The Miliuseae revisited : phylogenetic, taxonomic, and palynological studies in a major clade of Annonaceae

Chaowasku, T.

Chapter 6

A taxonomic revision and pollen morphology of the genus *Dendrokingstonia* (Annonaceae)

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Abstract

The genus *Dendrokingstonia* (Annonaceae) is taxonomically revised and palynologically studied. Three species are recognized, one of which, *D. gardneri*, is described as new to science. One new combination, *D. acuminata*, is made. The genus occurs from southern Thailand to Peninsular Malaysia and Sumatra. On the basis of macromorphology and pollen characters, it is considered to be related to *Monocarpia*. Both genera show a combination of macromorphological characters that is rare in the family, i.e. considerably enlarged stigmas, leaves with percurrent tertiary veins, a highly reduced number of carpels per flower and relatively large monocarps with a thick, hard wall. Scanning and transmission electron microscopy show that the pollen grains of *Dendrokingstonia* and *Monocarpia* are monosulcate monads with a columellate infratectum and a more or less bulging intine at the sulcus.

Key words: new combination, new species, palynology, systematics, taxonomy

Introduction

Dendrokingstonia is one of the most poorly known genera of Asian Annonaceae. It was described by Hooker & Thomson (1872) as *Kingstonia* Hook.f. & Thomson. Rauschert (1982) found that this name was pre-occupied by *Kingstonia* Gray (Saxifragaceae) and proposed the replacement name *Dendrokingstonia* Rauschert. So far, only a single species, *D. nervosa* (Hook.f. & Thomson) Rauschert, has been recognized. The genus was primarily characterized by the presence of only a single carpel per flower. In contrast, most Annonaceae have a flower with two or more carpels. Recent collections from Thailand with a fruit containing one or sometimes two monocarp(s) (Fig. 1B) appeared to be an undescribed species of *Dendrokingstonia*. Further, material from Sumatra described as *Bergsmia acuminata* Miq. (Flacourtiaceae/Achariaceae) turned out to represent a third *Dendrokingstonia* species. These two species are coherent with the type species in sharing all important diagnostic characters for the genus, i.e. leaves with percurrent tertiary venation, axillary flowers/inflorescences, considerably enlarged stigmas, highly reduced carpel numbers to one or two per flower, huge, thick-walled monocarps and four-part-lamellate ruminations of the endosperm.

In order to investigate the systematic affinity of *Dendrokingstonia*, several pollen morphological characters were included in the present revision. The pollen of one species of *Dendrokingstonia* had been studied earlier by Walker (1971a) using light microscopy (LM). In the present study, the pollen of all three species is investigated using scanning (SEM) and transmission (TEM) electron microscopy.

Material and methods

The indumentum terminology used follows Hewson (1988). Pollen samples were taken from dried herbarium specimens. Following Chaowasku *et al*. (2008) and Couvreur *et al*. (2009), the pollen of *Dendrokingstonia* was not acetolysed for SEM; however, material used for comparison (*Monocarpia euneura* Miq.) concerns an acetolysed sample. For

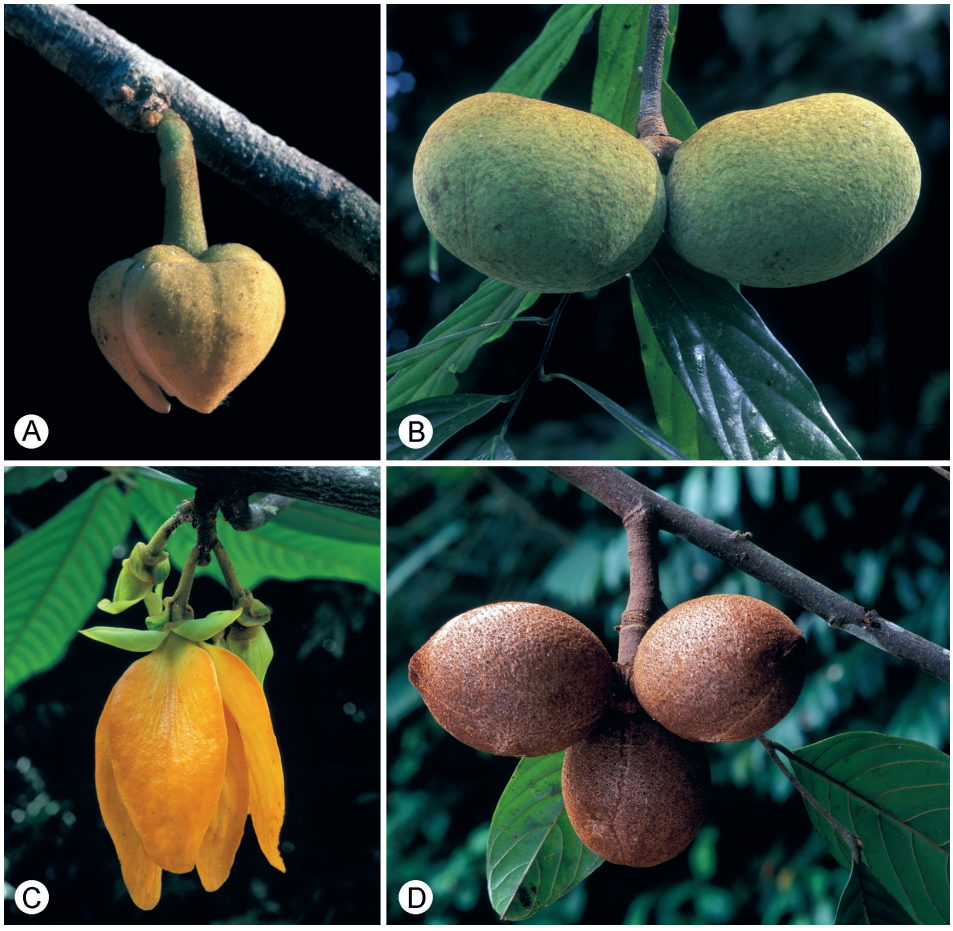

FIGURE 1. Flowers and fruits of *Dendrokingstonia* and *Monocarpia*. A, B, *Dendrokingstonia gardneri*: A, flower; B, fruit with two monocarps. C, D, *Monocarpia marginalis* (Scheff.) J.Sinclair: C, flowers; D, fruit with three monocarps. [All photographs: Simon Gardner.]

TEM, all material was prepared according to the techniques described by Van der Ham (1990). The subdivision of the exine into tectum, infratectum and basal layer, as described by Le Thomas (1980), is used. The terminology of pollen features follows Punt *et al*. (2007).

Voucher specimens for pollen morphological study:

D. acuminata: *Boschproefstation b.b. 2734* (L; SEM and TEM);
D. gardneri: *FRI 32134 (Wong Khoon Meng)* (L; TEM), *Kerr 19102* (K; SEM);
D. nervosa: *Rogstad 961* (L; SEM and TEM);
M. euneura: *Leighton 160* (L; SEM), *Sidiyasa 737* (L; TEM).

Specimens used in morphological study:

D. acuminata: *Boschproefstation b.b. 2734* (L); *b.b. 3068* (L); *Forbes 2654* (L); *Lörzing 5523* (L); *12332* (L); *16531* (L); *Teysmann HB 4559* (L, U).
D. gardneri: *FRI 6820 (Y.C. Chan)* (L); *32134 (Wong Khoon Meng)* (L); *Gardner & Sidisunthorn ST 2214* (L); *ST 2214a* (L); *ST 2575* (L); *ST 2575a* (L); *Kerr 19102* (K).
D. nervosa: *FRI 0608 (T.C. Whitmore)* (L); *2446 (K.M. Kochummen)* (L); *16131 (K.M. Kochummen)* (L); *17154 (Low Hoy Shing)* (L); *26628 (K.M. Kochummen)* (L); *Goodenough 1329* (K); *Rogstad 961* (L); *Singapore Field 40149 (J. Sinclair)* (L); *Wray 3376* (K).

Taxonomic treatment

Dendrokingstonia Rauschert, Taxon 31: 555 (1982). = *Kingstonia* Hook.f. & Thomson, Fl. Brit. India [J.D. Hooker] 1: 93 (1872), *nom. illeg*.
Type species:–*Dendrokingstonia nervosa* (Hook.f. & Thomson) Rauschert.

(Small- or) medium-sized trees, (6–)11–24 m tall. Young twigs glabrous or hairy. Leaves petiolate, (narrowly) elliptic or oblong, base wedge-shaped, obtuse, rounded or subcordate, apex obtuse, (sub)acute or caudate-acuminate, midrib sunken on upper surface, raised on lower surface, secondary veins prominent on lower surface, tertiary veins somewhat percurrent. Flowers bisexual, solitary or in fascicles, axillary (usually in axils of the fallen leaves), peduncles absent or inconspicuous, pedicels 3–8 mm long, distinctly thickened in fruit, bracts (and bracteoles) observed. Sepals (broadly) ovate (-triangular), free or connate, slightly overlapping at the base when free, persistent in fruit. Outer petals heart-shaped or (narrowly) ovate(-oblong). Inner petals ovate(-oblong) or narrowly oblong. Stamens 9–11, 14 or 50–56 per flower, connective tissue flat-topped. Carpels 1 or 2 per flower, stigmas (irregularly) peltate, ovaries flattened-ovoid or (ellipsoid-)cylindrical, ovules 3–10 per ovary, lateral, uni- or biseriate. Torus flat or elevated, enlarged in fruit (= carpophores) when elevated. Monocarps 1 or 2 per fruit, sessile on unenlarged torus or on carpophores, subglobose or (irregularly) cylindrical, surface often wrinkled when dry, sometimes (coarsely) constricted (when dry), indumentum dense and short, monocarp wall rather thick, hard when dry. Seeds 2 to 9 per monocarp, in one or two rows, (flattened-)ellipsoid or (flattened-)D-shaped, raphe nearly flat or ridged,

endosperm ruminations lamelliform, divided into four equal parts (cross-section).

Distribution:–Southern Thailand, Peninsular Malaysia to Sumatra (Indonesia) (Fig. 5).

Key to the species

1. Petioles 3–4 mm long, leaf base wedge-shaped, flowers solitary, sepals connate, torus elevated, enlarged in fruit (= carpophores), carpels 2 per flower, stamens 50–56 per flower ..... **2. *D. gardneri*, *sp. nov*.**
- Petioles 4–11 mm long, leaf base usually obtuse or rounded, flowers in fascicles, sepals free, slightly overlapping at the base, torus flat, not enlarged in fruit, carpels 1 (occasionally 2 in *D. acuminata*) per flower, stamens 9–11 or 14 per flower..... 2
2. Upper surface of the petioles grooved, flower buds globose, bracteoles generally placed at the midpoint of the pedicels, each fascicle usually with ≥ 15 flowers, pedicels 3–5(–6) mm long, outer petals and inner petals ovate(-oblong), outer petals 3.5–4 mm long, inner petals 2.9–3.5 mm long.....**1. *D. acuminata*, *comb. nov*.**
- Upper surface of the petioles not (or hardly) grooved, flower buds ellipsoid, bracteoles immediately placed below the sepals, each fascicle usually with < 15 flowers, pedicels (5.5–)6–8 mm long, outer petals narrowly ovate, ca. 8 mm long, inner petals narrowly oblong, ca. 7.1 mm long .....3*. D. nervosa*

1. *Dendrokingstonia acuminata* (Miq.) Chaowasku, *comb. nov*. (Figs. 2, 5)
= *Bergsmia acuminata* Miq., Fl. Ned. Ind., Eerste Bijv. 389 (Miquel, 1861).
Type:–Indonesia, Sumatra, Lampong, in fruit, *Teysmann HB 4559* (holotype L0189162!; isotype U!).

Trees 18–20 m tall. Young twigs glabrous to sparsely puberulous. Bud scales observed only at the base of new sprouting shoots, several, ovate to hemispherical, sometimes cup-shaped, basal ones smaller and smaller, respectively. Petioles 5–9 mm long, glabrous to sparsely (appressed-)puberulous, grooved above. Leaves elliptic, 6.5–16 × 2.8–5.7 cm, base usually obtuse, sometimes wedge-shaped or rounded, apex subacute to caudate-acuminate, lamina glabrous above, (almost) glabrous below, upper surface of midrib sunken, (almost) glabrous, raised on lower surface, glabrous to sparsely appressed-pilose, secondary veins 8–13 pairs per leaf, sometimes slightly impressed above, prominent below, angle with midrib 23°–45°. Flowers in fascicles, each fascicle usually with ≥ 15 flowers, axillary (mostly in axils of the fallen leaves), peduncles inconspicuous, pedicels 3–5(–6) mm long, (appressed-)tomentose, 6–9 × 3–4 mm in fruit, bracts several (to many), hemispherical-ovate, bracteoles usually 1 per flower, same shape as the bracts, usually placed at the midpoint of the pedicels. Sepals slightly ovate, slightly overlapping at the base, 1.7–1.9 × 1.6–2.1 mm, outside (appressed-)puberulous, denser near the base, margin puberulous, inside glabrous, persistent in fruit. Outer petals ovate(-oblong), 3.5–4 × 2.3–2.7 mm, outside (densely) (appressed-)tomentose, margin tomentose-cobwebbed, inside appressed-puberulous to tomentose, (much) sparser near the base. Inner petals same shape as the outer ones, 2.9–3.5 × 1.5–2.2 mm, indumentum on outside and margin same as the outer ones, inside (appressed-)villous, (much) sparser near the base. Stamens 9–11 per flower, 0.9–1 mm long. Carpels 1 (occasionally 2) per flower, 1.3–1.4 mm long, stigmas (irregularly) peltate with crenate margin, ca. 1 mm in diameter,

FIGURE 2. *Dendrokingstonia acuminata*: a, habit with flowers; b, upper leaf surface, showing grooved petiole; c, mature flower, side view; d, stamens surrounding single carpel; e, flower with petals, stamens and carpel detached, top view, showing flat torus and sepals slightly overlapping at the base; f, inside of outer petal; g, inside of inner petal; h, stamen, abaxial view; i, stamen, adaxial view; j, carpel; k, monocarp. [a–j, *Lörzing 12332*; k, *Boschproefstation b.b. 3068*.]

ovaries more or less ellipsoid-cylindrical, (appressed-)villous, slightly flattened on one side, ovules 3–6 per ovary, lateral, uni- or biseriate. Torus flat, not enlarged in fruit. Monocarps 1 per fruit, sessile on unenlarged torus, subglobose to slightly cylindrical, sometimes somewhat constricted at the middle of the monocarps (when dry), 3.8–5 × 2.8–3.3 cm, surface (a bit) wrinkled when dry, indumentum densely (appressed-)tomentose, monocarp wall ca. 2 mm thick. Seeds 2–6 per monocarp, in one or two rows, more or less ellipsoid to D-shaped, 2.6–2.7 × 1.4–1.5 cm, raphe ridged.

Distribution:–Endemic to Sumatra (Indonesia) (Fig. 5).

Habitat, ecology and phenology:–Occurring in primary forests on slopes. Elevation: 50–500 m. Flowering specimens: collected in November and February. Fruiting specimens: collected in May.

Field notes:–Branches many. Wood hard. Leaves faintly bluish, somewhat glossy, rather stiff (red–brown when young). Flowers fragrant, petals yellow. Fruits pale green with short brown hairs.

Vernacular names:–Bakbahan, Benitan teloer.

Notes:–Van Setten & Koek-Noorman (1992) studied and illustrated the fruit and seed morphology of *Lörzing 16531* under *Dendrokingstonia nervosa*.

According to Webber & Woodrow (2006), the genus *Bergsmia* Blume is now included in *Ryparosa* Blume (Achariaceae).

Based on macromorphology, *D. acuminata* is close to *D. nervosa*. It differs mainly in having (many) more flowers per fascicle, globose floral buds (ellipsoid in *D. nervosa*), usually (slightly) shorter pedicels and shorter petals (both whorls). Vegetatively, these two species are much alike, except for the petioles, which are grooved on the upper surface in *D. acuminata* (Fig. 2b), and are (hardly or) not grooved in *D. nervosa*.

2. *Dendrokingstonia gardneri* Chaowasku, *sp. nov*. (Figs. 1A, B, 3, 5)

Type:–Thailand, Trang, Khao Banthat Wildlife Sanctuary, Ton Plew Waterfall, x.2006, in fruit, *Gardner & Sidisunthorn ST 2575a* (holotype L0298137!; isotypes BKF, K).

Dendrokingstoniae nervosae et D. acuminatae aliquantum diversa, floribus solitariis (vs. fasciculatis), toro elevato (vs. plano), sepalis connatis (vs. liberis), staminum multum plurimorum differt. Praeterea in D. gardneri petioli plerumque breviores, folii basis semper cuneata, versus obtusa ad rotundata in alioribus.

Trees (6–)11–15(–20) m tall, (8–)17 cm in diameter, ca. 45 cm in girth. Young twigs sparsely appressed-puberulous. Petioles 3–4 mm long, almost glabrous to sparsely (appressed-) puberulous, slightly grooved above. Leaves (narrowly) elliptic to slightly oblong, 7.3–18.2 × 2.2–6 cm, base wedge-shaped, apex obtuse, subacute to caudate-acuminate, lamina glabrous above, (almost) glabrous below, domatia sometimes observed at axils of the secondary veins, each with a small hole or slightly sunken area, usually with few hairs, upper surface of midrib (slightly) sunken, glabrous, raised on lower surface, glabrous to very sparsely appressed-puberulous, secondary veins 6–11 pairs per leaf, prominent below, angle with midrib 26°–37°. Flowers solitary, axillary (in axils of the fallen leaves), peduncles absent, pedicels 4–5.2 mm long, (sparsely) (appressed-)tomentose, 7–8(–10) × 4–6 mm in fruit, bracts 2 or 3 per flower, hemispherical, ovate to triangular, one or two near the base, another a bit higher, slightly larger. Sepals broadly ovate(-triangular),

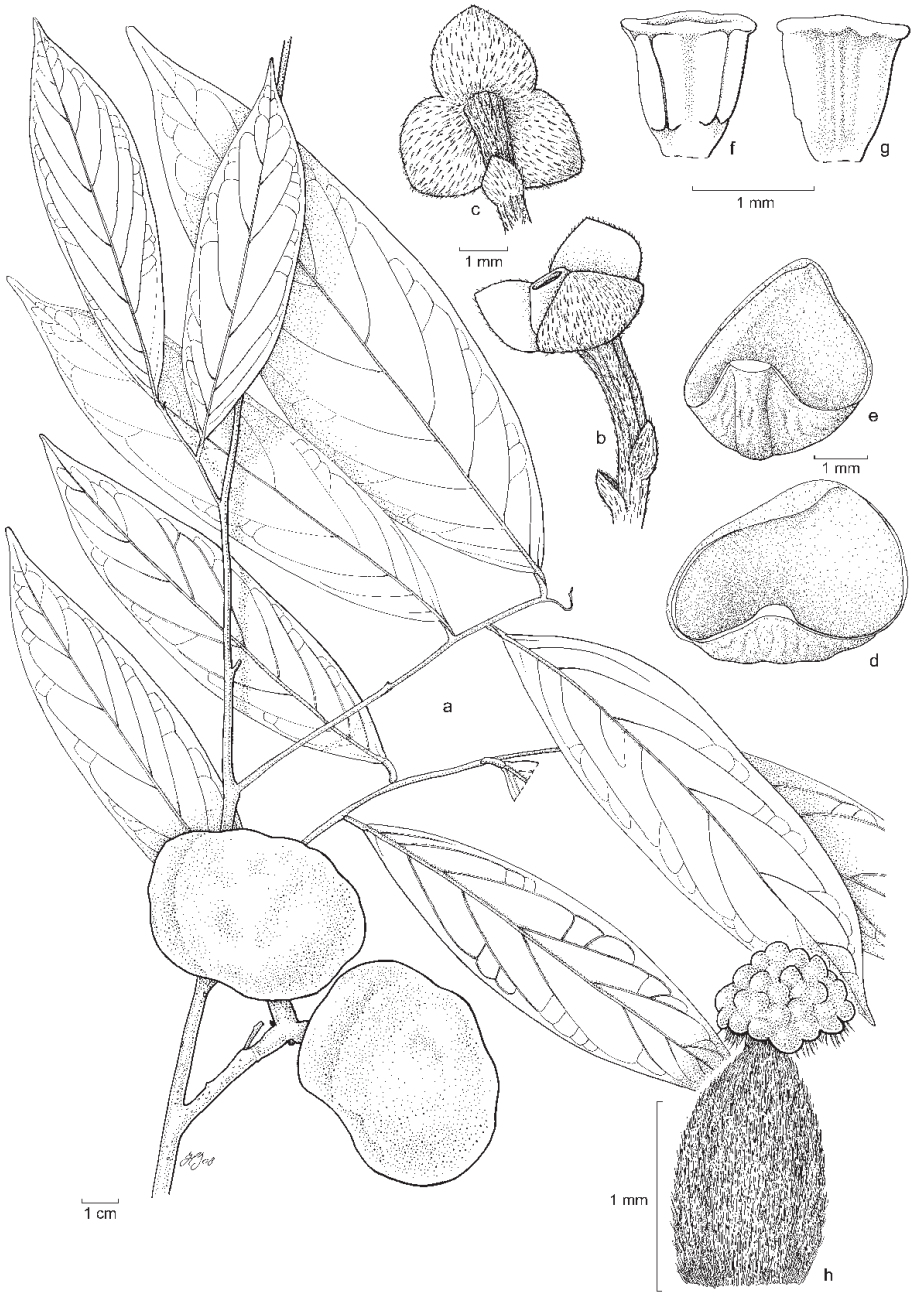

FIGURE 3. *Dendrokingstonia gardneri*: a, habit with fruit; b, flower with petals, stamens and carpels detached, side view, showing elevated torus; c, same as (b), but in bottom view, showing connate sepals; d, inside of outer petal; e, inside of inner petal, showing slightly saccate base; f, stamen, abaxial view; g, stamen, adaxial view; h, carpel. [a, *Gardner & Sidisunthorn ST 2214a*; b, c, h, *FRI 32134* (*Wong Khoon Meng*); d–g, *Kerr 19102*.]

connate (generally from the midpoint of their length through the base), 1.7–2 × 2.1–3 mm, outside and margin puberulous, inside glabrous, usually persistent in fruit. Outer petals ovate to slightly heart-shaped, 5.1–6.2 × 4.1–5.5 mm, outside and margin densely tomentose-cobwebbed, inside generally sparser, especially towards the base, base sometimes slightly saccate. Inner petals ovate, 5–6.1 × 3.1–3.5 mm, indumentum same as the outer ones, base slightly saccate. Stamens 50–56 per flower, 1–1.3 mm long. Carpels 2 per flower, 1.8–2.1 mm long, stigmas irregularly peltate, 0.8–1.2 mm in diameter, very sparsely puberulous at the base, ovaries flattened-ovoid, grooved on one side, densely (appressed-)tomentose, ovules 8–10 per ovary, lateral, biseriate. Torus elevated, truncated cone-shaped, 1.1–2 mm long, apex slightly sunken, base tomentose around the torus, which is enlarged in fruit (= carpophores). Monocarps 1 to 2 per fruit, sessile on carpophores, irregularly (slightly) cylindrical, 5.9–6.7 × 4.5–5 cm, surface often coarsely constricted (when dry), indumentum densely tomentose, monocarp wall 2–4 mm thick, carpophores woody, 3–6 × 7–10 mm for each monocarp. Seeds ca. 9 per monocarp, in two rows, flattened-ellipsoid to flattened-D-shaped, 3.2–3.6 × 2.3–2.4 cm, raphe nearly flat to slightly ridged.

Distribution:–Southern Thailand and northern Peninsular Malaysia (Fig. 5).

Habitat, ecology and phenology:–Occurring in undulating forests or in shady understorey of (primary) lowland (moist) evergreen forests; at base of limestone cliffs or on limestone tufa next to permanent waterfalls. Elevation: under 50 m to 130 m. Flowering specimens: collected in February and April. Fruiting specimens: collected in October, January and March.

Field notes:–Bole straight, monopodial. Bark smooth or rugged, dark brown, greyish-green, pale grey or midgrey, slash inner bark fibrous, yellow or brown, slash wood white or pale yellowish-white. Leaves glossy dark green above, paler green below, young leaves whitish. Flowers downturned, sepals yellow in open flowers, petals cream or dull brownish-yellow. Fruits pale brownish-yellow outside, pale yellow inside.

Etymology:–Named after the chief collector (Simon Gardner) who kindly sent the interesting specimens to L for identification.

Notes:–*Dendrokingstonia gardneri* is considerably different from the other two species in having solitary flowers (in fascicles in the other two species) with an elevated torus (Fig. 3b) that is enlarged in fruit (= carpophores, Fig. 3a) (flat and not enlarged in fruit in the others), connate sepals (Fig. 3c) (free in the others), thicker petals and many more stamens (50–56 vs. 9–11 or 14). The petioles are generally shorter and the leaf base is always wedge-shaped in *D. gardneri*, whereas it is usually obtuse or rounded in *D. nervosa* and *D. acuminata*.

The four-part-lamellate ruminations of the endosperm of *D. gardneri* are less pronounced than those of the other two species. They are more or less lamellate towards the raphe with some flattened pegs in the middle of the sides, as illustrated in figure 3 of Van Setten & Koek-Noorman (1992).

3. *Dendrokingstonia nervosa* (Hook.f. & Thomson) Rauschert (Figs. 4, 5). Taxon 31: 555 (1982).

= *Kingstonia nervosa* Hook.f. & Thomson[1], Fl. Brit. India [J.D. Hooker] 1: 93 (1872).
= *Bocagea nervosa* (Hook.f. & Thomson) Pierre, Fl. Forest. Cochinch. sub t. 16 (Pierre, 1881).

Type:–Peninsular Malaysia, Malacca, ix.1865–66, in flower, *Maingay 1054* (also under herbarium of the late A.C. Maingay, M.D. No. 22, distributed at the Royal Gardens Kew. 1871.) [lectotype K! (photograph), selected here].

Trees 12–24 m tall, 60–90 cm in girth. Young twigs sparsely puberulous to sparsely tomentose, isolated hairs occasionally stellate. Petioles 4–11 mm long, sparsely (appressed-)puberulous to sparsely tomentose, isolated hairs sometimes stellate, not (or hardly) grooved above. Leaves elliptic to slightly oblong, 8.5–22.4 × 3–8 cm, base obtuse to rounded, sometimes subcordate, apex acute to slightly caudate-acuminate, lamina glabrous both sides except the secondary veins on lower surface which is almost glabrous to appressed-pilose, upper surface of midrib sunken, less so near the petioles, sparsely pilose near the petioles, sparser to glabrous towards another end, raised on lower surface, (sparsely) appressed-pilose, sometimes also with shorter erect hairs, secondary veins 12–14 pairs per leaf, prominent below, angle with midrib 30°–43°. Flowers in fascicles, each fascicle usually with < 15 flowers, axillary (in axils of the fallen leaves), peduncles inconspicuous, pedicels (5.5–)6–8 mm long, (appressed-)tomentose, 1.1–1.4 × 0.4–0.6 cm in fruit, bracts several, hemispherical to ovate, bracteoles 1 or 2 per flower, same shape as the bracts, immediately placed below the sepals. Sepals slightly ovate, slightly overlapping at the base, ca. 2.8 × 2.4 mm, outside (appressed-)tomentose, margin tomentose, inside glabrous, persistent in fruit. Outer petals narrowly ovate, ca. 8 × 2.9 mm, outside and margin densely (appressed-)tomentose, inside shortly cobwebbed. Inner petals narrowly oblong, ca. 7.1 × 2.1 mm, indumentum a bit denser than the outer ones. Stamens 14 per flower, 1.1–1.3 mm long. Carpels 1 per flower, ca. 1.9 mm long, stigmas irregularly peltate, ca. 1 mm in diameter, ovaries more or less cylindrical, slightly grooved on one side, (appressed-)villous, ovules 6 or 7 per ovary, lateral, biseriate. Torus flat, not enlarged in fruit. Monocarps 1 per fruit, sessile on unenlarged torus, subglobose to slightly cylindrical, 4–5.1 × 3.3–3.9 cm, surface (a bit) wrinkled when dry, indumentum densely tomentose, monocarp wall 4–5 mm thick. Seeds 5 or 6 per monocarp, in two rows, more or less flattened-D-shaped, 2.6–3.1 × 1.2 cm, raphe almost flat to slightly ridged.

Distribution:–Peninsular Malaysia (Fig. 5).

Habitat, ecology and phenology:–Occurring in logged forests, disturbed forests or dense (primary) forests; on (steep) hillsides, on slight well-drained slopes with little humus accumulation or on flat lands; over granites or on sandy soils. Elevation: up to 300 m. Flowering specimens: collected in February. Fruiting specimens: collected in June and July.

Field notes:–Crown dense, rounded or bushy, sympodial or monopodial. Bark smooth or finely fissured and cracked, dark grey–green or black with grey patches, slash inner bark pale brown or orange brown, slash wood pale yellow or pale brown near white. New leaves pale pink. Mature petals yellow, with odor of ripe peaches, inner petals

[1] Incorrectly indicated as “nom. illeg.” in the original publication of this chapter.

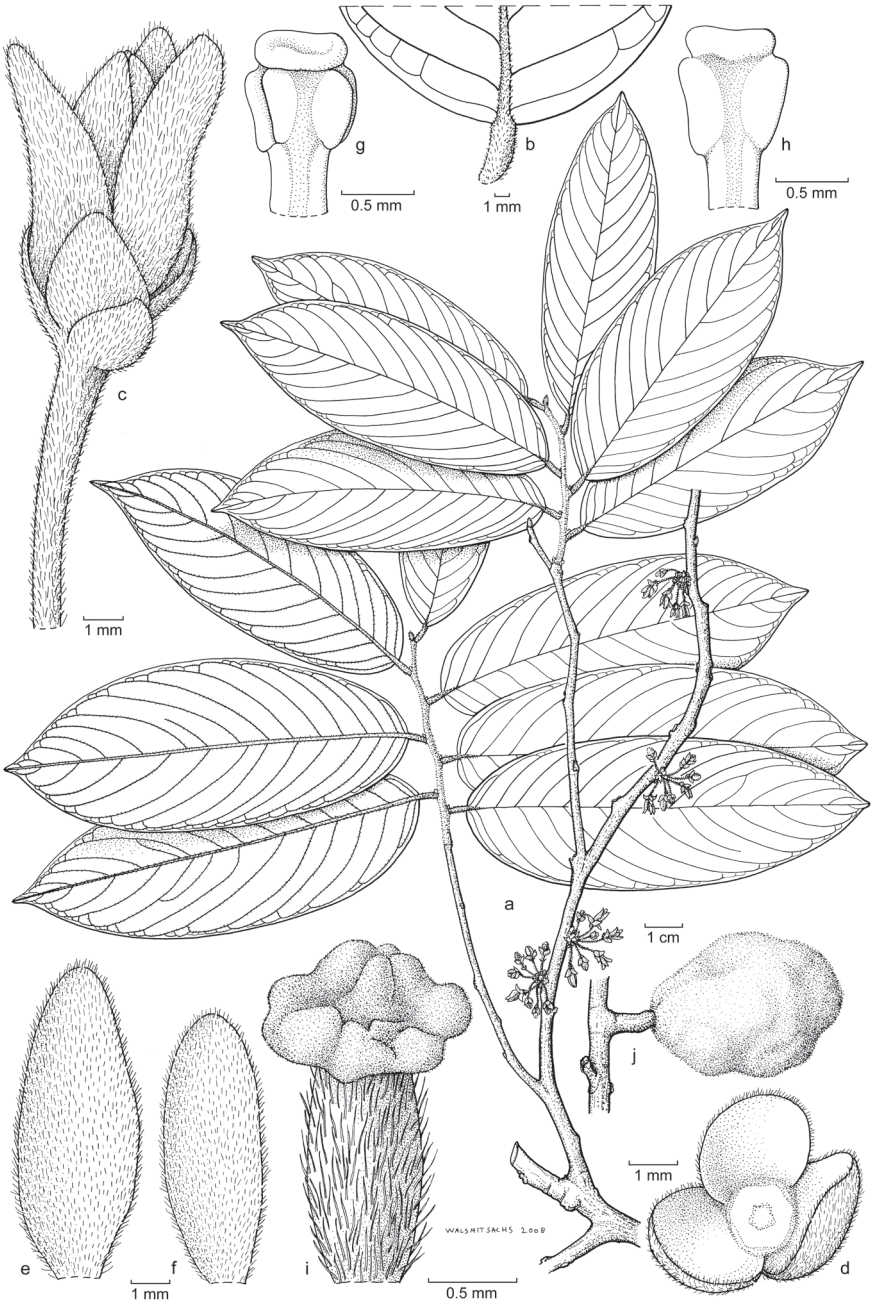

FIGURE 4. *Dendrokingstonia nervosa*: a, habit with flowers; b, lower leaf surface; c, slightly submature flower; d, flower with petals, stamens and carpel detached, top view, showing flat torus and sepals slightly overlapping at the base; e, inside of outer petal; f, inside of inner petal; g, stamen, abaxial view; h, stamen, adaxial view; i, carpel; j, monocarp. [a–i, *Rogstad 961*; j, *FRI 0608* (*T.C. Whitmore*).]

FIGURE 5. Distribution of *Dendrokingstonia*: *D. acuminata* (filled triangles); *D. gardneri* (filled squares); *D. nervosa* (filled circles).

overlapping in bud, stigmas turning black before pollen is released. Fruits (pale) brown, covered with fine hairs, shallowly ridged, mesocarp white, seeds pink, shiny.

Despite the noticeable differences between *D. acuminata* and *D. nervosa*, on the one hand, and *D. gardneri*, on the other, the three species are uniform in sharing a combination of several important characters (see Discussion and Conclusions).

Pollen description

Pollen grains (Figs. 7A–F, 8A–F) bilateral, monosulcate, medium-sized monads; long axis ca. 28–40 μm. Exine 0.8–1.6 μm thick, tectate; tectum 0.4–0.6 μm thick; infratectum columellate, up to ± as thick as the tectum; basal layer ± distinct, thinner than the tectum. Exine ornamentation psilate/perforate (*D. acuminata*, *D. gardneri*) or scabrate/verrucate/rugulate (*D. nervosa*). Intine moderately (*D. acuminata*, *D. nervosa*) or strongly (*D. gardneri*) bulging outwards from the sulcus, consisting of an exintinous and an endintinous sublayers.

Discussion

Systematic position of *Dendrokingstonia*

Dendrokingstonia exhibits a combination of several characteristics that is rather uncom-

mon in Annonaceae, i.e. leaves with percurrent tertiary veins, a highly reduced number of carpels per flower, considerably enlarged stigmas (Figs. 2j, 3h, 4i) and relatively large monocarps with a thick, hard wall (Fig. 1B).

Van Heusden (1992) found that the carpels of *Dendrokingstonia* resemble those of *Monocarpia* Miq. and *Piptostigma* Oliv., two 'short branch clade[2]' (SBC) genera outside the 'miliusoid clade[3]' (Richardson *et al*. 2004, Mols *et al*. 2004b; see Fig. 6). The SBC minus the miliusoid clade is referred to in the present article as the 'non-miliusoid grade' (NMG) (Fig. 6). On account of the carpel characters, *Dendrokingstonia* might be provisionally placed in the NMG, and is especially close to the small South-East Asian genus *Monocarpia* (Fig. 1C, D; Mols & Keßler 2000b), as both genera possess all four characters mentioned above. However, the position and appearance of the flowers/inflorescences of the two genera differ: terminal, conspicuous in *Monocarpia* (pers. ob. TC; Fig. 1C) vs. axillary, inconspicuous in *Dendrokingstonia* (Fig. 1A). Their endosperm ruminations are also different: spiniform in *Monocarpia* vs. lamellate in four parts in *Dendrokingstonia* (Van Setten & Koek-Noorman 1992).

The genus *Platymitra* Boerl., which belongs in the miliusoid clade of the SBC (Richardson *et al*. 2004, Mols *et al*. 2004b), also possesses a reduced number of carpels per flower and large, hard-walled monocarps. However, it lacks the percurrent tertiary veins of the leaves and the elaborated stigmas (Keßler 1988b).

It is important to note that most genera in the SBC, including the earlier mentioned genera (*Monocarpia*, *Piptostigma*, *Platymitra*) have spiniform ruminations of the endosperm (Van Setten & Koek-Noorman 1992). This type of endosperm ruminations is considered to be one of the synapomorphic characters of the SBC. The four-parted lamelliform ruminations of the endosperm appear to be a derived character. They only occur in certain genera in the NMG (Chatrou 1998) and the miliusoid clade (Mols *et al*. 2004a).

Several carpel characters of *Dendrokingstonia* also occur outside the SBC, in the more distant 'ambavioid clade' [the ambavioid clade is redefined here; it comprises *Ambavia* Le Thomas, *Cleistopholis* Pierre ex Engl., *Mezzettia* Becc. and *Tetrameranthus* R.E.Fr., as originally circumscribed by Doyle & Le Thomas (1996) and Le Thomas & Doyle (1996); the ambavioid clade in a redefined sense is sister to the canangoid clade (see Surveswaran *et al*. 2010); both clades differ in chromosome numbers (Okada & Ueda 1984, Morawetz & Le Thomas 1988), floral morphology (pers. obs. TC; see also Van Heusden 1992 for more details on each genus) and, probably, the branching architecture (Johnson 2003; pers. obs. TC)] and 'canangoid clade' (see Pirie *et al*. 2006: figure 2 for the phylogenetic position of both clades in Annonaceae). The reduction in carpel numbers to one per flower and the huge, stony-walled monocarps are found in *Mezzettia* Becc. and *Cyathocalyx* Champ. ex Hook.f. & Thomson *sensu stricto* (Van der Heijden & Keßler 1990, Surveswaran *et al*. 2010). *Cyathocalyx s.s.* also has greatly enlarged stigmas (Van Heusden 1992).

The occurrence of the characters mentioned above is summarized in Table 1.

Pollen morphology

Walker (1971a) described the pollen of *D. nervosa* (as *Kingstonia nervosa*), using LM, as

[2] Now recognized as subfamily Malmeoideae (see Chatrou *et al*. 2012).

[3] Equivalent to the recircumscribed Miliuseae of Chatrou *et al*. (2012).

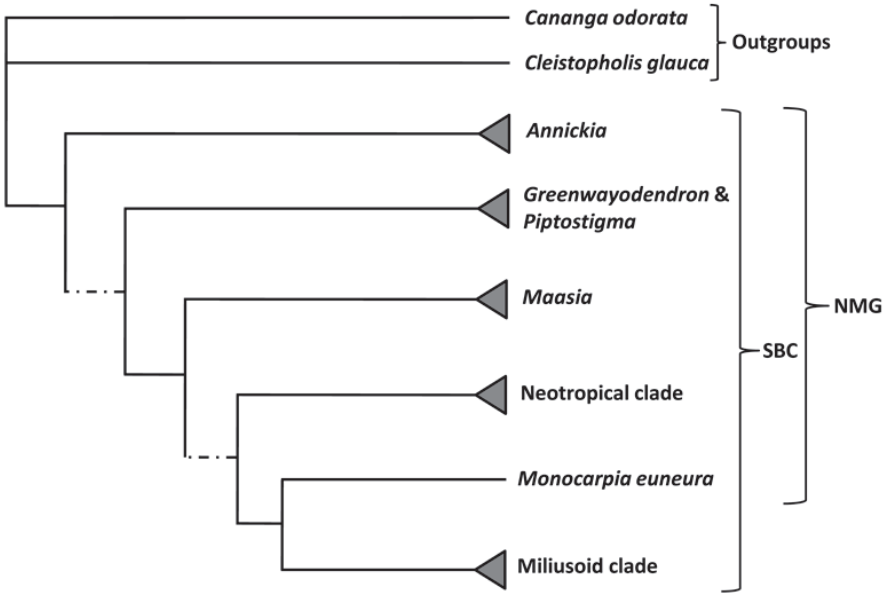

FIGURE 6. Simplified cladogram adapted from figure 4 of Pirie *et al*. (2006). Triangles signify at least two terminal taxa. Branches with Bayesian posterior probabilities lower than 0.95 are shown as broken lines. NMG, 'non-miliusoid grade'; SBC, 'short branch clade'.

TABLE 1. Phylogenetic placement and occurrence of important characters found in *Dendrokingstonia* and other (related) genera.

Character	Genus				
	Dendrokingstonia	*Monocarpia*	*Platymitra*	*Cyathocalyx s.s.*	*Mezzettia*
- Tertiary venation of leaves	Percurrent	Percurrent	Reticulate	Percurrent/ intermediate	Reticulate
- Flower/inflorescence position	Axillary	Terminal	Axillary	Terminal	Axillary
- Enlarged stigmas, ± peltate	+	+	-	+	-
- Reduced number of carpels to 1–4 per flower	+	+	+	+	+
- Relatively large monocarps with hard and thick wall	+	+	+	+	+
- Ruminations of endosperm	Four-part-lamellate	Spiniform	Spiniform	Intermediate	Irregular
- Major pollen types	Monosulcate	Monosulcate	Cryptoaperturate	Inaperturate	Inaperturate
- Phylogenetic position	SBC-NMG?	SBC-NMG	SBC-miliusoid	Canangoid	Ambavioid

+, present; -, absent; NMG, 'non-miliusoid grade'; SBC, 'short branch clade'

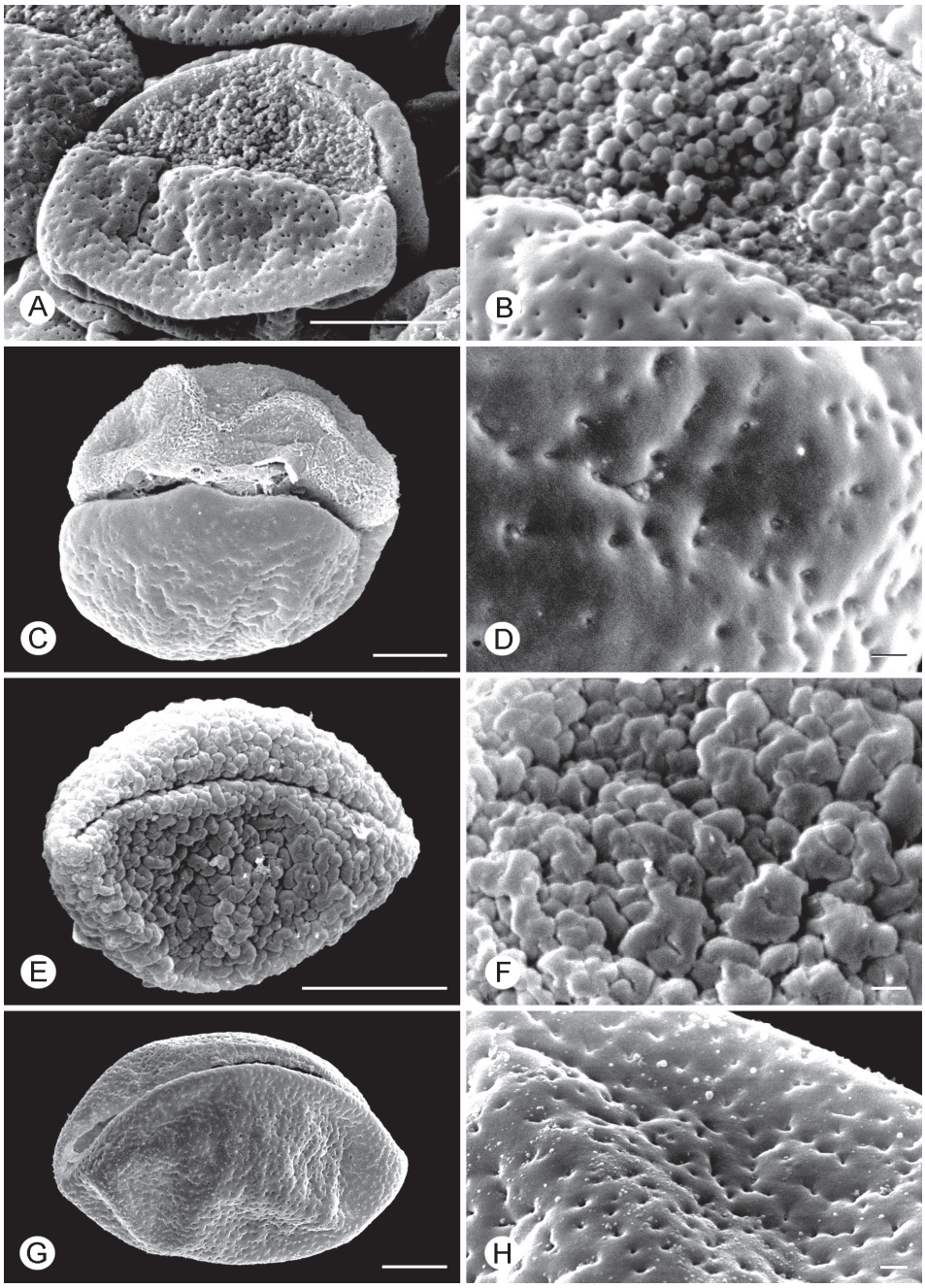

FIGURE 7. Pollen of *Dendrokingstonia* and *Monocarpia* (scanning electron microscopy). A, B, *D. acuminata*: A, pollen grain, collapsed, showing psilate/perforate exine (below) and granular sulcus membrane (above); B, detail of (A), showing exine ornamentation. C, D, *D. gardneri*: C, pollen grain, showing psilate/perforate exine (below) and bulging intine (above); D, detail of (C), showing exine ornamentation. E, F, *D. nervosa*: E, pollen

...continued on page 103

boat-shaped, monosulcate, medium-sized monads with a well-developed columellate infratectum. He did not describe the exine ornamentation, but his LM illustrations show an exine with verrucate to scabrate elements. We obtained the same results for *D. nervosa*. The exines of the pollen of *D. acuminata* and *D. gardneri* are much like that of *D. nervosa*, except for their ornamentation, which is psilate/perforate.

Within the SBC, the combination of a monosulcate aperture, a columellate infratectum and a more or less bulging intine is known only from several genera in the NMG: *Bocageopsis* R.E.Fr., *Malmea* R.E.Fr., *Unonopsis* R.E.Fr. (Waha 1985), *Maasia* Mols, Kessler & Rogstad [under '*Polyalthia*' *sumatrana* (Miq.) Kurz; Waha & Hesse 1988], *Monocarpia* (Figs. 7G–H, 8G–H) and *Mwasumbia* Couvreur & D.M.Johnson (Couvreur *et al*. 2009). The NMG is largely African-American; *Maasia* and *Monocarpia* are the only Asian genera. So far, the pollen of all genera studied in the NMG is monosulcate. It is expected that other genera in the NMG that have not been palynologically investigated also possess monosulcate pollen. The pollen morphology has shifted from monosulcate to cryptoaperturate/disulculate in the miliusoid clade (Mols *et al*. 2004a, Chaowasku *et al*. 2008).

Dendrokingstonia is unlikely to be part of the ambavioid, canangoid or miliusoid clades because all members of these clades do not exhibit the combination of pollen characters mentioned above (Le Thomas 1980, Hesse & Waha 1984, Mols *et al*. 2004a, Wang 2004, Chaowasku *et al*. 2008).

Conclusions

Macromorphological, pollen morphological and geographical evidence indicates that the systematic affinity of *Dendrokingstonia* is with the NMG, the basal part of the SBC. *Dendrokingstonia* might be closely related to *Monocarpia*, because both genera share several crucial characters (Table 1).

Dendrokingstonia consists of three species (*D. acuminata*, *D. gardneri* and *D. nervosa*) and is presently circumscribed by having the following characters:

1. Leaves with percurrent tertiary venation.
2. Axillary flowers/inflorescences.
3. Considerably enlarged stigmas.
4. Carpel numbers reduced to one or two per flower.
5. Massive monocarps with a thick, hard wall.
6. Four-lamellate ruminations of the endosperm.
7. Monosulcate pollen grains, with a columellate infratectum and a more or less bulging intine at the sulcus.

grain, collapsed, showing scabrate/verrucate exine with invaginated sulcus; F, detail of (E), showing ornamentation. G, H, *Monocarpia euneura*: G, pollen grain, collapsed, showing psilate/perforate exine with invaginated sulcus; H, detail of (G), showing ornamentation. Scale bars: 10 µm (A, C, E, G); 1 µm (B, D, F, H).

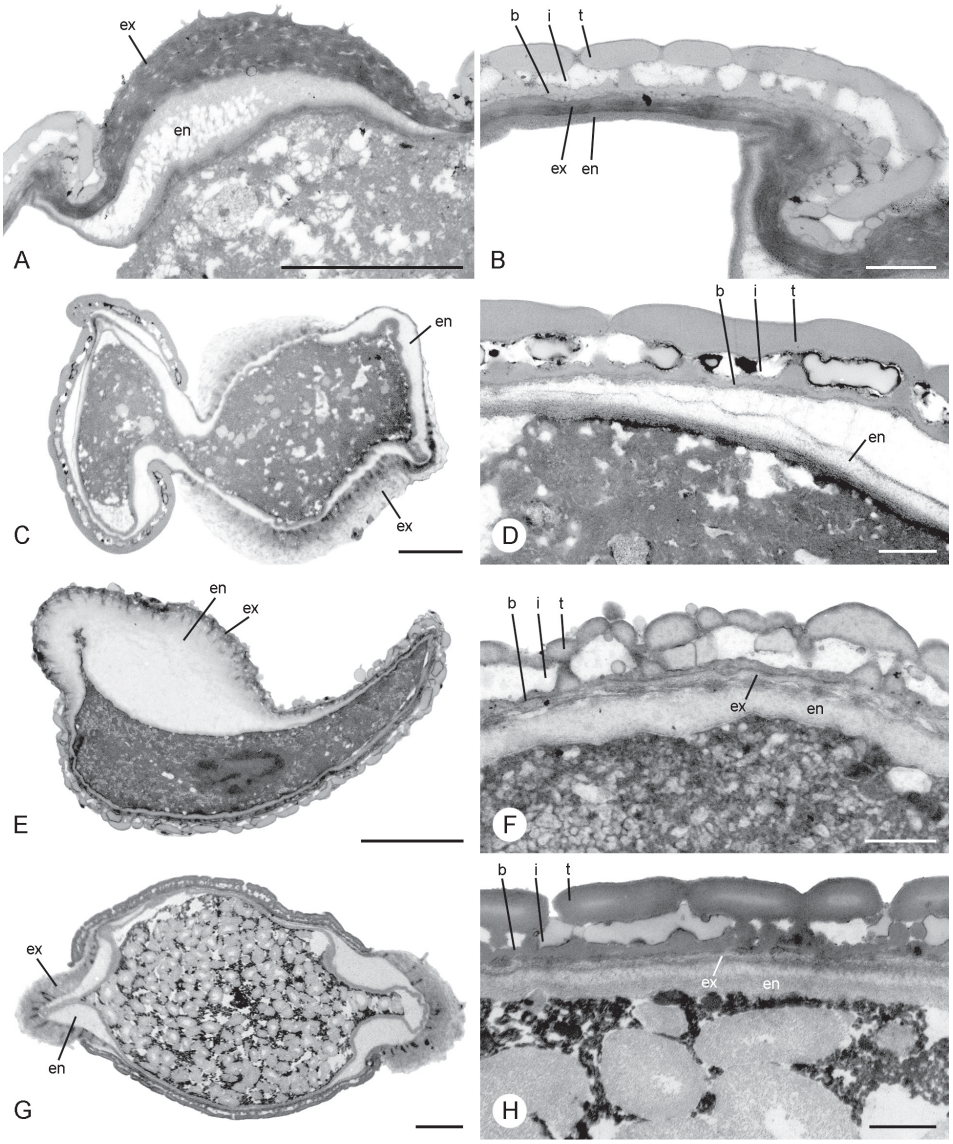

FIGURE 8. Pollen of *Dendrokingstonia* and *Monocarpia* (transmission electron microscopy). A, B, *D. acuminata*: A, cross-section of sulcus with intine moderately bulging outwards (exintine dark, endintine light); B, cross-section of exine near sulcus (right), showing tectum, columellate infratectum and basal layer. C, D, *D. gardneri*: C, cross-section of pollen grain, showing exine (left) and intine (right) strongly bulging outwards; D, cross-section of exine, showing tectum,columellate infratectum and basal layer. E, F, *D. nervosa*: E, cross-section of pollen grain, showing exine (below) and intine (above) moderately bulging outwards; F, cross-section of exine, showing tectum, columellate infratectum and basal layer. G, H, *Monocarpia euneura*: G, pollen grain, showing two cross-sections of the long sulcus with intine moderately bulging outwards; H, cross-section of exine, showing tectum, columellate infratectum and basal layer. Scale bars : 5 µm (A, C, E, G); 1 µm (B, D, F, H); b, basal layer; en, endintine; ex, exintine; i, infratectum; t, tectum.