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Unique pollen types in the Caesalpinioideae (Leguminosae)

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In the legumes several pollen types were encountered during a survey of the Caesalpinioideae that were previously unknown or poorly known for the subfamily: Viscin threads (*Jacqueshuberia*), periporate pollen (*Hardwickia, Colophospermum*), diporate pollen with a single continuous colpus (*Duparquetia*), tetracolporate pollen (*Ceratonia*), and pollen tetrads (*Afzelia, Diptychandra*).

Key words: Leguminosae, Caesalpinioideae, unique pollen

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A two-year multidisciplinary study on tribal classification in the Leguminosae recently culminated in the International Legume Conference (August, 1978), Royal Botanic Gardens, Kew. As part of this project a survey was made of pollen morphology in the Caesalpinioideae, and several pollen types unusual or unique in the legumes were encountered. The taxonomic results of the study will be published in the symposium volume (Graham & Barker, in press) and details of pollen structure treated later when the survey is more complete. At present representatives from ca. 118 of the 152 genera presently assigned to the Caesalpinioideae (excluding the Swartzieae to be removed to the Faboideae) have been surveyed using light and scanning electron microscopy.

MATERIAL AND METHODS

Pollen material was prepared by the standard acetolysis treatment and transferred in vials of 95% ethanol to the SEM facilities, Smithsonian Institution, Washington, D.C. Pollen was mounted on cover slips by evaporation of the ethanol and these afixed to aluminium stubs with Aqua-Dag. The pollen was sputter-coated with Gold-Palladium, and SEM-micrographs made with a Cambridge Mark IIA Stereoscan. Reference material is vouchered at US.

VISCIN THREADS

The genus *Jacqueshuberia* (Tribe Caesalpinieae) consists of three species confined to the Amazon region of Brazil (*J. amplifolia, J. purpurea, J. quinquangulata*). The taxonomy of the genus is presently under review by da Silva. The unique feature of the genus, from the standpoint of palynology, is that the pollen grains have viscin threads (Fig. 1 A–F). Skvarla et al. have made a detailed study of viscin threads in the Onagraceae, and mention (1978: 461) earlier reports for *Rhododendron* of the Ericaceae by Erdtman (1952), Bowers (1931), and Ikuse (1954), but this is the first record of the structures in the Leguminosae.

The pollen of *Jacqueshuberia* is spherical and ca. 75–80 μm in diameter. The exine structure is semitectate, reticuloid, consisting of folded, tectal mural elements, coalescing directly with the nexine. The surface of the lumina is scabrate (Fig. 1 F). Distinct apertures were not visible with either light or scanning electron microscopy.

The viscin threads are smooth under both the light and SEM magnification used here. They are about 2 μm in diameter throughout the length of the thread. The attachment appears as a branch off the muri without the bulbous base that characterizes

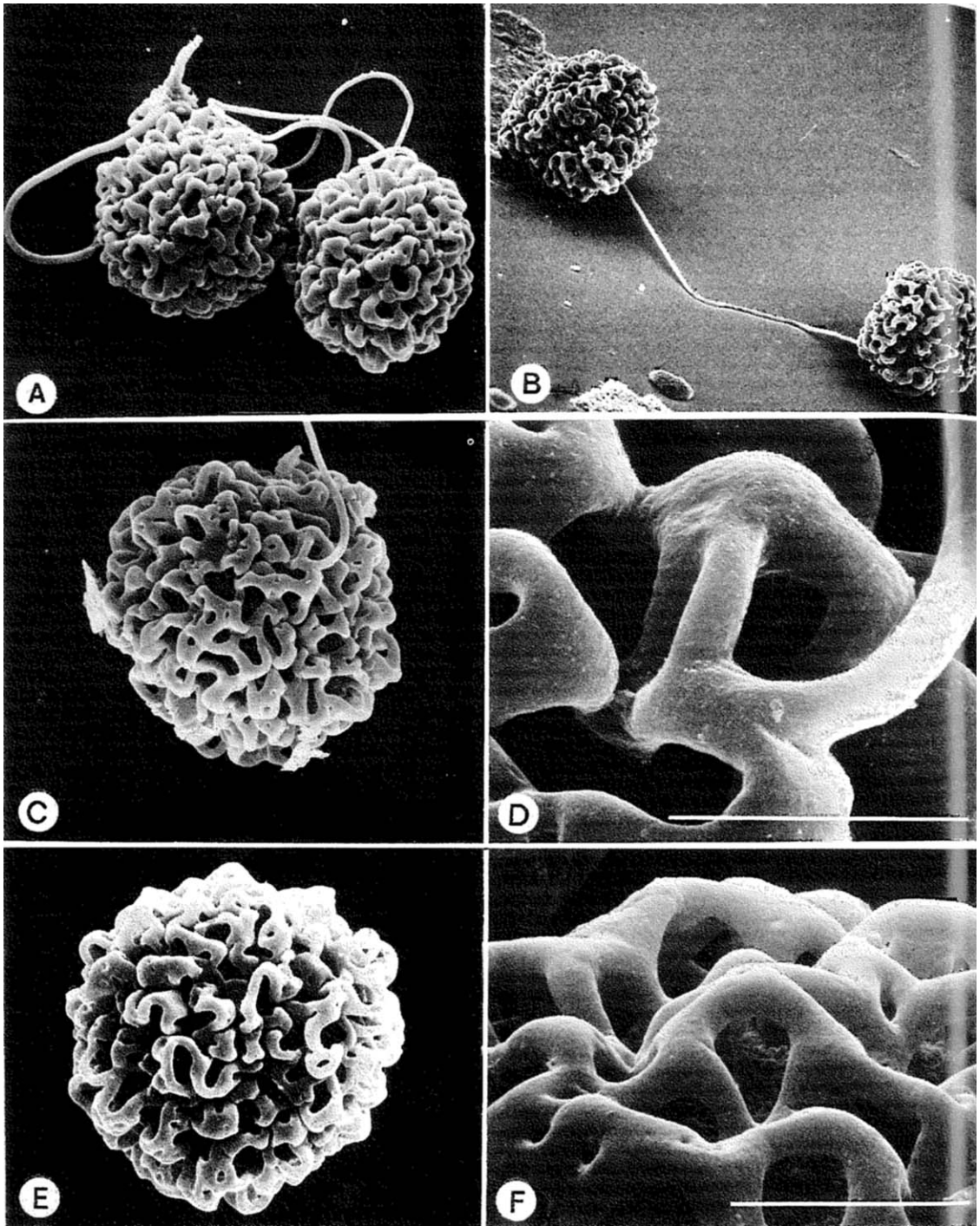

Fig. 1. Jacqueshuberia. (A, C–E) *J. purpurea* (A) ×700, (C) ×900, (D) ×6000, (E) ×1000. (B, F) *J. amplifolia* (B) ×500, (F) ×4800. The scale lines correspond to 10 μm.

some viscin threads in the Onagraceae (Fig. 1 C, D; Skvarla et al. 1978). The length of the threads is difficult to determine because they are frequently broken, folded, or portions overlain by the grains, and are likely to vary between grains. Maximum lengths observed were ca. 175–200 μm.

The number of threads per grain is also difficult to determine accurately. In a count of 100, about 35% showed no evidence of threads (Fig. 1 E), probably because they were broken at or near the base. Distinct threads, or at least attached fragments, occurred on the remainder. A common observation was one (Fig. 1 B) or two (Fig. 1 A) threads extending between two grains. Clusters of two to several grains entangled by the threads are common on the slides even after acetolysis. It is assumed the viscin threads reflect an adaptation to entomophily, but the pollination biology of *Jacqueshuberia* has not been studied.

PERIPORATE POLLEN

Periporate pollen grains occur in two genera of the Caesalpinioideae and both are in the tribe Detarieae. *Hardwickia* (Fig. 2 A, B) is an apetalous, presumably wind pollinated genus consisting of two species (Airy Shaw 1966) in India. The grains of *H. binata* are spherical and measure 45–50 μm in diameter. The pores are spherical, ca. 5 μm in diameter, and typically eight in number. The pore margins are diffuse and a granular membrane is frequently present. The grains are semitectate with irregularly shaped small supratectal processes, some of which are pointed with rounded apices approaching echinae.

The genus *Colophospermum* (Fig. 2 C) consists of a single species, *C. mopane*, confined to tropical south Africa. Only limited amounts of pollen material were available and most grains on the stubs were folded or collapsed. The grains are spherical, 45–50 μm in diameter, and periporate. The pores are circular, ca. 5 μm in diameter, with diffuse margins, and occasionally with a granular pore membrane. The principal difference between *Colophospermum* and *Hardwickia* pollen is that the former is reticulate whereas the latter is microreticulate. The reticulum is closed and regular. The diameter of the larger lumina are ca. 3 μm and the smaller ca. 1–2 μm. The muri are relatively straight with entire margins and ca. 1 μm in width.

DIPORATE POLLEN

The pollen of *Duparquetia* (tribe Cassieae; 1 species, *D. orchadacea*, tropical West Africa) is unique among the legumes and perhaps among the angiosperms. The grains are oblate to oblate-spheroidal with three thickened, meridionally elongated, equatorially arranged, equidistant ridges ca. 20 μm in length (Fig. 2 D). In polar view these resemble three protrusions but the pores are actually two in number, one located at each pole. Running through the pores is a single colpus-like extension along one side of two of the ridges. The grains are 30–35 μm in diameter (including the ridges), tectate, and psilate. The ridges are ca. 5 μm thick. The pores are circular, ca. 3 μm in diameter, with a faint annulus ca. 1–2 μm wide.

The uniqueness of the pollen is matched by an equally unusual floral morphology. There is partial fusion of the petals to give an orchidaceous aspect to the flower. *Duparquetia* has traditionally been placed in the Cassieae, but H. S. Irwin and R. C. Barneby (1978: personal communication) are placing it in a separate subtribe on the basis of distinct floral and palynological characters.

TETRACOLPORATE POLLEN

The genus *Ceratonia* (Cassieae) is monotypic (*C. siliqua*) and confined to the Mediterranean region. The pollen is unusual in the legumes in being tetracolporate (Fig. 2 E, F). The grains are oblate to oblate-spheroidal and 35–40 μm in diameter. The colpi are long (ca. 25–30 μm), equatorially arranged, meridionally elongated, equidistant, tapering to an acute apex, margins entire. The endopores are oval, situated at the mid-point of the colpus, equatorially elongated, with entire margins and ca. 4×8 μm. The exine is microreticulate in the mesocolpial regions and with tectum perforatum at the poles (i.e., nearing the poles the width of the muri begins to exceed the diameter of the lumina).

Consistently tetra-aperturate grains, as opposed to an occasional one among otherwise tri-aperturate forms, are unusual in the legumes. It was initially thought the reference material may have been from a polyploid population. In many angiosperm groups the number of apertures frequently increases with polyploidy (e.g., Graham & Tomb 1974, 1977). In *Ceratonia*, however, pollen material was available from three separate collections and all grains ob-

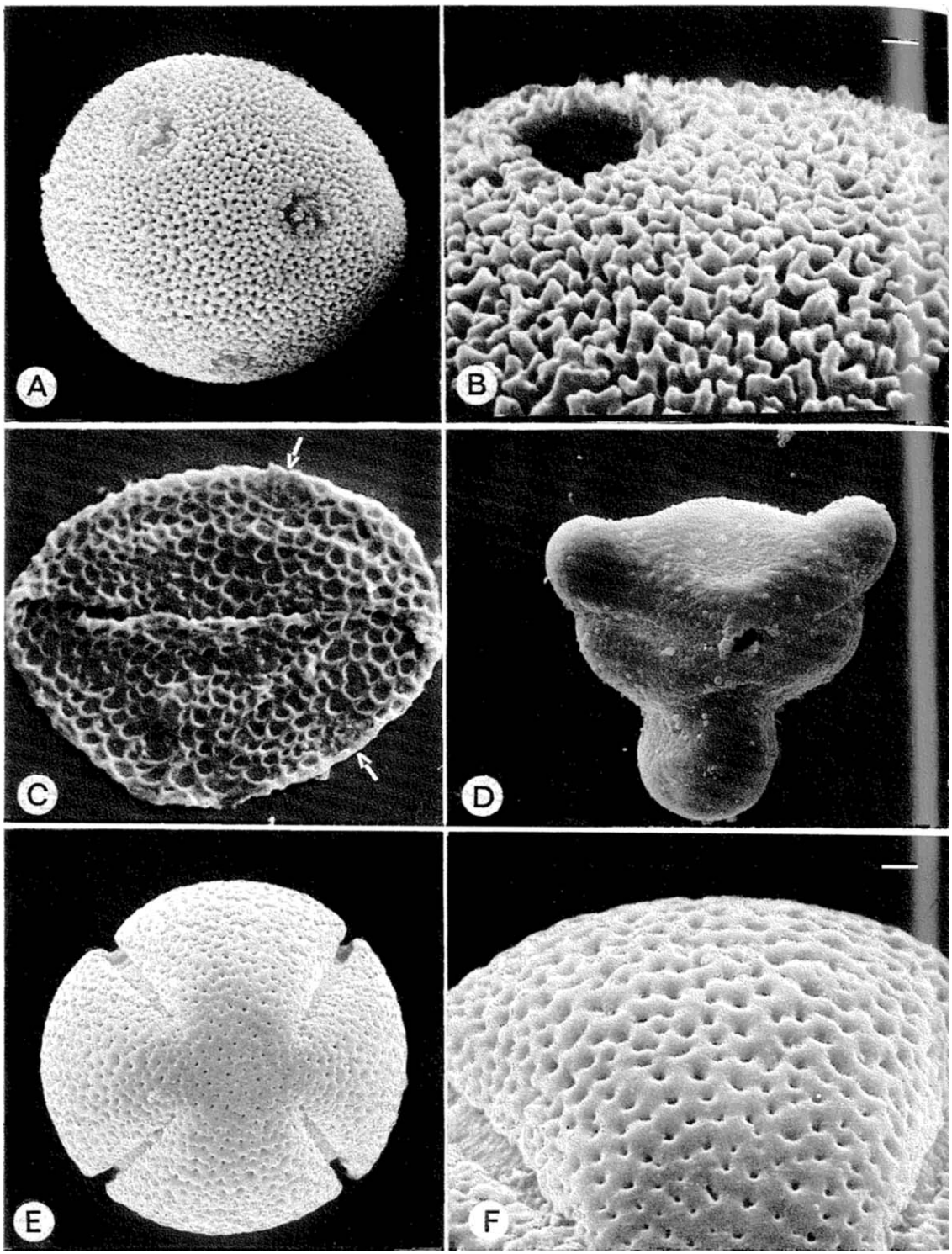

Fig. 2. (A, B) *Hardwickia binata* (A) ×2000, (B) ×7500. (C) *Colophospermum mopane*. ×1800, arrows indicate position of pores. (D) *Duparquetia orchadacea*, ×2500. (E, F) *Ceratonia siliqua* (E) ×2800, (F) ×7000. The scale lines correspond to 1 μm.

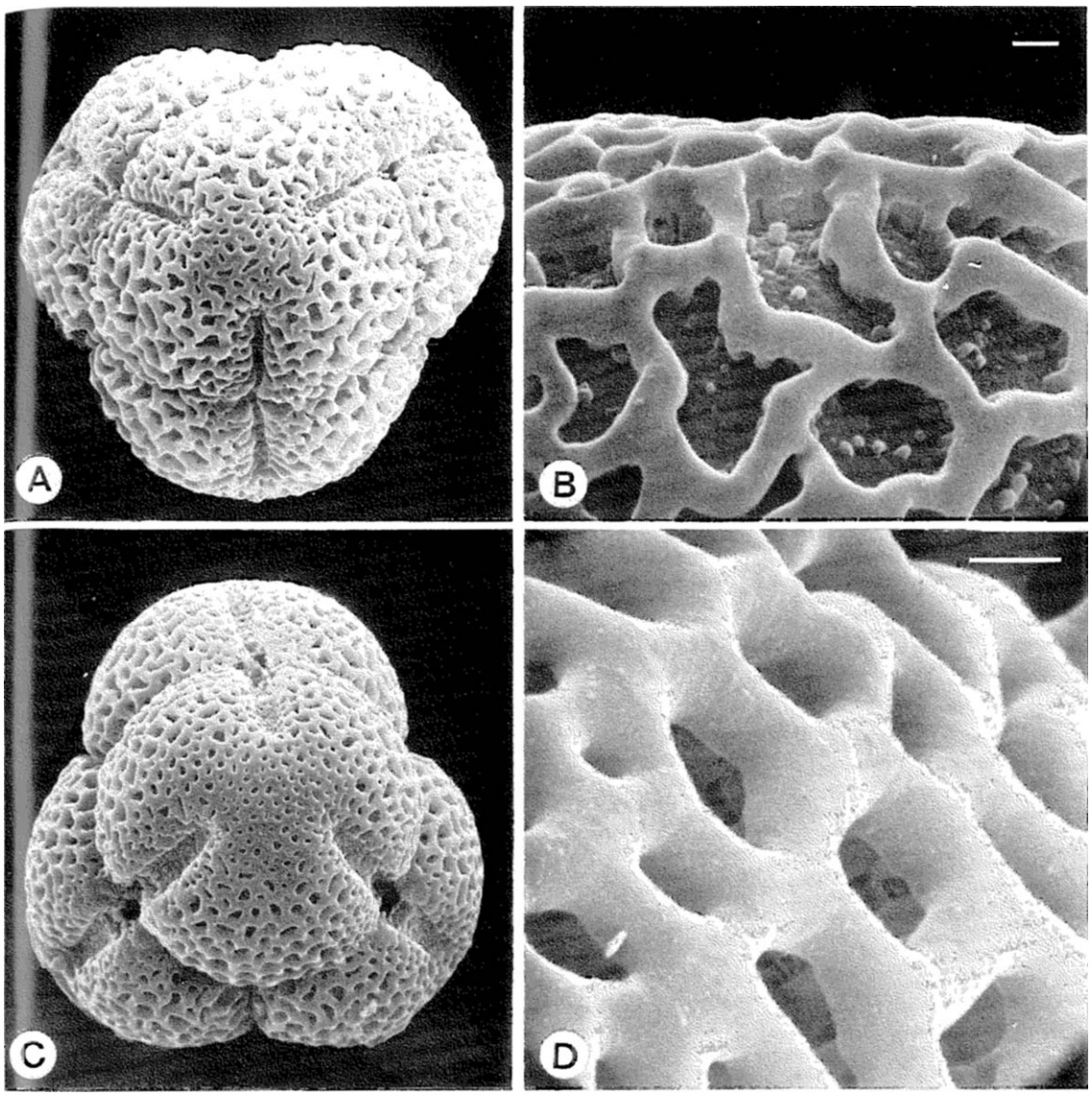

Fig. 3. Diptychandra. (A, B) *D. glabra* (A) ×1 600, (B) ×7 500. (C, D) *D. aurantiaca* (C) ×1 500, (D) ×15 000. The scale lines correspond to 1 μm.

served in each collection were tetracolporate. In the chromosome survey of legumes by P. Goldblatt (1978: personal communication) there is, as yet, no evidence of polyploidy in *Ceratonia*, and the tetracolporate condition is apparently an established and consistent morphological feature in the genus.

TETRADS

Pollen tetrads are most typical of the Mimosoideae but they do also occur in two genera of the Caesalpinioideae. The genus *Afzelia* (Detarieae, 14 species, Africa, Asia) studied by Senesse (1976) includes both monad and tetrad forms. In the genus *Diptychandra* (Caesalpineae, 3 species, Bolivia, Brazil) Guinet (1965) reported tetrads in two of the three species and we have found them in the third (Fig. 3 A–D). In *Diptychandra* the grains are in tetrahedral tetrads measuring ca. 55 μm. The individual grains are ca. 40 μm in diameter and tricolporate with the colpi meeting at the contact between

grains in the tetrad. The grains are reticulate, with the diameter of the lumen ca. 2μm in the mesocolpal region, becoming finer toward the poles. The muri are straight (Fig. 3C, D) to slightly sinuous (Fig. 3A, B) in both species, psilate and with entire edges. Free sexine elements occur sparsely in the lumina of the reticulum (Fig. 3B).

The occurrence of pollen tetrads in a single genus of both the Detarieae and Caesalpineae is not interpreted to mean the genera are related or are misplaced in their current tribal assignment. Pollen tetrads have developed independently in many taxonomically unrelated groups, probably in response to the selective factor of pollination efficiency. In any plant with more than one ovule per ovary, and not obligatorily wind pollinated, the presence of tetrads will likely be selected for, or at least not selected against, because it permits multiple fertilizations from a single pollination event. The same is probably true for viscin threads in entomophilous species. The periporate condition is one method of maximizing contact between cuticular-dissolving enzymes of the intine and the stigmatic surface, and the widespread occurrence of the punctate to reticulate exine pattern effects release of the recognition proteins stored between the columella (Heslop-Harrison 1971, 1976). The only pollen type among these legumes difficult to relate to factors of pollination biology and physiology are the unique grains of *Duparquetia*. Eventually the significance of the diporate condition and the meridional ridges will be determined. For the moment palynological studies have contributed to a better taxonomic understanding of the genus in that the uniqueness of the pollen is now reflected in separate subtribal status for *Duparquetia*.

SPECIMENS STUDIED

Afzelia: A. africana Smith, Zenker 224 Kamerun (US). *A. bella* Harms, Zenker 347 Kamerun (US). *A. bipindensis* Harms, Zenker 277 Kamerun (US). *Ceratonia: C. siliqua* L., Fause 15.10.1934 Algeria (US). Whitehead (Indiana Univ.) pollen exchange (MO). van der Hammen (Amsterdam) pollen exchange. — *Colophospermum: C. mopane* (Kirk ex Benth.) Kirk ex Léon, Winter 8673 Pretoria (K). — *Diptychandra: D. glabra* Benth., Maguire et al. s.n., Mato Grosso Brazil (US). *D. aurantiaca* Tul., Macedo 1302 Brazil (US). *Duparquetia: D. orchadacea* Baill., Vigne 376 Gold Coast Africa (US). Zenker 96 Kamerun (US). — *Hardwickia: H. binanta* Roxb., Khan 2319 India (K). — *Jacqueshuberia: J. purpurea* Ducke, Froes 25253 Brazil (US). *J. amplifolia* Cowan, Zarucchi 2137 Colombia (US).

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