POLLENMORPHOLOGICAL NOTES ON THE GENUS DIMOCARPUS (SAPINDACEAE)

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SUMMARY

The pollen morphology of all 5 species of the genus Dimocarpus was studied. General pollen morphology is rather uniform and only one main type is present, which could be subdivided into 7 subtypes on minor differences in shape, aperture, and exine pattern. Intraspecific variability is present in some species. Morphological trends are established and related to the taxonomic subdivision. Taxa which are macromorphologically advanced appear to have developed also derived pollen subtypes.

I. INTRODUCTION

The present note is complementary to the taxonomic revision of Dimocarpus by Leenhouts in this volume. All five species recognized by him were available for palynological investigation. The variable species D. longan, in which two subspecies and five varieties are recognized, was studied in some detail in order to elucidate intraspecific pollen variability. Although the pollen of Dimocarpus is all of the same general type, various morphological trends could be established. This made it desirable to recognize subtypes, which serve to indicate both the amount of intraspecific variability and the evolutionary level reached. They are indicated by letters A—F. Methods of investigation were the same as used in a previous study on the genus Lepisanthes (Muller, 1970). Unless otherwise indicated the material used originated from the Rijksherbarium (L).

The photomicrographs of Plate IV were taken with a Cambridge A II Scanning Electron Microscope, by courtesy of Dr. Th. S. Krans at the Geological Institute, University of Leiden. Acetolysed grains, coated with gold were used for this purpose. The author is again indebted to Dr. P. W. Leenhouts for stimulating discussions.
II. GENERAL MORPHOLOGY

The pollen grains in *Dimocarpus* are single, isopolar, and nearly always tricolporate (exceptionally tetracolporate). Average size varies between 20 and 30 μ. Shape as defined by the ratio between length polar axis and equatorial axis (P/E) varies between suboblate and spherical-subprolate. The equatorial outline is mostly circular to rounded triangular but in suboblate grains often semi-lobate with apertures at the angles (Pl. II, 14b). Wall stratification is uniformly developed and endexine and ekteaxine, the latter generally differentiated into an inner layer of columellae and an outer tectum, being present. Wall thickness is either uniform (Pl. II, 9b) or more or less greater on mesocolpia (Pl. II, 14b). The use of the terms endexine and ekteaxine is purely topographical. No evidence for subdivision of the endexine or for the presence of a foot layer could be found.

The endexine is generally rather thin, in some cases rather thick or slightly thickened alongside the ektoapertures (Pl. II, 2).

The columellae layer is often indistinct. The columellae are small, more or less regularly scattered or arranged in a substrate to striate pattern, in conformity with the sculptural pattern of the tectum.

The tectum may be smooth (Pl. II, 1), slightly undulating (Pl. IV, 1), finely perforate to reticulate or rugulate, with lumina which may be rather irregularly shaped (Pl. I, 10a; Pl. IV, 2, 3), or substrate (Pl. I, 11) to striate (Pl. III, 10a; Pl. IV, 4—9). The rather irregular pattern of the striate sculpture is especially evident on Pl. IV, 8, where it appears that on some parts of the grain two differently oriented systems of striae are superimposed. In other striate grains minute perforations are present in the grooves between the striae (Pl. III, 9; Pl. IV, 5, 7), which suggests that the striae were deposited on an originally perforated tectum. The width of the striae is rather constant and can be estimated from the stereoscan photomicrographs to be around 0.4 μ. The diameter of the perforations is 0.2—0.3 μ.

The sculptural pattern may be finer alongside the ektoapertures.

The ektoapertures are colpate, meridionally oriented, and their relative length is expressed in the ratio between equatorial diameter and total length ektoaperture (E/c). The endapertures are situated on the equator and are rather variably developed. In some cases only equatorial bridging of the ektoapertures is observed (Pl. III, 3). In a further stage they are developed as double circular apertures on each side of the ektoapertures (Pl. III, 1), while generally they are single circular or oval apertures which, in the latter case, are meridionally elongated (Pl. III, 8; Pl. IV, 8). Sometimes the ekteaxine and endexine separate in the endoapertural region (Pl. II, 14b; ‘fastigiate’ acc. to Reitsma, 1970).

The stereoscan pictures have shown that the apertures can be more or less completely covered with sculptured ekteaxinous material. On Pl. IV, 6 a rather long, narrow ektoaperture, closed by a smooth membrane is visible. On Pl. IV, 8 the membrane is covered with irregular verrucate to substrate sculpturing. On Pl. IV, 2 the ektoapertures are very indistinctly outlined because of a dense covering of rugulate ekteaxinous sculpturing.

It will be evident that the preceding account forms the description of the general *Dimocarpus* pollen type and that the variability which exists is of a minor character only and, moreover, continuous. On shape, length of ektoapertures, and exine pattern 'subtypes' can be recognized, however. In the following systematic descriptions the samples will be grouped already according to these subtypes, the definition and further evaluation of which will follow in chapter IV.
III. SYSTEMATIC DESCRIPTIONS

**DIMOCARPUS LOUR.**

**Dimocarpus dentatus** W. Meijer ex Leenh.

Subtype B — Pl. I: 1—2.

Material studied. Borneo, Sabah: *Ahwing SAN 38200*.

Pollen grains spherical-suboblate, P/E 0.93, equatorial outline circular, tricolporate. Size: P 22 (23.7) 26 μ, E 24 (25.6) 31 μ. Ektoapertures indistinct, 12 (16.0) 19 μ long, E/c 1.60. Endoapertures circular-elliptical, meridionally elongated, 3 (4.7) 6 μ. Total wall thickness 1.1 μ on poles, 1.5 μ on mesocolpia, 1.0 μ near apertures. Endexine 0.5 μ thick. Columellae indistinct, 12 (16.0) 19 μ long, E/c 1.60.

Subtype D — Pl. I: 3—5; Pl. IV: 4—5.

Material studied. Borneo: *Gansau SAN 54466; Endert 5414*.

**Dimocarpus foveolatus** (Radlk.) Leenh.


Material studied. Philippines, Luzon: *Ramos B.S. 7370 (M)*.

Pollen grains spherical-suboblate, P/E 0.96 (0.98) 0.99, equatorial outline circular, tricolporate. Size: P 23.1 (24.0) 24.9 μ, E 23.2 (24.2) 25.7 μ. Ektoapertures indistinct, tapering, 14.5 (15.1) 15.7 μ long, E/c 1.60 (1.62) 1.64. Endoapertures circular-elliptical or irregularly shaped, meridionally elongated, 4.2 (4.5) 4.8 μ. Total wall thickness 1.3 μ on poles, 1.5 μ on mesocolpia, 1.5 μ near apertures. Endexine 0.75 μ thick. Columellae fairly distinct, <0.5 μ in diameter, arranged in a stratified pattern. Tectum finely striate-reticulate, lumina isodiametric, <0.5 μ in diameter, striae <0.5 μ wide, irregular.

**Dimocarpus fumatus** (Bl.) Leenh.

Subtype G.


Material studied. Borneo: *Castro NBFD A 853; Endert 5243; Lajangah SAN 44665; Rundi SAN 43178; Sibat ak Luang S 23271*.

ssp. *indochinensis* Leenh.

Material studied. Indochina: *Eberhardt 4803 (P)*.
ssa. javensis (Radlk.) Leenh.

Material studied. Java: Koorders 11130 (BO).

Pollen grains spherical-subprolate, P/E 0.98 (1.01) 1.04, equatorial outline circular, rarely subtriangular, tricolporate. Size: P 20.6 (22.4) 23.9 μ, E 21.0 (22.2) 23.1 μ. Ektoapertures rather distinct, variably developed, sometimes equatorially bridged or as wide as endoapertures, 15.7 (17.8) 20.0 μ long, E/c 1.13 (1.25) 1.42. Endoapertures rather indistinct and irregularly shaped or circular, 2.5 (3.6) 4.7 μ. Total wall thickness 1.1 μ on poles, 1.4 μ on mesocolpia, 0.9 μ near apertures. Endexine 0.5 μ thick. Columellae absent or very indistinct. Tectum finely striate or rugulo-sтратиate with minute perforations between the striae.

**Dimocarpus gardneri** (Thw.) Leenh.

Subtype A — Pl. II: 1—5; Pl. IV: 1.

Material studied. Ceylon: Meijer 345.

Pollen grains suboblate, P/E 0.78, equatorial outline rounded triangular, tricolporate. Size: P 15 (17.3) 20 μ, E 20 (22.1) 24 μ. Ektoapertures rather distinct, tapering, 3—4 μ wide at equator, 15 (19.8) 24 μ long, E/c 1.12. Endoapertures circular or irregular, 3 (3.6) 4 μ. Total wall thickness 1.0 μ on poles, 1.6 μ on mesocolpia, 0.8 μ near apertures. Endexine <0.5 μ thick. Columellae indistinct, <0.5 μ in diameter. Tectum psilate.

**Dimocarpus longan** Lour.

ssa. longan var. longan.

Subtype A.


Pollen grains suboblate, P/E 0.76, equatorial outline semi-lobate, tricolporate, Size: P 15 (15.9) 19 μ, E 19 (21.0) 23 μ. Ektoapertures rather distinct, tapering, 11 (14.0) 15 μ long, E/c 1.50. Endoapertures indistinct, irregularly shaped, 3 (2.3) 4 μ. Total wall thickness 1 μ on poles, 1 μ on mesocolpia, 0.5 μ near apertures. Endexine <0.5 μ thick. Columellae very indistinct. Tectum psilate.

Comment. This sample probably originates from a cultivated plant.

Subtype B — Pl. II: 6—11; Pl. IV: 2—3.


Pollen grains spherical-suboblate, P/E 0.86 (0.89) 0.94, equatorial outline rounded triangular, tricolporate. Size: P 18.2 (19.6) 21.7 μ, E 20.4 (22.5) 26.4 μ. Ektoapertures distinct, tapering, 14.6 (15.1) 19.9 μ long, E/c 1.21 (1.32) 1.41. Endoapertures circular or irregularly shaped, 3.0 (3.7) 4.5 μ. Total wall thickness 1 μ on poles, 1.4 μ on mesocolpia, 0.9 μ near apertures. Endexine <0.5 μ thick. Columellae distinct or rather indistinct, <0.5 μ in diameter, irregularly scattered. Tectum smooth or very finely reticulate to rugulate, lumina approx. 0.5 μ in diameter.

The stereoscan photomicrographs (Pl. IV: 2—3) have shown that the shape of these
Plate I. Fig. 1, 2: *Dimocarpus dentatus* (Ahwing SAN 38200). — Fig. 3—5: ditto (Endert 5414). — Fig. 6—9: *D. foveolatus* (Ramos B.S. 7370). — Fig. 10, 11: *D. fumatus ssp. fumatus* (Castro NBFD A 853). — Fig. 12: ditto (Rundi SAN 43178). All 1000 x, O.I.
Plate II. Fig. 1—5: Dimocarpus gardneri (Meijer 345). — Fig. 6—8: D. longan ssp. longan var. longan (Griffith 998). — Fig. 9—11: ditto (Popta 863/210). — Fig. 12, 13: D. longan ssp. longan var. obtusus (Poilane 127). — Fig. 14, 15: D. longan ssp. malesianus var. malesianus (Parker 2717). All 1000 x, O.I.
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Plate III. Fig. 1: Dimocarpus longan ssp. malesianus var. malesianus (Pierre 4114). — Fig. 2—4: ditto (Elmer 21354). — Fig. 5—7: ditto (Sihat ak Luang S 23086). — Fig. 8, 9: ditto (Sulit PNH 32819). — Fig. 10—13: ditto (Sumague PNH 37299). All 1000 x, O.I.
Plate IV. Stereoscan photomicrographs. Fig. 1, 1580 x: Dimocarpus gardneri (Meijer 345). Fig. 2, 1580 x, Fig. 3, 6000 x: D. longan sp. longan var. longan (Poite 863/210). Fig. 4, 1570 x, Fig. 5, 6230 x: D. dentatus (Endert 5414). — Fig. 6, 1570 x, Fig. 7, 6000 x: D. longan sp. longan var. longan (Poite 127). — Fig. 8, 1550, Fig. 9, 6100 x: D. longan sp. longan var. malesianus (PNH 37299).
lumina may be highly irregular and variable. All transitions are present between shallow depressions in the rugulate tectum surface, elongated and branched fossae, and isodiometric pits.

ssp. longan var. obtusus (Pierre) Leenh.

Subtype F — Pl. II: 12—13; Pl. IV: 6—7.

Material studied. Indo China: Pierre 4115 (P); Poilane 127 (P).

Pollen grains spherical-suboblate, P/E 0.89 (0.92) 0.94, equatorial outline circular to rounded triangular, tricolporate. Size: P 20.6 (21.9) 23.2 μ, E 23.2 (23.9) 24.6 μ. Ektoapertures rather distinct, narrow, 17.5 μ long, E/c 1.33 (1.37) 1.40. Endoapertures circular or elliptical and meridionally elongated, 4.0 (4.5) 4.9 μ. Total wall thickness 1.2 μ on poles, 1.4 μ near apertures. Endexine <0.5 μ thick. Columellae very indistinct, ± arranged in a substrate pattern. Tectum striate, striae 0.5 μ wide, curvilinearly arranged on poles, between striae minute indistinct perforations may be present.

ssp. malesianus Leenh. var. malesianus.

Subtype A — Pl. II: 14—15; Pl. III: 1.


Pollen grains suboblate, P/E 0.77 (0.82) 0.86, equatorial contour rounded triangular to semi-lobate, tricolporate. Size: P 17.9 (19.8) 21.6 μ, E 21.9 (24.1) 26.2 μ. Ektoapertures distinct, tapering, rather narrow, occasionally equatorially bridged, 15.3 (16.8) 19.5 μ long, E/c 1.24 (1.45) 1.68. Endoapertures rather indistinct, developed as equatorial bridges, dumbbell shaped or irregularly circular, 2.0 (3.6) 5.1 μ. Total wall thickness 1.1 μ on poles, 1.5 μ on mesocolpia, 0.7 μ near apertures. Endexine up to 0.5 μ thick. Columellae indistinct to rather distinct, <0.5 μ in diameter, densely spaced. Tectum psilate, occasionally finely reticulate, lumina <0.5 μ in diameter.


Material studied. Sumatra: BB F 713. Borneo, Tawau: Aban Gibot SAN 31241; Bakar SAN 25025; Elmer 21834 (Bo); Rundi SAN 43034.

Pollen grains spherical-suboblate, P/E 0.85 (0.94) 1.05, equatorial contour circular to rounded triangular, tricolporate. Size: P 19.8 (23.1) 26.6 μ, E 21.4 (24.4) 28.6 μ. Ektoapertures distinct or indistinct, tapering, 14.7 (18.8) 21.3 μ long, E/c 1.13 (1.33) 1.45. Endoapertures rather indistinct, developed as equatorial bridges, irregularly shaped or circular, 3.1 (4.2) 5.6 μ. Total wall thickness 1.1 μ on poles, 1.4 μ on mesocolpia, 1.1 μ near apertures. Endexine <0.5 μ thick. Columellae rather distinct, <0.5 μ in diameter, up to 0.5 μ high, densely evenly scattered. Tectum psilate or very finely reticulate, lumina <0.5 μ in diameter.

Subtype C — Pl. III: 5—7.

Material studied. Borneo, E. Kutei: Kostermans 5331; Sarawak: Sibat ak Luang S 23086; Sibat ak Luang S 26148.

Pollen grains spherical, P/E 0.92 (0.95) 0.96, equatorial contour circular, tricolporate,
occasionally tetracolporate. Size: P 24.1 (25.4) 27.8 μ, E 25.3 (26.9) 28.4 μ. Ektoapertures rather indistinct, narrow, 14.6 (16.3) 18.0 μ long, E/c 1.54 (1.65) 1.84. Endoapertures indistinct or circular-elliptical, meridionally elongated, 5.5 (5.2) 6.3 μ. Total wall thickness 1.8 μ on poles, 1.5 μ on mesocolpia, 1.5 μ near apertures. Endexine 0.5—1.5 μ thick. Columellae distinct, <0.5 μ in diameter, 0.5 μ high, regularly, fairly densely spaced. Tectum psilate or finely reticulate, luminae <0.5 μ in diameter.


Material studied. Philippines, Mindoro: Sulit PNH 32819.

Pollen grains spherical, P/E 0.98, equatorial contour circular, tricolporate. Size: P 26 (29.5) 32 μ, E 25 (30.2) 33 μ. Ektoapertures rather distinct, narrow, parallel sides, 15 (20.2) 24 μ long, E/c 1.50. Endoapertures elliptical, meridionally elongated, 5 (7.8) 10 μ. Total wall thickness 1.2 μ on poles, 1.5 μ on mesocolpia, 1.0 μ near apertures. Endexine <0.5 μ thick. Columellae distinct, <0.5 μ in diameter, rather widely evenly spaced in a striate pattern. Tectum finely striate with minute perforations between the striae, striae supported by columellae, <0.5 μ wide.

Subtype E — Pl. III: 10—13; Pl. IV: 8—9.

Material studied. Philippines, Luzon: Barnes FB 331 (K); Cuming 1131; Sumague PNH 37299.

Pollen grains suboblate, P/E 0.84 (0.87) 0.92, equatorial contour rounded triangular to semilobate, tricolporate. Size: P 20.9 (21.0) 21.1 μ, E 23.0 (24.4) 25.1 μ. Ektoapertures rather distinct, tapering, sometimes equatorially bridged, 15.7 (17.5) 19.7 μ, E/c 1.28 (1.40) 1.46. Endoapertures rather distinct, irregularly shaped, 3.2 (3.5) 3.8 μ. Total wall thickness 1.3 μ on poles, 1.7 μ on mesocolpia, 0.6 μ near apertures. Endexine <0.5 μ thick. Columellae rather distinct <0.5 μ in diameter, 0.5 μ high on mesocolpia, shorter near apertures, scattered or in a faintly striate pattern. Tectum more or less distinctly striate. Striae <0.5 μ wide, often in a curvilinear or, occasionally, in a starshaped pattern.

IV. POLLEN SUBTYPES

A synthesis of the descriptive data presented in the preceding chapter, leads to the following diagnoses of the subtypes:

Subtype A.

Suboblate, P/E 0.76 (0.81) 0.86, equatorial contour rounded triangular to semi-lobate. Ektoapertures medium long, E/c 1.12 (1.42) 1.68. Wall conspicuously thickened on mesocolpia. Columellae small or indistinct. Tectum psilate, rarely finely reticulate.

This subtype occurs in D. gardneri, D. longan var. longan, and D. longan var. malesianus.

Subtype B.

Spherical-suboblate, P/E 0.82 (0.92) 1.05, equatorial contour circular to rounded triangular. Ektoapertures medium long, E/c 1.13 (1.36) 1.60. Wall slightly thickened on mesocolpia. Columellae rather distinct, scattered, rarely in a striate pattern. Tectum psilate or finely reticulate.

This subtype occurs in D. dentatus, D. foveolatus, D. longan var. longan, and D. longan var. malesianus.
Subtype C.
Spherical-suboblate, P/E 0.92 (0.95) 0.96, equatorial contour circular. Ektoapertures short, E/c 1.54 (1.65) 1.84. Wall thickness uniform. Columellae rather distinct, evenly scattered. Tectum psilate to finely reticulate.
This subtype occurs in D. longan var. malesianus.

Subtype D.
Spherical-suboblate, P/E 0.96 (0.98) 0.99, equatorial contour circular. Ektoapertures short, E/c 1.50 (1.58) 1.64. Wall thickness rather uniform. Columellae rather distinct, substriately arranged. Tectum substriate-perforate.
This subtype occurs in D. dentatus, and D. longan var. malesianus.

Subtype E.
Suboblate, P/E 0.84 (0.87) 0.92, equatorial contour rounded triangular to semi-lobate. Ektoapertures medium long, E/c 1.28 (1.40) 1.46. Wall thickened on mesocolpia. Columellae rather distinct, substriately arranged. Tectum striate.
This subtype occurs in D. longan var. malesianus.

Subtype F.
Spherical-suboblate, P/E 0.89 (0.92) 0.94, equatorial contour circular to rounded triangular. Ektoapertures medium long, E/c 1.33 (1.37) 1.40. Wall thickness rather uniform. Columellae very indistinct, substriately arranged. Tectum striate.
This subtype occurs in D. longan var. obtusus.

Subtype G.
Spherical-subprolate, P/E 0.98 (1.01) 1.05, equatorial contour circular to rounded triangular. Ektoapertures long, E/c 1.13 (1.25) 1.42. Wall slightly thickened on mesocolpia. Columellae absent or very indistinct. Tectum striate-perforate to rugulo-striate.
This subtype occurs in D. fumatus ssp. fumatus, ssp. indochinensis, and ssp. javensis.

The interrelationships between these subtypes are shown on a scheme (fig. 1), on which they are arranged according to the most significant morphological features, viz. ektexine sculpturing and overall shape. The main differentiation is in ektexine pattern and the subtypes can be separated in group I (A, B, C) which has a simply built, psilate or perforate/reticulate pattern, and group II (D, E, F, G) which has a more or less distinct striate pattern. The latter group, and especially subtype G which occurs in one species only, is considered derived because of increased complexity of ektexine sculpture. It is more difficult to decide whether A or B and C are derived. The semi-lobate, suboblate grains with indistinct columellae, a smooth tectum, and a thicker wall on the mesocolpia of subtype A could be considered a functionally specialized grain, while B and C with a more spherical shape, rather distinct columellae, and a finely perforate-reticulate, equally thick wall may come close to a generalized pollen type. The geographical distribution of these subtypes does not give any clear further evidence, A being concentrated in SE. Asia and being conspicuously absent from Borneo.

In Dimocarpus no correlation exists between the length of the ektoapertures and the shape of the grain and this is different from the situation in Lepisanthes (Muller, 1970).
On pollenmorphological grounds only, it is therefore not yet possible to state which is the most primitive subtype. Investigation of related genera will probably throw more light on this problem.
Fig. 1. Pollenmorphological trends in Dimocarpus.

Fig. 2. Distribution of pollen types and taxonomic subdivision in Dimocarpus. (* cultivated, origin uncertain).
V. POLLEN MORPHOLOGY AND TAXONOMY

The occurrence of the pollen subtypes in the taxa recognized by Leenhouts is summarized in fig. 2. From this table it is apparent that *D. longan* ssp. *malesianus* shows the largest pollenmorphological variability, while according to Leenhouts it also shows the largest macromorphological variability. The derived subtypes D and E of this taxon are restricted to the Philippines, clearly a peripheral distribution. Subtypes B and C are restricted to Sumatra, Borneo, and the Philippines, but A is mainly concentrated in SE. Asia which might also be considered peripheral and could suggest that B and C are closer to the primitive pollen type. If confirmed, this would indicate a W. Malesian origin for *D. longan* ssp. *malesianus*. *D. longan* ssp. *longan*, which according to Leenhouts is slightly more derived than ssp. *malesianus*, has in var. *longan* subtype B in common with the latter, but has also developed in var. *obtusus* a derived subtype of its own, G. Of interest is further that subtype A has not been found in this ssp., which has a SE. Asian distribution. This indicates origin from West Malesian populations of ssp. *malesianus* rather than from SE. Asian ones which are characterized by subtype A.

*D. foveolatus* may be related to *D. longan* ssp. *malesianus* from Luzon since they share pollen subtype B.

*D. dentatus* may, on the presence of subtype B, be similarly related to *D. longan* ssp. *malesianus* from Borneo, but has evolved locally the derived subtype D, which is rather in contrast to its macromorphological uniformity.

*D. gardneri* which in Leenhouts's opinion is 'macromorphologically as well as geographically fairly isolated and may be old' is characterized by pollen subtype A, which suggests a relationship to the SE. Asian populations of *D. longan* ssp. *malesianus*. There is no palynological evidence for a close relationship between *D. gardneri* and *D. dentatus* as might be suggested by the dentate leaflets which characterize both species.

*D. fumatus*, finally, has evolved the most clearly derived pollen subtype, G, which is in good agreement with the presence of a reduced corolla, also a derived condition. Because of the relatively small differences involved, the above suggestions must be considered as tentative. They could be further substantiated by a more detailed study, especially of the variable species *D. longan*, and of course by a comparison with the related genera of the tribe *Nepheleae* which will be investigated at a later date.

REFERENCES

