revisions of South-East Asian Ebenaceae Gürke were compiled in the first half of the 20th century, independently and by regions, i.e., Indochina (= Cambodia, Laos and Vietnam) by Lecomte (1928a, 1928b, 1930), the Malesian Archipelago and Pacific region by Bakhuizen van den Brink (1933, 1936, 1937, 1938, 1941, 1955) and Siam (= Thailand) by Craib (1912, 1920) and Fletcher (1937, 1938). These authors were based in different countries and herbaria (P, BO, K and E, respectively; herbarium acronyms follow Thiers 2020) where their original material was deposited and studied. Ebenaceae in Thailand and Malaysia then were revised by Phengklai (1972, 1978, 1981) and Ng (1977, 1978, 2001, 2002), respectively. In Vietnam and Laos, only handbooks, synopses or checklists were compiled (Pham-Hoang 1991, 1999; Nguyen 1996; Newman *et al.* 2007).

As part of the ongoing study of *Diospyros* in Cambodia, Laos, Thailand and Vietnam (hereinafter referred to as 'Indochina'), the authors have examined the type specimens of most taxa. By comparing specimens of Indochinese *Diospyros* with material from the rest of South-East Asia, we noticed that some species concepts differed across borders. These inconsistencies are embedded in the current literature available for the region, and inevitably lead to the misuse of names and misunderstanding in species distribution. Commonly misidentified species in the herbaria include *D. apiculata* Hiern, *D. strigosa* Hemsl., *D. bejaudii* Lecomte, *D. dictyoneura* Hiern and *D. borneensis* Hiern. Here we clarify the circumscription of these taxa, and apply changes that include synonymisations and resurrections, in line with the rules of the Code (Turland *et al.* 2018).

Material and methods

We investigated taxonomic publications and type specimens of the Indochinese species. Specimens from general, national and regional herbaria (A, BKF, BM, BO, BRUN, E, FI, K, KEP, L, NY, P, PSU, SING, VNM) were examined either onsite or online. Height and colour of bark, flower, and fruit were observed directly from the plants in the field or obtained from the specimen labels. Measurements of the floral parts were taken from dried mature flowers, unless otherwise stated. The type material of each name was located and lectotypifications were made for untypified species when possible. To verify the annotations on specimens, especially types, we compared the handwriting with letters or other autographed material. Updated descriptions and comparative tables are provided.

The distribution, with at least one voucher specimen per province or state, is listed. When collector numbers are not available, barcode numbers are provided instead. Occurrence maps based on the refined data points were drawn using RStudio and R (RStudio Team 2020; R Core Team 2021). Other miscellaneous information, such as ecology, uses and vernacular names, were obtained directly from the verified specimens and the literature.

Results

Clarification of Diospyros apiculata, D. strigosa and D. tamiriensis

Three problematic species of *Diospyros*, including *D. apiculata*, *D. strigosa* and *D. tamiriensis* Lecomte, have been mistakenly treated in Indochina. Chronologically, *D. apiculata* was first described from Peninsular Malaysia (Hiern 1873), followed by *D. strigosa* from Hainan (Hemsley 1910). A decade later, when *D. similis* Craib from Siam (Thailand) was described, Craib (1920) stated that this species is morphologically close to *D. strigosa* but differs slightly in the corolla length. In Cambodia, Lecomte (1928a, 1930) listed *D. tamiriensis* as an endemic species, found only in one location in the country. In the same accounts of the Indochinese Ebenaceae, he defined several varieties of *D. eriantha* Champ. ex Benth. (var. *balansae* Lecomte, *conica* Lecomte, *fragrans* Lecomte and *latifolia* Lecomte), all based

Table 1 Morphological comparison between *Diospyros apiculata* Hiern, *D. eriantha* Champ. ex Benth. var. *eriantha*, *D. strigosa* Hemsl. and *D. tamiriensis* Lecomte.

Characters	***D. apiculata***	***D. eriantha* var. *eriantha***	***D. strigosa***	***D. tamiriensis***
Number of lateral veins	10–13 on each side	5–9 on each side	(5–)7–9(–12) on each side	7–9 on each side
Tertiary veins	Finely scalariform	Reticulate	Reticulate	Coarsely scalariform
Petiole length	2–3 mm	2–5 mm	2–5 mm	(4–)8–10 mm
Hair density on leaf blade	Densely to sparsely hairy on both sides (Fig. 1A)	Sparsely hairy or subglabrous on both sides (Fig. 1C)	Subglabrous on upper surface, densely hairy on lower surface (Fig. 1E)	Subglabrous on upper surface, sparsely hairy on lower surface (Fig. 1G)
Hair on veins	Glabrous to subglabrous on upper side, densely to sparsely hairy on lower side	Glabrous on upper side, densely hairy on lower side	Densely hairy on both sides	Subglabrous on upper side, sparsely hairy on lower side
Hair type	Straight or slightly curved and soft hairs, 1–1.5 mm long (Fig. 1A)	Straight and soft hairs, 1.5–2.5 mm long (Fig. 1C)	Curved and stiff hairs (strigose), 1–1.5 mm long (Fig. 1E)	Straight or curved and soft hairs, 0.5–1.5 mm long (Fig. 1G)
Imbricate scale covering terminal buds	Not present	Present, 3–13 scales	Present, 2–5 scales	Not present
Merosity	4, rarely 5	4	4	4–5
Calyx division	Divided to the base	Divided ⅔ of the way to the base	Divided ⅔ of the way to the base	Divided nearly to the base
Calyx lobe	Lanceolate (male) or elliptic-oblong (female), 4–6 mm long	Ovate (male and female), 3–4 mm long	Narrowly triangular (male) or triangular (male and female), 3–5 mm long	Ovate or elliptic (female), 1–1.5 cm long
Corolla shape	Salverform (Fig. 1B)	Salverform (Fig. 1D)	Salverform (Fig. 1F)	Urceolate (flask-shaped) (Fig. 1H)
Corolla division	±Halfway to the base	±Halfway to the base	⅓ of the way to halfway to the base	Very shallowly divided
Corolla indumentum	Glabrous outside	Densely hairy outside	Densely hairy outside	Hairy along the midveins outside
Fruiting calyx	Fruiting calyx not obviously accrescent	Fruiting calyx accrescent, 8–10 mm long	Fruiting calyx accrescent, 8–13 mm long	Not known
Number of seeds	4	2	2, sometimes fused into 1	Not known

on Vietnamese specimens. In later years, Phengklai (1978, 1981) cited *D. similis* and *D. tamiriensis* as synonyms of *D. apiculata*, and a decade later, Pham-Hoang (1991, 1999) and Nguyen (1996) also included *D. eriantha* var. *conica* as a synonym of *D. apiculata*. As a result, *D. apiculata* had become a species with multiple synonyms and an extremely wide distribution range throughout continental South-East Asia. Additionally, Nguyen (1996) synonymised all varieties of *D. eriantha* except var. *conica* into *D. eriantha* var. *eriantha*.

In this study, we found that *D. eriantha* var. *balansae* is the only variety of *D. eriantha* that truly matches the type specimens of *D. eriantha* var. *eriantha*. The varieties *fragrans* and *latifolia* share the hairy stems and leaves, and small ovoid fruits but they are significantly different from *D. eriantha*, most noticeably in their corolla, calyx, leaf venation and indumentum, and these characters match with *D. strigosa* (Fig. 1, Table 1). The Cambodian species, *D. tamiriensis*, does not belong to *D. strigosa* nor other species and has significant morphological differences, especially in its flask-shaped corolla with four strips of hairs. As a result, *D. apiculata* is thus restricted to the lower Malay Peninsula (Malaysia and Southern Thailand), *D. tamiriensis* is reinstated and endemic to Cambodia, and *D. strigosa*, also resurrected from synonymy, has a wide distribution range from Southern China to Indochina. *Diospyros similis*, *D. eriantha* var. *conica*, var. *fragrans* and var. *latifolia* are treated here as synonyms of *D. strigosa*.

Below, we present the nomenclatural changes, descriptions and occurrence maps of *D. apiculata*, *D. strigosa* and *D. tamiriensis* (Fig. 2). The distinctive morphological characters of *D. eriantha* var. *eriantha* are also provided (Fig. 1C–D, Table 1).

Class Magnoliopsida Brongn.
Order Ericales Bercht. & J.Presl
Family Ebenaceae Gürke, nom. cons.
Genus *Diospyros* L.

Diospyros apiculata Hiern
Figs 1A–B, 2

Transactions of the Cambridge Philosophical Society 12: 186 (Hiern 1873). – **Type**: PENINSULAR MALAYSIA • Penang, Govt. Hill [Government Hill or later known as Penang Hill]; s.d. (distributed to K in 1871); *Maingay s.n.* [*Kew Distrib.* no. *1514*]; lectotype: K[K000792352]!, designated by De Kok & Puglisi (2021).

Ridley (1923: 285); Bakhuizen van den Brink (1937: 170; 1955: pl. 1, fig. I); Fletcher (1938: 364); Ng (1977: 212; 1978: 61); Phengklai (1978: 86, pro parte; 1981: 376, pro parte); Gardner *et al.* (2015: 487, 687, pro parte).

Description

Small tree, ca 2 m tall. *Young twigs* densely hairy with long ferruginous hairs. *Bark* dark grey, tuberculate, inner bark reddish brown, sapwood creamy white. *Leaves* ovate-oblong, obovate-lanceolate to obovate-oblong, 9–15 × 3–6 cm, base cordate, subcordate or rounded, apex caudate, 1–1.5 cm long, blade densely to sparsely hairy on both sides, more densely hairy on the veins, hairs filiform and straight or slightly curved, soft, 1–1.5 mm long; lateral veins 10–13 on each side, arched and anastomosing near the margin, tertiary veins conspicuously scalariform; petiole short, 2–3 mm long, covered by ferruginous hairs; glands inconspicuous. *Male inflorescences* axillary, subsessile, solitary to few-flowered, usually 3-flowered. *Calyx* campanulate in outline, hairy on both sides, glabrous inside near the base, margin entire, ciliate; lobes 4, rarely 5, divided to the base, lanceolate, 4–6 mm long, not spreading. *Corolla*

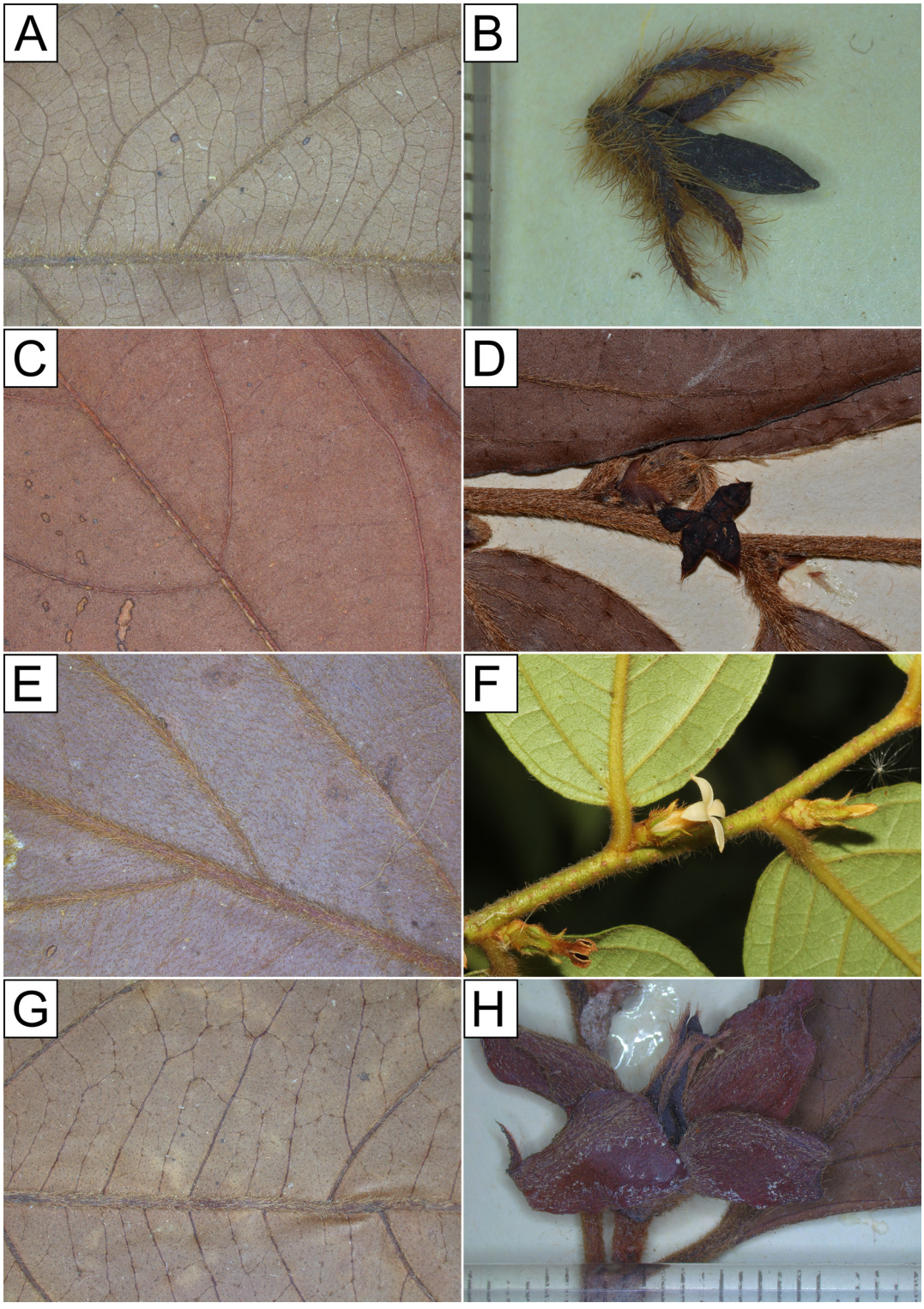

Fig. 1. A–B. *Diospyros apiculata* Hiern. **A**. Lower surface of leaf (*Curtis 1584* K[K001345613]). **B**. Male flower (*Maingay s.n.* [*Kew Distrib.* no. *1514*] K[K000792352]). **C–D**. *D. eriantha* Champ. ex Benth. var. *eriantha.* **C**. Lower surface of leaf (*Champion 133* K[K000792287]). **D**. Female flower (*Champion s.n.* K[K000792289]). **E–F**. *D. strigosa* Hemsl. **E**. Lower surface of leaf (*Collins 506* K[K001361689]). **F**. Female flower. **G–H**. *D. tamiriensis* Lecomte. **G**. Lower surface of leaf. **H**. Female flower (*Pierre 5029* K[K001361754]). Photographed by N. Meeprom and S. Duangjai.

creamy white, tubular when closed, salverform when opened, 0.8–1 cm long, glabrous on both sides; lobes 4, divided about halfway to the base, ovate or ovate-oblong, 3–5 mm long, sinistrorsely contorted, spreading when opened, apex obtuse or acute. *Stamens* 6–12, unequal in length, glabrous; anthers linear-oblong, apex cuspidate; filaments often geniculate, dilated and connate at base and inserted at the base of the corolla tube (the stamen characteristics obtained from Hiern, 1873). Rudimentary *ovary* small, hairy. *Bracteoles* lanceolate to ovate, 2–3 × 1 mm, hairy. *Female inflorescences* axillary, 1–3-flowered cyme, hairy. *Female flowers* similar to male flowers but with broader calyx lobes (elliptic-oblong). *Fruits* solitary, ovoid-conical, ca 2.5 × 1.3–1.7 cm, base rounded, apex apiculate, subsessile, subglabrous but hairy near the tip with yellowish hairs, 4-locular. *Fruiting calyx* slightly accrescent, hairy on both sides, glabrous near the base of each lobe; lobes 4, rarely 5, divided to the base, linear-oblong, 6 mm long, spreading, apex acuminate, margin flat. *Seeds* 4, ellipsoid in outline, concave, ca 1.5 cm long; endosperm smooth.

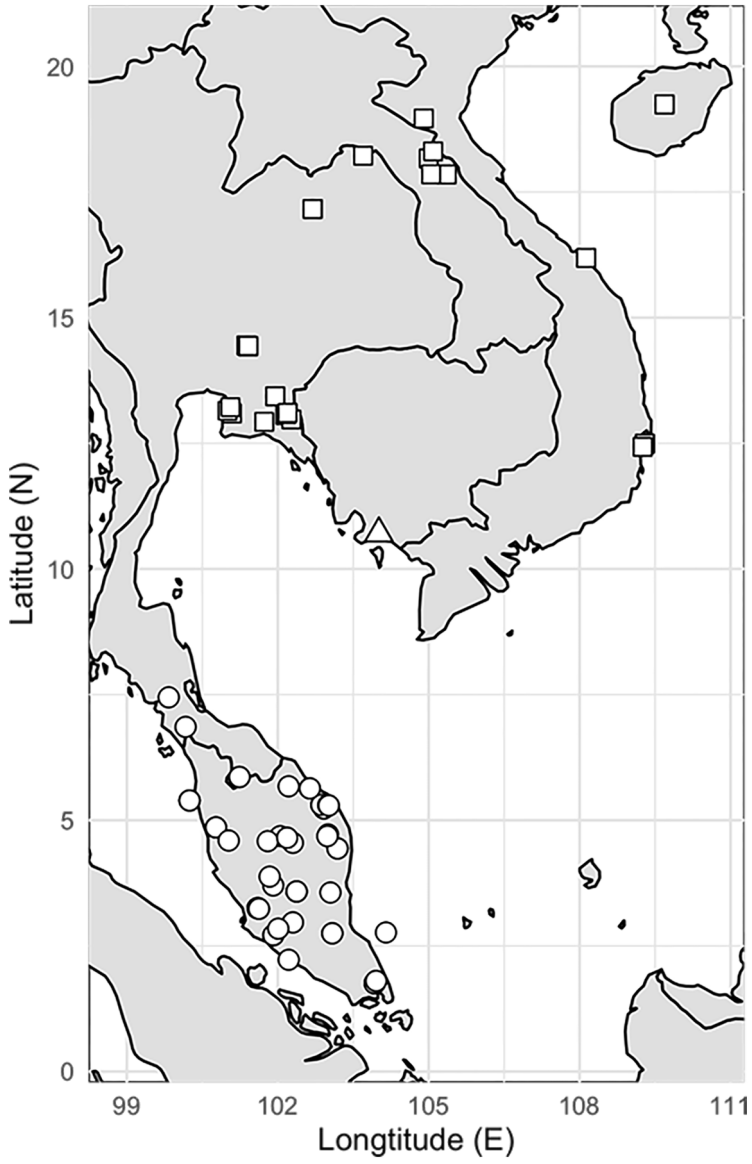

Fig. 2. Occurrence map of *D. apiculata* Hiern (○), *D. strigosa* Hemsl. (□) and *D. tamiriensis* Lecomte (△).

Distribution

THAILAND • Satun [*Kerr 14457* (K)], Yala [*Pooma 4420* (BKF), *5077* (BKF), *Satthaphorn 94* (PSU)]. Gardner *et al.* (2015) also listed *D. apiculata* in Krabi and Trang Provinces: two associated collections from Krabi [*Sidisunthorn ST1200* (BKF)] and Trang [*Gardner ST2465* (K, BKF)] that might belong to *D. apiculata* but they could not be confidently verified due to a lack of mature reproductive characters and were therefore excluded from the occurrence map.

PENINSULAR MALAYSIA • Johor [*Corner SFN29359* (K, SING), *Sinclair 10600* (SING)], Kelantan [*Abu Baker 10596* (KEP)], Malacca [*Alvins s.n.* (SING)], Negeri Sembilan [*Alvin 2077* (SING), *LaFrankie 2728* (KEP), *3024* (KEP)], Pahang [*Chew T1073e* (KEP), *Chua FRI40630* (K, KEP), *Henderson 22296* (SING)], Penang [*Curtis 1584* (K, SING), *Maingay s.n.* [*Kew Distrib.* no. *1514*] (K)], Perak [*King's Collector 5727* (SING), *6770* (SING)], Selangor [*Ali KEP51954* (KEP), *Asnah FRI35593* (SING), *Sow KEP52256* (KEP)], Terengganu [*Cockburn FRI10714* (K), *Corner SFN30368* (SING), *Sinclair SFN39953* (K), *Whitmore FRI20303* (K, KEP, L, SING)].

Ecology

Diospyros apiculata is found in lowland rain forest, up to 750 m elevation (Fig. 2), in the bioregion south of the Isthmus of Kra (Parnell 2013).

Notes

Singh (2005) listed *D. apiculata* in India but he noted that this species in India differs from the type by having a hairy corolla. We could not verify whether Singh's material matches with the typical *D. apiculata*.

Gardner *et al.* (2015) illustrated the typical form of *D. apiculata* from Southern Thailand, showing the scalariform venation, glabrous corolla (outside), and lanceolate calyx lobes of a male flower.

Diospyros strigosa Hemsl.
Figs 1E–F, 2

Bulletin of Miscellaneous Information, Royal Gardens, Kew 1910 (6): 193 (Hemsley 1910). – **Type**: CHINA • Hainan; Nov. 1889; *Henry 8741*; lectotype: K[K000792329]!, **here designated**; possible isolectotype: P[P00721454]!. – **Notes**: Hemsley (1910: 193) cited the gathering of *Henry 8741* from Hainan in the protologue of *D. strigosa*. Two sheets have been located at K and P. As Hemsley was based in Kew (Stafleu & Cowan 1979) and the only sheet in K has Hemsley's protologue attached, this sheet is designated here as the lectotype. The sheet of *Henry 8741* at P is a possible isolectotype because the leaf shape does not perfectly match the sheet at K. While the specimen still appears to belong to *D. strigosa*, it might have been collected from a different tree.
Lee *et al.* (1996: 231).

Diospyros similis Craib, *Bulletin of Miscellaneous Information (Royal Gardens, Kew)* 1920 (9): 303 (Craib 1920), syn. nov. – **Type**: THAILAND • Siam, Sriracha [Chon Buri, Si Racha]; 23 Sep. 1911; *Kerr 2112*; lectotype: K[K000792526]!, **here designated**; isolectotypes: BM[BM000884634]!, E [E00318464]!. – **Notes**: Craib (1920) cited *Kerr 2112* as the reference material of this species. Specimens of this gathering have been found in BK, E and K and the sheet at K is selected here as Craib was based in Kew when he was writing the Flora of Siam (Hill 1933; Stafleu & Cowan 1976).
Lecomte (1930: 968); Fletcher (1938: 380).
Diospyros cardiophylla Merr., *Philippine Journal of Science* 21 (4): 352 (Merrill 1922). – **Type**: CHINA • Hainan, Ng Chi Leng; Dec. 1921; *McClure 8349*; syntypes: A[A00010557]!, BISH[BISH001283]!,

BM[BM000997436]!, CAS[CAS0033254]!, K[K000792328]!, NY[NY00335006]!, P[P00721453]!, US[US00113421]!.

Diospyros eriantha Champ. ex Benth. var. *conica* Lecomte, *Flore Générale de l'Indo-Chine* 3 (7): 952 (Lecomte 1930), syn. nov. – **Type**: VIETNAM • Annam, Col des Nuages, près Tourane [Hai Van Pass]; 18 Sep. 1923; *Poilane 8080*; lectotype: P[P00721421]!, designated by Meeprom *et al.* (2022); isolectotype: P[P05197352]!.

Diospyros eriantha Champ. ex Benth. var. *fragrans* Lecomte, *Flore Générale de l'Indo-Chine* 3 (7): 952 (Lecomte 1930), syn. nov. – **Type**: VIETNAM • Annam, Nhatrang Prov., Ile My Giang (près Ninh Hoa) [Khanh Hoa, My Giang Island]; 24 Apr. 1923; *Poilane 6064*; lectotype: P [P00721503]!, designated by Meeprom *et al.* (2022); isolectotypes: P[P00721504, P00721505]!.

Diospyros eriantha Champ. ex Benth. var. *latifolia* Lecomte, *Flore Générale de l'Indo-Chine* 3 (7): 952 (Lecomte 1930), syn. nov. – **Type**: VIETNAM • Annam, Nhatrang Prov., Presqu'île de Han Heo [Khanh Hoa, Hon Heo Peninsula]; 12 Jun. 1923; *Poilane 6837*; lectotype: P[P00721419]!, designated by Meeprom *et al.* (2022); isolectotype: P[P00721420]!.

Diospyros apiculata [non Hiern] sensu auctorum et pro parte: Phengklai (1978: 86, fig. 51A, D; 1981: 376, fig. 51A, D); Pham-Hoang (1991: 811; 1999: 642); Nguyen (1996: 63).

Description

Small tree or shrubby tree, up to 10 m tall. *Young twigs* sparsely to densely hairy. *Bark* brown, scaly, inner bark orange-brown, sapwood creamy white. Terminal and axillary buds, including inflorescence buds, covered by 2–5 imbricate scales. *Leaves* lanceolate, elliptic-lanceolate to elliptic-oblong, 7–15 × 2.5–5 cm, base rounded to slightly cordate, apex acuminate to caudate, blade pubescent or sparsely hairy on upper surface, sometimes glabrescent, lower surface strigose; lateral veins (5–)7–9(–12) on each side, curved but not arched near the margin, tertiary veins reticulate, sometimes coarsely scalariform; petiole short, 2–5 mm long, sparsely to densely hairy. *Male flowers* solitary or in short, few-flowered fascicle, axillary. *Calyx* campanulate, 4–7 mm long, hairy on both sides; lobes 4, divided halfway to ⅔ of the way to the base, triangular to narrowly triangular, ca 4–5 mm long, valvate, margin entire and flat. *Corolla* salverform, ca 1 cm long, hairy outside, glabrous inside; tube tubular, slightly widened in the middle; lobes 4, divided ⅓ of the way to the base, ovate, 3–4 mm long, curved outward. *Stamens* not seen. *Female flowers* solitary, axillary, sessile. *Calyx* campanulate, 5–6 mm long, hairy outside, glabrous inside; lobes 4, divided ⅔ of the way to the base, triangular, 3–4 mm long, valvate, margin reflexed. *Corolla* salverform, ca 1 cm long, hairy outside, glabrous inside; tube ovoid; lobes 4, divided ⅓ to halfway to the base, curved outward. *Fruits* sessile, ovoid, 2.5–2 × 1–1.5 cm, 2-locular, apex acute or cuspidate (hardened stigma), hairy and later glabrescent, green when mature and turning reddish brown when ripe. *Fruiting calyx* slightly accrescent, hairy on both sides; lobes 4, divided nearly all the of the way to the base, lanceolate to ovate, 0.8–1.3 cm long, spreading or enclosing the fruits, margin flat or revolute. *Seeds* 2, sometimes both seeds fused into one.

Distribution

CHINA • Hainan [*Henry 8741* (K, P), *McClure 8349* (A, BISH, BM, CAS, K, NY, P, US)].

LAOS • Locality not specified [*Massie s.n.* (P[P00721748])], Bolikhamxai [*Svengsuksa 84* (BKF)], Khammouane [*Newman LAO 66* (BKF, E)].

THAILAND • Bueng Kan [*Kerr 8538* (K)], Chanthaburi [*Geesink 6751* (BKF, K), *Larsen 31970* (BKF), *Tagane 1811* (BKF)], Chonburi [*Collins 506* (K), *1982* (K), *Kerr 2112* (K), *Maxwell 74-1090* (BKF)], Nakhon Nayok [*Smitinand 10877* (BKF, K), *Poopath 6139* (BKF)], Nakhon Ratchasima [*Charoenphol 4387* (BKF, K)], Sa Kaeo [*Middleton 201* (BKF, E, K)], Udon Thani [*Suddee 3019* (BKF)].

VIETNAM • Hai Van Pass (Da Nang & Thua Hien Hue) [*Poilane 7769* (P), *8080* (P)], Khanh Hoa [*Poilane 6064* (P), *6837* (P)], Nghe An [*Du 3141* (K)].

Ecology

Diospyros strigosa is usually found near streams in lowland forest, 20–800 m elevations (Fig. 2).

Diospyros tamiriensis Lecomte
Figs 1G–H, 2

Notulae Systematicae 4 (4): 119 (Lecomte 1928a). – **Type**: CAMBODIA • In montibus Tamire [Kampot, Mt. Phnum Tamei]; May 1870; *Pierre 5029*; lectotype: P[P00721751]!, designated by Meeprom *et al.* (2022); isolectotypes: A[A00011098, A00353513]!, K[K001361754]!, L[L.2664519]!, NY[NY00334762]!, P[P00721506, P00721507, P00721508, P00721749, P00721752]!, VNM [VNM00002310, VNM00015396]!.
Lecomte (1930: 965, fig. 110).

Description

Medium-sized tree (Lecomte 1930). *Young twigs* densely hairy, hairs straight or slightly curved, 0.5–1.5 mm long. *Leaves* elliptic to elliptic-ovate, 8–13 × 3–7 cm, base cuneate, apex acuminate to caudate, blade glabrous or sparsely hairy on upper surface, lower surface sparsely hairy, more densely hairy on the midrib and lateral veins on both sides of the leaf, hairs same as on twigs but generally straighter; lateral veins 7–9 on each side, arched near the margin, tertiary veins coarsely scalariform and reticulate; petiole (0.4–)0.8–1 cm long, hairy. *Female flowers* axillary, solitary; pedicel ca 3 mm long, hairy. *Calyx* spreading, ca 2 cm in diam., hairy on both sides; lobes 4–5, divided nearly to the base, ovate or elliptic, 1–1.5 cm long, apex acuminate to caudate. *Corolla* urceolate (flask-shaped), hairy outside along the midveins; lobes 4–5, shallowly divided near the tip, broadly ovate, 1–2 mm long, apex acuminate. *Ovary* ovoid, densely hairy. Staminodes absent. *Male flowers*, *fruits* and *seeds* not seen.

Distribution

CAMBODIA • Kampot, Phnum Tamie [*Pierre 5029* (A, K, L, NY, P, VNM)]. This species is endemic to Cambodia and only known from the type collection (Fig. 2). A gathering included in Lecomte's original material of *D. tamiriensis* from Laos [*Massie s.n.* (P[P00721748])] belongs to *D. strigosa* Hemsl.

Notes

Diospyros tamiriensis is resurrected here from synonymy of *D. apiculata* (Phengklai 1978, 1981; Pham-Hoang 1991, 1999; Nguyen 1996; POWO 2022).

Recircumscription of Diospyros bejaudii Lecomte and resurrection of D. retrofracta Bakh.

Lecomte (1929, 1930) described the male and female forms of *D. bejaudii* Lecomte separately but the specimens corresponding to each sex are clearly two different species. De Kok & Puglisi (2021) selected the male specimen, *Béjaud 23* at P as the lectotype of *D. bejaudii* (P000721441, Fig. 3; isolectotype P02141496). This species is diagnosed by the presence of a pair of leaf basal veins, 4-merous flowers with pubescence on both sides of the calyx, calyx divided halfway to the base, nearly glabrous corolla with hairs restricted to the midvein of each lobe, corolla divided halfway to the base, fruiting calyx with raised rim inside at the base of the lobes, and with spreading or slightly curved calyx lobes (Figs 3, 4A–D).

The female form in the original publication of *D. bejaudii* is morphologically different and certainly not conspecific. The matching material is characterised by the coriaceous or subcoriaceous leaves, shallowly lobed calyx in male flowers, calyx divided ⅓ of the way to the base into 4–5 lobes in female flowers, corolla with sericeous hairs outside, and strongly reflexed fruiting calyx (Figs 4E–H, 5). The

oldest name that is best applied to this species is *D. retrofracta*. This name was published four years after *D. bejaudii* (Bakhuizen van den Brink 1933) from the specimens from Southern Thailand.

Previously, Phengklai (1978) treated *D. retrofracta* as a synonym of *D. bejaudii*, and in a later work (Phengklai 1981), the description of *D. bejaudii* was based almost entirely on the typical characters of *D. retrofracta* rather than *D. bejaudii*. This altered definition of *D. bejaudii* was carried over in subsequent accounts of the Ebenaceae in Thailand (Gardner *et al.* 2015) and Vietnam (Nguyen 1996). Moreover, the illustrations of *D. bejaudii* drawn by Pham-Hoang (1991, 1999) and the description and photos from Gardner *et al.* (2015) represent *D. retrofracta* rather than *D. bejaudii*.

Here, we provide updated nomenclature, description and distribution of *D. bejaudii* and *D. retrofracta*. Additionally, *D. pubicalyx* Bakh. is treated here as a new synonym of *D. bejaudii*.

Fig. 3. Lectotype of *D. bejaudii* Lecomte (*Béjaud 23* P[P00721441]) (Muséum National d'Histoire Naturelle 2022).

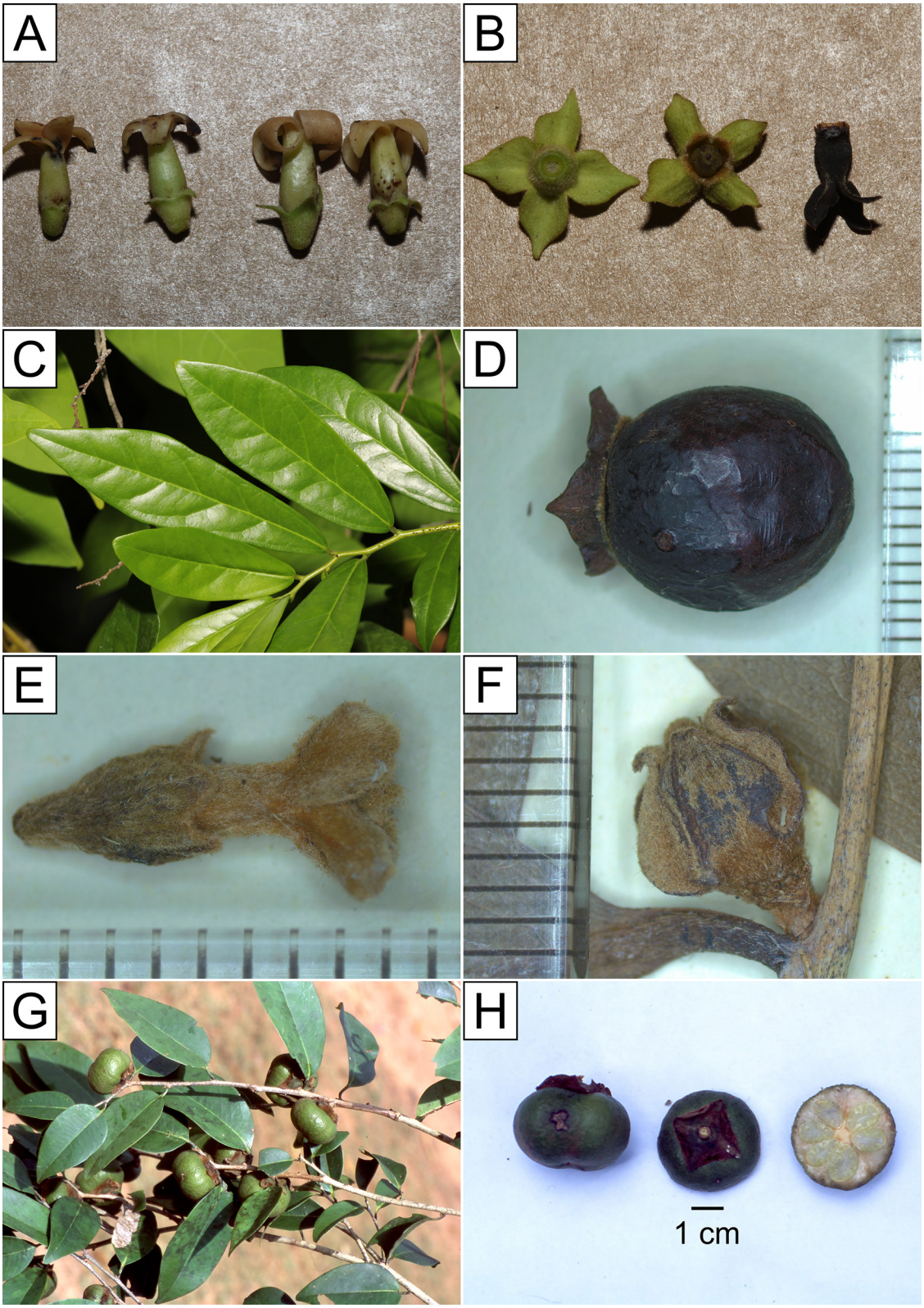

Fig. 4. A–D. *Diospyros bejaudii* Lecomte. **A**. Male flowers. **B**. Female calyx and corolla. **C**. Twig with leaves. **D**. Fruit (*Put 3161* K[K001361559]). **E–H**. *D. retrofracta* Bakh. **E**. Male flower (*Kerr 10718* K[K001361567]). **F**. Remaining calyx of female flower (*Kerr 12697A* K[K001361574]). **G**. Twigs with leaves and fruits. **H**. Fruits. Photographed by N. Meeprom and S. Duangjai.

Diospyros bejaudii Lecomte
Figs 3, 4A–D, 6

Bulletin du Muséum National d'Histoire Naturelle, séries 2 1: 430 (Lecomte 1929). – **Type**: CAMBODIA • 18 Apr. 1929; *Béjaud 23*; lectotype: P[P00721441]!, designated by De Kok & Puglisi (2021); isolectotype: P[02141496]!.
Lecomte (1930: 936).

Diospyros odoratissima Lecomte var. *oblonga* Lecomte, *Notulae Systematicae* 4 (4): 109 (Lecomte 1928), syn. nov. – **Type**: CAMBODIA • Région de Kompong Cham [Kampong Cham]; 28–30 Dec. 1917; *Chevalier 35881*; lectotype: P[P00721654]!, designated by Meeprom *et al.* (2022).
Lecomte (1930: 940).

Fig. 5. Isolectotype of *D. retrofracta* Bakh. (*Haniff & Nur 3984* K[K000792535]) (Royal Botanic Gardens, Kew 2022).

Diospyros pubicalyx [as '*pubicalix*'] Bakh., *Gardens' Bulletin, Straits Settlements* 7 (2): 182 (Bakhuizen van den Brink 1933), syn. nov. – **Type**: THAILAND • Lower Siam, Hat Sunuh or Lajburi, S. West Siam [Prachuap Khiri Khan, Hat Sanuk]; 16 Apr. 1919; *Hamid C.F. 3827*; lectotype: SING[SING0052425]!, designated by De Kok & Puglisi (2021); isolectotype: K[K001089523]!.

Bakhuizen van den Brink (1938: 179; 1955: pl. 39, fig. II); Fletcher (1938: 377); Phengklai (1978: 62, fig. 33A; 1981: 344, fig. 33A); Gardner *et al.* (2015: 510, 692).

Diospyros montana [non Roxb.] sensu Ng (2001: 310, pro parte, quod syn. *D. pubicalyx* Bakh.

Description

Tree, up to 30 m in *Kerr 10773*. *Bark* greyish black, scaly-fissured (resembles bark of *Tamarindus indica* L.) or smooth, inner bark pale yellow, sapwood creamy white. *Young twigs* sparsely hairy, old twigs glabrous. *Leaves* oblong, oblong-oblanceolate to oblong-obovate, noticeably roughly pentangular in outline, 6–11 × 2–4.5 cm, base rounded or subcordate, apex obtuse, acute or rounded, blade glabrous on both sides except the midrib sparsely hairy to pubescent; petiole 4–7 mm long, pubescent or glabrescent; lateral veins 6–10 on each side, arched and anastomosing near the margin, with 1–2 pairs of basal veins branching in narrower angle than the upper pairs of lateral veins, tertiary veins reticulate; glands 1–6 on each side. *Male inflorescences* 3-flowered fascicle, peduncle 1–5 mm long, pubescent. *Calyx* campanulate; lobes 4, divided about halfway to the base, triangular, spreading or slightly reflexed, valvate, apex acute-obtuse, margin slightly revolute. *Corolla* short-salverform, ca 1 cm long, glabrous except along the midvein outside of each lobe; lobes 4, divided about halfway to the base, elliptic, twisted, apex obtuse. *Stamens* not seen. *Female flowers* solitary (observed from female specimens with fallen corolla and fruits), corolla similar to male flowers but corolla tube widened in the middle. *Calyx* campanulate, sparsely hairy on both sides; lobes 4, divided halfway to ⅔ of the way to the base, ovate, reflexed when mature, apex acute-obtuse to acuminate-obtuse. *Fruits* subglobose, black when dried, 1.2–1.5 × 1–1.4 cm, subglabrous, 8-locular. *Fruiting calyx* accrescent, 0.8–1.5 cm in diam., subglabrous on both sides except the middle part inside sericeous (when the fruit removed); lobes 4, divided halfway to ⅔ of the way to the base, broadly ovate, spreading, slightly to strongly reflexed but not plicate, base with raised rim, apex acute, margin slightly revolute. *Seeds* 8, concave, thin.

Distribution

CAMBODIA • Kampong Cham [*Béjaud s.n.* (K[K001361045], P[P00721713, P00721442], VNM[VNM00015139], *23* (P), *24* (A, P), *Chevalier 35581* (P), *35582* (P)].

THAILAND • Chonburi [*Collins 1506* (K), *2259* (K), *Phengklai 11942* (BKF), *11977* (BKF), *13259* (BKF)]; Prachuap Khiri Khan [*Hamid 3827* (K, SING), *Kerr 10773* (K), *Middleton 1210* (BKF), *Put 3161* (K)]; Phetchaburi [*Kaewmuan 22* (BKF)].

Ecology

Diospyros bejaudii is distributed in dry evergreen forest or beach forest at or near sea level (Fig. 6).

Notes

Diospyros bejaudii is morphologically close to *D. ebenum* J.Koenig as they both have a raised rim inside the fruiting calyx and their leaves usually have basal veins. They can be distinguished by the shape of calyx lobes. Male calyx lobes of *D. bejaudii* are triangular with acute to acuminate apex while those of *D. ebenum* are semicircular with rounded apex. Female calyx lobes of *D. bejaudii* are spreading or curved outward while they are abruptly reflexed in *D. ebenum*.

Previously, *D. pubicalyx* was either cited as a synonym of *D. montana* by Ng (2001) or treated as a good species by Gardner *et al.* (2015). The type specimens of *D. pubicalyx* are not morphologically different

from *D. bejaudii* and here treated as its new synonym. In addition, *D. odoratissima* Lecomte var. *oblonga* Lecomte morphologically and geographically matches with *D. bejaudii*. However, *D. odoratissima* var. *oblonga* (published in 1928) must be treated here as a synonym of *D. bejaudii* (published in 1928) because the infraspecific epithet '*oblonga*' has been taken by another species.

Diospyros retrofracta Bakh.
Figs 4E–H, 5, 6

Gardens' Bulletin Straits Settlements 7 (2): 183 (Bakhuizen van den Brink 1933). – **Type**: THAILAND • Lower Siam, Pungah [Phang-nga]; 7 Dec. 1918; *Haniff & Nur 3984*; lectotype: BO [1 sheet without barcode]!, designated by De Kok & Puglisi (2021); isolectotype: K[K000792535]!.
Bakhuizen van den Brink (1938: 361; 1955: pl. 89, fig. 1); Fletcher (1938: 378).

Diospyros bejaudii Lecomte, *Bulletin du Muséum National d'Histoire Naturelle, séries 2* 1: 430 (Lecomte 1929).
Lecomte (1930: 936); Phengklai (1978: 90, fig. 53; 1981: 378, fig. 53); Pham-Hoang (1991: 812; 1999: 643); Nguyen (1996: 63); Gardner *et al.* (2015: 488, 688); Tagane *et al.* (2018: 50).

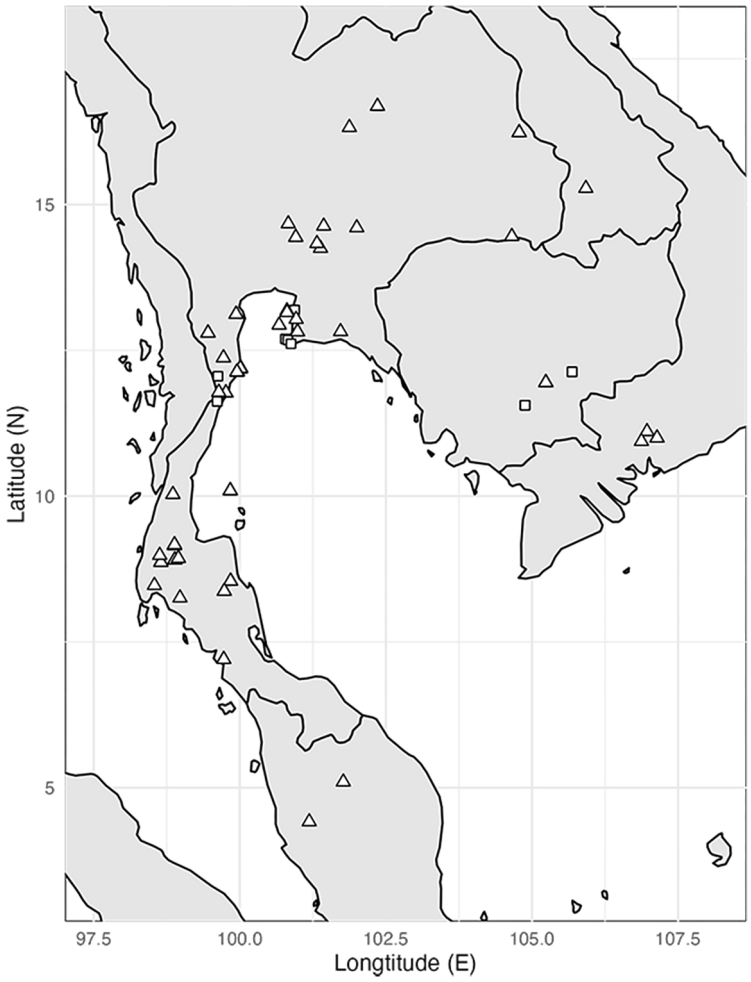

Fig. 6. Occurrence of *D. bejaudii* Lecomte (□) and *D. retrofracta* Bakh. (△) in mainland South-East Asia.

Description

Tree, up to 30 m tall. *Twigs* white or grey, glabrous. *Bark* dark grey, scaly, inner bark brown, sapwood creamy white. *Leaves* ovate, elliptic-ovate, elliptic to elliptic-lanceolate, 5–11 × 2.5–5 cm, base rounded, apex acute-obtuse, blade coriaceous, glabrous on both sides; lateral veins 8–11 on each side, arched and sometimes anastomosing near the margin, tertiary veins distinctly reticulate (areolate); petiole 0.5–1 cm long, glabrous. *Male inflorescences* axillary or subterminal, few-flowered fascicle. *Male flowers* subsessile, scented. *Calyx* campanulate or short-tubular, hairy outside, glabrous inside; lobes 4, divided ⅓ of the way to the base, broadly triangular, valvate, 1–2 mm long, apex acute. *Corolla* white, tubular when closed, salverform when opened, 0.8–1.5 cm long, sericeous outside, glabrous inside; lobes 4, divided ⅓ of the way to base, ovate, 3–4 mm long, twisted, spreading or revolute. *Stamens* 12; filaments short, anthers sagittate. Rudimentary *ovary* present, sericeous. *Female flowers* axillary or subterminal, solitary, subsessile. *Calyx* campanulate, hairy on both sides; lobes 4, rarely 5, divided halfway to ⅔ of the way to the base, broadly ovate or heart-shaped, valvate, erect, not spreading or reflexed, 4–5 mm long, apex acute, slightly curved outward, margin sometimes undulate. *Corolla* tubular when closed, opened corolla not seen, sericeous outside. *Ovary* ovoid, sericeous. *Fruits* solitary, subglobose, oblate and depressed at both ends, 1.5–2.5 × 2–3 cm, glabrous, light green when young, covered by brownish or golden hairs. *Fruiting calyx* brown, accrescent and hardened, 1.5–2.5 cm in diam., hairy on both sides; lobes 4, rarely 5, divided ⅓ of the way to halfway to the base, strongly reflexed. *Seeds* 4, commonly abortive, 1.2–1.5 × 0.7–0.9 cm; endosperm ruminate.

Distribution

MYANMAR • Tanintharyi [*Tagane et al. MY293* (KYO, RAF, TNS)] (Tagane *et al.* 2018).

CAMBODIA • Kampong Cham [*Bejaud s.n.* (P(P04569441, P04569443, P04569444, P04569446))], ‘Tonlap (Krek)’ [*Bejaud*, *6* (P), *26* (P), *812* (P)].

LAOS • Champasak [*Tagane et al. L2418* (KAG)].

THAILAND • Chonburi [*Collins 1267* (K), *Maxwell 93-830* (BKF), *Puudjaa 595* (BKF)], Krabi [*Gardner ST2163* (BKF), *Kerr 19394* (K)], Mukdahan [*Wongprasert 981020* (BKF)], Nakhon Nayok [*Koyoma T-30227* (BKF)], Nakhon Si Thammarat [*Thavorn 275* (K, P)], Phang-nga [*Haniff 3894* (K), *Shimizu T-29213* (BKF)], Phetchaburi [*Kerr 10718* (K), *11001* (K), *11093* (K), *Middleton 902* (BKF, E, K), *911* (BKF, E, K)], Prachuap Khiri Khan [*Larsen 33669* (BKF, P), *33674* (P), *33689* (P), *33708* (P), *33721* (BKF, P), *Newman 1176* (BKF, E), *Santisuk 555* (BKF, K)], Ranong [*Middleton 3819* (BKF, E, K)], Rayong [*Phonsena 5542* (BKF)], Saraburi [*Maxwell 05-463* (BKF)], Si Sa Ket [*Pooma 6071* (K)], Surat Thani [*Gardner ST1964* (BKF, K), *ST1966* (BKF), *Kerr 11174* (K), *12697* (K), *12697A* (K), *Middleton 1497* (E, K), *Niyomdham 1276* (BKF, K, P), *Pooma 3553* (BKF, K)], Trang [*Kerr 19108* (K)].

VIETNAM • Dong Nai [*Pierre 1289* (P), *Poilane 19626* (K, P), *21337* (P)].

PENINSULAR MALAYSIA • Kelantan [*Whitmore FRI4233* (K, KEP, L)], Perak [*Ng FRI5841* (K, KEP, L)]. Fig. 6.

Additional material

Photographs of *D. bejaudii* in Gardner *et al.* (2015) well illustrate the fresh characters of *D. retrofracta*.

Ecology

Diospyros retrofracta is commonly found on limestone hills, sometimes along streams, at 50–350 m elevations (Fig. 6).

Table 2 Morphological comparison between *Diospyros dictyoneura* Hiern and *D. hasseltii* Zoll.

Characters	*D. dictyoneura*	*D. hasseltii*
Leaf texture	Coriaceous when dried	Chartaceous to subcoriaceous and usually crispy when dried
Lateral veins	6–9 on each side, not parallel	9–15 on each side, usually parallel
Tertiary veins	Reticulate, not scalariform	Reticulate, commonly scalariform
Flower merosity	5-merous, rarely 4-merous	4-merous
Fruit shape and size	Elongated, ovoid to ellipsoid, 3.5–5 × 2–2.5 cm	Subglobose to ovoid, 2.5–4 × 1.5–2.5 cm, usually compressed at both ends
Fruit indument	Hairy outside with brownish or yellowish hairs and glabrescent when old	Usually covered by blackish or brownish hairs and glabrescent when old
Fruiting calyx	2.5–3 cm in diam. (4–6 cm in diam. when fully spread)	1.5–2.5 cm in diam. (2.5–3(–4) cm in diam. when fully spread)
Fruit stalk	1–2.5(–4) cm long	0.5–1 cm long

Diospyros dictyoneura Hiern does not occur in Indochina

Diospyros dictyoneura was described from material from Borneo, where it is widespread, and is also found in Peninsular Malaysia (Johor, Pahang and Terengganu). This species has been reported in Thailand (Phengklai 1978, 1981; Gardner *et al.* 2015) and Vietnam (Pham-Hoang 1991, 1999; Nguyen 1996). We found that all the specimens from Thailand and Vietnam determined as *D. dictyoneura* were in fact misidentifications, mostly of *D. hasseltii* Zoll. These two species are similar in their enlarged and plicate fruiting calyx, but they have significantly different leaf texture, flower merosity, fruit shape, fruiting calyx size and fruit stalk (Fig. 7, Table 2).

The ambiguity might be a result of the revision by Bakhuizen van den Brink (1938) as discussed in Ng (1977). In his treatment of *D. dictyoneura*, he cited some Thai specimens that belong to *D. hasseltii* and he also noted that he only saw photos of the type specimens of *D. dictyoneura*. Fletcher (1938) also cited a specimen of *D. hasseltii* as *D. dictyoneura* in Thailand. In the present study, we have not seen specimens of *D. dictyoneura* in Thailand and Vietnam. Hence, we conclude that *D. dictyoneura* should be excluded from the flora account of *Diospyros* in Thailand and Vietnam.

Diospyros dictyoneura Hiern
Fig. 7A–C

Transactions of the Cambridge Philosophical Society 12: 192 (Hiern 1873). – **Type**: MALAYSIAN BORNEO • Sarawak, Mt. Mattang, near Kuching; Sep. 1866; *Beccari PB 2615*; lectotype: K[K000792679]!, designated by De Kok & Puglisi (2021); isolectotypes: FI[FI008993]!, P[P00721798]!.

Bakhuizen van den Brink (1938: 257; 1955: pl. 57 figs y–z); Ng (1977: 218; 1978: 68; 2002: 55).

Description

Tree, 8–25 m tall. *Leaves* elliptic to elliptic-oblong, 9–17 × 5–7 cm, base rather rounded, apex acute-round or acuminate-rounded, blade coriaceous when dried, glabrous on both sides; lateral veins 6–9

on each side, not parallel, anastomosing near the margin, raised below, tertiary veins reticulate; petiole 1–1.5 cm long, glabrous. *Male inflorescences* 3–6-flowered, 3–4 cm long, hairy. *Calyx* campanulate, subglabrous to hairy on both sides; lobes 5, rarely 4, divided ⅔ of the way to the base, broadly ovate, 3–5 × 3–5 mm, apex acuminate to caudate. *Corolla* tubular when closed, hairy outside, opened male corolla not seen; lobes 5, divided about ⅓ of the way to the base, ovate, apex rounded. *Female inflorescences* 1–3-flowered, 2–3 cm long, hairy. *Female calyx* and *corolla* similar to male flowers. *Fruits* elongated, ovoid to ellipsoid, 3.5–5 × 2–2.5 cm, hairy outside with brownish or yellowish hairs when young, glabrescent when old; fruit stalk stout to slender, 1–2.5(–4) cm long. *Fruiting calyx* strongly accrescent, campanulate, 2.5–3 cm in diam. (4–6 cm in diam. when fully spread), subglabrous to pubescent on both sides; lobes 5, rarely 4, divided ⅔ of the way to the base, oblong or ovate, 2–2.5 × 2–3 cm, apex acute or acuminate, curved inward enclosing the base of the fruit, never reflexed, base plicate. *Seeds* ca 2 × 1 cm; endosperm smooth.

Distribution

BRUNEI • Location not specified [*Ashton 7868* (K), *Bernstein 179* (BURN, K)], Belait [*Ashton 7868* (BRUN), *Azlan BRUN23480* (BRUN, K, SING), *Chin 4602* (BRUN), *Kalat BRUN21980* (BRUN), *Ogata Og-B16* (BRUN), *Smythies SAN17466* (BRUN, K, L, KEP, SING)], Temburong [*Ashton 2989* (BRUN), *Project Team (25 Ha Forest Dynamics Plot) 12-4613* (BRUN), *Tan 317* (BRUN)], Tutong [*Suzuki K12569* (BRUN)].

INDONESIAN BORNEO • Kalimantan [*Neth.Ind.For.Service bb.29031* (K)].

MALAYSIAN BORNEO • Sabah [*Caudra A1349* (K, P), *Madani 36752* (K), *Madani 39879* (K), *Sundaling SAN96659* (K)], Sarawak [*Beccari 2615* (FI, K, P), *Chai S.19326* (K), *Galau S15705* (K), *Galau Tree No.521* (K), *Paie S.38428* (K, L), *Othman S.36992* (K, L), *Smythies SAN17466* (K), *Yii S.48415* (K)].

PENINSULAR MALAYSIA • Johor [*Corner 37029* (K)], Pahang [*Abu FRI46749* (K), *Kochummen FRI16198* (K)], Terengganu [*Whitmore FRI20200* (K)].

Ecology

Diospyros dictyoneura is found in evergreen forest at 100–1000 m elevations.

Diospyros hasseltii Zoll.
Fig. 7D–F

Natuurkundig Tijdschrift voor Nederlandsch-Indië 14: 159 (Zollinger 1857). – **Type**: Illustration of Kuhl & Hasselt No. 2b.; holotype, probably at BO (not seen).

Hiern (1873: 265); Bakhuizen van den Brink (1938: 254); Ng (1977: 221; 1978: 73); Phengklai (1978: 66, fig. 38; 1981: 352, fig. 38); Pham-Hoang (1991: 818; 1999: 648); Nguyen (1996: 67); Gardner *et al.* (2015: 500, 690).

Diospyros horsfieldii Hiern, *Transactions of the Cambridge Philosophical Society* 12: 193 (Hiern 1873). – **Type**: INDONESIA • Java; s.d.; *Horsfield 1182*; lectotype: K[K000792680]!, designated by De Kok & Puglisi (2021).

Ridley (1923: 293); Lecomte (1930: 932); Fletcher (1938: 372).

Diospyros brachiata King & Gamble, *Journal of the Asiatic Society of Bengal. Part 2. Natural History* 74: 224 (King & Gamble 1906). – **Type**: PENINSULAR MALAYSIA • Penang, Waterfall valley; 1888; *Curtis 1453*; lectotype: K[K000792583]!, designated by De Kok & Puglisi (2021: 295); isolectotype: SING[SING0052913]!.

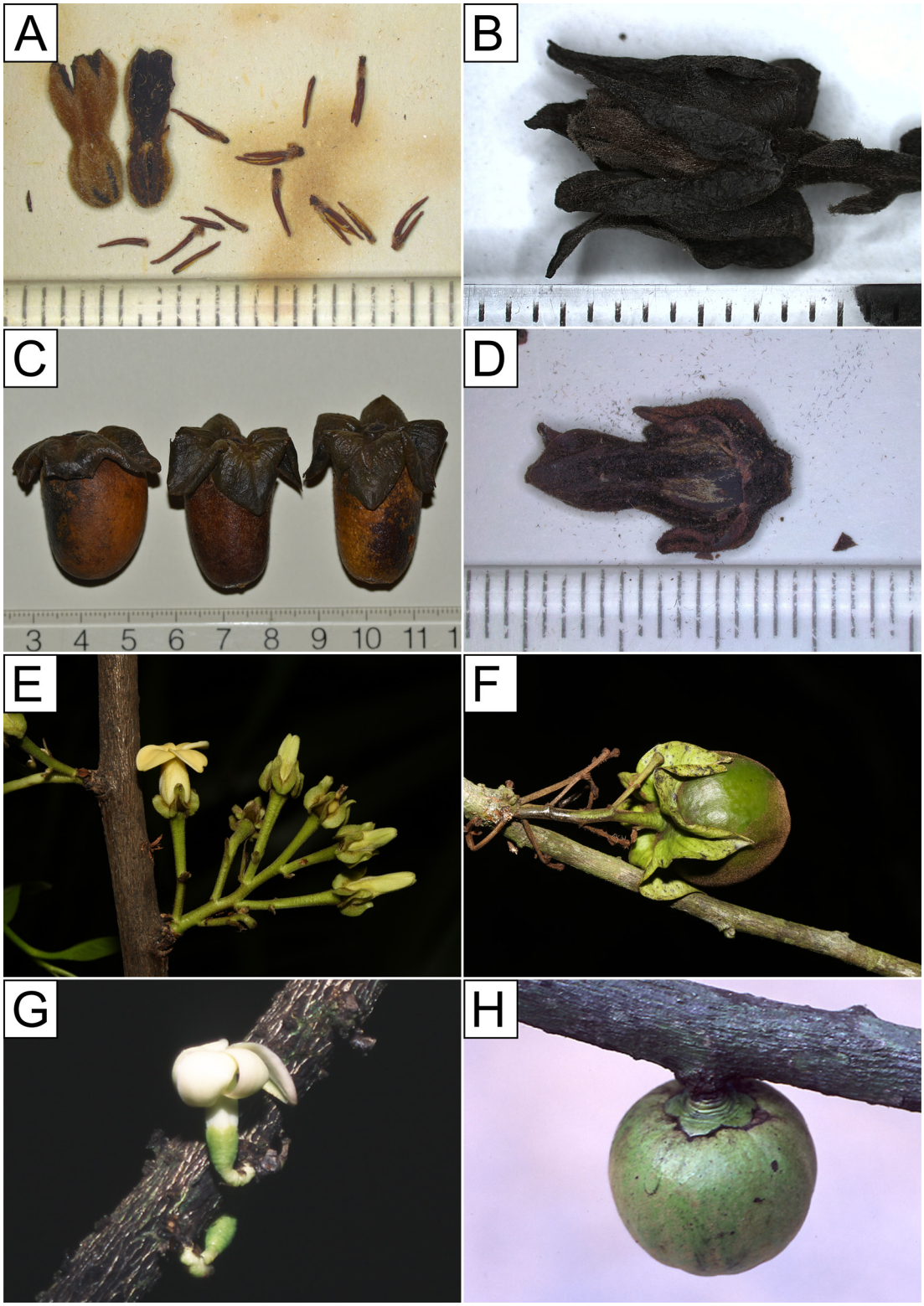

Fig. 7. A–C. *Diospyros dictyoneura* Hiern. **A**. Corolla and stamen of male flower (*Beccari 2615* K[K000792678]). **B**. Female flower (*Galao S15705* K[K001423314]). **C**. Fruits (*Bernstein 179* K[without barcode]). **D–F**. *D. hasseltii* Zoll. **D**. Male flower with front calyx lobe removed (*Smitinand 46521* K[K001361167]). **E**. Female inflorescences. **F**. Fruits. **G–H**. *D. fecunda* H.R.Fletcher. **G**. Male inflorescence; **H**. Fruit. Photographed by N. Meeprom and S. Duangjai.

Ridley (1923: 293); Fletcher (1938: 364).

Diospyros brachiata King & Gamble var. *atra* C.E.C.Fisch., *Bulletin of Miscellaneous Information* (*Royal Gardens, Kew*) 1927 (7): 314 (Fischer 1927). – **Type**: MYANMAR • South Tenasserim; 28 Feb. 1926; *Parkinson 1957*; holotype: K[K000792407]!. – **Notes**: Fischer (1927) cited *Parkinson 1957* collected from Tenasserim as the original gathering. To the best of our knowledge, the only sheet of this collection has been found in K and is considered the holotype of this taxon.

Fletcher (1938: 364).

Diospyros brachiata King & Gamble var. *lanceolata* H.R.Fletcher, *Bulletin of Miscellaneous Information* (*Royal Gardens, Kew*) 1937 (7): 383 (Fletcher 1937). – **Type**: THAILAND • Puket, Kamala [Phuket, Kamala Beach]; *Kerr 17412*; lectotype: K[K001361057]!, **here designated**; isolectotypes: BK[BK257846]!, E[E00318456]!, K[K000792556]!. – **Notes**: Fletcher (1937) cited only *Kerr 17412* from Puket [Phuket] as the original material, and several sheets have been located at BK, E and K. As the only sheet, K001361057, was annotated as 'type' while the others were either unannotated or annotated as 'co-type' in Fletcher's own handwriting, the sheet is selected here as the lectotype.

Fletcher (1938: 364).

Diospyros dictyoneura [non Hiern], sensu auctorum: Bakhuizen van den Brink (1938: 257, pro parte; 1955: pl. 57 figs a–x); Fletcher (1938: 368); Phengklai (1978: 82, fig. 49; 1981: 373, fig. 49); Pham-Hoang (1991: 815; 1999: 645); Nguyen (1996: 65); Gardner *et al.* (2015: 500, 690).

Description

Tree, up to 15 m tall. *Bark* black, smooth or scaly and sparsely lenticellate, inner bark reddish brown, sapwood white, young twigs green, glabrous, older twigs blackish-brown. *Leaves* elliptic, elliptic-lanceolate to narrowly elliptic, 15–30 × 5–10 cm, base rounded or cuneate, apex acuminate or caudate (usually missing in herbarium specimens), blade chartaceous to subcoriaceous and usually crispy when dried, glabrous on both sides; lateral veins 9–15 on each side, usually parallel, curved near the margin, sunken above and distinctly raised below, tertiary veins reticulate, commonly scalariform; petiole 1–1.5 cm long, glabrous. *Male inflorescences* compound cymes, ca 5 cm long, many-flowered, on young or old branches; bracts and bracteoles present. *Calyx* campanulate in outline, hairy on both sides; lobes 4, divided at least ⅔ of the way to the base, ovate, 5–7 × 4–6 mm, valvate, base plicate which makes each calyx lobe look like heart-shaped, apex acuminate. *Corolla* tubular when closed, salverform when opened, 1.5–2.5 cm long, densely hairy outside, hairs usually black, sometimes brown, subglabrous inside; tube with 4 longitudinal ridges outside; lobes 4, divided halfway to the base, oblong 0.7–1 cm long, apex obtuse. *Female inflorescences* similar to male inflorescence but with fewer flowers. *Female calyx* and *corolla* similar to male flowers. *Fruits* subglobose to ovoid, 2.5–4 × 1.5–2.5 cm, usually depressed at both ends, dark green when young and turning yellow when ripe, usually covered by blackish or brownish hairs when young, glabrescent when mature, 8(–10)-locular; fruit stalk 0.5–1 cm long. *Fruiting calyx* accrescent, 1.5–2.5 cm in diam. (2.5–3(–4) cm in diam. when fully spread); lobes 4, divided ⅔ of the way to the base, broadly ovate, ca 1.5 × 1.5 cm, spreading or curved inward, not reflexed, base plicate, apex acute, margin sometimes undulate or reflexed. *Seeds* 8(–10), sometimes abortive, crescent-shaped, 1.5–2 × 0.7–1 cm; endosperm smooth.

Distribution

MYANMAR • Tanintharyi [*Parkinson 1957* (K000792407)].

CAMBODIA • Kandal [*Bejaud 811* (P), *Chevalier 31833* (P)].

LAOS • Sainyabuli [*Thorel 3076* (P)].

THAILAND • Bangkok [*Kerr 4229* (K, P), *Marcan 1893* (K)], Bueng Kan [*Kerr 21337* (K)], Chonburi [*Phengnaren 556* (BKF)], Chumphon [*Williams 1263* (BKF)], Kanchanaburi [*Maxwelll 93-295* (BKF)], Krabi [*Chamchumroon 6* (BKF), *Kerr 12432* (K), *Pooma 3633* (BKF, K)], Lampang [*Winit 1651* (BKF, K)], Loei [*Smitinand s.n.* (BKF [BKF019432])], Nakhon Si Thammarat [*Maxwell 85-883* (BKF), *Suvarnakoses 776* (BKF, K), *Thavorn 1007* (BKF)], Narathiwat [*Lakshnakara 624* (K), *Niyomdham 8216* (BKF)], Phang-nga [*Gardner ST0854* (BKF, K), *Geesink 5022* (BKF, K), *Kerr 18351* (K), *Meeboonya RM289* (BKF), *Maudsub 45* (BKF) *Promdej 286* (BKF)], Phrae [*Phengklai 73* (BKF, K), *Smitinand 10824* (BKF, K), *Smitinand 46521* (BKF, K), *Winit 1674* (K)], Phuket [*Kerr 17412* (K, lectotype of *D. brachiata* King & Gamble var. *lanceolata* H.R.Fletcher), Ranong [*Gardner ST0864* (BKF, K), *Geesink 4915* (BKF), *Kerr 16993* (K), *17019* (K)], Satun [*Gardner ST0245* (BKF, K), *ST1479* (BKF, K), *ST1529* (BKF, K), *ST1536* (BKF, K), Surat Thani [*Damrongsak s.n.* (BKF [BKF018899, BKF197556], *Prapat 42* (K)], Trang [*Larsen 33291* (BKF, P), *Phengklai 1572* (BKF), *Phengnaren 87* (BKF), *Sinbunroong 28* (BKF), *Vanpruk 663* (K, Bakhuizen van den Brink (1938: 259) mentioned this specimen under *D. dictyoneura*), *Williams 2020* (BKF)].

PENUNSULAR MALAYSIA • Kedah [*Kochummen 8969* (K)], Kelantan [*Corner SFN10202* (K), *33416* (K)], Malacca [*Griffith* (Herb. Griffith No.) *3620* (K), *Griffith s.n.* (K001346333), *Wight s.n.* (K001345340)], Penang [*Curtis 1453* (K, SING), *1454* (K, SING), *3591* (K, SING)].

SUMATRA • Locality not specified [*Forbes 2330* (P), *Yates 1588* (K)].

JAVA • East Java [*Backer 18218* (K), *Koorders 28903/b* (L)], Semarang [*Kooders 26239/b* (K)], West Java [*Bakhuizen van den Brink 6718* (L)], locality not specified [*Horsfield 1182* (K), *Koorders 1672* (K)].

VIETNAM • Ha Noi [*Fleury 37752* (P)], Nghe An [*Chevalier 30192* (P)], Tonkin Meriodinal [*Bon 416* (P)].

Ecology

Diospyros hasseltii is found in evergreen or dry evergreen forest, usually found near streams, at 0–800 m elevations.

Notes

Although the type of *D. hasseltii* has not been seen by the authors, the species is easy to recognise and has consistent morphological characters. Moreover, the original description of *D. hasseltii* clearly depicted the noticeable characters of this species (4-ridged corolla tube covered by black hairs and 8-locular fruits).

Diospyros fecunda H.R.Fletcher is not a synonym of D. borneensis Hiern

In Thailand, *D. fecunda* has long been recognised as a synonym of *D. borneensis* (Phengklai 1978, 1981; Gardner *et al.* 2015). We found that these two species share a truncate fruiting calyx that splits unevenly, but other characters are clearly different, especially the presence of the intramarginal vein in *D. borneensis* which does not occur in *D. fecunda* (Fig. 8, Table 3).

Here, we resurrect *D. fecunda* as a species distributed in Peninsular Thailand. We also exclude *D. borneensis* from the Thai flora as this Bornean species only reaches Peninsular Malaysia (Johor). We provide morphological comparison between these two species (Table 3) and updated taxonomic information concerning *D. fecunda* including lectotypification. A thorough description of *D. borneensis* can be found in Ng (2002).

Table 3. Morphological comparison between *Diospyros borneensis* Hiern and *D. fecunda* H.R.Fletcher.

Characters	***D. borneensis***	***D. fecunda***
Leaf shape and size	Oblong, up to 20 cm long	Elliptic, up to 15 cm long
Lateral vein number	10–14 on each side	6–9 on each side
Intramarginal line	Present, continuous from leaf base to apex (Fig. 8)	Not present
Lateral vein colour (when dried)	Conspicuously darker colour than leaf blade	Not obviously darker than leaf blade
Tertiary veins	Coarsely scalariform	Reticulate or somewhat irregularly scalariform
Fruit shape and size	Globose, 3.5–4 × 3.5–4 cm	Broadly ovoid, 3–4 × 3–4 cm
Fruit lobes (when mature and dried)	Usually deeply splitting throughout the fruit	Usually shallowly splitting, sometimes deeply splitting near the base
Fruit indument	Conspicuously hairy with rusty hairs	Subglabrous, usually hairy near the base, hairs yellowish
Fruiting calyx	Irregularly splitting into 3–5 lobes, 1.5–2 cm in diam.	Irregularly splitting into 3–7 lobes, 1–1.5 cm in diam.
Fruit stalk length	1–2 cm long	Subsessile, up to ca 0.5 cm long
Number of seeds	8	(8–)12–16

Diospyros fecunda H.R.Fletcher
Figs 7G–H, 9

Bulletin of Miscellaneous Information (*Royal Gardens, Kew*) 1937 (7): 387 (Fletcher 1937). – **Type**: THAILAND • Siam, Pattani, Yala, Betong; 26 Aug. 1923; *Kerr 7658*; lectotype: K[K000792545]!, **here designated**; isolectotypes: BM[BM00084634]!, E[E00318461]!, K[K000792546, K000792547, K000792548, Carpological Collection]!). – **Notes**: Fletcher (1937) cited *Kerr 7658* as the only gathering accompanying the original description of *D. fecunda.* Specimens have been located at BM, E and K, and all are well preserved. Four sheets in K were annotated as 'type' while the other sheets in BM, E and K were either unannotated or annotated as 'co-type' in H.R. Fletcher's handwriting. Among those sheets in K, we select the most complete specimen (K000792545) with fruit attaching on a twig as the lectotype.

Fletcher (1938: 369).

Diospyros borneensis [non Hiern], sensu auctorum: Phengklai (1978: 72; 1981: 359); Gardner *et al.* (2015: 489, 688).

Description

Tree, 7–20 m tall. *Twigs* glabrous. *Bark* brown, shallowly fissured, inner bark brown, sapwood whitish yellow. *Leaves* elliptic, 8–15 × 3.5–6 cm, base attenuate, slightly decurrent, apex acuminate or subcaudate with obtuse tip, blade glabrous on both sides; lateral veins 6–9 on each side, arched near the margin but not directly anastomosing, tertiary veins reticulate or irregularly scalariform; petiole slender, 0.5–1 cm long, glabrous. *Male inflorescences* ramiflorous in short fascicle. *Calyx* green, tubular-campanulate; lobes 4, shortly divided, semicircular. *Corolla* creamy white, salverform; lobes 4, divided ± halfway to

the base, oblong, curved outward. *Female flowers* not seen. *Fruits* solitary, green, turning black when dried, broadly ovoid, 3–4 × 3–4 cm, usually slightly wider than long, subglabrous, usually hairy near the base with yellowish hairs, pericarp smooth, shallowly lobed or longitudinally splitting near the base when dried; fruit stalk very short (subsessile) to ca 0.5 cm long, stout. *Fruiting calyx* slightly accrescent, 1–1.5 cm in diam.; lobes 3–7, irregularly divided when mature, spreading or reflexed, glabrescent outside, rather densely hairy inside. *Seeds* (8–)12–16, flat, asymmetrically elliptic, 1.5–2.5 × 0.7–1 cm; endosperm smooth.

Distribution

THAILAND • Phatthalung [*Sinbumrong 355* (BKF)], Songkhla [*Niyomdham 3065* (BKF)], Yala [*Kerr 7658* (BM, E, K); *Middleton 2950* (BKF)]. Specimens of this species have been rarely collected. It is found in the very southernmost tip of Thailand and may also occur in Peninsular Malaysia.

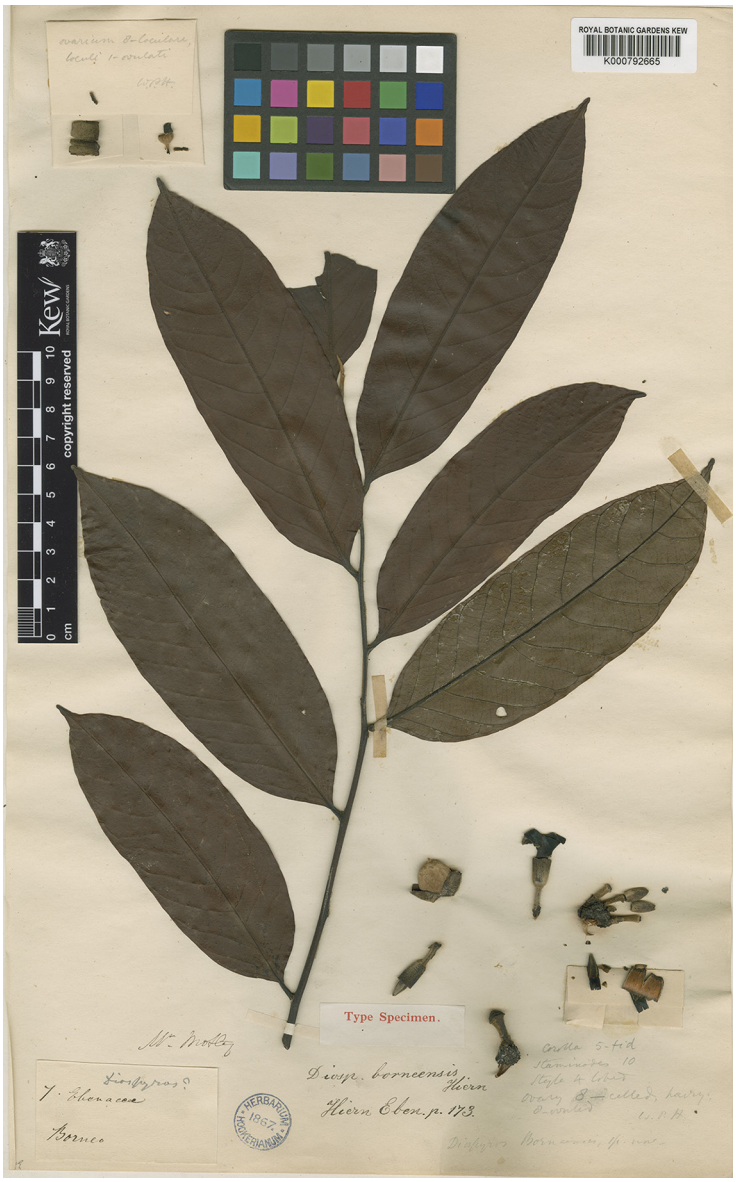

Fig. 8. Holotype of *D. borneensis* Hiern (*Motley 7* K[K000792665]) (Royal Botanic Gardens, Kew 2022). The red arrow points at lateral veins forming the intramarginal line.

Ecology

Diospyros fecunda is endemic to Thailand and found in evergreen forest at 400–650 m elevations.

Discussion

The early collections of plant specimens from Asia were usually deposited in European herbaria, mainly due to the European colonial expansion (Bridson & Forman 2013). Although Thailand was not colonised, it formed a strong botanical connection with European herbaria in the early 20th century (Jacobs 1962). In these herbaria, multiple authors began compiling the first treatments of the Ebenaceae in South-East Asia. There were obvious limitations to these accounts, including the reduced access to the type material of the extant species, the overall small number of specimens available for study from the country under investigation, and crucially, the even lower number of specimens from the neighbouring countries. Yet, the majority of the known species of *Diospyros* were described for the first time in these monographs and typified accordingly on specimens held in Europe. Type and historical specimens of old

Fig. 9. Lectotype of *D. fecunda* H.R.Fletcher (*Kerr 7658* K[K000792545]) (Royal Botanic Gardens, Kew 2022).

names, therefore, are not readily available in the regional herbaria where botanists identify specimens and conduct biodiversity research.

As a result, some specimens are inevitably misidentified, and modified species concepts may become locally established and perpetrated in the literature. Sometimes, it is the lack of a designated lectotype from among mixed gatherings that causes misidentification (Forsberg 1992), such as in *D. bejaudii* and *D. tamiriensis*. Alternatively, a broad morphological species concept may be applied to some taxa, as observed in *D. apiculata* and *D. borneensis*, which include in synonymy an array of different species, only superficially similar.

As historical type specimens, general collections and botanical literature have become widely available online (Heberling *et al.* 2019), our aim to update the taxonomy of *Diospyros* with a more comprehensive study of the species has resulted in multiple taxonomic changes and provided a framework for future taxonomic revisions.

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