Colophospermum reduced to Hardwickia (Leguminosae-Caesalpinioideae)

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ABSTRACT

KEY WORDS

Colophospermum, Hardwickia, India, Southern Africa, Mopane. The genus *Colophospermum*, described in 1949, known from its only species *C. mopane* from southern Africa, is congeneric with the monotypic *Hardwickia* described from India in 1811. The new combination *H. mopane* is made. The taxonomic study is accompanied by a palynological as well as a wood anatomical study.

RÉSUMÉ

MOTS CLÉS Colophospermum, Hardwickia, Inde, Afrique méridionale, Mopane. Le genre *Colophospermum*, décrit en 1949, connu par son unique espèce *C. mopane* d'Afrique tropicale méridionale, paraît congénérique de *Hardwickia*, genre monotypique décrit de l'Inde en 1811. La nouvelle combinaison *H. mopane* est proposée. L'étude taxonomique est accompagnée des résultats de recherches palynologiques et anatomiques du bois.

Hardwickia was described by ROXBURGH and illustrated in his Plants of the Coast of Coromandel in 1811, based on H. binata (Fig. 1). Two more species H. pinnata Roxb. ex DC. (1825) and H. alternifolia (Elm.) Elm. (ELMER 1907, 1908) were described later, but afterwards both proved to belong in the genus Kingiodendron Harms (KNAAP-VAN MEEUWEN 1970) ren-

dering the genus monotypic again. *Hardwickia* differs from *Kingiodendron* notably in having only two leaflets with flabellately arranged nerves and in lacking bracteoles on the flower stipe. Also, the wood of *Hardwickia* differs significantly from that of *Kingiodendron* in lacking axial gum ducts (KNAAP-VAN MEEUWEN 1970).

LÉONARD (1949) described Colophospermum to



. Hardanken lombe

Fig. 1.—Hardwickia binata: plate 209, reproduced from Roxburgh (1811).

accommodate the aberrant Copaifera? (Colophospermum) mopane Kirk ex Benth. BENTHAM (1865a), on account of having fruiting material only, did not want to describe it as a genus distinct from Copaifera, although KIRK, the collector of the type, suggested this, and proposed Colophospermum as its name. Léonard's original publication of Colophospermum does not show

that any comparison was made with extra African genera, although *Copaifera* as well as *Hardwickia* were currently classified (BENTHAM 1865b; TAUBERT 1894) in the same tribe namely Cynometreae, which are now named Detarieae. Most characters which are mentioned by LEONARD to distinguish *Colophospermum* from *Copaifera* are in fact characters that characterize

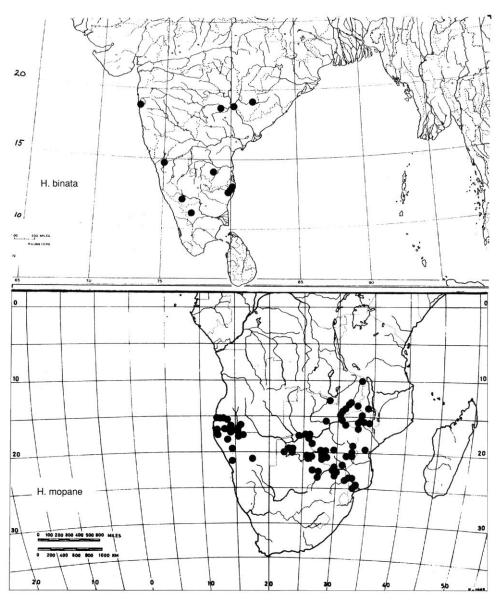


Fig. 2.—Distribution of *Hardwickia binata* (above) and of *H. mopane* (below).

Hardwickia, such as the foliaceous "prolongation" of the leaf rachis, the absence of bracteoles, the single ovule, and the corrugated cotyledons. More characters that are common to both genera can be added, such as those found in the pollen structure (Graham & Barker 1981; this paper) and in the basic chromosome number (GOLDBLATT 1981). The characters shared by Colophospermum and Hardwickia are listed below. Added, are the characters in which both taxa differ.

Characters common to Colophospermum and Hardwickia

Leaves 2-foliolate with a much reduced, deciduous, united, secondary pair of leaflets in between.

Leaflets with translucent dots.

Flowers without bracteoles.

Flowers actinomorphic, apetalous.

Filaments long, thread-like, anthers large, versatile.

Stigma large, ± peltate.

Ovary with 1 ovule only.

Seeds narrowly winged, furrowed.

Cotyledons corrugated.

Cotyledons epigeous.

Wind pollinated.

Chromosome number n = 17.

straight, without resin vesicles.

Differences between Colophospermum and Hardwickia

Colophospermum: 4 sepals; 20-25 stamens; seed ± reniform, with resin vesicles.

Hardwickia: (4-)5 sepals; 10(-11) stamens; seed

A number of the characters shared by the two monotypic genera are quite unique in the Detarieae or even in the Caesalpinioideae. As such may be mentioned the lack of bracteoles on the flower stipe, the flower and pollen structure that indicates wind pollination, and the chromosome number. The foliaceous appendage on the leaf may be added. This "prolongation" of the leaf beyond the pair of fully developed leaflets is foliaceous, conduplicate and mostly soon deciduous. The morphology is the same in both genera. In the original publication of *Colopho-*

spermum, LÉONARD (1949) did not express his opinion about the morphological nature of this element, but later he named it a terminal foliole (LÉONARD 1957). CUSSET (1970) was certain that it represents a foliole. In this paper the foliar element is indicated as a much reduced, secondary pair of united leaflets, not a single terminal leaflet. This is more in accordance with the paripinnate nature of the leaves. Moreover, the cotyledons in *Colophospermum*, whether they are true cotyledons or paracotyledons (DE VOGEL 1979), look like a pair of united leaflets, when the nervation pattern is considered. As such they appear the same as the reduced pair of leaflets.

Two characters, viz the uniovulate ovary and the corrugated cotyledons, are also found in the following genera: Gossweilerodendron, Kingiodendron, Oxystigma and Prioria, in which the latter has more or less flat cotyledons.

KNAAP-VAN MEEUWEN (1970) described the *Hardwickia* leaflets as without pellucid dots. However, *Hardwickia* also has pellucid dots, although they are much less numerous and less distinctive.

The ecology of *Hardwickia binata* (ROY 1996) is rather similar to that of *Colophospermum mopane* (ROSS 1977; MAPAURE 1994) as both taxa are encountered in rather dry savannas, the first in India north of the equator, the second south of the equator in southern Africa (Fig. 2).

POLLEN MORPHOLOGY

(by I.K. FERGUSON).

The pollen morphology of the two monotypic genera *Hardwickia* (*H. binata*) and *Colophospermum* (*C. mopane*) has only been described comparatively recently. FASBENDER (1959) described the pollen of *Hardwickia* as tricolporate. This would appear to be based on an incorrectly identified specimen. VAN ZINDEREN BAKKER & COETZEE (1959) described *Colophospermum* as pantoporate. It was not appreciated that these two taxa had similar pantoporate pollen until GRAHAM et al. (1980) drew attention to the unusual pollen and further described the pollen of the two taxa (GRAHAM & BARKER 1981) but without drawing taxonomic conclusions.

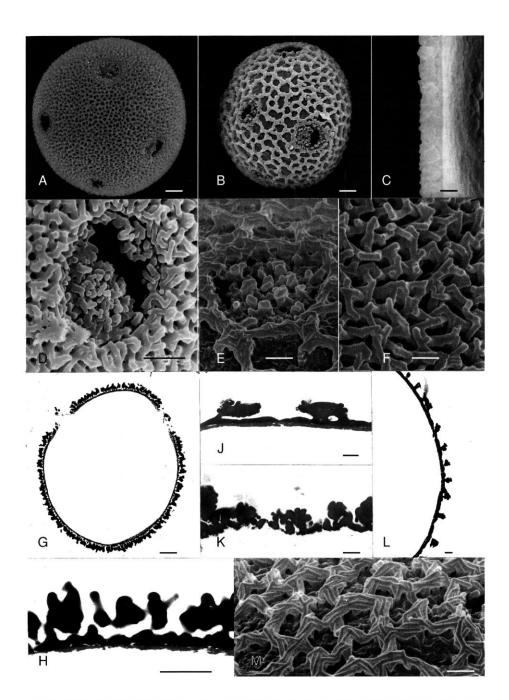


Fig. 3.—A, C, D, F, G, H, *Hardwickia binata*; B, E, J-M, *H. mopane*: A, pantoporate pollen with microreticulate exine; **B**, pantoporate pollen with reticulate exine; **C**, detail of exine stratification showing thick sexine and thin nexine; **D**, detail of pore with aperture membrane; **E**, detail of pore with aperture membrane; **F**, exine ornamentation showing scabrate muri; **G**, thin section of whole pollen grain showing 2 apertures and thin nexine; **H**, thin section detail of exine stratification with thin endexine, clear foot layer, columellae layer, thick tectum with scabrate surface; **J**, thin section detail of exine stratification with thick columellae; **K**, thin section detail of aperture membrane; **L**, thin section of part of pollen showing thin nexine and widely spaced sexine elements; **M**, exine ornamentation showing striate muri. (A, C, D, G, *Khan 2319*; B, J-L, *Lugard 243*; E, M, *Torre 7326*; F, *Gamble 874*. A-F, L, SEM micrographs; G-K, TEM micrographs. Scale A, B, G = 10 μm; C-F, H-M = 1 μm).

FERGUSON (1987) in a study of the exine stratification emphasized that similarity in the details of the pantoporate apertures and the very thin exine. He suggested, and it was supported further by GUINET & FERGUSON (1989), that the thin walled pantoporate pollen might be associated with wind pollination, citing the suggestion of ROSS (1977) that *Colophospermum* is wind pollinated.

Hitherto no taxonomic evaluation of the two taxa incorporating pollen morphological data has been made.

Materials and methods

Material was obtained from the Herbarium, The Royal Botanic Gardens, Kew (K). The pollen samples were prepared by the methods described by FERGUSON et al. (1994). SEM = Scanning electron microscope, TEM = Transmission electron microscopy.

General pollen description.—Fig. 3.

Pollen spheroidal, 36-50 μm in diameter, pantoporate with 8-12 pores 5-7 μm in diameter, pores with a granular or rugulate membrane. Ornamentation reticulate or microreticulate/rugulate. Exine 1-1.5 μm thick, nexine thin, sexine well developed 1 μm or greater thick. In TEM endexine thin, foot layer distinct, columellae short and tectum well developed ca. 1 μm thick.

Colophospermum (Fig. 3B, E, J-M).

Pores 6-7 µm in diameter with a granular membrane. Ornamentation reticulate, lumina (1.5)2-4(-5) µm on the longest axis, muri distinctly striate. Columellae comparatively sparse and thick.

SPECIMENS EXAMINED.—Botswana: *Lugard 243*; Mozambique: *Torre 7326*.

Hardwickia (Fig. 3A, C-D, F-H).

Pores ca. 5 µm in diameter with a comparatively finer scabrate membrane than *Colophospermum*. Ornamentation microreticulate/rugulate, lumina about or less than 0.5 µm on the longest axis, muri scabrate giving a somewhat overall rugulate appearance to the surface of the exine.

Columellae comparatively denser and thinner.

SPECIMENS EXAMINED.—India: Gamble 874, Gamble 15258, Khan 2319.

Discussion

The pantoporate pollen is remarkable, occurring very rarely not only in the Caesalpiniodeae where it occurs in the two species under investigation and in one or two species of *Bauhinia*, but also occurring only in 2 genera of Papilionoideae (GUINET & FERGUSON 1989).

The similarity in the structure of the apertures, the aperture membrane, pollen size, shape and thin exine are especially noteworthy. The exine ornamentation and stratification differs sufficiently to allow the pollen of the two species to be easily distinguished. Nonetheless the reticulate pattern, thin exine and its stratification are basically very similar.

Previous workers have noted the similarities in pollen morphology (GRAHAM et al. 1980; GRAHAM & BARKER 1981; FERGUSON 1987) but drew no taxonomic conclusions. GUINET & FERGUSON (1989) emphasized the unique pantoporate pollen type in the Caesalpinioideae and suggested that the pollen might be a secondary adaptation to wind pollination.

Modification of exine ornamentation as a development of pollination strategy has been suggested by a number of authors as a widespread syndrome in both Papilionoideae and Caesalpinioideae (FERGUSON & SKVARLA 1982; FERGUSON & PEARCE 1986; GUINET & FERGUSON 1989; KLITGAARD & FERGUSON 1992). The occurrence of this unique pantoporate pollen type in two geographically isolated species could be interpreted as a convergent modification to wind pollination. However, it is significant that the occurrence of this unique pantoporate pollen in the two geographically isolated species agrees well with several macromorphological features, some quite unique as well. Therefore these common morphological features could support the view that the similar pollen type found in Hardwickia and Colophospermum may indeed be indicative of relationship. This relationship may in turn underlie the expression of a secondary modification to wind pollination.

WOOD ANATOMY (by P.E. GASSON & B.J.H. ter Welle).

Colophospermum mopane is a medium-sized to large tree, usually ca. 10 m tall, but ranging from 4-18 m. It is dominant in large areas of hot, low-lying, mainly alluvial, but also alkaline and poorly-drained soils, and often forms pure stands. The heartwood is dark reddish-brown to almost black, very durable, hard and heavy and difficult to work, but subject to termite attack (CUTLER, pers. comm.). It is commonly used for mine props and railway sleepers, and makes very good firewood (COATES PALGRAVE 1988; PRIOR & CUTLER 1996). There is much literature on the species, including several papers with information on wood properties, summarised by TIMBERLAKE (1995).

Hardwickia binata is a moderate-sized to large tree from drier areas. The heartwood is dark red to dark brown, with darker streaks and often with a purplish cast, and is probably the hardest and heaviest Indian wood, which is difficult to work when seasoned (RAMESH RAO & PURKAYASTHA 1972; PEARSON & BROWN 1932). It is used for mine props, posts and beams, cartwheel naves and spokes, ploughs, railway sleepers, and is a moderately good fuelwood. In 1897 H. pinnata was transferred by HARMS to Kingiodendron (as K. pinnatum), although PEARSON & BROWN (1932) still described the two species under Hardwickia, viz. H. binata and H. pinnata. Kingiodendron pinnatum is characterized by the presence of axial gum canals and noncrystalliferous axial parenchyma and GAMBLE (1902) states that the tree (which he calls H. pinnata) also yields a valuable balsam like copaiba. These characters are all indications validating the transfer by HARMS (1897) of H. pinnata to another genus. A wood anatomical description of Hardwickia is provided by JUTTE (1965) who studied some genera of the Cynometreae.

Colophospermum mopane (Fig. 4).

Growth rings distinct, marked by tangential lines of axial parenchyma one to two cells wide.

Vessels diffuse, solitary (8-38%), usually in radial multiples of 2-4, occasionally to at least 12, sometimes in 2 immediately adjacent rows,

or in irregular clusters of 2-6, round to oval, 19-47(15-67) per sq. mm, diameter 52-80(12-108) mm. Vessel element length: 161(45-271) mm. Perforations simple. Intervascular pits alternate, vestured, round or oval to polygonal, sometimes elongated, often with coalescent apertures, 2-5 mm. Vessel-ray and vessel-parenchyma pits similar, but half-bordered. Yellow to dark-brown organic deposits common to abundant.

Fibres thick-walled, with simple pits, more frequent on the radial than the tangential walls, lumen up to 5 µm in diameter, walls up to 2-4 µm thick. Very few fibres gelatinous. Length: 600(465-725) µm in Kw7103.

Axial parenchyma scanty paratracheal, incompletely vasicentric, vasicentric-aliform (lozengetype), some diffuse, and terminal tangential bands one to two cells wide. Crystalliferous chambered parenchyma strands with prismatic crystals abundant, up to 19-24 crystals per strand. These strands very often in contact with the rays. Strands 2-4 cells long.

Rays 7-8(5-10) per mm, 2(-3)-seriate, few uniseriate, the uniseriate rays up to 7-8 cells (= 140-150 mm) high, the multiseriate rays up to 16-27 cells (= 310-440 mm) high, homocellular, composed of procumbent cells. Yellow to brown organic deposits common to abundant.

SPECIMENS EXAMINED.—Zimbabwe: J. Prior s.n.; Rhodesia 12.1954 (Kw 7103); Botswana: Terry et al. 185 (Kw 72242); Angola: Dechamps et al. 1194 (Uw 23528); Namibia: Pettinen s.n. (ex RHBw 14016); South Africa: CSIR IND. 78 (ex RHBw 15178).

Hardwickia binata (Fig. 5).

Growth rings distinct, marked by tangential lines of axial parenchyma one to several cells wide.

Vessels diffuse, solitary (22-100%), and in radial multiples of 2-3, occasionally up to 6, round to oval, 6-9(3-13) per sq. mm, diameter 77-108(12-173) mm. Vessel element length: 137(60-217) mm. Perforations simple. Intervascular pits alternate, vestured, round to oval, occasionally with coalescent apertures, 2-5 mm. Reddish-brown deposits common.

Fibres thick-walled, with simple pits, more frequent on the radial than the tangential walls,

lumen up to 7.5 μ m in diameter, walls 2.5-7.5 μ m thick. Fibres often gelatinous, but not found in Kw7306. Length: 875-994(390-1469) μ m (280-1700 μ m in PEARSON & BROWN 1932).

Axial parenchyma scanty paratracheal and

incompletely vasicentric, ocasionally forming lateral wings (i.e. winged aliform), also diffuse and in terminal tangential lines, in Kw21524 many tangential bands up to 10 cells wide. Crystalliferous chambered parenchyma strands

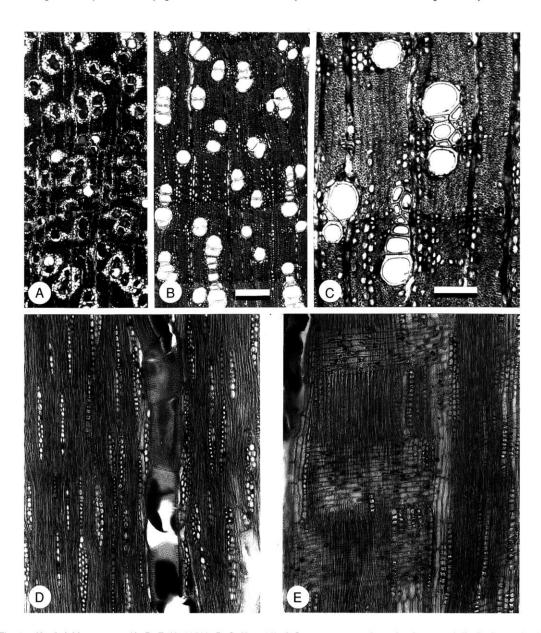


Fig. 4.—*Hardwickia mopane*: (A, D, E, Uw23528; B, C, Kw7103). A-C, transverse sections showing vessel distribution and axial parenchyma patterns; **D**, tangential longitudinal section showing ray width and height, chains of prismatic crystals, many immediately adjacent to rays, and vessels with pitting and dark contents; **E**, radial longitudinal section showing procumbent ray cells and chains of prismatic crystals. Scale lines: For A-B (on B) is 200 μm; for Figs C-E (on C) is 100 μm.

with prismatic crystals abundant, up to 15 crystals per strand. These strands usually bordering the rays. Strands 2-4 cells long.

Rays 4-9 per mm, 3-4-seriate, up to 22 cells high (= 420-540 mm), homocellular, composed

of procumbent cells. Brown organic deposits common.

NOTE.—Kw7303 has abundant traumatic canals in wide axial parenchyma bands, finer

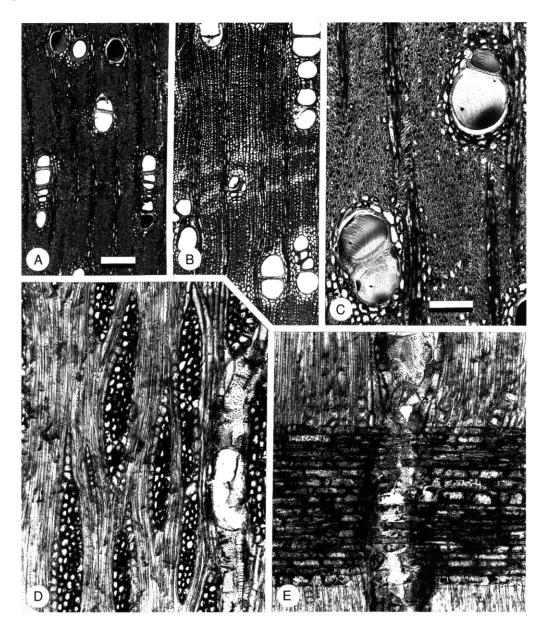


Fig. 5.—*Hardwickia binata*: A-C, transverse sections showing vessel distribution and axial parenchyma patterns; **D**, tangential longitudinal section showing ray width and height and chains of prismatic crystals mainly adjacent to rays; **E**, radial longitudinal section showing procumbent ray cells, intervessel and vessel-ray pitting, and chains of prismatic crystals. Scale lines: For Figs A, B (on A) is 200 μm, for Figs C-E (on C) is 100 μm. All Royal Botanic Gardens, Calcutta, 1868.

intervessel pitting, axial parenchyma strands of considerably more than 4 cells, and prismatic crystals in ray cells. This combination of characters strongly indicates that this sample is incorrectly named. Pearson & Brown (1932) refer to Kanehira (1924) reporting horizontal (i.e. radial) gum canals in the wood.

SPECIMENS EXAMINED.—Calcutta: Anderson 1868, cultivated in Royal Botanic Gardens (Kw7306); Gamble 143, Madhya Pradesh (Kw 21523); Gamble 4020 (see Gamble 1902), Coimbatore (Kw 21524); East India Museum (Kw 7303), this sample is misidentified (see note above).

The wood anatomy of the two genera is very similar in most respects. Vessels are diffusely arranged, and there tend to be more radial multiples in Colophospermum. However, the greater proportion of solitary vessels in Hardwickia is partly explained by their larger size, with fewer vessels per mm². The intervessel pitting is very similar in both genera. The fibres are thick-walled, with virtually no lumina in both, and gelatinous fibres are variably present. Axial parenchyma patterns are variable within each species, but the overall range from scanty paratracheal to more abundant paratracheal, and diffuse parenchyma are present in both genera. This range of parenchyma distribution is found in many legume genera. Prismatic crystals are abundant in both, and are often found in chambered parenchyma cells directly adjacent to the rays. The rays are slightly wider in *Hardwickia*, but in many taxa, variation in ray width is not unusual. Both have homocellular rays composed of procumbent cells. Organic deposits are common in both, although they are of different colours (yellow-brown in Colophospermum, brown to reddish-brown in Hardwickia). In the absence of chemical tests, the significance of these differences is not known. The differences in quantitative characters (i.e. vessel diameter and element length, vessel density and fibre length) may all be attributable to differences in cambial age of the samples, since the Hardwickia samples were all

from mature trunk wood, whereas the *Colophospermum* samples were from narrower stems. This could also explain the more frequent vessel groupings in *Colophospermum*, since such groupings tend to be more frequent in narrower stems and branches.

The wood of the two taxa is very similar anatomically, but there are many examples in the legumes of taxa that look similar but are not particularly closely related. In this case, the lack of a feature (axial canals) is probably very important. In the legumes these are found only in Detarieae and Amherstieae, including, in COWAN & POLHILL's (1981) Crudia group of the Detarieae, Kingiodendron pinnatum (once included in Hardwickia), Prioria, Oxystigma Gossweilerodendron (see table in GASSON 1994; BARETTA-KUIPERS 1981; ILIC 1991; WHEELER et al. 1986). These genera are all grouped by Breteler (1996) in the apetaliferous Hymenaea complex of the Detarieae. If Colophospermum and Hardwickia truly belong in this group, then it is likely that they are more closely related to each other than to the genera with axial canals. Although Colophospermum lacks canals, the wood is reported by SMITH & SHAH-SMITH (in press) to be resinous, presumably as a result of contents in the lumina of the vessels and parenchyma cells.

After these studies, it is concluded that the two genera have to be united under the name *Hardwickia*.

TAXONOMY (by F.J. Breteler).

HARDWICKIA Roxb.

Pl. Coromandel 3: 6, t. 209 (1811).—Type: *H. binata* Roxb.

Colophospernum Kirk ex J. Léonard, Bull. Jard. Bot. Brux. 19: 390 (1949).—Type: C. mopane (Kirk ex Benth.) Kirk ex J. Léonard.

This genus contains two species which may be distinguished as follows:

Hardwickia binata Roxb.

Pl. Coromandel 3: 6, t. 209 (1811).—Type: t. 209 (ROXBURG 1811). For additional references see KNAAP-VAN MEEUWEN (1970).

SPECIMENS EXAMINED.—INDIA: Beddome 2550, Cuddapah Hills (BM); Herb. Benthamianum s.n., N.W. Bengal, ? Tilothue (K); Bourne 2154, Clingleput distr., Kambakan (K); Bourne s.n., Myosore, near Hangal (K); Buchanan s.n., Myosore (BM); Forest Service s.n., Coimbatore (L, WAG); Gamble 11086, Madras, Auaukapur, Muchakola (K); Gamble 15258, Madras, Kotealeota (K); Haines 5615, Bihar, near Daltongang (K); Herb. Madras 9963, Mamandur (K); Hooker & Thomson 299, Bihar, upper part of Soane (K); Jacquemont 237 (P); Lushington (Herb. Gamble) s.n., Madras, Somanaparam (K); Matthew & Paramasivan RHT 24304, Dharmapuri, Kambalai (K); Matthew & Paramasivan RHT 24305 (L); Mooney 239, Narepa, Telagu (K); Mooney 2143, Bastar State, Pilur (K); Khan in Herb. Mooney 2319, Bastar State, Bhopalpatnam (K); Pierre 122, Coromandel (P); Roxburgh s.n. (BM); Fischer in herb. Sedgwick & Bell 5957, N. Bombay (K); Wight 874, Madras (K, P, WAG).-Cultivate: Andersen 28, Botanical Garden Calcutta (P); Japin 2780, Hyderabad, Miami forest (K); Pierre s.n., Botanical Garden Calcutta (P); Wood s.n. (K).

Hardwickia mopane (Kirk ex Benth.) Breteler, comb. nov.

Copaifera? (Colophospermum) mopane Kirk ex Benth., Trans. Linn. Soc. London 25: 317, t. 43A (1865).— Colophospernum mopane (Kirk ex Benth.) Kirk ex J. Léonard, Bull. Jard. Bot. Brux. 19: 390 (1949).— Type: Kirk s.n., Mozambique, Lupata (holo-, K!). For additional references see Léonard (1949).

SPECIMENS EXAMINED.—ANGOLA: Bamps et al. 4086, Km 54 Roçadas-Pereira d'Eca (WAG); Barbosa 9778, Moçamedes, Caraculo (K); Brito et al. 7843 A, Huila, Roçadas, Cumato (WAG); Couto 191, Cunene, Roçadas, Chicusse Chama (K); Couto 370, Km 92 Sa da Bandeira-Moçamedes (K); Dechamps et al. 1193, 1194, Moçamedes, near Capangombe (K, WAG); Exell & Mendonça 2339, Moçamedes, Birei (BM); Exell & Mendonça 2880, Huila, between Donguna and Ruacana (BM); Gossweiler 11.000, Moçamedes, Mubi-Bero (K); Grandvaux Barbosa & Correia 9111, Moçamedes, Caraculo (BM); Humbert 16492, between Moçamedes and Villa Arriaga (BM, P); Mendes 1133, Huila, Quihita (BM); Mendes 1722, Huila, Cahama (BM); Menezes & Henriques 4, Huila, Cureca (K); de Menezes 1036, Huila, Gambos (BM, K, P); de Menezes 1403, Huila, Mupa (BM, K, P); de Menezes 3661, Huila, Gambos (BM, K, P); Pearson 2562, between Gambos and Cahama (K); Powell-Coltan 1529, Huila, Cuamato (BM); Santos 153, Moçamedes Dois Irmãos (BM); C.F. & J.D. Ward 45, Moçamedes, Tona Nat. Park (K); Welwitsch 605, near Bumbo (BM, K, P).—BOTSWANA: Allen 249, 255, Orapa (K); de Beer 85, Serowe (K); Drummond 5272, Madisiara (K); Erens 200, Martins Drift Trading Station (K); Erens 308, Maun Camp, Thamalakane R. (K); Iwley 1081, Moremi (K); Leach & Noel 257, Radisele (K); Lugard 243, Ngamiland (K); Lugard 296, near Tklakane Pits (K); Miller B 113, Kazangulu (BM); Paterson 30, Makarikari-pan (K); Pole Evans 3219, Seruli (BM, K); Smith 1226, Thamalakane R. (K); Yalala 145, Palapye (K).—MALAWI: Burtt 5999, Shire Valley (BM, P).—MOZAMBIQUE: Correia & Marques 915, Gaza, Canicado (WAG); Gomes e Sousa 4771, Chioca (K): Grandvaux Barbosa & Carvalho 3161, 3166, Salima (K); Grandvaux Barbosa & Carvalho 3263, 40.5 km Tete-Chioca Rd. (K); Grandvaux Barbosa & Carvalho 3279, 76 km Tete-Chioca Rd. (K); Grandvaux Barbosa & Carvalho 3408, 38 km Chioca-Chetima Rd. (K); Grandvaux Barbosa & Carvalho 3448, Massamba (K); Grandvaux Barbosa & Carvalho 3595, 59 km Furancungo-Regulo Bene Rd. (K); Grandvaux Barbosa & Lemos 8191, Massingir (K); Grandvaux Barbosa & Lemos 8625, 14 km Mabalane-Mapai (K); Kirk s.n., Lupata (K, type); Livingstone s.n. (K); Mendonça 4038, Vila Machado (BM, K); Pedrogão 227, 239, Mucatine (K); Pedrogão 287, Chicholo (K); Torre 7326, Magude (BM).-NAMIBIA: Baum 978, Nakapi (BM, K); Coppejans 653A, Outjo (WAG); de Winter 3066 (K); de Winter 5293, near Ohopaho (K); de Winter 9198, Katima (K); Germishuizen 2569, 80 km Outjo-Khorixas (WAG); Giess 7766, Farm Grootberg (K, WAG); Immelman 490, Farm Mosella, Ugab R. (WAG); Lubenberg 4905, Okjiwarango (K); Merxmuller 1422, Outjo (K); Moss et al. 2126, Marienfluss (WAG); Pegel 90, Brandberg (K); Rautanen 432, Hereroland, Okaukuejo (BM, K); Rautanen 524, Ondonga (K); Rodin 2623, 8963, Oshikango (K); Rodin 9041, NW of Engela (K); Schinz s.n., Ovamboland (K); Walter 1033, Outjo (BM).—SOUTH AFRICA: Andrews 1275, Venda, Nwandedi Park (K); Breyer 18391, Mokutsi (K); Cocks 4827, Zoutpansberg (K); Codd 4827, (K); Codd & de Winter 5570, Letaba (K); de Winter 8673, S of Messina(K); Eicker et al. 193, Greefswald (K); Hutchinson 2303, Dongolo (K); I.B.P.E. 1464, Sandy Spruit (K); I.B.P.E. 1918, 1960, Messina (K); Lambinon & Reekmans 82/104, Kruger Park (WAG); Rogers 22549, Messina (K); Schlieben 9256, Zoutpansberg (K); Schlieben & Hartmann 12307, between Mopane and Vivo (K, WAG); Small 467, 60 km N of Louis Trichardt (K); van der Schiff 3546, Kruger Park, Letaba (K); van Vuuren 1625, 37 km N of Louis Trichardt (WAG); Verdoorn 2082, Limpopo R. (K).—ZAMBIA: Angus 2237, S of Kafue, Kafue R. (K); Bingham 7687, Nyamaluma (WAG); Bush 60, W

Lupande R. (K); Fanshawe 735, Ndola (K); Gairdner 557, Kazungula (K); Grant 4509, near Livingstone (WAG); Greenway & Trapnell 5604, Hupane (Chinsenga) (K); Robson 956, Changwe (BM); Rodin 4501, Victoria Falls (K); Shantz 412, (K); Shantz 439, Kafue (K); Swynnerton 1250, Muchukwana (BM, K); Symoens 11451, 10 km S of Livingstone (K); Trapnell 1823, Luangwa (K); van Rensburg KBS 1798, Kafue R. (K); van Rensburg KBS 2134, Fort Jameson (K); Yilger 604, Kalambola (K).—ZIMBABWE: Biegel 791, Gwelo (K); Burtt-Davy 18121, Bosoli Siding (BM); Chase 1482, Hot Springs (BM); Chase 2507, Ndanga (BM, K); Cosby 1071, Chipinga (K); Drummond 6020, Beitbridge (K); Exell et al. 444 (BM); Gibbs 204, S of Matopo Hills (BM); Malaisse 12177, Beitbridge-Victoria Rd. (WAG); Mason s.n., Victoria Falls (K); Myres 853, Odzi R. (K); Norrgrann s.n., Dombodema (WAG); Obermeyer 2371, Birchenough Bridge (K); Phipps 2414, Mkumburu R. (K); Plowers 1536, Nyamandhlovu (K); Rushworth 1459, Wankie (K); Shantz 414, Tjolotjo (K); Soane 232, Sabi Valley (K); Stace 1482 (K); Wild 2372 (K).—Cultivate: Fanshawe 9070 & 9389, from forest nursery (K).

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