POLLEN MORPHOLOGY OF THE GENUS HYDNOCARPUS (FLACOURTIACEAE) with notes on related genera

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SUMMARY

Pollen grains of 34 species of the genus Hydnocarpus (Flacourtiaceae) are described. Two pollen types, one of which is subdivided in two subtypes, are distinguished. Within Flacourtiaceae the pollen of Hydnocarpus is more or less isolated, but the related genus Chlorocarpa has rather similar pollen. In sculpture there exists some resemblance to Paropsia (Passifloraceae).

I. INTRODUCTION

The present study forms part of a general pollenmorphological survey of the family Flacourtiaceae, initiated at the Rijksherbarium in collaboration with Dr. H. Sleumer. The genus Hydnocarpus was selected for the first detailed study because it proved to have rather characteristic pollen types and is concentrated in SE. Asia and the Malesian region. Moreover, an adequate amount of well-determined material as well as a recent revision of the genus (Sleumer, 1954) were available. In total 34 species could be investigated, representing 85 % of the total number of species known. In addition, the pollen of a large number of other Flacourtiaceae was cursorily examined, in order to assess the pollen morphological relationships of Hydnocarpus within the family. The pollen of the genera Neoptychocarpus and Chlorocarpa, which resemble that of Hydnocarpus most, is described in more detail.

Previously, only Erdtman (1952) has, very briefly, described the pollen of *Hydnocarpus* elmeri which, however, proved to be rather atypical of the genus.

The pollen material was acetolysed for two minutes, mounted in glycerin jelly and photographed with a Leitz apochromatic OI objective (90/1.40). Acetolysed grains, covered with a thin layer of gold, were photographed under a Cambridge AII Scanning Electron Microscope at the Geological Institute, University of Leiden. Unless indicated otherwise, all material examined originated from the Rijksherbarium (L).

This study was performed under supervision of Mr. J. Muller. I express my sincere thanks to Dr. H. Sleumer for providing the material on which this study is based, for discussions and taxonomic corrections, and to Mr. Muller for critically examining the manuscript. Finally, I take this opportunity to convey my gratitude to Professor C. G. G. J. van Steenis, who has been my teacher in plant taxonomy and under whose guidance I have had the privilege of working in the Rijksherbarium for two and a half years.

II. GENERAL MORPHOLOGY

The pollen grains in Hydnocarpus are single, isopolar and tricolporate. Average size varies between 17 and 42 μ . Shape, as defined by the ratio of length polar axis (P) to length equatorial axis (E), is generally spherical but may vary between suboblate, subprolate and, rarely, prolate. The equatorial outline is always circular.

Size measurements were taken, whenever possible, from ten well developed grains and minimum, average, and maximum sizes are given separately for P and E. Under the lightmicroscope an endexine and an ektexine can be recognized, while the latter is further differentiated into a layer of columellae and a reticulate tectum. The inner surface of the endexine appears to be smooth. The columellae occur in two different types, a) supporting columellae which are more or less distinctly arranged in single rows in a reticulate pattern and which support the muri of the reticulum with their somewhat swollen heads, and b) free columellae, which are shorter, with rounded tops, more variable in diameter and occurring scattered in the lumina of some species. The presence or absence of these free columellae forms an important criterium for the definition of pollen types in Hydnocarpus. Size and distribution pattern of the lumina are also important for this purpose. Some species are characterized by a finer reticulum on the poles, others by a more even size distribution of the lumina or by finer lumina near the ektoapertures. There is also a rather marked difference between grains with a finely reticulate and those with a coarsely reticulate tectum, although transitions occur. The muri are biconvex in cross-section, exceptionally conical. The pollen grains are invariably tricolporate. The apertures in the ektexine (ektoapertures) are meridionally elongated slits (colpi); their relative length is indicated by the polar index (PI = width polar field/E) which varies between 0.23 (long colpi) and 0.75 (short colpi). In grains with short colpi, the width of the polar field may be difficult to measure and in such cases the length of the colpi is also indicated. The short colpi in coarsely reticulate grains may be rather inconspicuous.

The endexinous apertures are generally oval-subrectangular, as wide as, or slightly wider than colpi and sometimes indistinctly costate on polar sides.

III. SYSTEMATIC DESCRIPTIONS

A. HYDNOCARPUS GAERTN.

Section Taraktogenos (Hassk.) Warb.

Hydnocarpus annamensis (Gagnep.) Lescot & Sleum. — Pl. I: 1—5.

Material studied. Indo-China: Balansa 2400.

Pollen grains suboblate to subprolate, P/E 0.83 (0.96) 1.20, equatorial outline circular, tricolporate. Size: P 27 (28.7) 30 μ , E 24 (29.8) 35 μ . Ektoapertures 1 μ wide at equator, sides parallel, tips pointed, PI 0.25 (0.33) 0.42. Endoapertures distinct, oval, 7 μ long, 5 μ wide, equatorially elongated. Total wall thickness 3 μ throughout. Endexine 1 μ thick. Supporting columellae reticulately arranged, 0.5 μ in diameter, rather variable,

circular to oval in cross-section, I μ high; free columellae 0—3 per lumen, size variable, up to 0.5 μ high. Tectum coarsely to finely reticulate, lumina isodiametric to slightly elongated, 2—3 μ in diameter, finer on poles, muri straight to curved, 0.5 μ wide, I μ high.

Hydnocarpus calophylla (Ridl.) Sleum. — Pl. I: 6—9; Pl. VI: 1—2.

Material studied. Borneo: Jacobs 5181.

Pollen grains spherical, P/E 0.89 (0.93) 0.97, equatorial outline circular, tricolporate. Size: P 33 (35.9) 39 μ , E 35 (38.6) 41 μ . Ektoapertures 3.5—5 μ wide at equator, sides parallel at equator, tapering to pointed tips, PI 0.42 (0.47) 0.51. Endoapertures distinct, rectangular-oval, 18 μ long, 7 μ wide, elongated in equatorial direction. Total wall thickness 4.5 μ throughout. Endexine 2—4 μ thick. Supporting columellae reticulately arranged, 1.5—2 μ in diameter, rather variable, subangular-circular to -oval in cross-section, 1.5 μ high; free columellae 2—8 per lumen, size variable, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 2—5 μ in diameter, uniformly distributed, muri straight to curved, 1 μ wide, 1 μ high.

Hydnocarpus hainanensis (Merr.) Sleum.

Material studied, Hainan: F. C. How 70706.

Pollen grains spherical, P/E 0.89 (0.94) 1.04, equatorial outline circular, tricolporate. Size: P 23 (25) 27 μ , E 25 (26.5) 28 μ . Ektoapertures I μ wide at equator, sides parallel, tips pointed, PI 0.19 (0.28) 0.31. Endoapertures indistinct, oval to rectangular, \pm 6 μ long, \pm 1.5 μ wide, elongated in equatorial direction. Total wall thickness 2.5—3 μ throughout. Endexine I μ thick. Supporting columellae reticulately arranged, 0.5 μ in diameter, rather variable, subangular-circular to -oval in cross-section, 0.5—I μ high; free columellae 0—2 per lumen, size variable, up to 0.5 μ high. Tectum rather finely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, I—3 μ in diameter, uniformly distributed, muri straight to curved, I μ high, \pm 0.5 μ wide.

Hydnocarpus heterophylla Bl. — Pl. I: 10—13; Pl. VI: 3—4.

Material studied. Philippines: BS 41600, PNH 23029 (ssp. philippinensis Sleum.). — Java: Unesco 43, Kostermans c.s. 400 (ssp. heterophylla).

Pollen grains suboblate to subprolate, P/E 0.78 (0.97) 1.23, equatorial outline circular, tricolporate. Size: P 21 (28.5) 38 μ , E 22 (29.6) 38 μ . Ektoapertures 1—1.5 μ wide at equator, sides parallel, tips pointed, PI 0.20 (0.28) 0.40. Endoapertures indistinct to rather distinct, oval, \pm 6—10 μ long, \pm 3—7 μ wide. Total wall thickness 2.5—3 μ throughout. Endexine \pm 1 μ thick. Supporting columellae reticulately arranged, 0.5—1.5 μ in diameter, rather variable, subangular-circular to -oval in cross-section, 1—1.5 μ high; free columellae 0—5 per lumen, size variable, up to 0.5 μ high. Tectum finely to coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 1—4 μ in diameter, uniformly distributed, muri straight to curved, 0.5—1 μ wide, 0.5—1 μ high.

Hydnocarpus ilicifolia King. — Pl. II: 1—8.

Material studied. Laos: Kerr 21293.

Pollen grains spherical, P/E 0.93 (1.00) 1.10, equatorial outline circular, tricolporate.

Size: P 27 (30.1) 33 μ , E 29 (30) 31 μ . Ektoapertures I—2 μ wide at equator, sides parallel, tips pointed, PI 0.21 (0.27) 0.33. Endoapertures indistinct, oval, \pm 7 μ long, \pm 3 μ wide. Total wall thickness 3.5 μ throughout. Endexine 1.5 μ thick. Supporting columellae reticulately arranged, 0.5 μ in diameter, rather variable, subangular-circular to -oval in cross-section, I μ high; free columellae 0—2 per lumen, size variable, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, variable in shape, 1.5—2.5 μ in diameter, finer on poles, muri straight to curved, I μ wide, I μ high.

Hydnocarpus kunstleri (King) Warb.

Material studied. Borneo: Jacobs 5246. — Sumatra: Forbes 3033.

Pollen grains spherical, P/E 0.85 (0.99) 1.08, equatorial outline circular, tricolporate. Size: P 22 (26.1) 30 μ , E 22 (25.9) 30 μ . Ektoapertures 0.5—1.5 μ wide at equator, sides parallel, tips pointed, PI 0.23 (0.35) 0.41. Endoapertures oval, 9 μ long, 4 μ wide, elongated in equatorial direction. Total wall thickness 3 μ throughout. Endexine 1—1.5 μ thick. Supporting columellae reticulately arranged, 0.5 μ in diameter, rather variable, subangular-circular to -oval in cross-section, 0.5—1 μ high; free columellae 0—2 per lumen, up to 0.5 μ high. Tectum coarsely reticulate. lumina irregularly shaped, isodiametric to slightly elongated, 2—2.5 μ in diameter, uniformly distributed, muri straight to curved, 1 μ wide, 1 μ high.

Hydnocarpus kurzii (King) Warb.

Material studied. Burma: (cult. Hawaii) Gillet 1943. — Thailand: Kerr 15038.

Pollen grains spherical to subprolate, P/E 0.87 (1.02) 1.21, equatorial outline circular, tricolporate. Size: P 25 (26.9) 29 μ , E 24 (26.7) 28 μ . Ektoapertures 1.5—2.5 μ wide at equator, sides parallel, tips pointed, PI 0.22 (0.30) 0.37. Endoapertures oval, 10 μ long, 3—4 μ wide, elongated in equatorial direction. Total wall thickness 3 μ throughout. Endexine 1 μ thick. Supporting columellae reticulately arranged, 0.5—1 μ in diameter, rather variable, subangular-circular to -oval in cross-section, 1 μ high; free columellae 0—1 per lumen, up to 0.5 μ high. Tectum coarsely reticulate. lumina irregularly shaped to slightly elongated, 2—3 μ in diameter, finer on poles, muri straight to curved, 1 μ wide, 1 μ high.

Hydnocarpus tenuipetala Sleum.

Material studied. Borneo: S 25371.

Pollen grains spherical, P/E 0.92 (0.94) 1.00, equatorial outline circular, tricolporate. Size: P 22 (23.1) 24 μ , E 24 (24.5) 25 μ . Ektoapertures I—I.5 μ wide at equator, sides parallel, tips pointed, PI 0.32 (0.36) 0.39. Endoapertures indistinct. Total wall thickness 3 μ throughout. Endexine I μ thick. Supporting columellae reticulately arranged, 0.5—I μ in diameter, rather variable, subangular-circular to -oval in cross-section, I μ high; free columellae 0—I per lumen, up to 0.5 μ high. Tectum finely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, I—2 μ in diameter, finer on poles, muri straight to curved, 0.5—I μ wide, I μ high.

Hydnocarpus wrayi King.

Material studied. Perak: Wray 2608.

Pollen grains spherical, P/E 0.89 (0.98) 1.08, equatorial outline circular, tricolporate. Size: P 23 (24.3) 27 μ , E 25 (25.3) 26 μ . Ektoapertures 1 μ wide at equator, sides parallel, tips pointed, PI 0.19 (0.24) 0.30. Endoapertures rather indistinct, oval, 7 μ long, 2 μ wide, equatorially elongated. Total wall thickness 3 μ throughout. Endexine 1 μ thick. Supporting columellae reticulately arranged, 1 μ in diameter, rather variable, subangular-circular in cross-section, 1 μ high; free columellae 2—5 per lumen, size variable, up to 1 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 1.5—3.5 μ in diameter, uniformly distributed, muri straight to curved, 1 μ wide, 1 μ high.

Section Hydnocarpus

Subsection OLIGANTHERA Warb.

Hydnocarpus alcalae C. DC. — Pl. II: 9—11; Pl. VI: 5—6.

Material studied. Philippines: PNH 5870.

Pollen grains spherical, P/E 0.92 (0.96) 1.04, equatorial outline circular, tricolporate. Size: P 27 (30.5) 33 μ , E 30 (31.4) 33 μ . Ektoapertures 8 (10) 12 μ long, PI \pm 0.62, 1—2.5 μ wide at equator, sides parallel, tips pointed. Endoapertures indistinct, circular, 3—4 μ in diameter. Total wall thickness 3.5 μ throughout. Endexine 1—1.5 μ thick. Supporting columellae reticulately arranged, 0.5—1 μ in diameter, rather variable, subangular-circular in cross-section, 1 μ high; free columellae 5—20 per lumen, size variable, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 2—5 μ in diameter, uniformly distributed, muri straight to curved, 1 μ wide, 1 μ high.

Hydnocarpus alpina Wight.

Material studied. Madras: Beddome 1873.

Pollen grains spherical, P/E 1.03 (1.11) 1.24, equatorial outline circular, tricolporate. Size: P 29 (31.8) 36 μ , E 27 (28.6) 31 μ . Ektoapertures 1 μ wide at equator, sides parallel, tips pointed, PI 0.21 (0.31) 0.39. Endoapertures oval, 9 by 5 μ , elongated in equatorial direction. Total wall thickness 3 μ . Endexine 1 μ thick. Supporting columellae indistinctly reticulately arranged, 0.5—1 μ in diameter, rather variable, subangular-circular in cross-section, 1—1.5 μ high; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, 1—1.5 μ in diameter, uniformly distributed, muri straight to curved, 1 μ wide, 0.5—1 μ high.

Hydnocarpus anthelmintica Pierre.

Material studied. Philippines (cult.): PNH 36211.

Pollen grains spherical, P/E 0.86 (0.94) 1.04, equatorial outline circular, tricolporate. Size: P 27 (29.5) 31 μ , E 30 (31.4) 33 μ . Ektoapertures 12 (14.2) 16 μ long, 1—2 μ wide at equator, sides parallel, tips pointed, PI \pm 0.65. Endoapertures distinct, oval, 4 μ long, 2 μ wide, elongated in equatorial direction. Total wall thickness 3.5 μ throughout.

Endexine 1.5—2 μ thick. Supporting columellae indistinctly reticulately arranged, 0.5—1 μ in diameter, rather variable, subangular-circular in cross-section; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, \pm 0.5 μ in diameter, uniformly distributed, muri straight to curved, 0.5 μ wide, 1 μ high.

Hydnocarpus beccariana Sleum.

Material studied. Borneo: S 25381.

Pollen grains spherical, P/E 0.92 (1.03) 1.15, equatorial outline circular, tricolporate. Size: P 40 (42) 45 μ , E 38 (40.6) 44 μ . Ektoapertures 1—2 μ wide at equator, sides parallel, tips pointed, PI 0.27 (0.34) 0.47. Endoapertures irregularly shaped, isodiametric to oval, 4—8 μ in diameter, elongated in equatorial direction. Total wall thickness 2.5—3 μ throughout. Endexine I μ thick. Supporting columellae indistinctly reticulately arranged, I μ in diameter, rather variable, subangular-circular to -oval in cross-section, I—1.5 μ high; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, 0.5—I μ in diameter, uniformly distributed, muri straight to curved, I μ wide, I μ high.

Hydnocarpus borneensis Sleum.

Material studied. Borneo: SAN 36211.

Pollen grains spherical, P/E 0.97 (1.07) 1.27, equatorial outline circular, tricolporate. Size: P 35 (38.9) 45 μ , E 34 (36.4) 39 μ . Ektoapertures I μ wide at equator, sides parallel, tips pointed, PI 0.31 (0.34) 0.39. Endoapertures rather distinct, oval, 8—11 μ long, 5—6 μ wide, elongated in equatorial direction. Total wall thickness 3—3.5 μ throughout. Endexine I—1.5 μ thick. Supporting columellae reticulately arranged, I μ in diameter, rather variable, subangular-circular to -oval in cross-section, I μ high; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, I—2 μ in diameter, uniformly distributed, muri straight to curved, I μ wide, I μ high.

Hydnocarpus castanea Hook. f. & Thoms. — Pl. II: 12; Pl. III: 1—4; Pl. VII: 1—2.

Material studied. Thailand: Kerr 18342.

Pollen grains spherical, P/E 0.93 (0.98) 1.07, equatorial outline circular, tricolporate. Size: P 31 (32.8) 34 μ , E 32 (33.4) 34 μ . Ektoapertures I μ wide at equator, sides parallel, tips pointed, PI 0.28 (0.36) 0.48. Endoapertures distinct, oval, 7 μ long, 5 μ wide, elongated in equatorial direction. Total wall thickness 3 μ throughout. Endexine I μ thick. Supporting columellae reticulately arranged, 0.5—I μ in diameter, rather variable, subangular-circular to -oval in cross-section, I μ high; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, uniformly distributed, I—2 μ in diameter, muri straight to curved, I μ wide, I μ high.

Hydnocarpus cucurbitina King.

Material studied. Perak: Scortechini 2056.

Pollen grains spherical to subprolate, P/E 1.00 (1.14) 1.26, equatorial outline circular, tricolporate. Size: P 22 (26.3) 29 μ , E 22 (22.5) 23 μ . Ektoapertures 1 μ wide at equator, sides parallel, tips pointed, PI 0.27 (0.29) 0.30. Endoapertures oval, 6 by 1.5 μ , elongated in equatorial direction. Total wall thickness 2 μ throughout. Endexine 1 μ thick. Support-

ing columellae very indistinctly arranged in a reticulate pattern, 0.5 μ in diameter, rather variable, subangular to circular in cross-section, 0.5 μ high; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, I μ in diameter, uniformly distributed, muri straight to curved, 0.5 μ wide, I μ high.

Hydnocarpus curtisii King.

Material studied. Penang: Curtis 1535.

Pollen grains spherical, P/E 0.94 (1.06) 1.17, equatorial outline circular, tricolporate. Size: P 30 (31.8) 35 μ , E 28 (30.1) 32 μ . Ektoapertures 0.5 μ wide at equator, sides parallel, tips pointed, PI 0.21 (0.26) 0.30. Endoapertures rather indistinct, oval, 6 μ long, 2.5 μ wide, elongated in equatorial direction. Total wall thickness 3 μ throughout. Endexine 1 μ thick. Supporting columellae reticulately arranged, 0.5—1 μ in diameter, rather variable, subangular to circular in cross-section, 1 μ high; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, 1—1.5 μ in diameter, uniformly distributed, muri straight to curved, 0.5—1 μ wide, 1 μ high.

Hydnocarpus elmeri Merr. — Pl III: 5-8; Pl. VII: 3-4.

Material studied. Borneo: Elmer 20736.

Pollen grains spherical, P/E 1.00 (1.12) 1.21, equatorial outline circular, tricolporate. Size: P 17 (17.7) 19 μ , E 14 (16.9) 17 μ . Ektoapertures 1 μ wide at equator, sides parallel, tips pointed, PI 0.27 (0.32) 0.38. Endoapertures very indistinct. Total wall thickness 2 μ throughout. Endexine 1 μ thick. Supporting columellae reticulately arranged, 0.5 μ in diameter, 0.5 μ high, rather variable, subangular to oval in cross-section; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, 0.5 μ in diameter, slightly finer near ektoapertures, muri straight to curved, 0.5 μ wide, 0.5 μ high, upper surface conical in cross-section.

Hydnocarpus glaucescens Bl.

Material studied. Sumatra, Padang: Beccari 948.

Pollen grains spherical, P/E 0.96 (1.05) 1.14, equatorial outline circular, tricolporate. Size: P 22 (24) 25 μ . Ektoapertures I μ wide at equator, sides parallel, tips pointed, PI 0.32 (0.36) 0.40. Endoapertures very indistinct. Total wall thickness 3 μ . Endexine 1.5 μ thick. Supporting columellae reticulately arranged, I μ in diameter, rather variable, subangular to oval in cross-section, I μ high; free columellae I—4 per lumen, 0.5 μ in diameter, 0.5 μ high. Tectum finely to coarsely reticulate, lumina 1.5—3 μ in diameter, uniformly distributed, irregularly shaped, isodiametric to elongated, muri straight to curved, I μ wide, I μ high.

Hydnocarpus nana King.

Material studied. Perak: King's collector 5828.

Pollen grains spherical, P/E 0.81 (0.88) 1.00, equatorial outline circular, tricolporate. Size: P 17 (17.9) 19 μ , E 19 (20.3) 21 μ . Ektoapertures 0.5 μ wide at equator, sides parallel, tips pointed, PI 0.45 (0.48) 0.50. Endoapertures rather indistinct, oval, \pm 4 by 1 μ , elongated in equatorial direction. Total wall thickness 2 μ throughout. Endexine 0.5—1 μ

thick. Supporting columellae reticulately arranged, 0.5μ in diameter, rather variable, circular to oval in cross-section, 0.5μ high; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, $1-1.5 \mu$ in diameter, uniformly distributed, muri straight to curved, 0.5μ wide, 0.5μ high.

Hydnocarpus pentagyna Sloot. — Pl. III: 9—13.

Material studied. Borneo: SAN 15170, S 22116.

Pollen grains spherical to prolate, P/E 0.90 (1.10) 1.36, equatorial outline circular, tricolporate. Size: P 28 (33.9) 41 μ , E 28 (30.7) 35 μ . Ektoapertures 0.5—1 μ wide at equator, sides parallel, tips pointed, PI \pm 0.23. Endoapertures distinct, oval, \pm 10 μ long, \pm 5 μ wide, elongated in equatorial direction. Total wall thickness 3 μ throughout. Endexine 1 μ thick. Supporting columellae indistinctly reticulately arranged, 0.5 μ in diameter, subangular-circular to -oval in cross-section, 1—1.5 μ high; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, 0.5—1 μ in diameter, uniformly distributed, muri straight to curved, 0.5—1 μ wide, 1 μ high.

Hydnocarpus pentandra (Buch,-Ham.) Oken; H. laurifolia (Dennst.) Sleum.

Material studied. India: Hook. f. & Thoms. s.n.

Pollen grains spherical, P/E 0.91 (1.07) 1.23, equatorial outline circular, tricolporate. Size: P 21 (24) 27 μ , E 20 (22.3) 24 μ . Ektoapertures 1—2 μ wide at equator, sides parallel, tips pointed, PI 0.27 (0.33) 0.39. Endoapertures oval, 10 μ long, 3—4 μ wide, elongated in equatorial direction. Total wall thickness 3 μ throughout. Endexine 1 μ thick. Supporting columellae indistinctly reticulately arranged, 0.5 μ in diameter, rather variable, subangular-circular to -oval in cross-section, 1 μ high; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, 1—2 μ in diameter, uniformly distributed, muri straight to curved, 1 μ wide, 1 μ high.

Hydnocarpus subfalcata Merr.

Material studied. Borneo: S 18087.

Pollen grains spherical, P/E 0.93 (0.98) 1.07, equatorial outline circular, tricolporate. Size: P 25 (28.5) 32 μ , E 26 (29.2) 32 μ . Ektoapertures 1—2 μ wide at equator, sides parallel, tips pointed, PI 0.46 (0.50) 0.56. Endoapertures indistinct or distinct, 3 μ wide, length variable, equatorially elongated and sometimes nearly merging with each other. Total wall thickness 4—4.5 μ . Endexine 1.5—2 μ thick, occasionally somewhat thickened up to 2.5 μ around the endoapertures. Supporting columellae reticulately arranged, 0.5—1 μ in diameter, rather variable, subangular-circular to -oval in cross-section; free columellae 1—6 per lumen, size variable, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric, 2—4 μ in diameter, uniformly distributed, muri straight to curved, 1 μ wide, 1 μ high.

Hydnocarpus sumatrana (Miq.) Koord.

Material studied. Philippines: FB 3916.

Pollen grains spherical, P/E 1.11 (1.15) 1.21, equatorial outline circular, tricolporate. Size: P 35 (35.3) 37 μ , E 29 (31.7) 35 μ . Ektoapertures 1 μ wide at equator, sides parallel, tips pointed. PI 0.35 (0.37) 0.39. Endoapertures indistinct. Total wall thickness 3 μ .

Endexine I μ thick. Supporting columellae reticulately arranged, I μ in diameter, rather variable, subangular-circular in cross-section, I.5 μ high; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, 0.5—I μ in diameter, uniformly distributed, muri straight to curved, I μ wide, I.5 μ high.

Hydnocarpus venenata Gaertn.

Material studied. Ceylon: Thwaites 1630.

Pollen grains spherical, P/E 0.97 (1.00) 1.04, equatorial outline circular, tricolporate. Size: P 27 (28.1) 29 μ , E 27 (28.2) 29 μ . Ektoapertures 0.5—1 μ wide at equator, sides parallel, tips pointed, PI 0.21 (0.26) 0.32. Endoapertures distinct, oval, 8 μ long, 3 μ wide, elongated in equatorial direction. Total wall thickness 4 μ throughout. Endexine 1.5 μ thick. Supporting columellae reticulately arranged, 0.5—1 μ in diameter, rather variable, subangular-circular to -oval in cross-section, 1 μ high; free columellae 0—2 per lumen, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 2—4 μ in diameter, finer on poles, muri straight to curved, 1 μ wide, 1 μ high.

Hydnocarpus yatesii Merr.

Material studied, Sumatra: R. Si Toroes 4644.

Pollen grains spherical, P/E 0.88 (0.96) 1.05, equatorial outline circular, tricolporate. Size: P 21 (21.6) 22 μ , E 21 (22.5) 24 μ . Ektoapertures 0.5—1 μ wide at equator, sides parallel, tips pointed, PI 0.18 (0.23) 0.27. Endoapertures oval, 7 μ long, 2—2.5 μ wide, elongated in equatorial direction. Total wall thickness 5 μ throughout. Endexine 1—1.5 μ thick. Supporting columellae reticulately arranged, 0.5—1 μ in diameter, rather variable, subangular-circular to -oval in cross-section, 1 μ high; free columellae 1—4 per lumen, size variable, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 2—3 μ in diameter, uniformly distributed, muri straight to curved, 0.5—1 μ wide, 0.5 μ high.

Subsection PLEIANTHERA Warb.

Hydnocarpus crassifolia Sleum.

Material studied. Borneo: Beccari 3972.

Pollen grains spherical, P/E 0.91 (0.99) 1.10, equatorial outline circular, tricolporate. Size: P 32 (35.2) 38 μ , E 32 (35.4) 38 μ . Ektoapertures 8—10 μ long, PI \pm 0.75, 0.5—1 μ wide at equator, sides parallel, tips pointed. Endoapertures indistinct. Total wall thickness 5—6 μ . Endexine 2.5—3 μ thick. Supporting columellae reticulately arranged, diameter 1.5—2.5 μ , rather variable, subangular-circular or -oval in cross-section, 1—1.5 μ high; free columellae 4—14 per lumen, size variable, up to 1 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 2.5—3.5 μ in diameter, uniformly distributed, muri straight to curved, 1.5 μ wide, 1.5 μ high.

Hydnocarpus octandra Thwait.

Material studied. Ceylon: Thwaites 2640.

Pollen grains spherical, P/E 0.93 (0.99) 1.14, equatorial outline circular, tricolporate. Size: P 28 (29.4) 32 μ , E 28 (29.7) 32 μ . Ektoapertures 1—2 μ wide at equator, sides

parallel, tips pointed, PI 0.35—0.40. Endoapertures indistinct, oval. Total wall thickness 4 μ . Endexine 1.5 μ thick. Supporting columellae reticulately arranged, 1—1.5 μ in diameter, rather variable, subangular-circular to -oval in cross-section, 1 μ high; free columellae 3—12 per lumen, size variable, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 3—5 μ in diameter, uniformly distributed, muri straight to curved, 1 μ wide, 1—1.5 μ high.

Hydnocarpus woodii Merr. — Pl. IV: 1-6.

Material studied. Borneo: SAN 20859.

Pollen grains spherical, P/E 0.86 (1.03) 1.14, equatorial outline circular, tricolporate. Size: P 28 (29.2) 31 μ , E 24 (28.4) 31 μ . Ektoapertures 0.5—1 μ wide at equator, sides parallel, tips pointed, PI 0.28 (0.34) 0.40. Endoapertures rather indistinct, 6 μ long, 3.5 μ wide, elongated in equatorial direction. Total wall thickness 3.5—4 μ throughout. Endexine 1.5 μ thick. Supporting columellae reticulately arranged, \pm 1 μ in diameter, rather variable, subangular-circular or -oval in cross-section, 1 μ high; free columellae 1—7 per lumen, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 2—4 μ in diameter, uniformly distributed, muri straight to curved, 1—1.5 μ wide, 1 μ high.

Section Asteriastigma (Bedd.) Warb.

Hydnocarpus anomala (Merr.) Sleum. — Pl. IV: 7—13; Pl. VII: 5—6.

Material studied. Borneo: SAN 35247.

Pollen grains suboblate to spherical, P/E 0.83 (1.00) 1.02, equatorial outline circular, tricolporate. Size: P 28 (32) 37 μ , E 30 (32.1) 37 μ . Ektoapertures 11 (13.7) 15 μ long, 2—4 μ wide at equator, PI \pm 0.60—0.65, tips pointed. Endoapertures distinct, oval, 7—10 μ long, 5—6 μ wide, elongated in equatorial direction. Total wall thickness 3—5 μ throughout. Endexine 1—1.5 μ thick. Supporting columellae reticulately arranged, 1—1.5 μ in diameter, subangular-circular to -oval in cross-section; free columellae 1—13 per lumen, size variable, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to elongated, 2—6 μ in diameter, uniformly distributed, muri straight to curved, 1 μ high.

Hydnocarpus gracilis (Sloot.) Sleum.

Material studied. Sumatra: Krukoff 4085.

Pollen grains spherical, P/E 0.94 (1.04) 1.07, equatorial outline circular, tricolporate. Size: P 29 (31) 32 μ , E 28 (29.7) 31 μ . Ektoapertures I μ wide at equator, sides parallel, tips pointed, PI 0.40 (0.48) 0.53. Endoapertures distinct, oval, 10 μ long, 5 μ wide, elongated in equatorial direction. Total wall thickness 3.5—5 μ . Endexine 1.5 μ thick, 2.5 μ thick around the endoapertures. Supporting columellae reticulately arranged, 1—2 μ in diameter, rather variable, subangular-circular to -oval in cross-section, I μ high; free columellae 2—7 per lumen, size variable, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 2—7 μ in diameter, uniformly distributed, muri straight to curved, I μ high, 1.5 μ wide.

Hydnocarpus macrocarpa (Bedd.) Warb. ssp. burmanica Sleum.

Material studied. Burma: Parkinson 402.

Pollen grains spherical, P/E 0.93 (1.01) 1.12, equatorial outline circular, tricolporate. Size: P 27 (28.1) 30 μ , E 26 (27.9) 30 μ . Ektoapertures 12 (13) 14 μ long, PI 0.61—0.67, 2.5—3 μ wide at equator, tips pointed. Endoapertures distinct, oval, 10 by 4—5 μ , elongated in equatorial direction. Total wall thickness 4 μ throughout. Endexine 1.5 μ thick. Supporting columellae reticulately arranged, 0.5—1 μ in diameter, rather variable, subangular-circular in cross-section, 1 μ high; free columellae 2—7 per lumen, size variable, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to elongated, 2—4 μ in diameter, uniformly distributed, muri straight to curved, 0.5—1 μ wide, 1.5 μ high.

Hydnocarpus polypetala (Sloot.) Sleum.

Material studied. Borneo: Jacobs 5313, Kostermans 21592.

Pollen grains spherical to subprolate, P/E 0.88 (1.05) 1.26, equatorial outline circular, tricolporate. Size: P 28 (34.5) 41 μ , E 26 (32.9) 41 μ . Ektoapertures 1—3 μ wide at equator, sides parallel, tips pointed, PI 0.27 (0.38) 0.47. Endoapertures distinct, oval, 10—14 μ long, 5—7 μ wide, elongated in equatorial direction. Total wall thickness 4—6 μ throughout. Endexine 1—2 μ thick. Supporting columellae reticulately arranged, 1—1.5 μ in diameter, rather variable, subangular-circular to -oval in cross-section, 1—2 μ high; free columellae 0—5 per lumen, size variable, up to 1 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 2—5 μ in diameter, uniformly distributed, muri straight to curved, 1—1.5 μ wide.

Section Kerrandrias Sleum.

Hydnocarpus calvipetala Craib. — Pl. V: 1-3.

Material studied. Thailand: Kerr 16518.

Pollen grains spherical, P/E 0.92 (1.03) 1.17, equatorial outline circular, tricolporate. Size: P 27 (31.2) 33 μ , E 27 (30.1) 32 μ . Ektoapertures 1.5—3 μ wide at equator, sides parallel, tips pointed, PI 0.20 (0.27) 0.37. Endoapertures distinct, oval, 8 μ long, 5 μ wide, elongated in equatorial direction. Total wall thickness 3.5 μ throughout. Endexine 1—1.5 μ thick. Supporting columellae reticulately arranged, 0.5—1 μ in diameter, rather variable, subangular-circular to -oval in cross-section, 1 μ high; free columellae 0—5 per lumen, scattered, size variable, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 3—5 μ in diameter, on poles 2—3 μ in diameter, muri straight to curved, 1 μ wide, 1 μ high.

B. CHLOROCARPA ALSTON

Chlorocarpa pentaschista Alston. — Pl. V: 4—9.

Material studied. Ceylon: Thwaites 2018 (BM).

Pollen grains subprolate, P/E 1.11 (1.18) 1.24, equatorial outline circular, tricolporate. Size: P 38 (39.6) 41 μ , E 32 (33.6) 36 μ . Ektoapertures 1 μ wide at equator, sides parallel,

tips pointed, PI 0.22 (0.27) 0.31. Endoapertures indistinct. Total wall thickness 2 μ . Endexine 0.5—I μ thick. Supporting columellae indistinctly reticulately arranged, 0.5—I μ in diameter, rather variable, round to oval in cross-section, I μ high; free columellae absent. Tectum finely reticulate, lumina irregularly shaped, isodiametric to elongated, 0.5—I μ in diameter, uniformly distributed, muri straight to curved, 0.5 μ wide, I μ high.

C. NEOPTYCHOCARPUS BUCHHEIM

Neoptychocarpus apodanthus (Kuhlmann) Buchheim.

Material studied. Brasil, Amazonas: Silva 57815.

Pollen grains spherical, P/E 0.88 (1.00) 1.07, equatorial outline circular, tricolporate. Size: P 22 (26.4) 30 μ , E 25 (26.4) 28 μ . Ektoapertures 0.5 μ wide at equator, sides parallel, tips pointed, PI 0.36—0.52. Endoapertures distinct, irregularly isodiametric to oval, 2.5—7 μ long, 3—5 μ wide. Total wall thickness 2 μ , around the endoapertures 5 μ . Endexine \pm 0.5 μ , thickened mainly on polar sides of the endoapertures, width of these thickenings up to 2.5 μ . Supporting columellae in single rows, reticulately arranged, 0.5 μ in diameter, rather variable, circular to oval in cross-section, \pm 1 μ high; free columellae 0—1 per lumen, size variable, up to 0.5 μ high. Tectum coarsely reticulate, lumina irregularly shaped, isodiametric to slightly elongated, 1.5—3 μ in diameter, smaller near the apertures, muri straight to angular, 0.5—1 μ wide, 0.5 μ high.

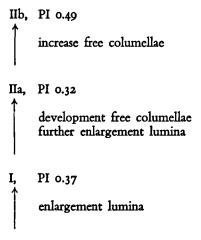
IV. POLLEN TYPES

From the preceding systematic descriptions it will be clear that the pollen of the *Hydno-carpus* species is of the same general type and that all other characters vary continuously between the species.

Based on a combination of characters, the following pollen types can nevertheless be recognized:

- Type I: Lumina $\leq 2 \mu$ in diameter, free columellae absent, supporting columellae often irregularly arranged, ektoapertures medium long.
- Type II: Lumina $\geq 2 \mu$, free columellae present or absent, supporting columellae in a reticulate pattern, length of ektoapertures variable.
 - Subtype IIa: 0—6 free columellae/lumen, lumina often finer on poles, ektoapertures long.
 - Subtype IIb: 0—20 free columellae/lumen, lumen size uniform, ektoapertures short, often indistinct.

If it is assumed that the small, finely reticulate pollen type which occurs in a majority of Flacourtiaceous genera, has been the ancestral type, a phylogenetic sequence of *Hydnocarpus* pollen types as shown in fig. I can be envisaged.



basic type of finely reticulate Flacourtiaceae pollen

Fig. 1. Pollenmorphological trends in Hydnocarpus.

This would indicate that the coarsely reticulate grains with short ektoapertures and abundant free columellae (pollen type IIb) form a derived pollen type. Hydnocarpus elmeri (pollen type I) shows the closest resemblance to the basic Flacourtiaceous pollen type.

V. POLLEN MORPHOLOGY AND TAXONOMY

The distribution of the investigated species over the types and subtypes is presented in Table I. From this table it would appear that subsection Oliganthera of section Hydnocarpus has preserved the most complete range of variation with both primitive and advanced types present. Subsection Pleianthera has only advanced pollen types. Section Taraktogenos lacks the primitive types but has developed a high percentage of IIa-type grains. Sections Asteriastigma and Kerrandrias show each a different derived type. Hutchinson (1967) has recently distinguished Taraktogenus Hassk. as a separate genus, while Sleumer (1954), following earlier authors, only accepts it as a subgenus of Hydnocarpus. Pollenmorphologically it clearly belongs to Hydnocarpus, which supports Sleumer's opinion.

Since it is also of interest to provide evidence for the taxonomic position of *Hydnocarpus* within *Flacourtiaceae*, a general survey of the pollen types present in this family was made. This survey was restricted to one or two representatives of each genus, as far as material was available, and is of a preliminary nature.

In general, pollen grains in *Flacourtiaceae* are fairly small, spherical to prolate and tricolporate. Ektoapertures are distinct, slitlike, endoapertures are variously developed and often elongated in equatorial direction. In some cases the endoapertures are much reduced and only developed as equatorial bridges in the colpate ektoapertures. Columellae are indistinct or distinct and often reticulately arranged.

Section	Taraktogenos	Hydnocarpus	arpus	Asteriastigma	Kerrandrias
Subsection		Oliganthera	Pleianthera		
d II	calophylla	alcalae yatesii	orassifolia octandra woodii	anomala gracilis macrocarpa polypetala	
II a	annamensis hainanensis heterophylla ilicifolia kunstleri kurzii tenuipetala	glaucescens subfalcata venenata			calvipetala
н		alpina anthelmintica beccariana borneensis cucurbitina curtisii elmeri nana pentagyna pentagyna sumatrana			·

Table I. Pollen types and taxonomic subdivision in Hydnocarpus

Based mainly on the development of the tectum, the following groups can be recognized:

- A. Tectum smooth or finely reticulate, columellae < 0.5 μ in diameter, grains generally small.
- B. Tectum reticulate to coarsely reticulate, columellae $> 0.5 \mu$ in diameter, grains fairly large (Hydnocarpus type).
- C. Tectum gemmate (Gynocardia type).
- D. Tectum areolate-perforate (Camptostylus type).
- E. Apertures porate (Lozania type).

In table II the distribution of these pollen types over the genera is indicated. It will be clear that the *Hydnocarpus* pollen type (B) is relatively infrequent. The pollen of the genus *Chlorocarpa* belongs to type B-I and this is also the genus which is taxonomically nearest to *Hydnocarpus*. Another genus with similar pollen is *Neoptychocarpus*, but this differs, as can be seen from the description in this paper, in the costate endoapertures and thinner wall. Besides, it belongs to quite a different tribe (*Casearieae*). The resemblance with pollen of *Trichostephanus* (*Trichostephaneae*) is not so striking, although it comes close to *Hydnocarpus* type I, from which it differs in the broader muri.

Outside *Flacourtiaceae* there is a distinct resemblance in sculpture with the pollen of *Paropsia*, a genus of *Passifloraceae* which has sometimes been referred to *Flacourtiaceae*. The aperture development in *Paropsia*, however, shows considerable difference and is typical for *Passifloraceae* (Pacqué, personal communication).

In conclusion it can be stated that, in contrast to the relative pollen morphological uniformity of *Flacourtiaceae*, within *Hydnocarpus* a derived pollen type has developed, characterized by a coarsely reticulate sculpture, free columellae, and a tendency to reduction of the ektoapertures. Within the genus this tendency is to a certain degree correlated with the taxonomic subdivision.

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SLEUMER, H. 1954. Flacourtiaceae. Flora Malesiana I, 5: 1-106.

A Pineda
A Pleuranthodendron

TABLE II. Distribution of pollen types (A-E) in relation to tribal subdivision (I-XI) in Flacourtiaceae.

		riacourtiaceae.		
I	Or	cobeae	VI	Homalieae
	Α	Rawsonia		A Byrsanthus
	A	Dasylepi s		A Gerrardina
	Α	Scottellia		A Homalium
	A	Berberidopsis		A Calantica
	A	Ahernia		A Bivinia
	Α	Erythrospermum		A Trimeria
	\mathbf{D}	Camptostylus		A Dissomeria
	Α	Poggea		
	Α	Peterodendron	VII	Phyllobotryeae
	Α	Grandidiera		no material available
	Α	Oncoba		
	A	Xylotheca	VIII	Flacourtieae
	A	Caloncoba		Flacourtiinae
	Α	Lindackeria		A Eichlerodendron
	Α	Mayna		A Xylosma
	Α	Carpotroche		A Azara
	A	Buchnerodendron		A Ludia
	A	Prockiopsis		A Tisonia
		•		A Aphloia
П	Par	ngieae		A Flacourtia
		dnocarpinae		A Dovyalis
	в	Hydnocarpus		A Neopringlea
	В	Chlorocarpa		
	С	Scaphocalyx		Idesiinae
	C	Trichadenia		A Bennettiodendron
	С	Gynocardia		A Cathayeia (= Idesia)
	Α	Pangium		A Poliothyrsis
	Α	Ryparosa		A Itoa
	C	Eleutherandra		
	C	Baileoxylon	IX	Casearieae
		•		A Lunania
	Kis	gelariinae		D Samyda
	A`	Kiggelaria		A Tetrathylacium
		Q 0		A Laetia
ш	Аb	atieae		A Bartholomaea
	Α	Abatia		A Euceraea
	A	Aphaerema		A Ophiobotrys
		•		A Osmelia
IV	Tri	chostephaneae		A Ryania
	В	Trichostephanus		A Hecatostemon
		4		A Zuelania
\mathbf{v}	Sco	olopieae		D Casearia
		lopiinae		B Neoptychocarpus
	A	Scolopia		
	Ā	Hemiscolopia	X	Bembicieae
	A	Streptothamnus		A Bembicia
	Ā	Pseudoscolopia		
			XI	Lacistemeae
	Pro	ckiinae		A Lacistema
	A	Prockia		E Lozania
	Ā	Hasseltia		
	A	Neosprucea		
	A			

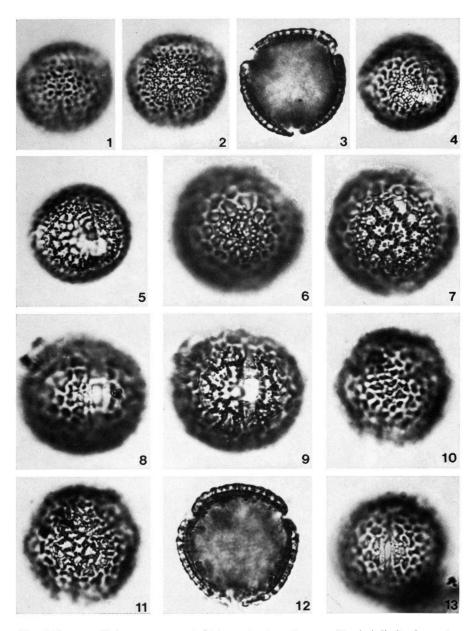


Plate I. Fig. 1—5: Hydnocarpus annamensis (Balansa 36211). — Fig. 6—9: H. calophylla (Jacobs 5181). — Fig. 10—13: H. heterophylla ssp. heterophylla (Kostermans 400). All × 1000.

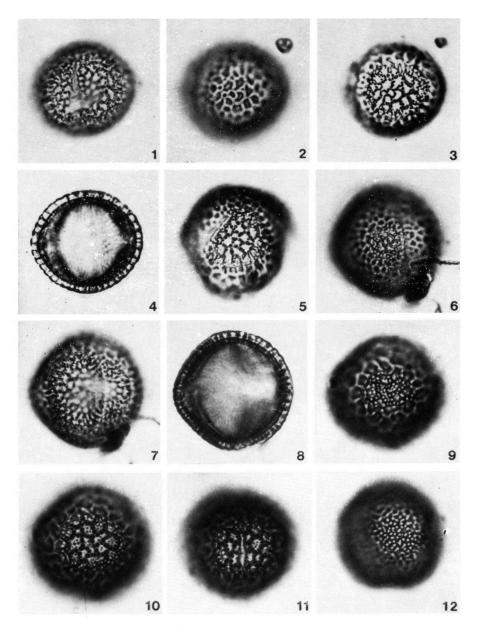


Plate II. Fig. 1—8: Hydnocarpus ilicifolia (Kerr 21293). Fig. 9—11: H. alcalae (PNH 58780). — Fig. 12: H. castanea (Kerr 18324). All \times 1000.

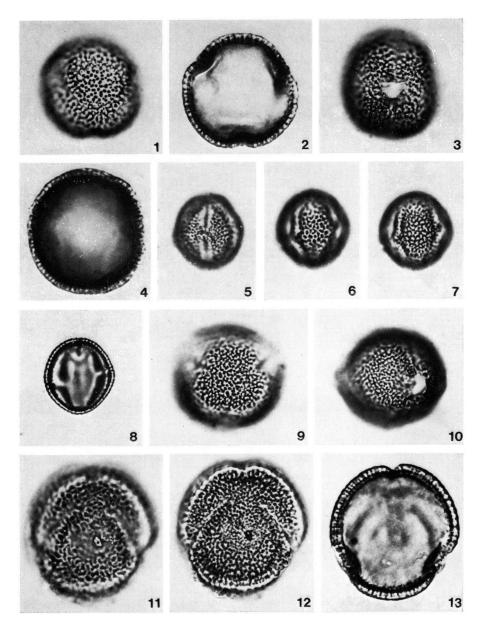


Plate III. Fig. 1—4: Hydnocarpus castanea (Kerr 18324). — Fig. 5—8: H. elmeri (Elmer 20736). — Fig. 9—10: H. pentagyna (S. 22116). — Fig. 11—13: H. pentagyna (SAN 15170). All × 1000.

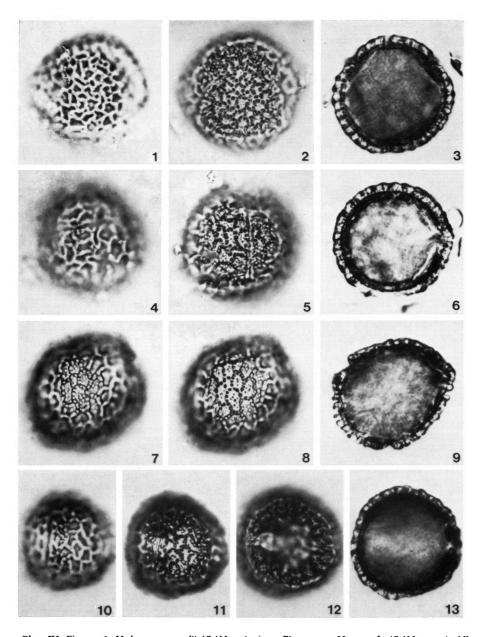


Plate IV. Fig. 1—6: Hydnocarpus woodii (SAN 20859). — Fig. 7—13: H. anomala (SAN 35247). All \times 1000.

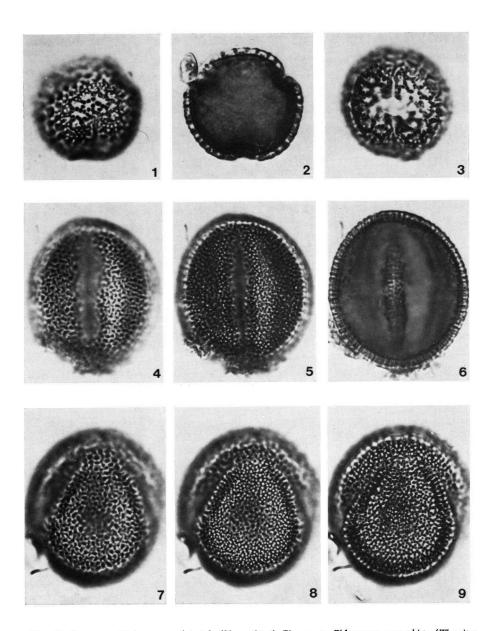


Plate V. Fig. 1—3: Hydnocarpus calvipetala (Kerr 16518). Fig. 4—9: Chlorocarpa pentaschista (Thwaites 2918). All \times 1000.

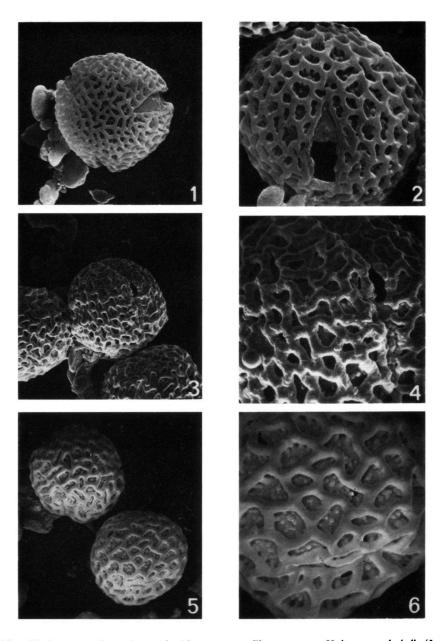


Plate VI. Stereoscan photomicrographs. Fig. 1, \times 1000. Fig. 2, \times 2000: Hydnocarpus calophylla (Jacobs 5181). Fig. 3, \times 1000, Fig. 4, \times 5000: H. heterophylla ssp. heterophylla (Kostermans 400). Fig. 5, \times 1000, Fig. 6, \times 2500: H. alcalae (PNH 58780).

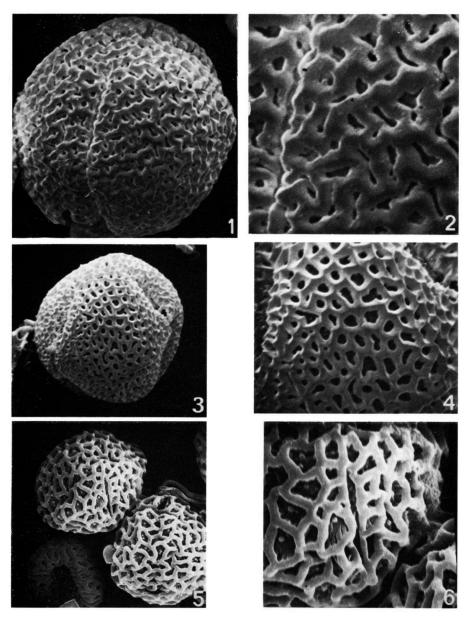


Plate VII. Stereoscan photomicrographs. Fig. 1, \times 2000, Fig. 2, \times 5000: Hydnocarpus castanea (Kerr 18324). Fig. 3, \times 2500, Fig. 4, \times 5000: H. elmeri (Elmer 20736). Fig. 5, \times 1000, Fig. 6, \times 2500: H. anomala (SAN 35247).

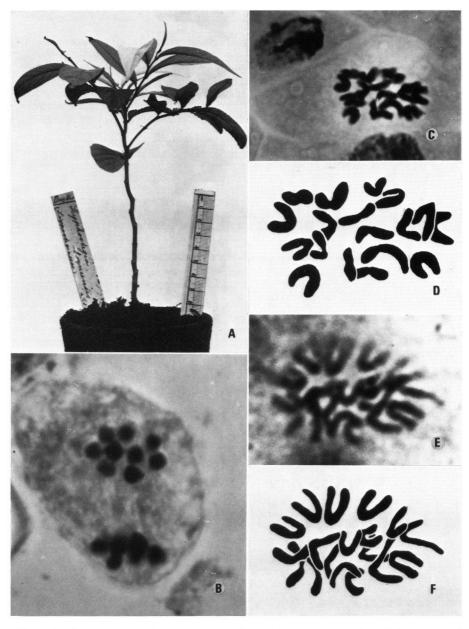


Plate I. Scyphostegia borneensis Stapf — A. young plant of about two years old. — B. late anaphase I, showing meiotic chromosomes in a pollen mother cell, n = 9. — C — F. mitotic chromosome complements, 2n = 18; C—D. chromosome complement of a vegetative cell of a flower-bud, with D illustrating the inked chromosomes of C; E—F. chromosome complement of a roottip cell, with F illustrating the inked chromosomes of E. — (B & D—F, \times 3000; C, \times 1500. A & E, Nooteboom & Aban 1600; B & C, Nooteboom & Aban 1539).