POLLEN MORPHOLOGY OF THE GENUS LEPISANTHES (SAPINDACEAE) IN RELATION TO ITS TAXONOMY

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CONTENTS

Summary 507
I Introduction 507
II. General morphology 508
III. Systematic descriptions. 511
IV. Pollen types 547
V. Pollen morphology and taxonomy 557
References 561

SUMMARY

The pollen morphology of 18 out of 22 species of the genus *Lepisanthes*, as recently revised, was studied. General pollen morphology is rather uniform, but taxonomically significant differences exist in shape, relative length of ektoapertures, endoaperture development, and in the sculpture of the tectum. Detailed descriptions are presented and special attention is given to intraspecific variability. 10 Pollen types are recognized, most of which are linked by transitions. Morphological trends are established and the extent to which they indicate natural relationships is evaluated. In subgenera *Lepisanthes* and *Erioglossum* a less evolved but more variable pollen morphology is present, while in subgenera *Otophora* and *Aphania* derived pollen types occur, which agrees well with macromorphological evidence. Subgenus *Erioglossum* appears pollenmorphologically closely related to subgenus *Lepisanthes*. Subgenus *Aphania* can, both macro- and pollenmorphologically, be derived from subgenus *Otophora*. Within *Lepisanthes tetraphylla* close parallels exist between macromorphological and palynological interpretations of natural affinities between the numerous races. *Lepisanthes fruticosa*, in contrast, shows on both counts rather wide and continuous intraspecific variability. Also in *Lepisanthes senegalensis* continuous pollenmorphological variability is present, but here a clinal pattern can be detected. In general, geographically isolated or endemic forms in *Lepisanthes* show a tendency to develop deviating pollen types.

I. INTRODUCTION

The recent taxonomic revision of the genus *Lepisanthes* by Leenhouts (1969), as a precursor to a future treatment of the *Sapindaceae* for the 'Flora Malesiana', provided an excellent opportunity to supplement his macromorphological approach with a detailed palynological survey.

As can be learned from his revision, Leenhouts has considerably altered the circumscription of the genus and significantly reduced the number of species. This was mainly possible because of the much more extensive material available to him than to his predecessor, Radlkofer, who last monographed the family for 'Das Pflanzenreich' in 1932.

Since the publication of his revision, Leenhouts has been able to make one additional taxonomic change: *L. borneensis* and *aphanococca* are now reduced as subspecies to *L. falcata* (Leenhouts, 1970).

Of the total of 22 species now recognized, only 18 yielded usable pollen slides. However, all subgenera and sections are represented by at least one species and it would appear that taxonomic coverage is broad enough to permit generalizations about the genus as a whole. In addition, the abundant material available for certain widespread and variable species, notably *L. tetraphylla*, *L. fruticosa*, and *L. senegalensis*, permitted a detailed study of intraspecific pollen variability, the results of which also proved to be of taxonomic significance.

Although Radlkofer himself already did study the pollen grains of *Sapindaceae* and attempted to utilize the results for his taxonomic work, very little has been published on the family since this pioneer effort. The family receives only the briefest treatment in Erdtman's handbook (1952) and the only more extensive recent study is by Merville (1965) who described the pollen of a number of West African representatives, among which is *Aphania senegalensis*, a species which is assigned by Leenhouts to the genus *Lepisanthes*.

So far, no fossil dispersed *Lepisanthes* pollen has come to light, but it is hoped that the detailed descriptions and illustrations presented here, will lead to the establishment of a fossil record for the genus. This will permit a test of the tentative phylogenetic interpretations presented in the last chapters of this study.

For the present palynological survey all specimens which bore sufficiently mature buds or flowers were examined and only of those which showed well developed anthers material was collected. In an attempt to correlate pollen development with flower type it was found that functionally male flowers and ripe buds showed the highest percentage of excellent pollen samples (38 %), but 'bisexual' (functionally female) flowers still yielded 25 % excellent samples. It would thus appear that *Lepisanthes*, as far as pollen production is concerned, does not show a sharp difference between functionally male and female flowers. The observations and measurements were restricted to samples which yielded at least ten well developed pollen grains.

The material investigated was acetolyzed (3 min), embedded in glycerin jelly, and examined and photographed with a Leitz apochromatic objective (O I, 90/1.40) or with phase contrast. Sections were cut after embedding in gum arabic according to Leins (1968).

The sequence of descriptions is the same as employed by Leenhouts (1969).

Photomicrographs were taken with ordinary light and magnified 1000 ×, unless otherwise stated. Series of a single grain at successive levels of focus are differentiated with a, b, c.

The author is deeply indebted to Dr. P. W. Leenhouts for his stimulating cooperation in the execution of this study. His critical comments are incorporated in chapter V.

II. GENERAL MORPHOLOGY

The pollen grains in *Lepisanthes* are single, isopolar, and in general tricolporate. Average size varies between 20—30 μ. Shape as defined by the ratio between length polar axis and equatorial axis (P/E) varies between oblate and subprolate and is important for taxonomic interpretation. The equatorial outline also shows variation, dependent on the state of expansion of the grain, however, and only significant in the few cases of angular to semilobate grains. Wall stratification appears uniformly developed, endexine and ektexine, the latter generally differentiated into an inner layer of columellae and outer tectum nearly always being present. In very thinwalled grains the ektexine may appear to be homogeneous, however. In a few cases the endexine in the apertural areas consists of a thick outer layer (endexine 1) and a very thin inner layer (endexine 2) which may close the aperture on the inner side (Fig. 1 A, B; Plate V: 7).

The development of the tectum shows significant variability and the principal types are

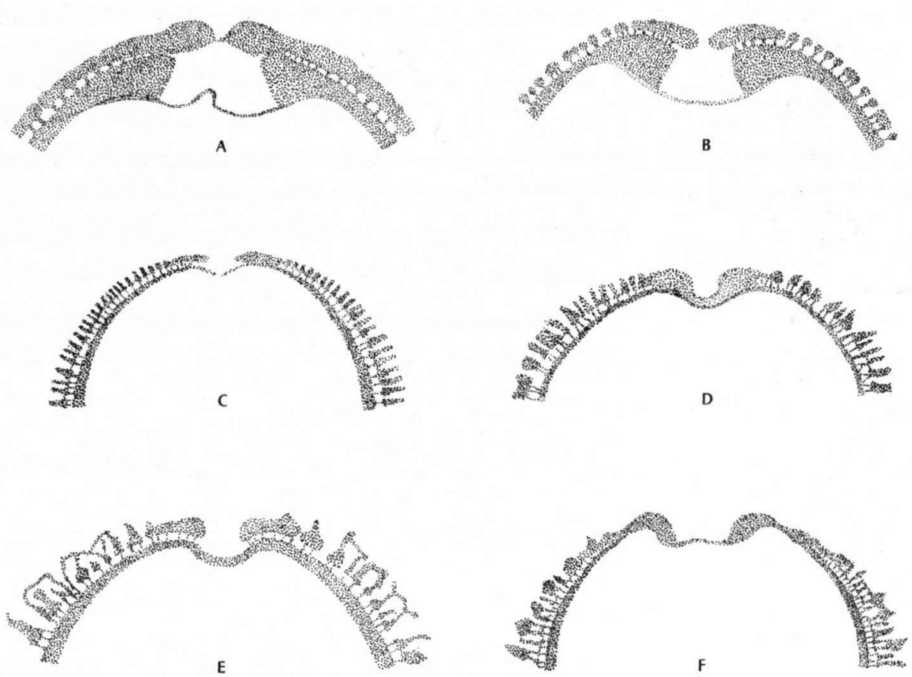

Fig. 1. Schematic sub equatorial cross sections of *Lepisanthes* pollentypes. A. *L. tetraphylla 'lamponga' (Maradjo 481)*. — B. *L. tetraphylla 'scortechinii' (Ridley 5360)*. — C. *L. amoena (Beccari 3359)*. — *L. bengalan (Kostermans 4889)*. — E. *L. fruticosa (Curran 5820)*. — F. *L. kinabaluensis (SF 26934)*.

schematically drawn in cross section on fig. 1. These drawings are based on a combination of surface views and thin sections.

In *L. tetraphylla 'lamponga'* (fig. 1 A) tectum and endexine are of equal thickness, while the columellae are rather distinct, except near the apertures where they are reduced. The tectum surface is nearly smooth with scattered fine perforations. The endexine 2 appears as a distinct inner membrane only in the apertural area.

The wall structure of *L. tetraphylla 'scortechinii'* (fig. 1 B) is basically similar, but the tectum is finely reticulate. The columellae are arranged in a reticulate pattern in single rows bearing on top the muri of the tectate reticulum, which are biconvex in cross section.

A rather different arrangement is seen in *L. amoena* (fig. 1 C). Here the endexine is gradually decreasing in thickness towards the aperture, whilst no trace of an endexine 2 can be detected. The columellae are thin, slightly decreasing in length towards the aperture, arranged in a reticulate pattern, and bearing a reticulate tectum. The muri are more or less bottle-shaped in cross section. The height of the muri and the diameter of the lumina gradually decreases towards the aperture.

L. bengalan (fig. 1 D) shows a further elaboration of this pattern. Here the endexine is uniformly thin, the columellae are long and slender and occasionally branched. The shape of the muri in cross section is more irregular, but they are also generally broadened at their base.

A more extreme pattern is exhibited by certain forms of *L. fruticosa* (fig. 1 E), where the tectum is developed into a highly complex reticulum. The muri are forked and sometimes connected at their tops, thus forming locally a second outer tectate layer, partially covering the coarsely reticulate pattern underneath. The muri are also conspicuously broadened at base, but the columellae are very thin and short.

On fig. 1 F, finally, another extreme form of tectate structure, as present in *L. kinabaluensis* is shown. The columellae again are very thin and short, the broadened bases of the muri appear to form an almost continuous layer, while at their tops the muri are locally swollen and fused, forming emerging subechinate-verrucate structures.

The reticulate grains show significant variations in lumen size and shape distribution, further details of which will be discussed in the specific pollen descriptions which follow this general chapter. The presence of tectate areas alternating with finely reticulate areas in certain forms of *L. senegalensis* and of a rugulate sculpture in one collection of *L. fruticosa* may be mentioned here already.

The apertures also show taxonomically important differences. They are nearly always composite and an ekto- and endoaperture can generally be distinguished. Their number is three, exceptionally four, they are meridionally oriented and situated on the equator and, in grains with a subtriangular equatorial outline, at the angles. The ektoapertures, restricted to the ektexine, are generally colpate, elongated in polar direction, and closed by a membrane which is probably endexinous in nature (fig. 1 C, D, E, F). In a few cases there appears to be also an ektexinous membrane covering the ektoaperture (fig. 1 A). The membrane often bears a sculpture consisting of a few minute scattered verrucae, one of the few characters which, according to Merville (1965), are present in most Sapindaceous pollen types, but which also occurs in other families such as *Hippocastanaceae* and *Anacardiaceae*. Exceptionally the ektoapertures are syncolpate or absent altogether. The relative length of the ektoaperture is expressed in the ratio between equatorial diameter and total length of ektoaperture (E/c) and was found to be very significant for taxonomic interpretation. This ratio was found to be more reliable and convenient to determine than the often used polar index. Width of the ektoapertures is dependent on the state of expansion of the grain and is much less significant.

The endoapertures are generally isodiametric or slightly elongated in polar direction. On fig. 1 A and B the equatorial section through the aperture system shows that the endexinous aperture is much wider than the ektoaperture and is surrounded by an annular thickening which, in surface view, is found to be circular and surrounding the aperture completely (see also Plate VII, fig. 2). In other grains the endoapertures are smaller, irregularly shaped with only indistinct polar thickenings, or, in extreme cases they may be only visible as equatorial constrictions of the ektoapertures or as irregular thin areas of the apertural membrane.

In general, in grains with a relatively short ektoaperture and a wider endoaperture, the wall structure is fairly simple and does not show a differentiation in coarseness of sculpture alongside the aperture (fig. 1 A, B). In grains with a long ektoaperture, however, a pronounced transition from coarse to fine sculpture parallel to the apertural margin and a reduction in total thickness or costate thickenings are present (fig. 1 C—E). In *L. kinabaluensis* (fig. 1F) a thickened margin borders the aperture which cannot be differentiated as to endexine or ektexine and is separated by a thin zone from the reticulate-subechinate mesocolpial field.

Although a certain amount of infolding of the entire aperture may occur, especially in grains with very long ektoapertures, the present author has not been able to observe any separate folding of the endexine near the aperture, forming the endexinal fold or *'replis'* described by Merville (1965) for *Lepisanthes (Aphania) senegalensis*. It may be pointed out that her illustrations for this species do not clearly show this feature in any case.

The use of the terms ektexine and endexine in this paper is purely topographical. Staining of the sections with basic fuchsin failed to give any clear differentiation. Electronmicroscopical investigation will have to reveal whether a foot layer is present and how the different layers recognized are to be homologized with those present in related taxa.

III. SYSTEMATIC DESCRIPTIONS

LEPISANTHES BL.

subgenus LEPISANTHES

section Lepisanthes

Lepisanthes andamanica King — Pl. I: 1—4.

Material studied. Andaman Isl.: *King s.n.*

Pollen grains suboblate, P/E 0.86, equatorial outline circular-rounded triangular, tricolporate. Size: P 20 (21.5) 23 μ, F 23 (25.0) 28 μ. Ektoapertures distinct, 20 (21.8) 24 μ long, E/c 1.15, 3 μ wide at equator, slightly tapering with rounded tips. Endoapertures rather distinct, circular, 3 (3.1) 4 μ. Total wall thickness 1 μ on poles, 1.7 μ on mesocolpia, 1 μ near apertures. Endexine < 0.5 μ thick. Columellae indistinct < 0.5 μ in diameter, < 0.5 μ long. Tectum very finely evenly reticulate, lumina isodiametric, < 0.5 μ in diameter, muri < 0.5 μ wide, < 0.5 μ high.

Lepisanthes tetraphylla (Vahl.) Radlk.

1. *Lepisanthes tetraphylla 'tetraphylla'* — Pl. I: 5—10.

Material studied. India: *Gamble 21747; Haines s.n.; Ritchie 98; Wallich 8040; Wight 530; Herb. Arn. Arbor. s.n.* cult. Calcutta. —Ceylon: *Thwaites 3508*. —Cambodia: *Béjaud 1938*. —Vietnam: *Pételot 936; Poilane 5536; Poilane 5545*. — Andaman Isl.: *Helfer 986/1*. —Java: cult. *H. Bog. III J. 34*. — Martinique: cult. *Duss 1837*.

Pollen grains spherical-suboblate, P/E 0.93, equatorial outline rounded-triangular, tricolporate, rarely triporate (*Poilane 5536*, Pl. I: 9 & 10!). Size: P 20 (22.6) 26 μ, E 22 (24.6) 29 μ. Ektoapertures rather distinct, 15 (20.9) 28 μ long, E/c 1.19, 2—3 μ wide at equator, tapering with pointed tips. Endoapertures rather distinct, circular-elliptical, 2 (3.4) 6 μ. Total wall thickness 1.1 μ on poles, 1.4 μ on mesocolpia, 0.9 μ near apertures. Endexine very thin, < 0.5 μ. Columellae rather indistinct, < 0.5 μ in diameter, < 0.5 μ long. Tectum in general finely, evenly reticulate (Pl. I: 8), occasionally nearly smooth or foveolate, lumina uniformly isodiametric or slightly irregularly shaped, < 0.5 μ in diameter, sometimes finer near apertures, muri < 0.5 μ wide, uniform in width or irregularly broadened, < 0.5 μ high.

Comment. In general this form has a rather uniform pollen type, only showing slight variability in shape of lumina and muri. One sample, however, *(Poilane 5536)* shows dimorphism and contains besides normal tricolporate grains, triporate grains with fairly large circular endoapertures which appear to be covered with a thin verrucate membrane.

3. *Lepisanthes tetraphylla 'deficiens'* — Pl. I: 11, 12.

Material studied. India: *Wight 535.*

Pollen grains suboblate, P/E 0.84, equatorial outline circular-rounded triangular, tricolporate. Size: P 23 (26.2) 32 μ, E 26 (31.6) 35 μ. Ektoapertures rather distinct, 20 (22.5) 24 μ long, F/c 1.40, 3—4 μ wide, sides parallel with rounded tips. Endoapertures distinct, circular, 3 (3.5) 5 μ, occasionally indistinctly annulate. Total wall thickness 1.0 μ on poles, 1.2 μ on mesocolpia, 1.0 μ near apertures. Endexine 0.5 μ thick. Columellae distinct, < 0.5 μ in diameter, 0.5 μ long, densely spaced. Tectum smooth or very finely reticulate, lumina uniform, isodiametric, < 0.5 μ in diameter, muri < 0.5 μ wide, < 0.5 μ high.

6. *Lepisanthes tetraphylla 'assamica'* — Pl. II: 1—3.

Material studied. Assam: *Gage 185.*

Pollen grains suboblate, P/E 0.87, equatorial contour rounded triangular, tricolporate. Size: P 21 (23) 25 μ, E 24 (26.5) 28 μ. Ektoapertures distinct, 18 (21.5) 25 μ long, E/c 1.23, 2 μ wide at equator, tapering, indistinctly costate (Pl. II: 2), apertural membrane occasionally finely verrucate. Endoapertures distinct, irregular shaped to circular, 2 (3.0) 4 μ. Total wall thickness 1.0 μ on poles, 1.5 μ on mesocolpia, 1.0 μ near apertures. Endexine < 0.5 μ thick, slightly thickened alongside ektoapertures. Columellae absent or very indistinct, < 0.5 μ in diameter, < 0.5 μ long. Tectum finely foveolate-reticulate (Pl. II: 3), lumina elliptical, irregularly shaped, slightly aligned, evenly distributed, up to 0.5 μ in diameter, muri up to 1 μ wide, variable in width, < 0.5 μ high.

8. *Lepisanthes tetraphylla 'basicardia'* — Pl. II: 4—6.

Material studied. Burma: *S. Mokim s.n.*

Pollen grains spherical-suboblate. P/E 0.94, equatorial outline circular, tricolporate. Size: P 22 (22.3) 23 μ, E 23 (23.8) 25 μ. Ektoapertures rather distinct, 18 (19.7) 22 μ long, E/c 1.21, 2 μ wide at equator, slightly tapering. Endoapertures distinct, circular, 2 (2.7) 3 μ. Total wall thickness uniformly 1 μ. Endexine 0.5 μ thick. Columellae indistinct, scarce, < 0.5 μ in diameter, < 0.5 μ long. Tectum finely evenly reticulate, lumina isodiametric, even in size, up to 0.5 μ in diameter, muri < 0.5 μ wide, < 0.5 μ high.

9. *Lepisanthes tetraphylla 'browniana'* — Pl. II: 7—9.

Material studied. Burma: *Gomez 342.*

Pollen grains suboblate, P/E 0.88, equatorial outline rounded triangular, tricolporate. Size: P 33 (33.5) 34 μ. E 34 (38.0) 40 μ. Ektoapertures indistinct (Pl. II, 8, 9), 6 (6.6) 7 μ long, E/c 1.71, 3 μ wide at equator, slightly tapering with rounded tips. Endoapertures rather distinct, circular, 6 (6.6) 7 μ. Total wall thickness uniformly 1 μ. Endexine 0.5 μ thick, slightly thickened on polar sides of endoapertures. Columellae distinct (Pl. II: 7a), variable in size, up to 0.5 μ in diameter, arranged in a subreticulate pattern, 0.5 μ long. Tectum finely reticulate, lumina uniformly isodiametric, up to 1 μ in diameter, slightly decreasing in size near apertures (Pl. II: 9), evenly distributed, muri up to 1.5 μ in width, occasionally multicolumellate, < 0.5 μ high.

12. *Lepisanthes tetraphylla 'siamensis'* — Pl. III: 1—2.

Material studied. Thailand: *Kerr 2563 A; Kerr 10641; Vanpruk 191.*

Pollen grains spherical suboblate, P/E 0.92, equatorial contour circular to rounded triangular, tricolporate. Size: P 20 (20.9) 24 μ, E 20 (22.8) 26 μ. Ektoapertures distinct, 15 (20.0) 23 μ long, E/c 1.14, constricted and up to 2 μ wide at equator (Pl. III; 2), tapering, indistinctly costate. Endoapertures indistinct, irregularly shaped, 2 μ. Total wall thickness 1.0 μ on poles, 1.5 μ on mesocolpia, 0.5 μ near apertures. Endexine < 0.5 μ thick. Columellae very indistinct, < 0.5 μ in diameter, < 0.5 μ long or absent. Tectum shallowly finely reticulate, lumina irregular elliptical, < 0.5 μ in diameter, finer near apertures, muri < 0.5 μ wide, 1 μ high on mesocolpia, < 0.5 μ high near apertures.

Comment. The rather massive, dark brown ektexine which is considerably thickened on the mesocolpia (Pl. III: 1 b) is unique for this form.

13. *Lepisanthes tetraphylla 'poilanei'* — Pl. III: 3—5.

Material studied. Thailand: *Kasin 364.*

Pollen grains spherical-suboblate, P/E 0.91, equatorial outline rounded triangular, tricolporate. Size: P 23 (25.3) 29 μ, E 26 (27.8) 29 μ. Ektoapertures rather indistinct, 19 (23.5) 26 μ long, E/c 1.17, 4 μ wide at equator, sides tapering. Endoapertures distinct, circular-elliptical, elongated in polar direction (Pl. III: 3), 4 (5.4) 6 μ. Total wall thickness uniformly 1 μ. Endexine < 0.5 μ thick. Columellae distinct, < 0.5 μ in diameter, < 0. 5 μ long, rather dense, arranged in a reticulate pattern. Tectum finely evenly reticulate, lumina up to 1 μ in diameter, slightly finer towards apertures and on poles, rather irregular in shape, isodiametric-elliptical, muri up to 0.5 μ in width, < 0.5 μ high, borne on single rows of columellae.

14. *Lepisanthes tetraphylla 'mekongensis'* — Pl. III: 6—8.

Material studied. Cambodia: *d'Alleizette 1393; Herb. Pierre 5669.*

Pollen grains spherical-suboblate, P/E 0.91, equatorial outline circular, tricolporate. Size: P 18 (19.6) 22 μ, E 20 (21.6) 24 μ. Ektoapertures distinct, 13 (18.2) 22 μ long, E/c 1.19, 2 μ wide at equator, tapering sides. Endoapertures rather indistinct (Pl. III: 7), circular, 2 (2.3) 3 μ. Total wall thickness uniformly 1 μ. Endexine < 0.5 μ thick. Columellae rather distinct, < 0.5 μ in diameter, < 0.5 μ high, rather densely evenly spaced. Tectum smooth or finely reticulate, lumina isodiametric, < 0.5 μ in diameter, muri < 0.5 μ wide, < 0.5 μ high.

15. *Lepisanthes tetraphylla 'langbianensis'.*

Material studied. S. Vietnam: *Poilane 18633.*

Pollen grains spherical-suboblate, P/E 0.94, equatorial outline circular, tricolporate. Size: P 21 (26.0) 28 μ, E 24 (27.5) 31 μ. Ektoapertures rather indistinct, 14 (18.6) 24 μ long, E/c 1.49, 1—2 μ wide at equator, sides parallel. Endoapertures distinct, circular, 2 (3.8) 5 μ. Total wall thickness 1.5 μ on poles, 2 μ on mesocolpia, 1.5 μ near apertures. Endexine 0.5 μ thick. Columellae indistinct, < 0.5 μ in diameter, 0.5 μ long. Tectum smooth or very faintly finely reticulate, lumina isodiametric, < 0.5 μ in diameter, muri < 0.5 μ wide, < 0.5 μ high.

Comment. The single sample available consisted of badly preserved, crumpled grains and the measurements are, therefore, not very reliable. Also the structure of the ektexine was difficult to elucidate.

16. *Lepisanthes tetraphylla 'tonkinensis'*.

Material studied. N. Vietnam: *Bon 2828.*

Pollen grains spherical, tricolporate. Size: 29.6 μ. Ektoapertures rather indistinct, 24.0 μ long, E/c 1.23, 4 μ wide at equator, sides slightly tapering. Endoapertures distinct, circular-elliptical, 5 μ, slightly annulate. Total wall thickness 2 μ on mesocolpia, 1 μ near apertures. Endexine 0.5 μ thick. Columellae very indistinct. Tectum psilate.
Comment. The single sample available did not contain well enough preserved grains to permit a complete description.

19. *Lepisanthes tetraphylla 'longifolia'* — **Pl. III: 9—11.**

Material studied. Malay Pen.: *Holttum SF 9049; Sinclair SF 40145.*

Pollen grains spherical-suboblate, P/E 0.89, equatorial outline circular, tricolporate. Size: P 30 (32.3) 35 μ, E 32 (36.1) 40 μ. Ektoapertures rather distinct, 18 (22.1) 26 μ long, E/c 1.63, 2 μ wide at equator, sides parallel, apertural membrane with scarce verrucae. Endoapertures distinct, circular, 4 (5.4) 6 μ, annulate. Total wall thickness 1 μ on poles, 1.5 μ on mesocolpia, 2.5 μ near apertures. Endexine 0.5 μ thick, thickened up to 1.5 μ around apertures. Columellae indistinct, < 0.5 μ in diameter, 0.5 μ long, densely spaced. Tectum 0.5—1 μ thick, smooth or very finely irregularly perforate, lumina < 0.5 μ in diameter.
Comment. *SF 40145* is characterized by an exceptionally heavy smooth tectum, *SF 9049* by a thinner, finely perforated tectum; otherwise the two samples appear identical.

20. *Lepisanthes tetraphylla 'scortechinii'* — **Fig. 1B; Pl. III: 12; Pl. IV: 1—3.**

Material studied. Malay Pen.: *Ridley 5360.*

Pollen grains spherical-suboblate, P/E 0.90, equatorial outline circular, tricolporate. Size: P 33 (37.0) 41 μ, E 36 (41.0) 44 μ. Ektoapertures rather distinct, 15 (21.5) 33 μ long, E/c 1.91, 2 μ wide at equator, sides parallel, with pointed tips. Endoapertures rather distinct, irregular-circular, 3 (7.0) 10 μ, annulate. Total wall thickness 1.5 μ on poles, 2.0 μ on mesocolpia, 3 μ near apertures. Endexine 0.5—1 μ thick, distinctly thickened, up to 2 μ, around endoaperture (Pl. IV, 3). Columellae indistinct, <0.5 μ in diameter, < 0.5 μ long. Tectum finely evenly reticulate (Pl. III, 12), lumina up to 1 μ in diameter, variable in shape, circular, elliptical, or elongated-irregular, muri up to 1 μ wide, < 0.5 μ high, biconvex in cross section (Pl. IV, 3).

21. *Lepisanthes tetraphylla '21'*.

Material studied. Malay Pen.: *Hume 9333.*

Pollen grains suboblate, P/E 0.84, equatorial outline circular, tricolporate. Size: P 25 μ, E 28 (29.9) 32 μ. Ektoapertures fairly distinct, 12 (15.9) 19 μ long, E/c 1.88, 1—2 μ wide at equator, sides parallel, with rounded tips. Endoapertures distinct, irregular-circular, 3 (4.4) 5 μ, annulate. Total wall thickness 1 μ on poles, 1.5 μ on mesocolpia, 2 μ near endoapertures. Endexine 0.5 μ, distinctly thickened around endoapertures. Columellae absent, ektexine smooth.

22. *Lepisanthes tetraphylla 'hirta'* — **Pl. IV: 4—6.**

Material studied. Malay Pen.: *Kiah SF 24307; Kostermans s.n.; Ridley 11085; Soh KEP 15491.* — Sumatra: *Rahmat si Toroes 4199; Soepadmo 190.*

Pollen grains spherical-suboblate, P/E 0.93, equatorial outline circular, tricolporate. Size: P 21 (27.0) 31 μ, E 23 (29.1) 34 μ. Ektoapertures rather indistinct (Pl. IV: 5), 11 (16.2) 22 μ long, E/c 1.80, 2—4 μ wide at equator, sides parallel, rounded tips. Endoapertures distinct, irregular circular-elliptical, 4 (5.7) 7 μ, equatorially elongated (Pl. IV: 5), irregularly annulate. Total wall thickness 1.2 μ on poles, 1.2 μ on mesocolpia, 2.2 μ near endoapertures. Endexine 0.5 μ, distinctly thickened around endoapertures. Columellae fine but distinct, < 0.5 μ in diameter, 0.5 μ long, medium dense, evenly distributed. Tectum smooth or finely perforate-reticulate, lumina isodiametric, up to 0.5 μ in diameter, muri variable in width, < 0.5 μ high.

Comment. The pollen of this form is rather variable in length of ektoapertures and in sculptural development.

24. *Lepisanthes tetraphylla 'cuneata'* — **Pl. IV: 7—8.**

Material studied. Malay Pen.: *Holttum 9583; SF 24519.*

Pollen grains spherical-suboblate, P/E 0.91, equatorial outline circular to rounded triangular, tricolporate. Size: P 22 (24.7) 28 μ, E 24 (27.4) 31 μ. Ektoapertures rather indistinct, 11 (16.0) 20 μ long, E/c 1.71, 2 μ wide at equator, sides parallel, rounded tips. Endoapertures distinct, circular-elliptical or irregularly shaped, 4 (5.0) 6 μ, annulate. Total wall thickness 1.0 μ on poles, 1.4 μ on mesocolpia, 2.5 μ around endoapertures. Endexine 0.5 μ thick, slightly thickened around endoapertures. Columellae absent or very indistinct, <0.5 μ in diameter, <0.5 μ long. Tectum smooth or with very few irregularly spaced perforations, lumina < 0.5 μ in diameter.

25. *Lepisanthes tetraphylla 'montana'* — **Pl. V. 1—6.**

Material studied. Malay Pen.: *Henderson 18372.* — Sumatra: *v. Steenis 3448; v. Steenis 3781.* — Java: *Koorders 39656; NN 143; v. Steenis 17342; Winckel 450 B;* cult. *H. Bog. III-B. 23.* — Borneo: *Kostermans 21072; Wood SAN 1995.*

Pollen grains spherical-suboblate, P/E 0.93, equatorial outline circular, tricolporate, occasionally tetracolporate (25 % in *v. Steenis 17342*). Size: P 23 (28.5) 36 μ, E 25 (30.9) 36 μ. Ektoapertures rather distinct or indistinct, 13 (19.5) 29 μ long, E/c 1.58, 2—4 μ wide at equator, sides parallel, rounded or pointed tips. Endoapertures distinct, circular, 3 (5.6) 10 μ, irregularly annulate. Total wall thickness 1.2 μ on poles, 1,5 μ on mesocolpia, 2.6 μ near apertures. Endexine 0.5 μ thick, thickened around endoapertures. Columellae rather distinct, < 0.5 μ in diameter, 0.5 μ long, densely spaced. Tectum smooth (Pl. V: 1, 4a) or finely, evenly reticulate, (Pl. V: 5) lumina isodiametric-irregularly shaped, 0.5 μ in diameter, muri < 0.5 μ wide, < 0.5 μ high.

Comment. The samples from the Malay Peninsula, Sumatra, and Borneo all posses a thin smooth tectum, while those from Java show a psilate, finely perforate or evenly finely reticulate tectum.

27. *Lepisanthes tetraphylla 'lamponga'* — Fig. 1a; Pl. V: 8, 9; Pl. VI: 1.

Material studied. Sumatra: *Bünnemeyer 637; Iboet 399; Lörzing 4699; Maradjo 481; Meijer 4466a; Raap 497; Rahmat si Toroes 5295; Yates 1962.*

Pollen grains spherical-suboblate, P/E 0.90, equatorial outline circular, tricolporate. Size: P 23 (26.3) 34 μ, E 23 (29.2) 41 μ. Ektoapertures rather distinct (Pl. V: 8a, 9), 8, (17.8) 26 μ long, E/c 1.63, 2—3 μ wide at equator, occasionally constricted, sides parallel, rounded tips, rarely excentric and longer on one hemisphere than on the other, indistinctly costate. Endoapertures distinct, circular or elliptical and equatorially elongated, 4 (5.6) 7 μ, annulate. Total wall thickness 1.5 μ on poles, 2.0 μ on mesocolpia, 3 μ near endoapertures. Endexine 0.5 μ thick, thickened up to 2 μ around endoapertures. Columellae rather distinct (Pl. V; 7, 8a), < 0.5 μ in diameter, 0.5 μ long, densely spaced. Tectum smooth, or very finely irregularly perforate, or shallowly pitted, lumina isodiametric, < 0.5 μ in diameter, 0.5 μ thick.

31. *Lepisanthes tetraphylla 'pallens'* — Pl. VI: 2—4.

Material studied. Timor: *Spanoghe 21; v. Steenis 18203.*

Pollen grains suboblate, P/E 0.86, equatorial outline rounded triangular, tricolporate. Size: P 23 (25.3) 30 μ, E 28 (29.7) 33 μ. Ektoapertures indistinct (Pl. VI: 3), 9 (16.0) 24 μ long, E/c 1.85, 2 μ wide at equator, sides parallel, rounded tips. Endoapertures rather distinct, circular, 4 (4.9) 6 μ, slightly annulate (Pl. VI: 3). Total wall thickness 1.0 μ on poles, 2.0 μ near apertures. Endexine 0.5—1 μ thick, slightly thickened around endoapertures. Columellae rather indistinct, < 0.5 μ in diameter, 0.5 μ long, arranged in a subreticulate pattern. Tectum finely evenly reticulate, lumina isodiametric, up to 0.5 μ in diameter, muri < 0.5 μ in width, < 0.5 μ high.

32. *Lepisanthes tetraphylla 'angustifolia'.*

Material studied. Java: *Korthals 8.*

Pollen grains spherical-suboblate, P/E 0.95, equatorial outline rounded triangular, tricolporate. Size: P 21 (23.0) 25 μ, E 23 (24.2) 26 μ. Ektoapertures indistinct, 9 (13.6) 15 μ long, E/c 1.78, 3 μ wide at equator, sides tapering with rounded tips. Endoapertures distinct, circular, 3 (4.1) 6 μ. Total wall thickness uniformly 1.0 μ. Endexine 0.5 μ thick. Columellae rather distinct, < 0.5 μ in diameter, 0.5 μ long, rather densely spaced. Tectum smooth or very finely perforate, lumina < 0.5 μ in diameter, < 0.5 μ thick.

33. *Lepisanthes tetraphylla '33'.*

Material studied. Anambas Isl.: *Henderson SF 20114.*

Pollen grains spherical-suboblate, P/E 0.91, equatorial outline circular, tricolporate. Size: P 24 (25.3) 28 μ, E 24 (27.9) 31 μ. Ektoapertures distinct, 9 (14.6) 18 μ long, E/c 1.91, 2—3 μ wide at equator, sides parallel, tips rounded or pointed. Endoapertures distinct, irregular-circular, 4 (5.1) 6 μ, distinctly costate on polar sides. Total wall thickness 1.4 μ on poles, 1.5 μ on mesocolpia, 1.9 μ near endoapertures. Endexine 0.5 μ thick, distinctly thickened on polar sides of endoapertures. Columellae rather distinct, < 0.5 μ in diameter, 0.5 μ long, medium dense, evenly spaced. Tectum smooth, 0.5 μ thick.

34. *Lepisanthes tetraphylla* '*heterolepis*'.

Within this form two different pollen types occur, provisionally designated A and B and described separately below.

Type A — **Pl. VI: 5—7.**

Material studied. Java: *Backer 1441.*

Pollen grains spherical, P/E 0.98, equatorial outline circular, tricolporate. Size: P 31 (32.8) 34 μ, E 31 (33.3) 35 μ. Ektoapertures indistinct, 18 (22.8) 26 μ long, E/c 1.46, 2.3 μ wide at equator. Endoapertures rather distinct, circular, 5 (5.9) 7 μ, indistinctly annulate. Total wall thickness 2 μ on poles, 2.5 μ on mesocolpia, 3 μ near apertures. Endexine 0.5 μ thick, slightly thickened around endoapertures. Columellae very indistinct, < 0.5 μ in diameter, < 0.5 μ long. Tectum finely reticulate, lumina isodiametric, rounded-subangular, up to 1 μ in diameter on mesocolpia, up to 0.5 μ on poles and near apertures, muri < 1 μ wide, < 0.5 μ high.

Type B — **Pl. VI: 8.**

Material studied. Borneo: *Kostermans 21046; v. Slooten 2250.*

Pollen grains suboblate, P/E 0.87, equatorial outline circular, tricolporate. Size: P 24 (26.1) 28 μ, E 26 (29.2) 32 μ. Ektoapertures indistinct, 11 (15.4) 18 μ long, E/c 1.90, 3—4 μ wide at equator. Endoapertures rather distinct, circular, 3 (5.6) 7 μ, indistinctly annulate. Total wall thickness uniformly 1 μ. Endexine indistinct. Columellae absent. Tectum smooth.

Comment. Although only three samples of this form could be investigated, the fact that the two Bornean samples are quite similar and markedly different from the Javanese sample appears significant. The palynological evidence thus confirms Leenhouts's opinion that the delimitation of this form is artificial. It would seem that two distinct, geographically isolated, and possibly not closely related forms have been united. Additional sampling will be necessary to clarify the situation further.

35. *Lepisanthes tetraphylla* '*35*' — **Pl. VII: 1, 2.**

Material studied. Borneo: *Anderson 4748; Clemens 30266; Clemens 50335; Endert 4176.*

Pollen grains spherical-suboblate, P/E 0.89, equatorial outline circular, tricolporate. Size: P 24 (28.7) 34 μ, E 30 (32.3) 37 μ. Ektoapertures distinct, 13 (18.3) 22 μ long, E/c 1.76, 2—4 μ wide at equator, parallel sides, rounded tips, apertural membrane occasionally covered with minute verrucae (Pl. VII: 2). Endoapertures distinct, circular-elliptical, equatorially elongated, 4.0 (6.0) 12.0 μ, distinctly annulate. Total wall thickness 1.4 μ on poles, 1.4 μ on mesocolpia, 2.4 μ near apertures. Endexine 0.5 μ thick, thickened around endoapertures. Columellae rather or very distinct, < 0.5 μ in diameter, 0.5 μ long, densely evenly spaced. Tectum smooth, < 0.5 μ thick.

Comment. Some variability is present in wall thickness and distinctness of columellate structure. The lowland samples *Anderson 4748* and *Endert 4176* have thick walls with distinct columellae while the Kinabalu samples from higher altitude *(Clemens 30266, 50335)* are characterized by very thin structureless walls.

36. *Lepisanthes tetraphylla* '*petiolaris*' — **Pl. VII: 3, 4.**

Material studied. Borneo: *Hose 551.*

Pollen grains suboblate, P/E 0.86, equatorial outline circular, tricolporate. Size: P 24 (25.0) 26 μ, E 28 (29.1) 30 μ. Ektoapertures rather distinct, 11 (14.1) 18 μ long, E/c 2.06, 2 μ wide at equator, sides parallel, rounded tips. Endoapertures distinct, elliptical, equatorially elongated, 5 (6.4) 8 μ, annulate. Total wall thickness 1.0 μ on poles, 1.0 μ on mesocolpia, 2 μ near apertures. Endexine 0.5 μ thick, thickened around endoapertures. Columellae rather distinct, < 0.5 μ in diameter, < 0.5 μ long, densely evenly spaced. Tectum smooth, < 0.5 μ thick.

37. *Lepisanthes tetraphylla* '*37*'.

Material studied. Borneo: *Endert 2823*; *Endert 3728.*

Pollen grains suboblate, P/E 0.78, equatorial outline circular, tricolporate. Size: P 24 (25.2) 26 μ, E 31 (32.5) 35 μ. Ektoapertures rather distinct, 12 (14.6) 18 μ long, E/c 2.23, 2 μ wide at equator, parallel sides, rounded tips. Endoapertures distinct, circular, 4 (4.9) 6 μ, annulate. Total wall thickness 2 μ on poles, 1.7 μ on mesocolpia, 2.7 μ near apertures. Endexine 1 μ thick, conspicuously thickened up to 2 μ around endoapertures. Columellae rather indistinct, < 0.5 μ in diameter, 0.5 μ long, scattered. Tectum smooth or finely perforate, lumina < 0.5 μ in diameter, 0.5 μ thick.

39. *Lepisanthes tetraphylla* '*39*'.

Material studied. Borneo: *Carr 26768.*

Pollen grains spherical-suboblate, P/E 0.93, equatorial contour circular, tricolporate. Size: P 30 (31.0) 32 μ. E 25 (33.4) 39 μ. Ektoapertures rather distinct, 13 (14.9) 18 μ long, E/c 2.24, 2 μ wide at equator, parallel sides, rounded tips. Endoapertures distinct, circular, 5 (5.6) 6 μ, annulate. Total wall thickness 1.2 μ on poles, 1.3 μ on mesocolpia, 3.0 μ near apertures. Endexine 0.5 μ thick, conspicuously thickened up to 2 μ around endoapertures. Columellae rather indistinct, < 0.5 μ in diameter, 0.5 μ long, scattered. Tectum smooth, 0.5 μ thick.

41. *Lepisanthes tetraphylla* '*41*'.

Material studied. Borneo: *Haviland 1624.*

Pollen grains spherical-suboblate, P/E 0.92, equatorial outline circular, tricolporate. Size: P 24 (26.6) 32 μ, E 25 (29.0) 30 μ. Ektoapertures rather distinct, 18 (19.7) 24 μ long, E/c 1.47, 1—2 μ wide, sides parallel, rounded tips. Endoapertures distinct, circular, 5 (5.8) 7 μ, slightly annulate. Total wall thickness 1.0 μ on poles, 1.3 μ on mesocolpia, 2 μ near apertures. Endexine 0.5 μ thick, slightly thickened around endoapertures. Columellae rather distinct, < 0.5 μ in diameter, 0.5 μ long, densely spaced. Tectum smooth, < 0.5 μ thick.

42. *Lepisanthes tetraphylla* '*42*'.

Material studied. Borneo: *Kadir & Enggoh BNB 10351.*

Pollen grains spherical-suboblate, P/E 0.94, equatorial outline circular, tricolporate. Size: P 32 (32.3) 33 μ, E 32 (34.3) 39 μ. Ektoapertures distinct, 22 (23.2) 24 μ long, E/c 1.48, 4 μ wide at equator, sides parallel, rounded tips. Endoapertures irregular-elliptical, equatorially elongated, 4 (5.5) 7 μ, annulate. Total wall thickness 1.0 μ on poles, 2.0 μ on mesocolpia, 2.7 μ near apertures. Endexine indistinct, < 0.5 μ thick. Columellae absent or very indistinct. Tectum finely irregularly perforate, lumina isodiametric, < 0.5 μ in diameter, < 0.5 μ thick.

43. *Lepisanthes tetraphylla 'schizolepis'* — Pl. VII: 5—9.

Material studied. Philippines: *Alvarez 22112; Cuming 785; Loher 13879; Loher 14124; Ramos BS. 42828; Ramos & Edaño BS 33478; Ramos & Edaño BS 48216.*

Pollen grains suboblate, P/E 0.76, equatorial outline rounded triangular to semi-lobate, tricolporate. Size: P 15 (21.4) 24 μ, E 23 (28.2) 33 μ. Ektoapertures indistinct or virtually absent, 3 (8.5) 18 μ long, E/c 3.31, 2 μ wide at equator, sides parallel. Endoapertures circular, 2 (3.3) 5 μ, sometimes indistinctly annulate. Total wall thickness 0.9 μ on poles, 1.1 μ on mesocolpia, 1.0 μ near apertures. Endexine, often indistinct, < 0.5 μ thick, possibly slightly thickened around endoapertures. Columellae absent or only faintly visible, < 0.5 μ in diameter, < 0.5 μ long. Tectum smooth, rarely faintly irregularly perforate, 0.5 μ thick.

46. *Lepisanthes tetraphylla '46'* — Pl. VII: 10.

Material studied. Philippines: *Wenzel 824; Wenzel 2857.*

Pollen grains oblate, P/E 0.71, equatorial contour rounded triangular to semi-lobate, tricolporate, rarely tetracolporate. Size: P 14 (19.9) 26 μ, E 23 (28.2) 33 μ. Ektoapertures distinct, 9 (12.1) 15 μ long, E/c 2.33, 2 μ wide at equator, sides tapering. Endoapertures distinct, circular, 3 (4.1) 6 μ. Total wall thickness 1.0 μ on poles, 1.1 μ on mesocolpia, 1.2 μ near apertures. Endexine distinct, 0.5 μ thick. Columellae indistinct, < 0.5 μ in diameter, < 0.5 μ long, scattered. Tectum faintly, irregularly rugulate-foveolate, depressions irregularly shaped, sometimes indistinctly aligned, < 0.5 μ in diameter, very shallow, total thickness 0.5 μ.

section **Hebecoccus**

Lepisanthes falcata ssp. **borneensis** Leenh. — Pl. VIII: 3—7.

Material studied. Borneo: *Chew, Corner & Stainton RSNB 2936; Clemens 29896; Smythies 15669.*

Pollen grains suboblate, P/E 0.79, equatorial outline rounded triangular or circular, tricolporate. Size: P 20 (22.7) 26 μ, E 20 (28.8) 36 μ. Ektoapertures rather distinct, 18 (22.6) 26 μ long, E/c 1.27, 3 μ wide at equator, sides tapering, indistinctly costate. Endoapertures circular or slightly irregular, 3 (4.5) 6 μ. Total wall thickness 1.1 μ on poles, 2 μ on mesocolpia, 1.3 μ near apertures. Endexine conspicuous, 0.5—1 μ thick. Columellae indistinct, causing a faint intragranulate pattern (Pl. VII: 6 a, 7).Tectum smooth, < 0.5 μ thick.

Comment. As already anticipated by Leenhouts (1969), this form, which had been described as a separate species has turned out to be conspecific with *L. falcata*. The three well preserved samples studied were very similar and only showed slight variation in size.

Lepisanthes banaensis Gagnep. — Pl. VIII: 1, 2.

Material studied. S. Vietnam: *Clemens 3892.*

Pollen grains suboblate, P/E 0.87, equatorial outline circular, tricolporate. Size: P 17 (18.3) 20 μ, E 20 (21.3) 22 μ. Ektoapertures rather distinct, 11 (13.0) 15 μ long, E/c 2.04, 1 μ wide at equator, sides parallel, costate. Endoapertures circular-elliptical, elongated equatorially, costate on polar sides. Total wall thickness 0.8 μ on poles, 1.1 μ on mesocolpia, 2 μ near apertures. Endexine 1 μ thick, distinctly thickened on polar sides of endoapertures, gradually tapering in poleward direction alongside ektoapertures. Columellae < 0.5 μ in diameter, 0,5 μ long, scattered. Tectum reticulate, lumina rather uniform in size, isodiametric, up to 0.5 μ in diameter, slightly smaller near apertures, muri < 0.5 μ wide, < 0.5 μ high.

Comment. The only pollen sample available for this species was extracted from a closed, probably male bud and contained a fairly high percentage of crumpled grains. The above description may, therefore, not be entirely representative.

Lepisanthes ferruginea (Radlk.) Leenh. — **Pl. VIII: 8—10.**

Material studied. Sumatra: *Lörzing 5560.* — Java: *Junghuhn s.n.; Zollinger 3459;* cult. *H. Bog. III. J 58a.*

Pollen grains suboblate, P/E 0.88, equatorial outline circular to rounded triangular, tricolporate. Size: P 23 (23.5) 24 μ, E 24 (26.6) 29 μ. Ektoapertures rather distinct, 13 (15.4) 20 μ long, E/c 1.73, 1.5 μ wide at equator, sides parallel, slightly costate. Endoapertures circular, 3 (3.3) 4 μ. Total wall thickness 1.3 μ on poles, 2 μ on mesocolpia, 1.3 μ near apertures. Endexine 1 μ thick, slightly thickened alongside ektoapertures. Columellae < 0.5 μ in diameter, < 0.5 μ long, rather densely scattered. Tectum irregularly finely perforate-foveolate, lumina irregularly shaped, occasionally interconnected (Pl. VIII: 10), up to 1 μ in diameter, muri variable in width, up to 2 μ wide, < 0.5 μ high.

Comment. This description is mainly based on *H. Bog. III. J. 58a,* which was the only sample available with rather well preserved, fully developed grains.

Lepisanthes simplicifolia (Thw.) Leenh. — **Pl. VIII: 11, 12; Pl. IX: 1—3.**

Material studied. Ceylon: *Thwaites CP 443.*

Pollen grains oblate, P/E 0.73, equatorial outline circular to rounded triangular, tricolporate. Size: P 19 (20.2) 21 μ, E 24 (27.5) 30 μ. Ektoapertures indistinct, 6 (7.6) 9 μ long, E/c 3.70, 4 μ wide at equator, sides tapering with rounded tips, sometimes congruous with endoaperture. Endoapertures circular, 3 (4.3) 5 μ, indistinctly annulate. Total wall thickness 1 μ, slightly thickened around endoapertures. Wall without visible structural differentiation, surface smooth.

subgenus OTOPHORA

section **Otophora**

Lepisanthes amoena (Hassk.) Leenh. — **Fig. 1c; Pl. IX: 4—10.**

Material studied. Malay Pen.: *Murdoch SF 199.* — Sumatra: *Forbes 2693.* — Java: *Nieuwenhuis 121; Teysmann 4772; Thorenaar T 63;* cult. *H. Bog. XI. B XV. 56.*

Pollen grains spherical, P/E 0.98, equatorial outline circular, rounded triangular, or semi-lobate, tricolporate, rarely tetracolporate. Size: P 23 (27.5) 31 μ, E 24 (28.0) 35 μ. Ektoapertures distinct, 19 (22.6) 26 μ long, E/c 1.24, 1—2 μ wide at equator, sides parallel, often inwardly folded (Pl. IX: 6). Endoapertures indistinct (Pl. IX: 7), irregularly shaped or circular, sometimes elliptical and equatorially elongated, 3 (4.1) 7 μ. Total wall thickness 1.4 μ on poles, 2 μ on mesocolpia, 1.0 μ near apertures. Endexine 0.7 μ thick, thinning towards apertures (fig. 1 C). Columellae very fine, < 0.5 μ in diameter, < 0.5 μ long, scattered in a reticulate pattern, absent from a narrow zone bordering the aperture. Tectum evenly finely reticulate, lumina isodiametric or irregularly elliptical, rather uniform in size and shape, slightly coarser, up to 1 μ in diameter on poles and mesocolpia, finer near apertures but transition very gradual, muri < 0.5 μ wide, slightly irregularly broadened at base, up to 1 μ high on mesocolpia, gradually becoming lower towards apertures.

Comment. The pollen of this species is very homogeneous, except for *Beccari 3359* in which, besides the normal tricolporate grains also a small percentage of tetracolporate and asymetrically-syncolpate grains occur.

Lepisanthes divaricata (Radlk.) Leenh. — Pl. X: 1—3.

Material studied. Borneo: *Brunig S 17527; Haviland s.n.* (1892); *SH s.n.* (1891).

Pollen grains spherical-suboblate, P/E 0.95, equatorial outline rounded triangular, tricolporate. Size: P 21 (22.7) 24 μ, E 20 (24.0) 29 μ. Ektoapertures distinct, 15 (19.5) 24 μ long, E/c 1.23, 1—2 μ wide at equator, sides parallel, indistinctly costate near endoapertures only. Endoapertures fairly distinct, circular, 2 (2.6) 4 μ. Total wall thickness 1.3 μ on poles, 2.0 μ on mesocolpia, 1.1 μ near apertures. Endexine 0.5 μ thick. Columellae indistinct, < 0.5 μ wide, < 0.5 μ long. Tectum evenly finely reticulate, lumina isodiametric, even in size and shape, up to 0.5 μ in diameter on poles and mesocolpia, slightly finer near apertures, muri < 0.5 μ wide, occasionally broadened at base, 1 μ high on mesocolpia, decreasing in height towards apertures.

Comment. It is not quite certain in how far the relatively small size of the grains may be due to immaturity of the anthers, as only relatively small buds were available.

Lepisanthes kinabaluensis Leenh. — fig. 1 f; Pl. X: 8—15; Pl. XI: 1—3.

Material studied. Borneo: *Carr SF 26934; Clemens 29017.*

Pollen grains spherical, P/E 0.99, equatorial outline circular, tricolporate. Size: P 26 (30.3) 33 μ, E 25 (30.7) 33 μ. Ektoapertures distinct, 20 (22.2) 29 μ long. E/c 1.38, up to 4 μ wide at equator, slightly tapering sides with rounded tips, bordered by low, 2 μ wide costae (Pl. X: 13), apertural membrane occasionally covered with scattered small verrucae. Endoapertures rather indistinct, circular-elliptical, elongated in polar direction, 2 (3.7) 4 μ. Total wall thickness 1.6 μ on poles, 3 μ on mesocolpia, 0.5—1.3 μ near apertures. Endexine 1—1.5 μ thick on mesocolpia, thinning towards apertures over a narrow zone surrounding the apertures, apparently fused with undifferentiated ektexine in the broad costate ridges bordering the ektoapertures. Columellae indistinct, < 0.5 μ in diameter , 0.5 μ high, scattered, disappearing towards the apertures. Tectum formed by a mosaic of irregularly shaped areas with a finely reticulate sculpture and irregularly shaped verrucae or echinae (Pl. X: 10; Pl. XI: 16). Lumina of reticulum isodiametric, up to 1 μ in diameter on poles and mesocolpia, finer towards apertures. Verrucae and echinae formed by fused upper parts of muri of reticulum (fig. 1 F), 1 μ in diameter at base, 1 μ high, tips rounded or pointed. This sculptural pattern is coarsest on the mesocolpia, gradually disappearing towards the apertures which are bordered by the smooth-surfaced thin-walled zones and ridges (fig. 1 F).

Lepisanthes multijuga (Hook. *f.*) Leenh. — **Pl. X: 4—7.**

Material studied. Borneo: *Ramos 1173; SAN 17575.*

Pollen grains suboblate, P/E 0.88, equatorial outline rounded triangular, tricolporate. Size: P 21 (23.0) 25 μ, E 24 (26.1) 30 μ. Ektoapertures distinct, 15 (18.8) 22 μ long, E/c 1.39, 2—3 μ wide at equator, sides parallel, costate. Endoapertures rather distinct, circular, 3 (3,5) 4 μ. Total wall thickness 1.5 μ on poles, 1.9 μ on mesocolpia, 1.0 μ near apertures. Endexine < 0.5 μ thick, slightly thickened along ektoapertures. Columellae indistinct, < 0.5 μ wide, 0.5 — 1 μ long, densely spaced. Tectum finely evenly reticulate, lumina isodiametric, < 0.5 μ in diameter, muri < 0.5 μ wide, 1 μ high.

section **Pseudotophora**

Lepisanthes bengalan Leenh. — **Fig. 1 D; Pl. XI: 4—8.**

Material studied. Borneo: *Kostermans 4889.*

Pollen grains spherical, P/E 0.98, equatorial outline circular, tricolporate. Size: P 27 (28.3) 29 μ, E 27 (29.2) 30 μ. Ektoapertures distinct, 21 (21.8) 22 μ long, E/c 1.34, 5 μ wide at equator, sides tapering, bordered by massive exinous zones (fig. 1 D). Endoapertures irregularly circular (Pl. XI: 8 a), 5 (5.7) 6 μ. Total wall thickness 2.0 μ on poles, 2.5 μ on mesocolpia, 1.5 μ near apertures. Endexine < 0.5 μ thick. Columellae < 0.5 μ in diameter, 0.5 μ long, scattered in a reticulate pattern in single rows, underlying muri of reticulum (Pl. XI: 7). Tectum reticulate, lumina variable in size and shape, isodiametric or elliptical and curved, up to 2 μ in diameter on mesocolpia and poles, gradually becoming finer towards apertures, muri up to 2 μ high on mesocolpia, 1 μ high near apertures, < 0.5 μ wide at top, irregularly broadened at base and fused with tops of columellae.

Lepisanthes fruticosa (Roxb.) Leenh. — **Fig. 1 E; Pl. XII: 1—10; Pl. XIII: 1—10; Pl. XIV: 1—9; Pl. XV: 1—5.**

Material studied. Vietnam: *Eberhardt 2656; Pierre 1283; Squires 850.* — Thailand: *SF 3933; Zimmerman 112.* — Malay Pen.: *Murdoch 86; SF 18759; Ridley 6948.* — Borneo: *Clemens 27612; Kostermans 7329; NBFD 3245; NBFD 5917; Nicholson NBFD 48511; Pingkun NBFD 8844; SAN 24654; Sar. For. Dept. S 25182; Wood 1784.* — Philippines: *Curran FB 5820; Curran FB 19325; Edaño PNH 26847; Lopez BS 41389 A; Merritt FB 3660; PNH 14388; Quisumbing PNH 8066; Ramos BS 39744.* — Celebes: *Rachmad 372.*

Grains spherical-suboblate, P/E 0.96, equatorial outline circular or rounded triangular, tricolporate. Size: P 20 (28.8) 36 μ, E 21 (30.0) 39 μ. Ektoapertures distinct, 13 (23.9) 34 μ long, E/c 1.26, exceptionally syncolpate (Pl. XIII: 2 a), 4 μ wide at equator, sides tapering. Endoapertures generally distinct (Pl. XII: 5), circular or elliptical 2 (4.2) 8 μ. Total wall thickness highly variable, 1—3 μ on poles, 2—5 μ on mesocolpia, 1 μ near apertures. Examples of respectively a thin walled grain and a thick walled grain are *S 25182* (Pl. XIII: 5 b) and *Curran 5820* (Pl. XV: 1, 3 b). Endexine 0.5—1 μ thick, occasionally thickened near apertures (Pl. XV: 1). Columellae variably developed, absent or very indistinct in finely reticulate grains (Pl. XIII: 5 b, 6 b, 7), distinct in coarsely reticulate grains (Pl. XII: 6 b; Pl. XIV: 6, 7 a), up to 0.5 μ in diameter, 0.5 μ long, only slightly

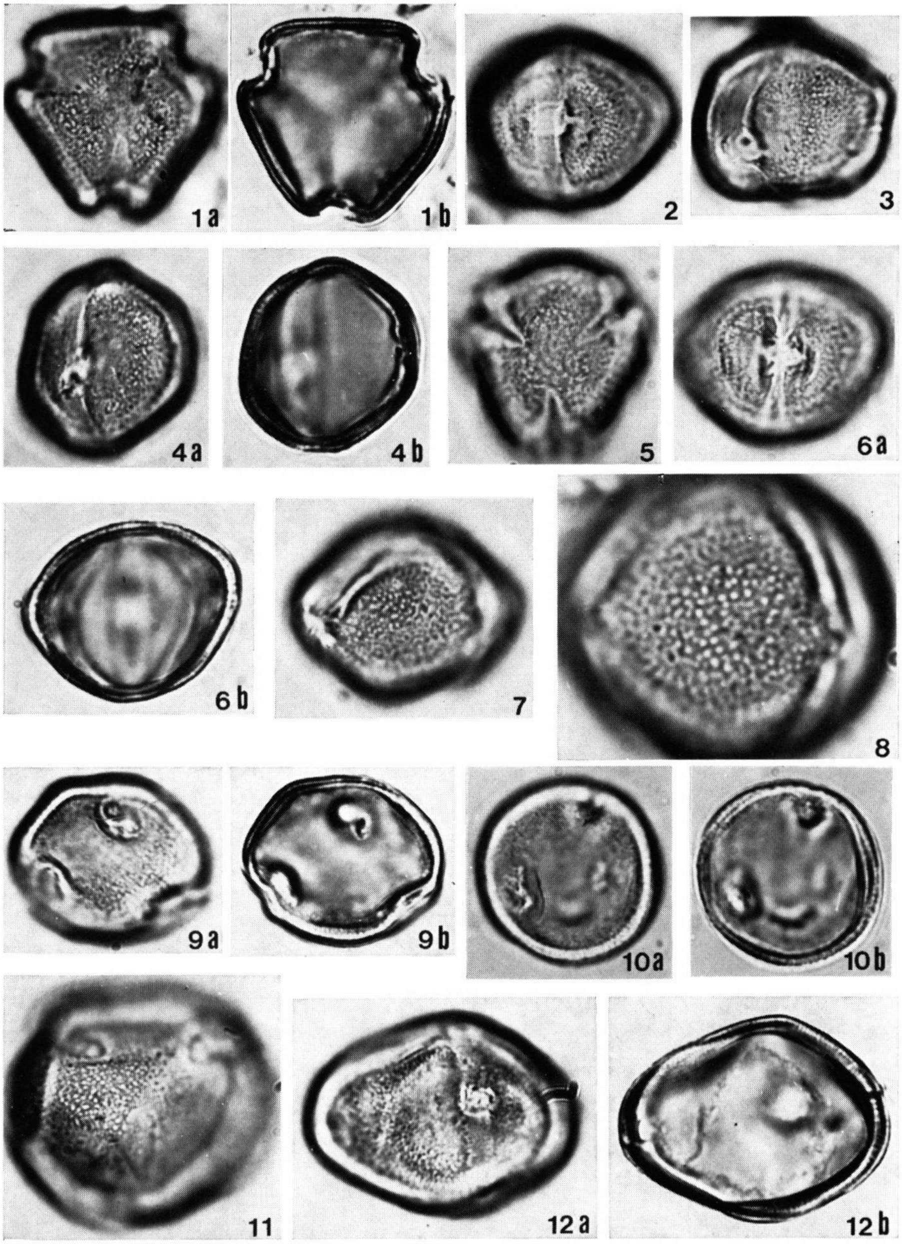

Plate I. Fig. 1—4: *L. andamanica (King s.n.)*. — Fig. 5—7: *L. tetraphylla 'tetraphylla' (Wight 530)*. — Fig. 8: *L. tetraphylla 'tetraphylla' (Gamble 21747)*. — Fig. 9, 10: *L. tetraphylla 'tetraphylla' (Poilane 5536)*. — Fig. 11, 12: *L. tetraphylla 'deficiens' (Wight 535)*. All 1000 x, except 8: 2000 x.

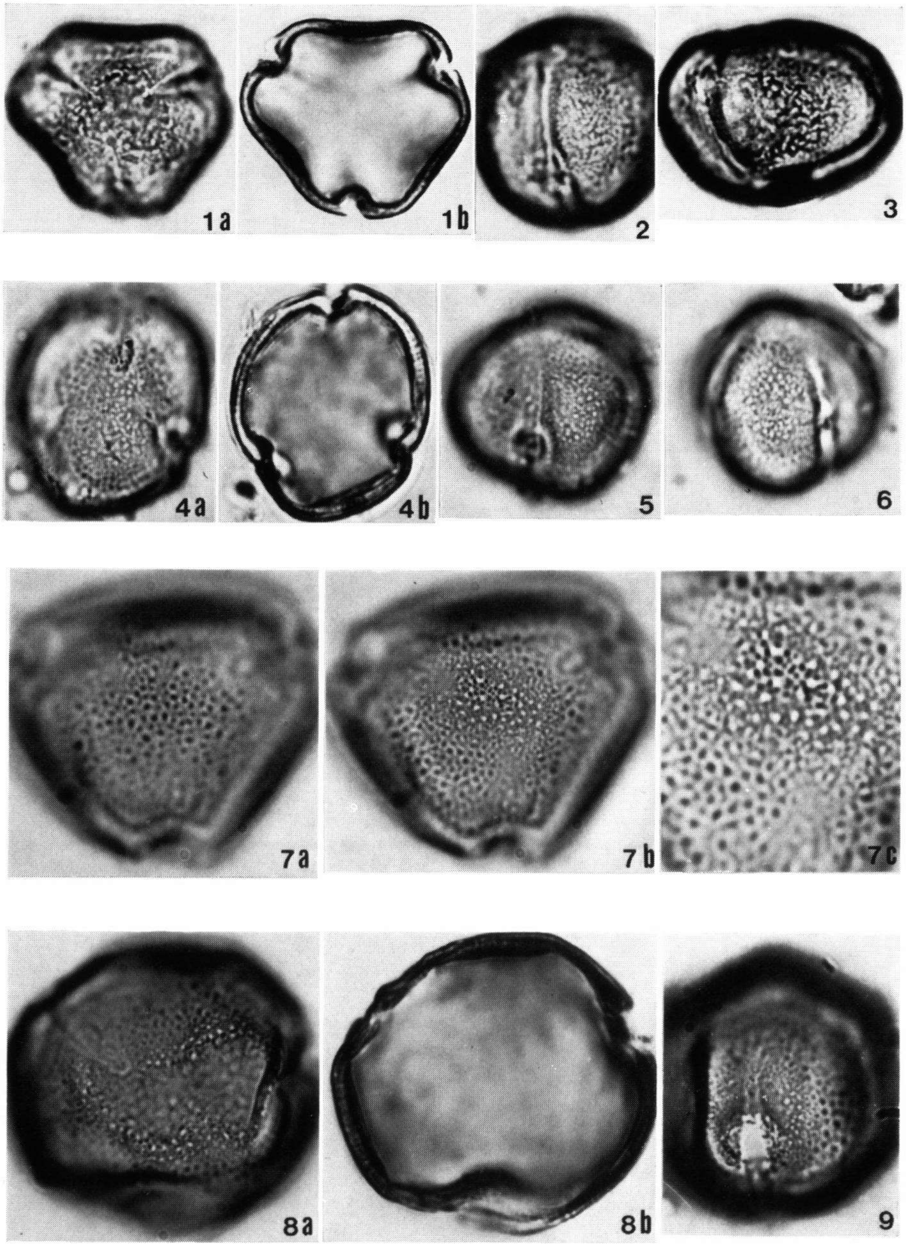

Plate II. Fig. 1—3: *L. tetraphylla 'assamica' (Gage 185)*. — Fig. 4—6: *L. tetraphylla 'basicardia' (Mokim s.n.)*. — Fig. 7—9: *L. tetraphylla 'browniana' (Gomez 342)*. All 1000 ×, except 7 c: 2000 ×.

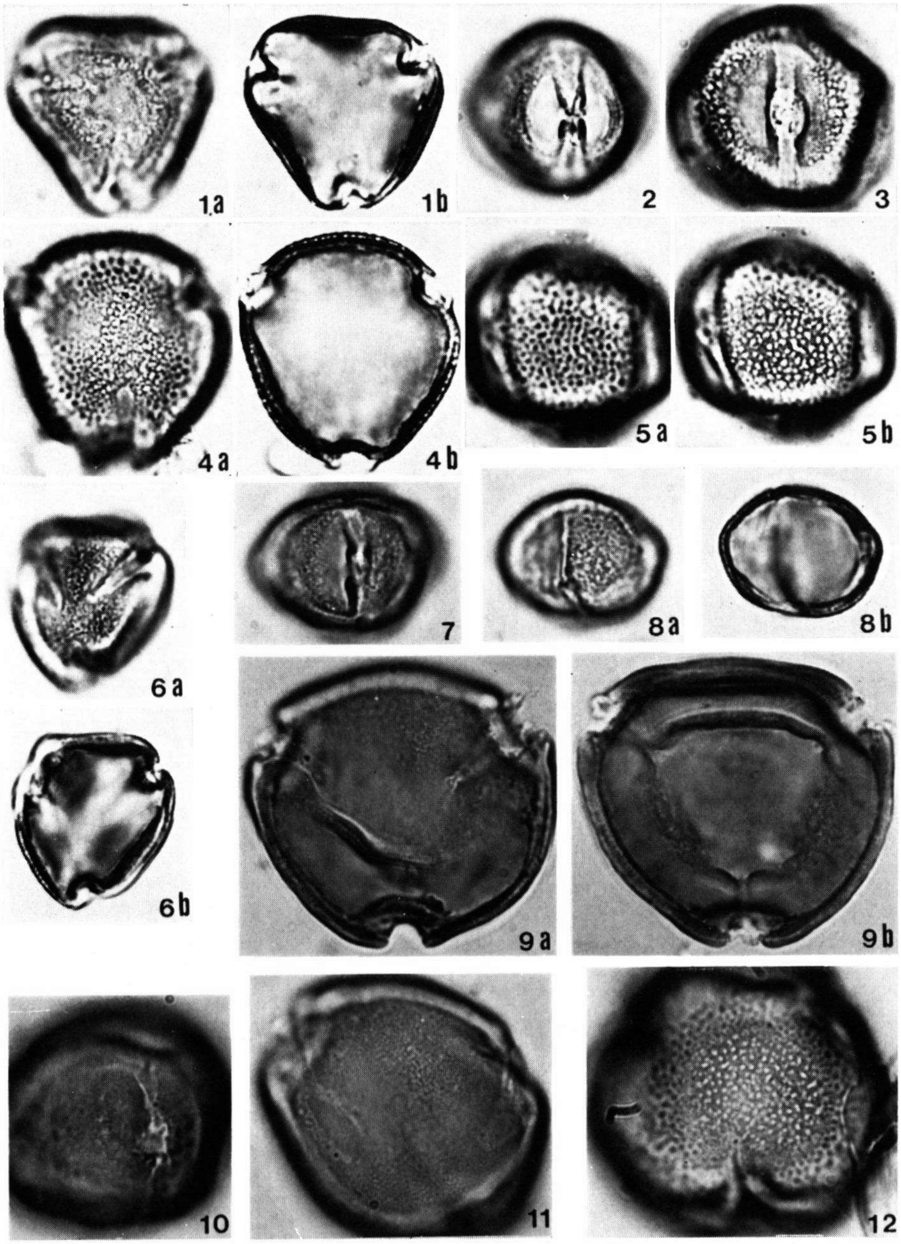

Plate III. Fig. 1, 2: *L. tetraphylla 'siamensis' (Vanpruk 191).* — Fig. 3—5: *L. tetraphylla 'poilanei' (Kasin 364).* — Fig. 6—8: *L. tetraphylla 'mekongensis' (D'Alleizette 1393).* — Fig. 9—11: *L. tetraphylla 'longifolia' (SF 40145).* — Fig. 12: *L. tetraphylla 'scortechinii' (Ridley 5360).* All 1000 ×, except 12: 2000 ×.

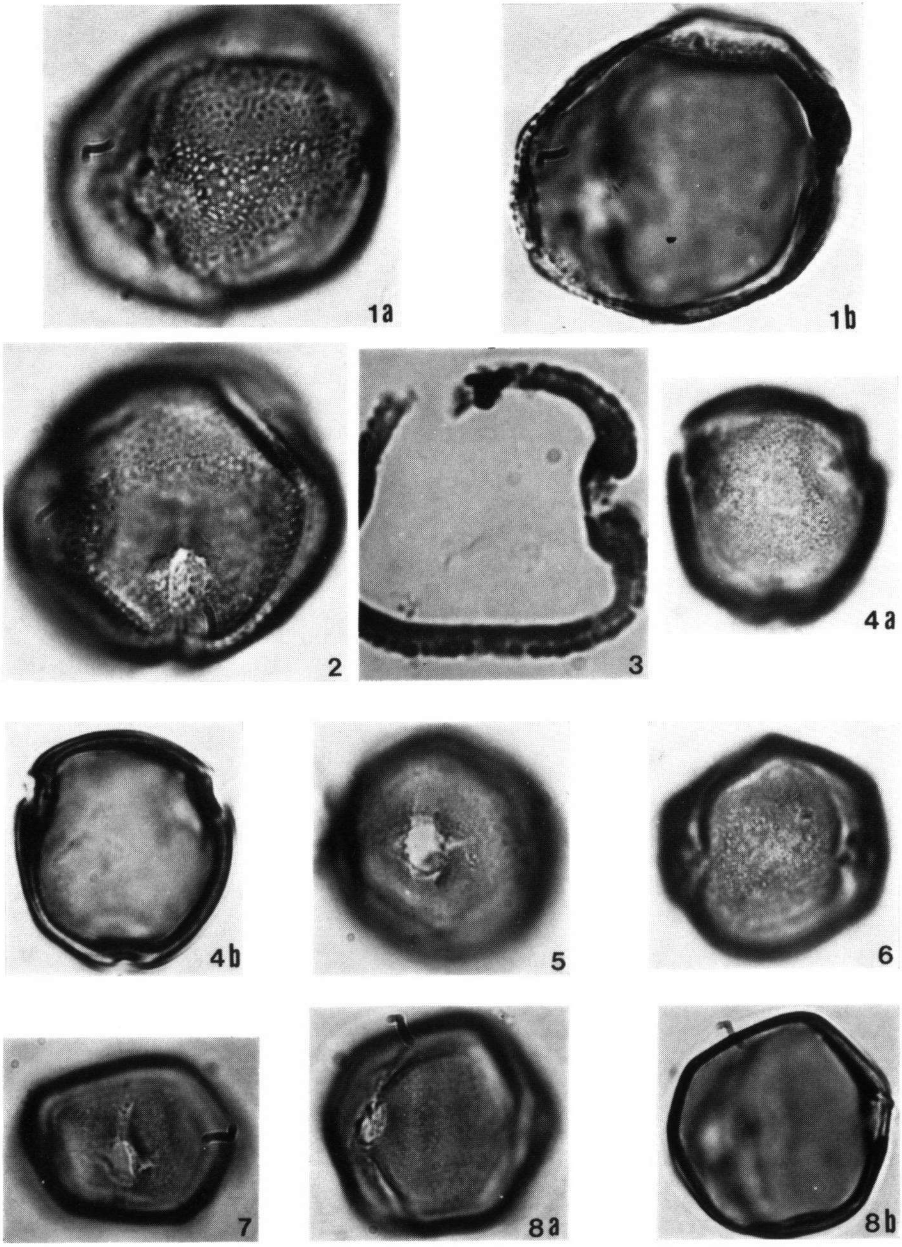

Plate IV. Fig. 1—3: *L. tetraphylla 'scortechinii' (Ridley 5360).* — Fig. 4—6: *L. tetraphylla 'hirta' (Rahmat 4199).* — Fig. 7, 8: *L. tetraphylla 'cuneata' (Holttum 9583).* All 1000 ×, except 3: 2000 ×.

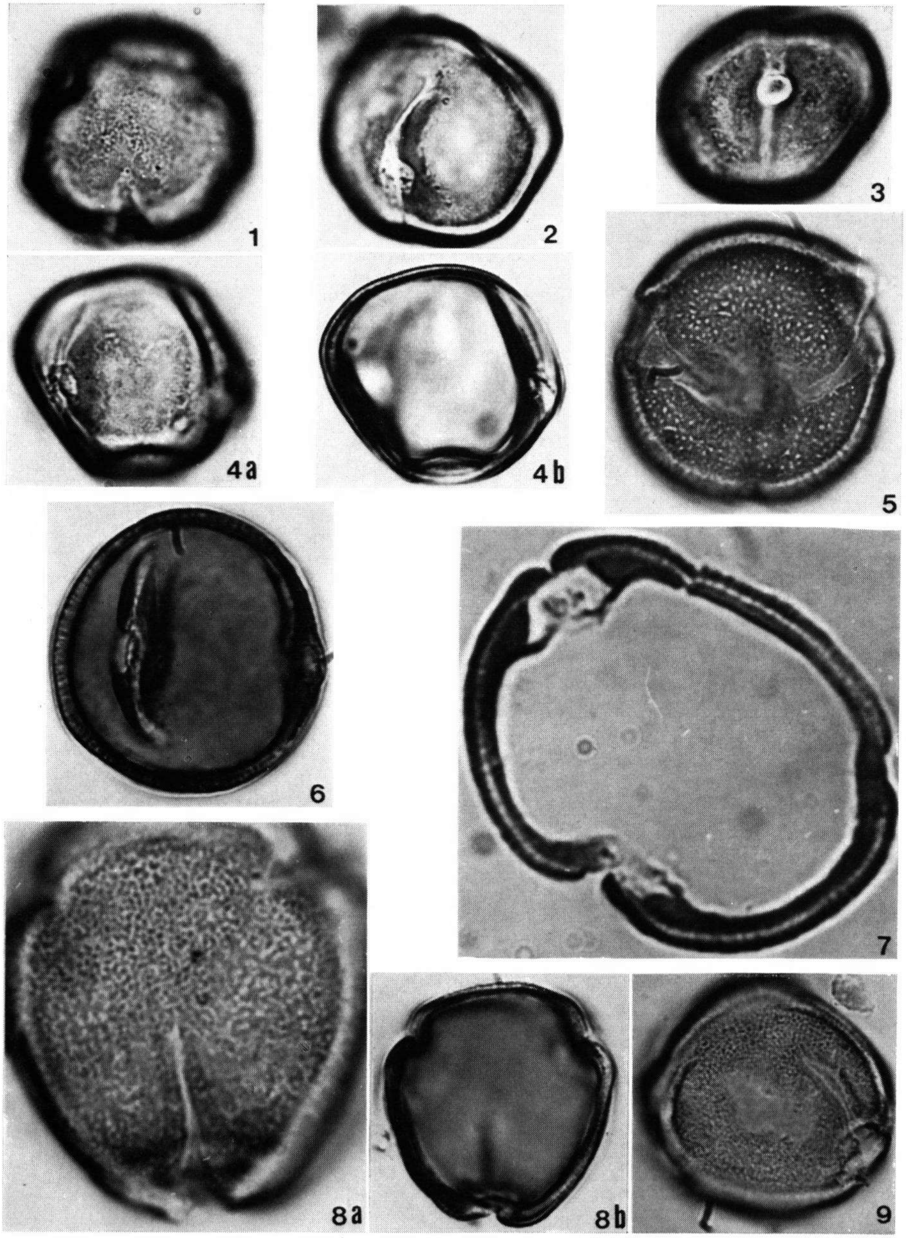

Plate V. Fig. 1—4: *L. tetraphylla* 'montana' (*Winckel 450*). — Fig. 5, 6: *L. tetraphylla* 'montana' (*Koorders 39656*). — Fig. 7: *L. tetraphylla* 'lamponga' (*Maradjo 481*). — Fig. 8, 9: *L. tetraphylla* 'lamponga' (*Rahmat si Toroes 5595*). All 1000 ×, except 7, 8: 2000 ×.

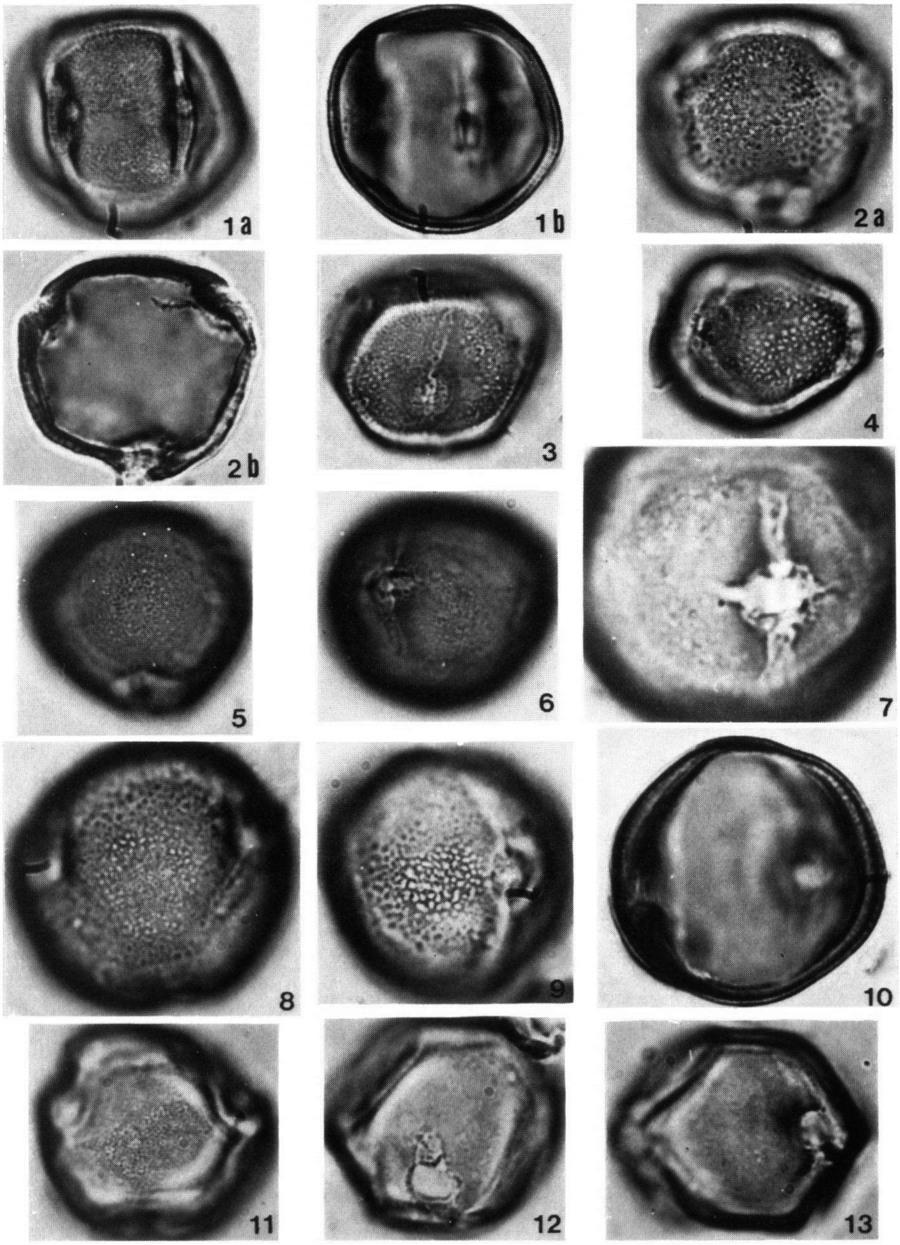

Plate VI. Fig. 1: *L. tetraphylla 'lamponga' (Rahmat si Toroes 5295)*. — Fig. 2—4: *L. tetraphylla 'pallens' (Spanoghe 21)*. — Fig. 5—7: *L. tetraphylla '33' (SF 20114)*. — Fig. 8—10: *L. tetraphylla 'heterolepis' A (Backer 1441)*. — Fig. 11—13: *L. tetraphylla 'heterolepis' B (v. Slooten 2250)*. All 1000 ×, except 7: 2000 ×.

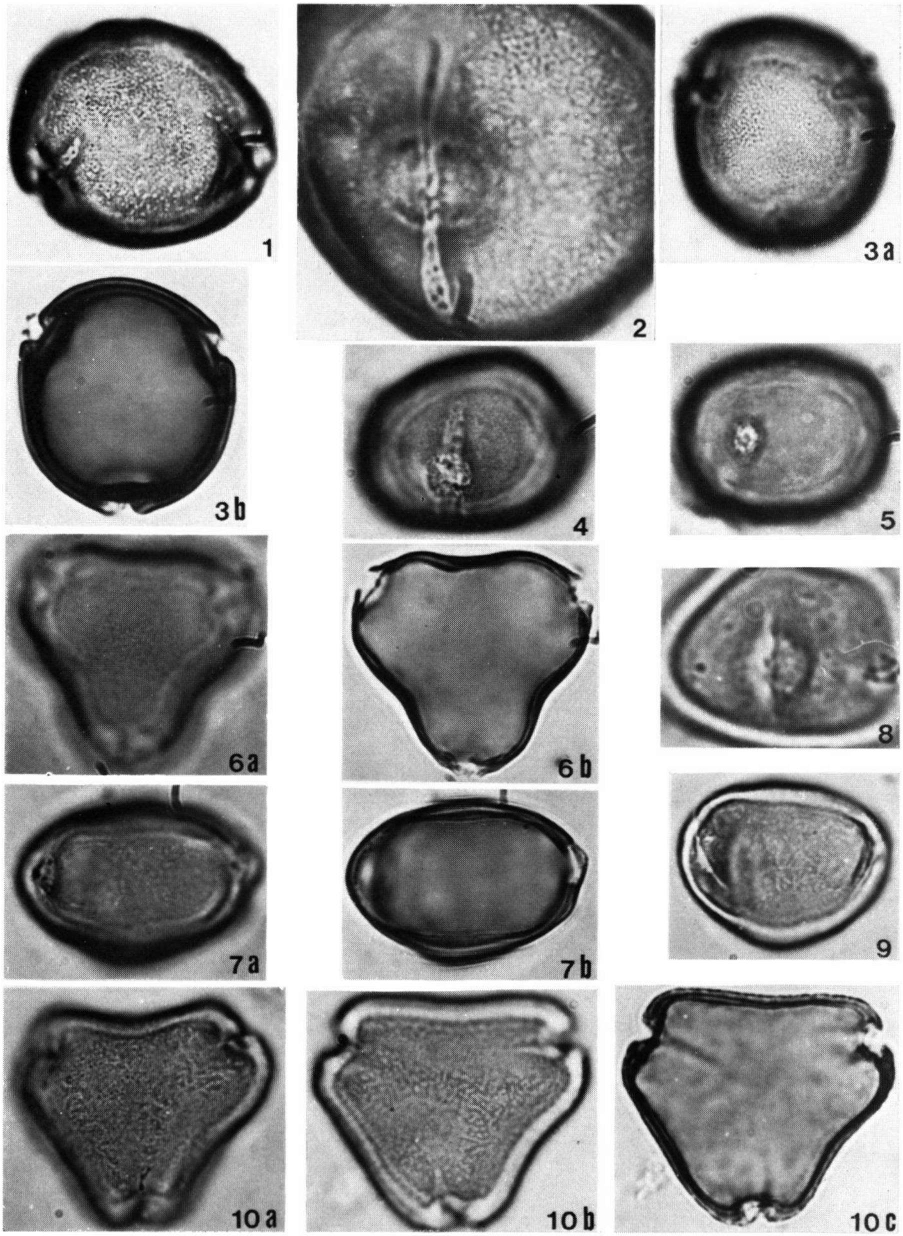

Plate VII. Fig. 1, 2: *L. tetraphylla '35' (Anderson 4748)*. — Fig. 3, 4: *L. tetraphylla 'petiolaris' (Hose 551)*. — Fig. 5: *L. tetraphylla 'schizolepis' (Cuming 785)*. — Fig. 6, 7: *L. tetraphylla 'schizolepis' (Loher 14124)*. — Fig. 8: *L. tetraphylla 'schizolepis' (Alvarez FB 22112)*. — Fig. 9: *L. tetraphylla '46' (Wenzel 824)*. All 1000 ×, except 2, 8: 2000 ×.

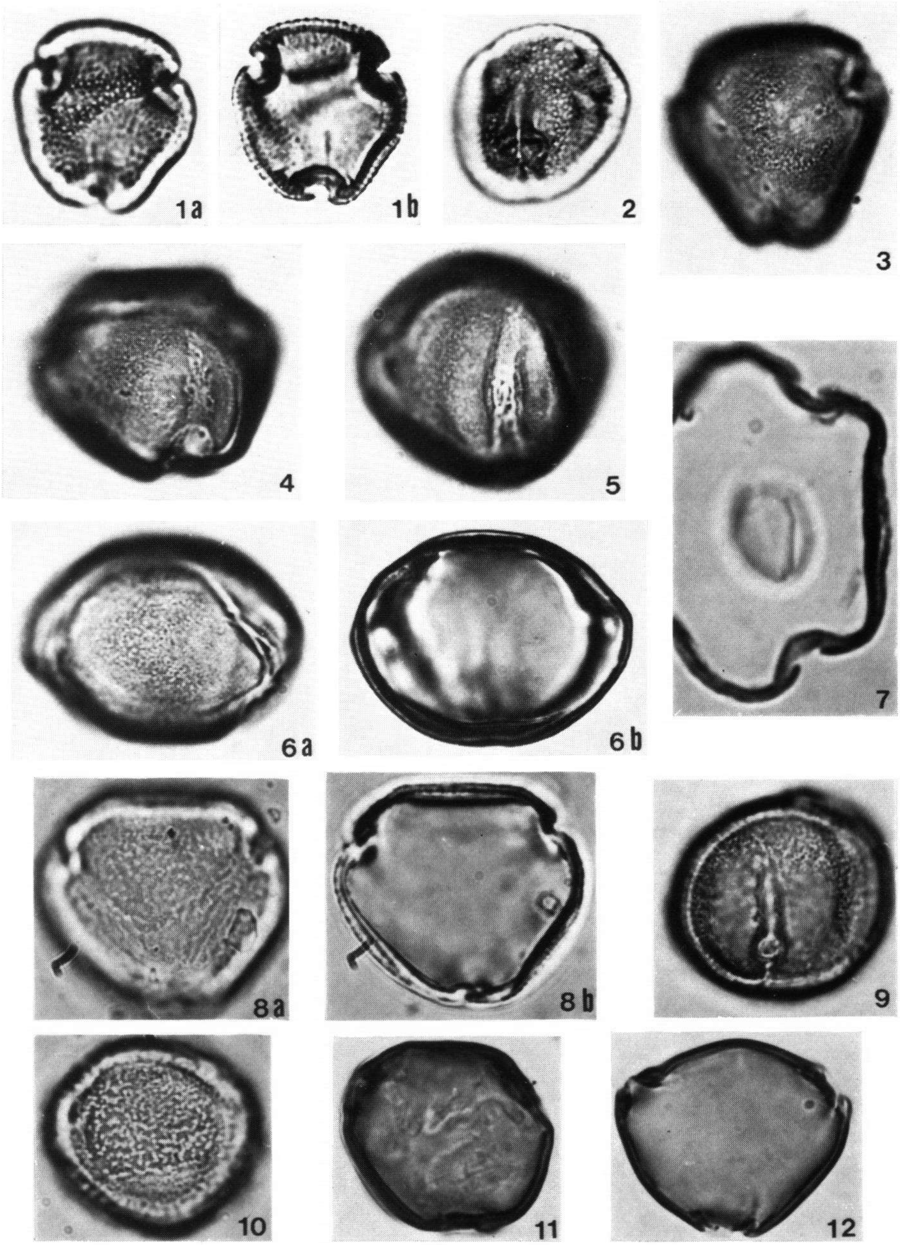

Plate VIII. Fig. 1, 2: *L. banaensis (Clemens 3892)*. — Fig. 3—7: *L. aphanococca* ssp. *borneensis (Clemens 29896)*. — Fig. 8—10: *L. ferruginea (H. Bog. III. J. 58a)*. — Fig. 11, 12: *L. simplicifolia (Thwaites 443)*. All 1000 ×, except 7: 2000 ×.

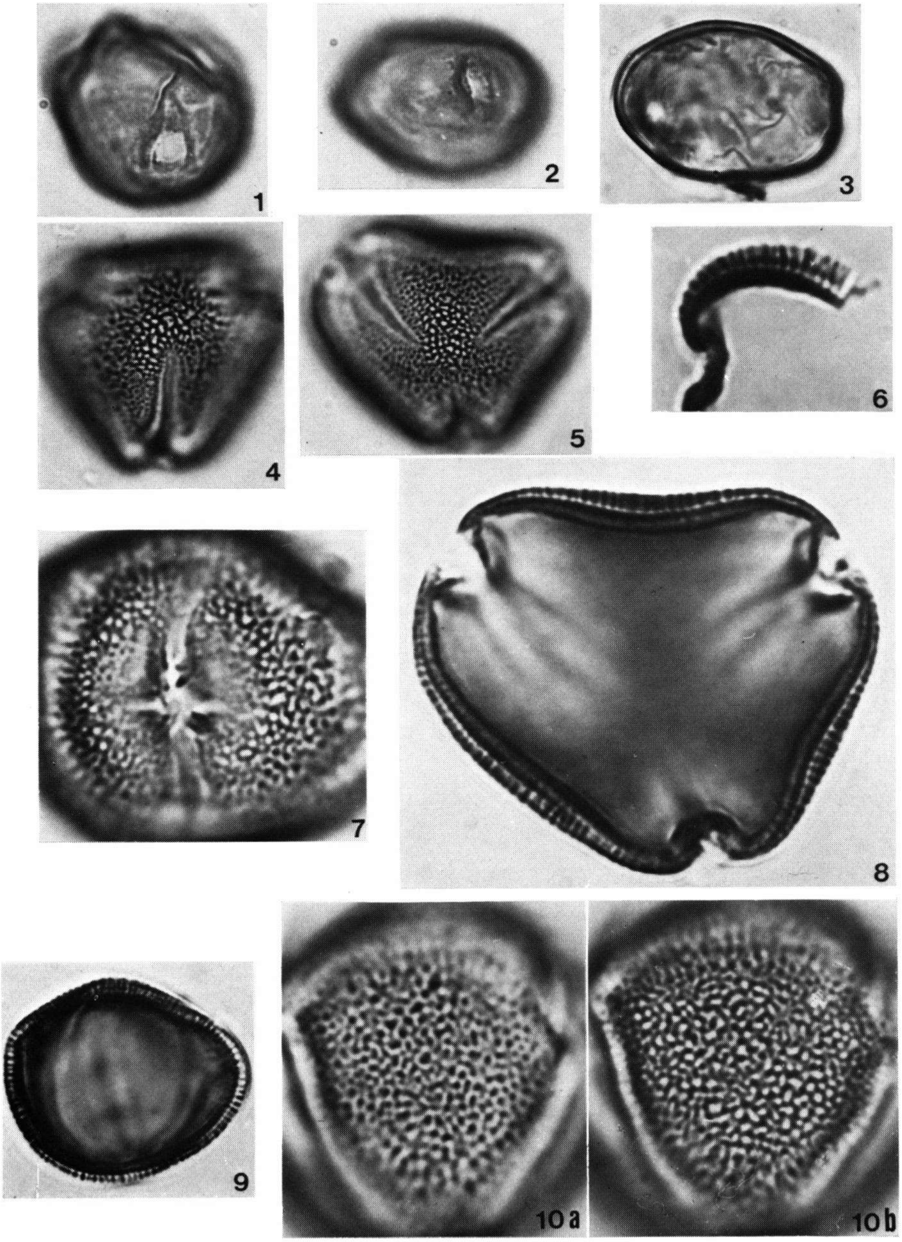

Plate IX. Fig. 1—3: *L. simplicifolia (Thwaites 443)*. — Fig. 4—10: *L. amoena (Beccari 3359)*. All 1000 ×, except 6, 7, 8, 10: 2000 ×.

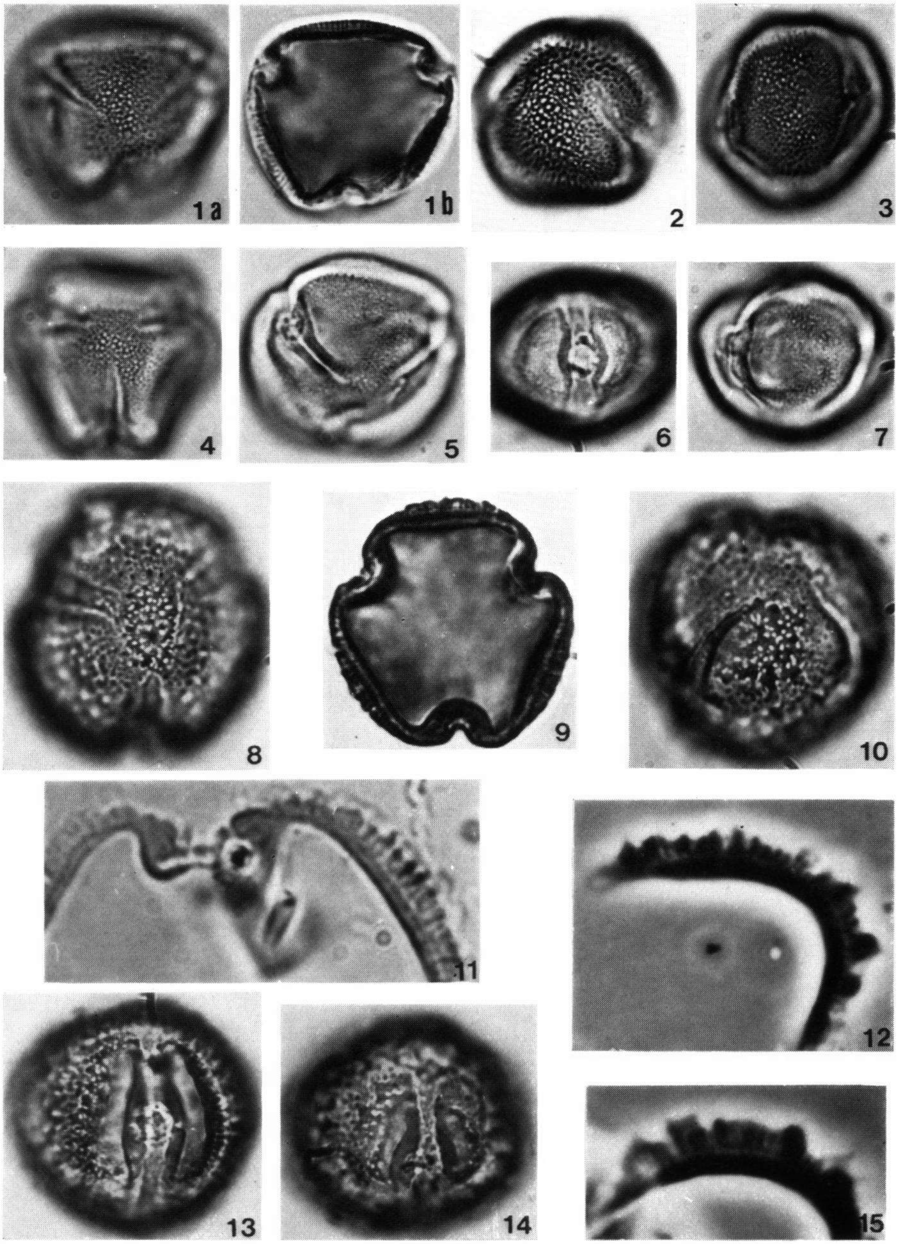

Plate X. Fig. 1—3: *L. divaricata (Haviland s.n.)*. — Fig. 4—7: *L. multijuga (SAN 17575)*. — Fig. 8—15: *L. kinabaluensis (SF 26934)*. All 1000 ×, except 11, 12 Ph.C., 15 Ph.C.: 2000 ×.

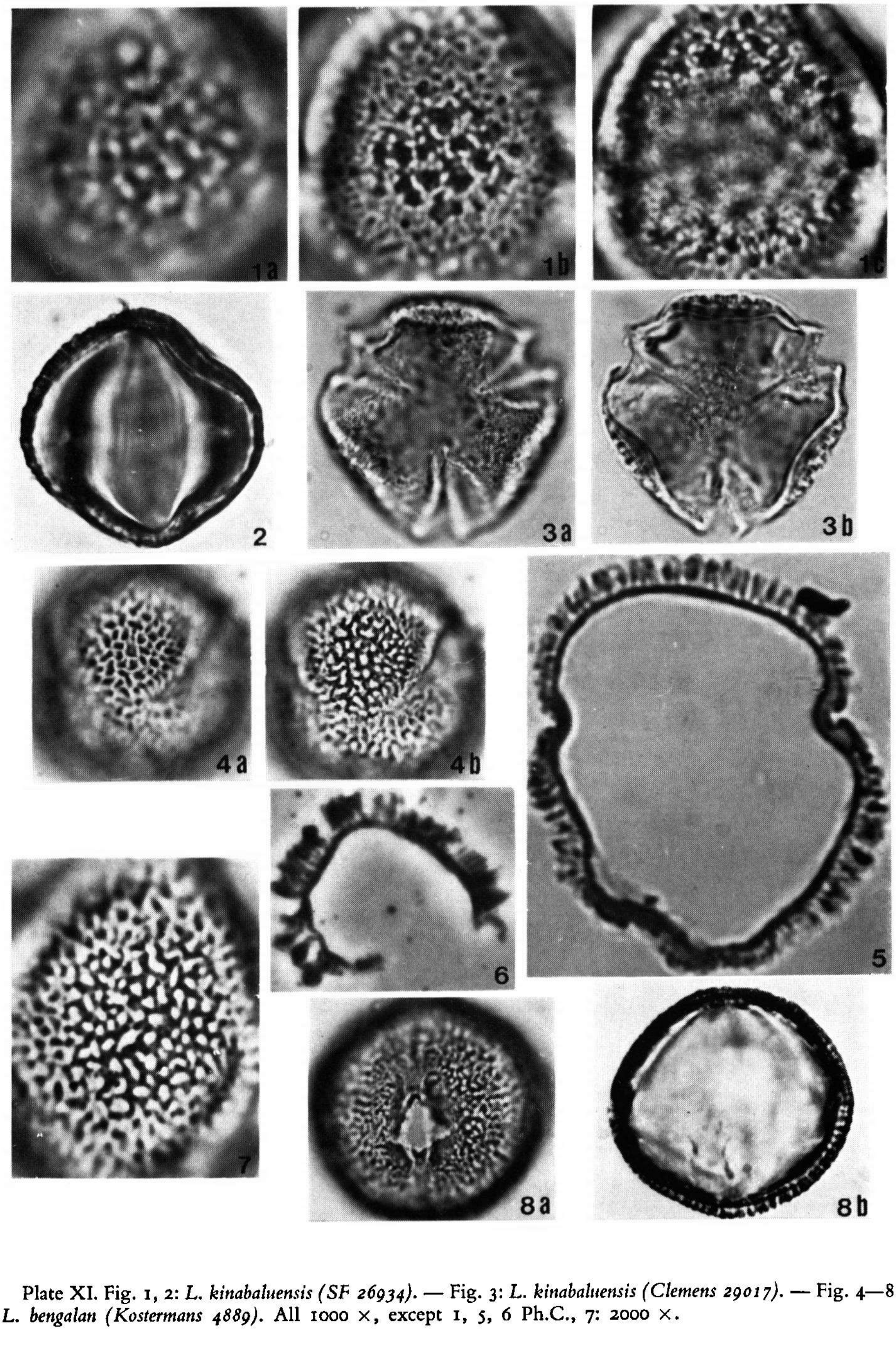

Plate XI. Fig. 1, 2: *L. kinabaluensis (SF 26934)*. — Fig. 3: *L. kinabaluensis (Clemens 29017)*. — Fig. 4—8: *L. bengalan (Kostermans 4889)*. All 1000 ×, except 1, 5, 6 Ph.C., 7: 2000 ×.

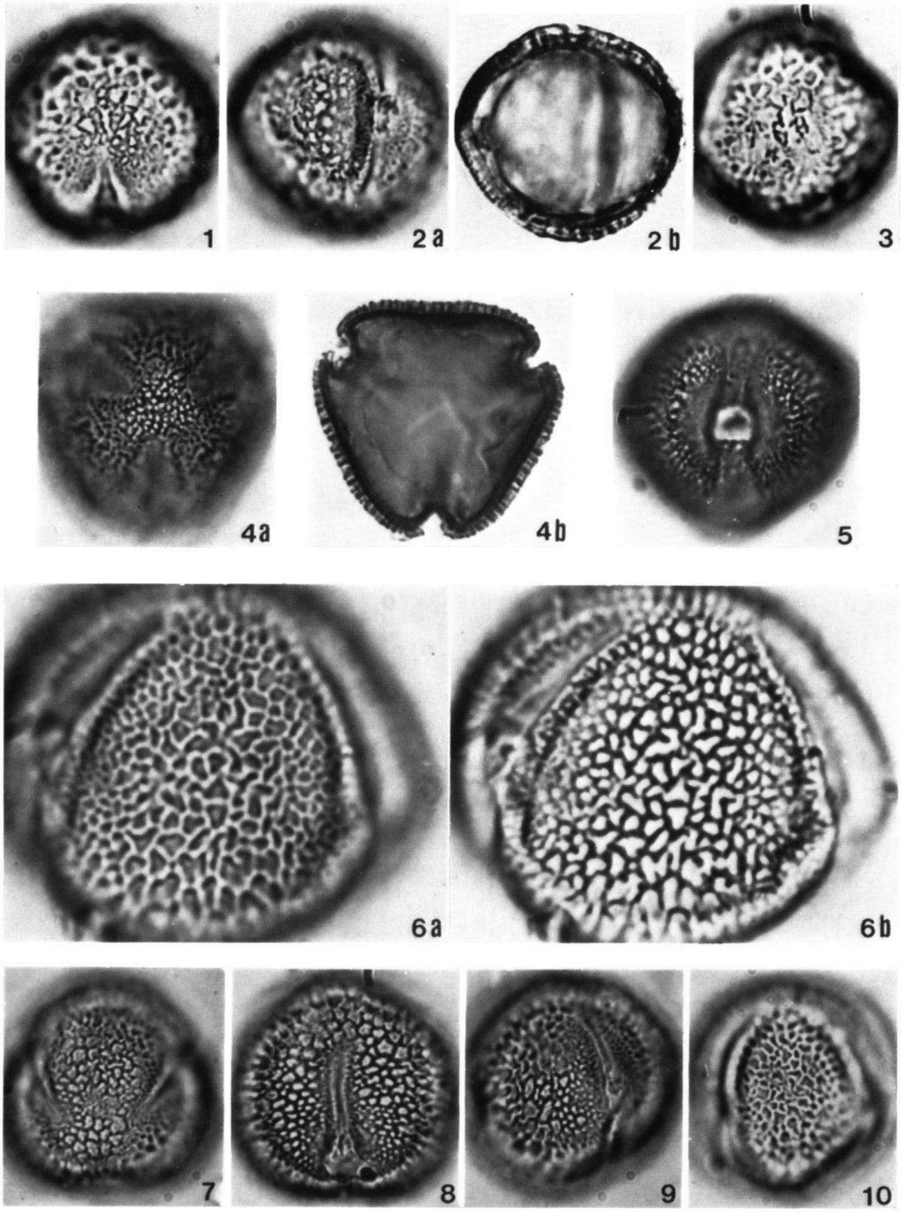

Plate XII. Fig. 1—3: *L. fruticosa (SF 3933)*. — Fig. 4—6: *L. fruticosa (Eberhardt 2636)*. — Fig. 7—10: *L. fruticosa 'erythrocalyx' (Kostermans 7329)*. All 1000 ×, except 6: 2000 ×.

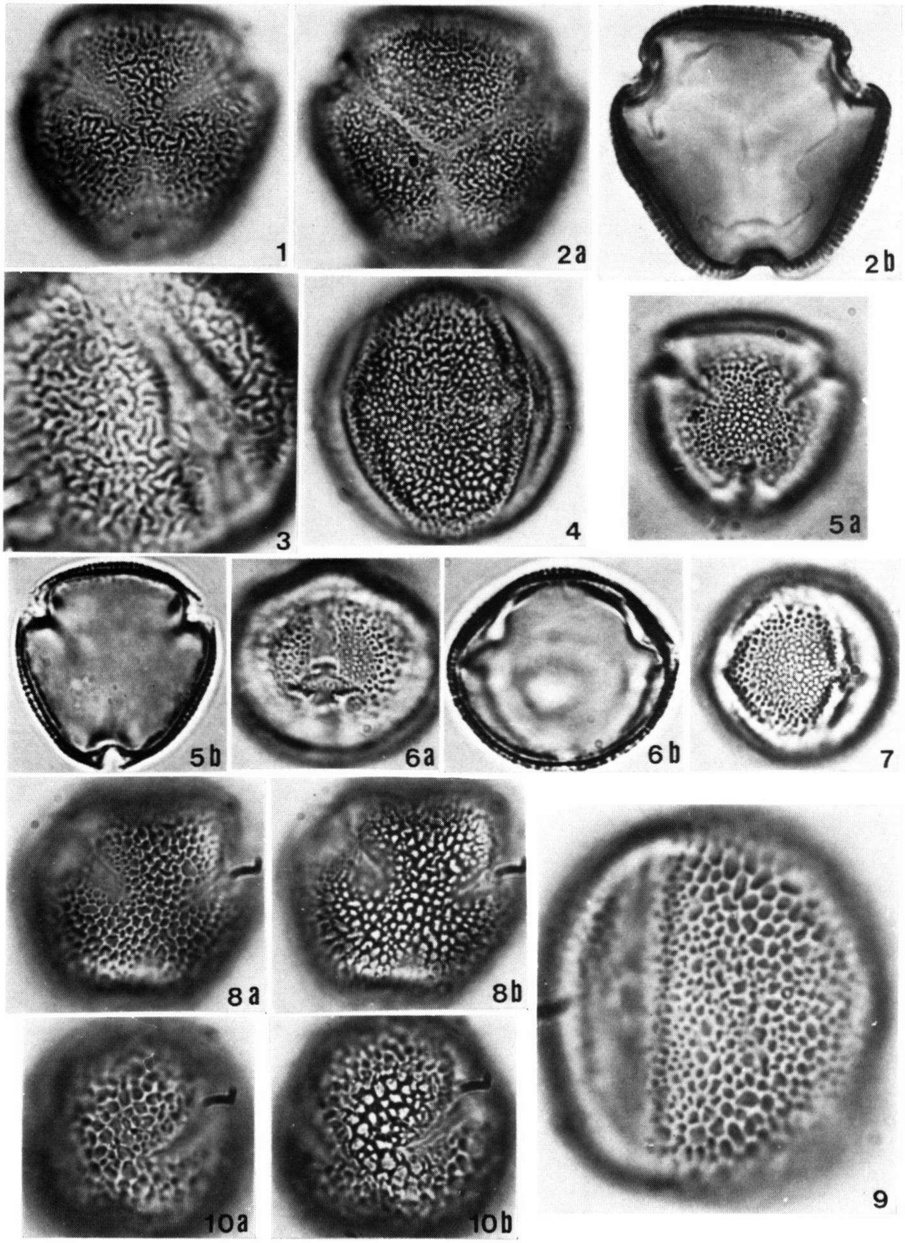

Plate XIII. Fig. 1—4: *L. fruticosa (Nicholson 48511).* — Fig. 5—7: *L. fruticosa 'glandulosa' (S 25182).* — Fig. 8, 9: *L. fruticosa (Clemens 27612).* — Fig. 10: *L. fruticosa (Rachmad 372).* All 1000 ×, except 3, 9: 2000 ×.

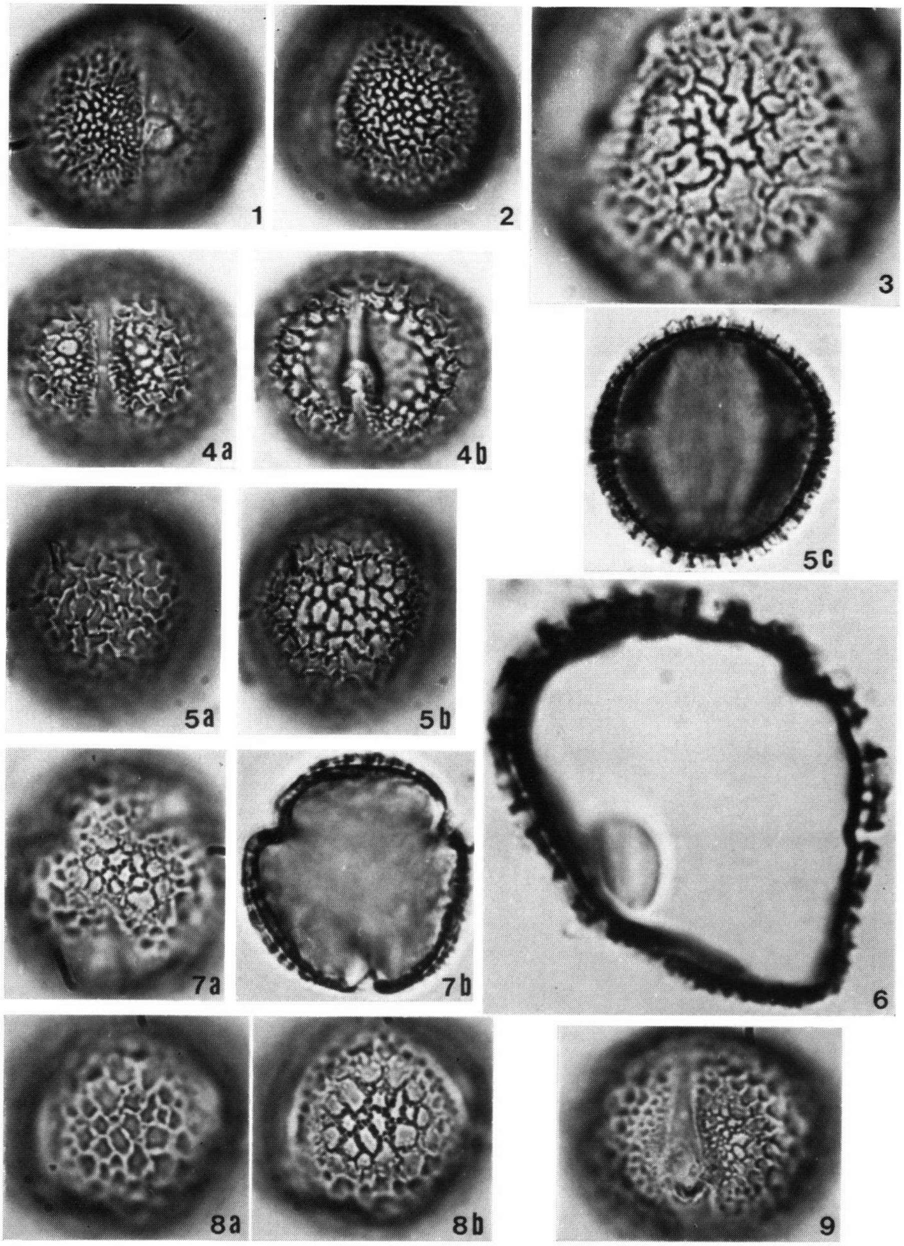

Plate XIV. Fig. 1—3: *L. fruticosa (Rachmad 372)*. — Fig. 4, 5: *L. fruticosa (Merritt FB 3660)*. — Fig. 6—9: *L. fruticosa (PNH 14388)*. All 1000 ×, except 3, 6: 2000 ×.

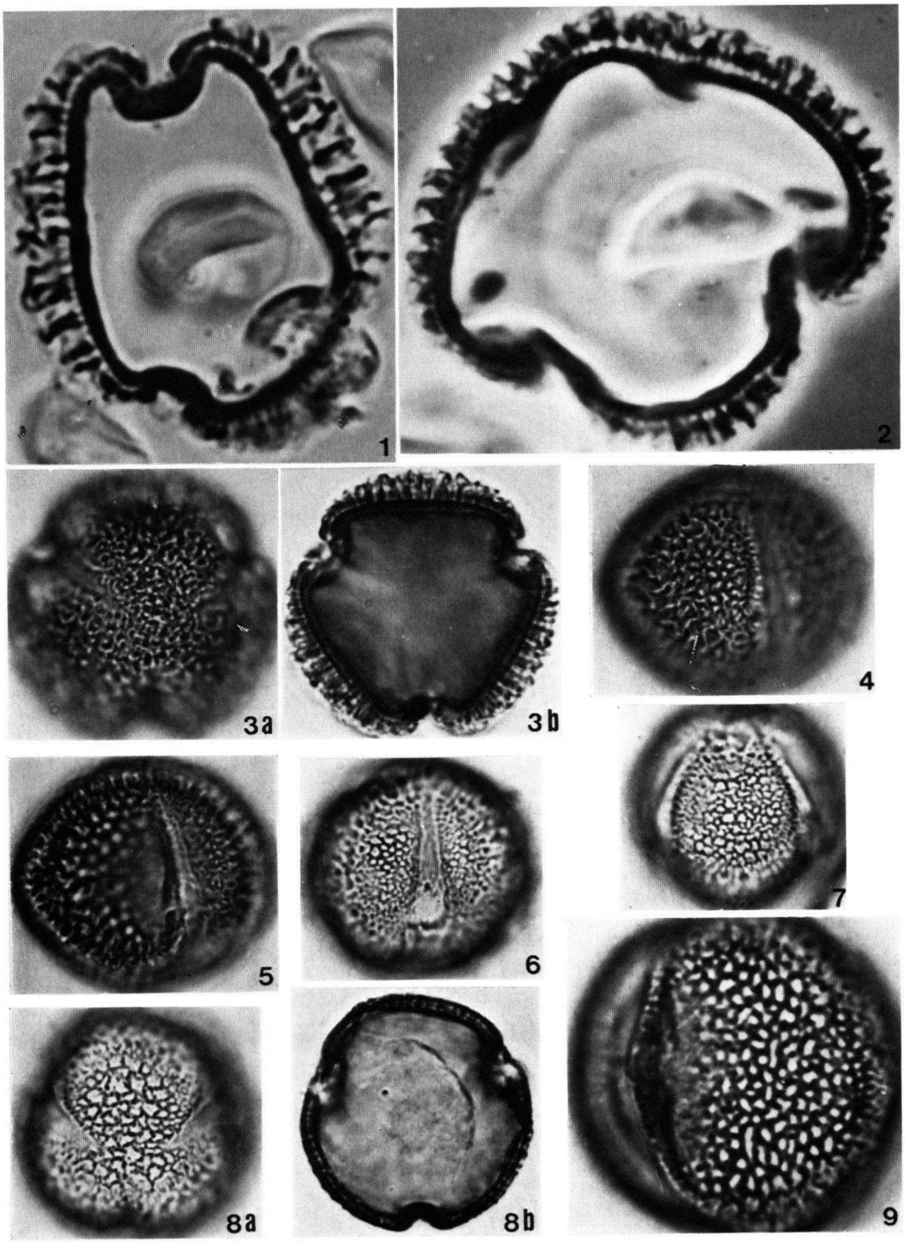

Plate XV. Fig. 1—5: *L. fruticosa (Curran 5820)*. — Fig. 6—8: *L. alata (Alston 13229)*. — Fig. 9: *L. alata (Zollinger 3456)*. All 1000 ×, except 1, 2 Ph.C., 9: 2000 ×.

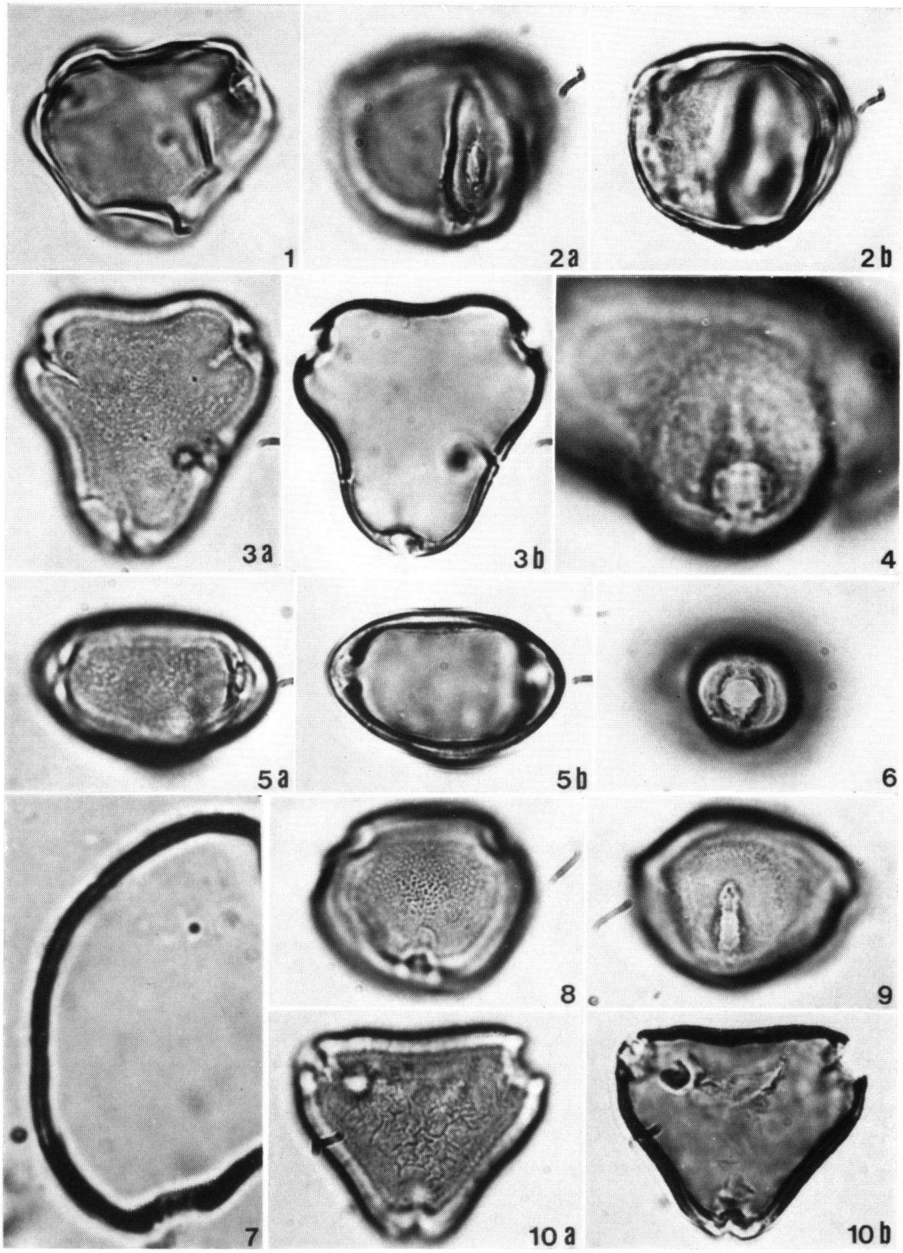

Plate XVI. Fig. 1, 2: *L. membranifolia (Beccari PP 307)*. — Fig. 3—6: *L. rubiginosa (de Vriese s.n.)*. — Fig. 7—9: *L. rubiginosa (Ramos BS 46362)*. — Fig. 10: *L. rubiginosa (Forman 329)*. All 1000 ×, except 4, 6, 7: 2000 ×.

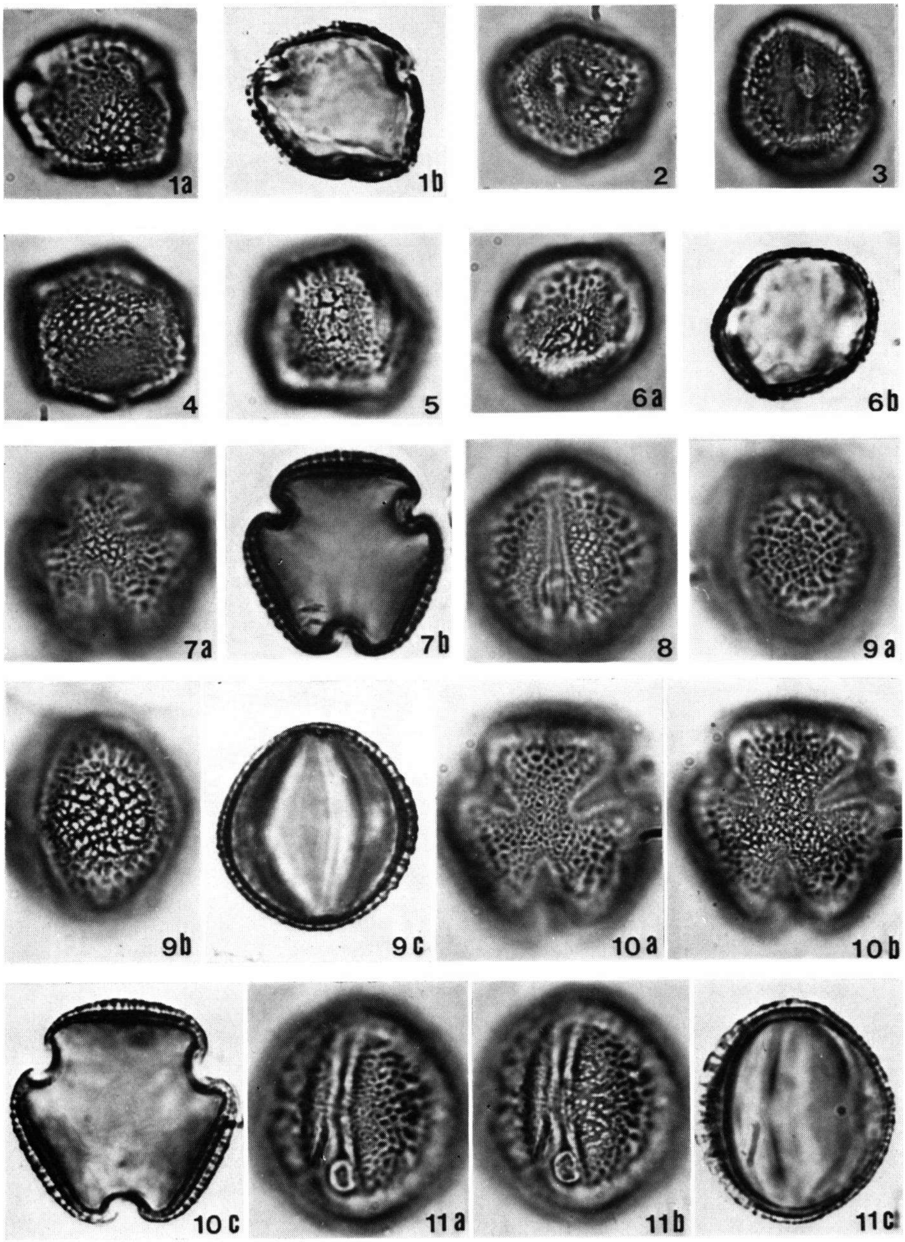

Plate XVII. Fig. 1—6: *L. mixta (Aet 679)*. — Fig. 7—9: *L. senegalensis 'senegalensis' (Warnecke 383)*. — Fig. 10, 11: *L. senegalensis 'senegalensis' (Tanner 1094)*. All 1000 ×.

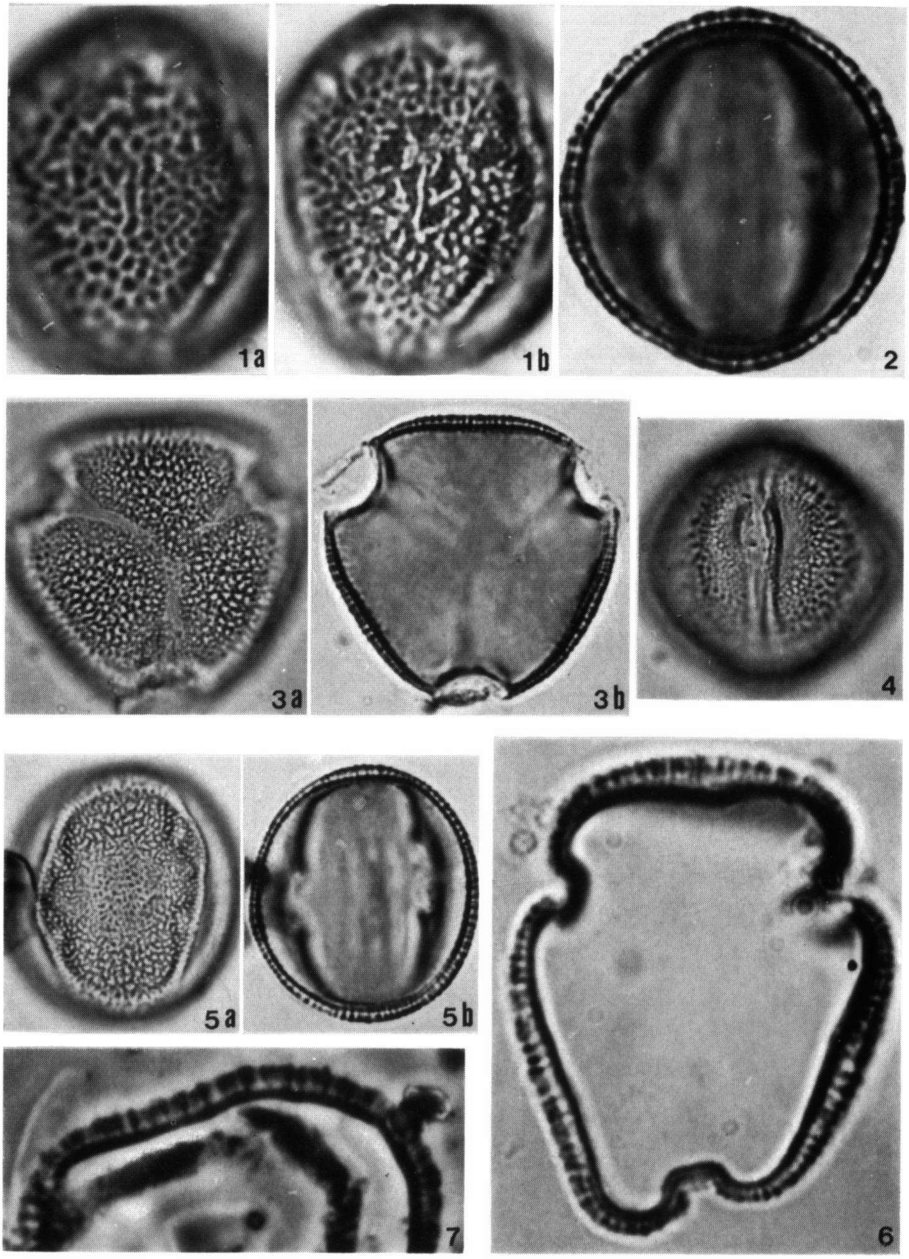

Plate XVIII. Fig. 1, 2: *L. senegalensis 'senegalensis' (Tanner 1094)*. — Fig. 3—6: *L. senegalensis 'danura' (Lace 4665)*. All 1000 ×, except 1, 6, 7 Ph.C.: 2000 ×.

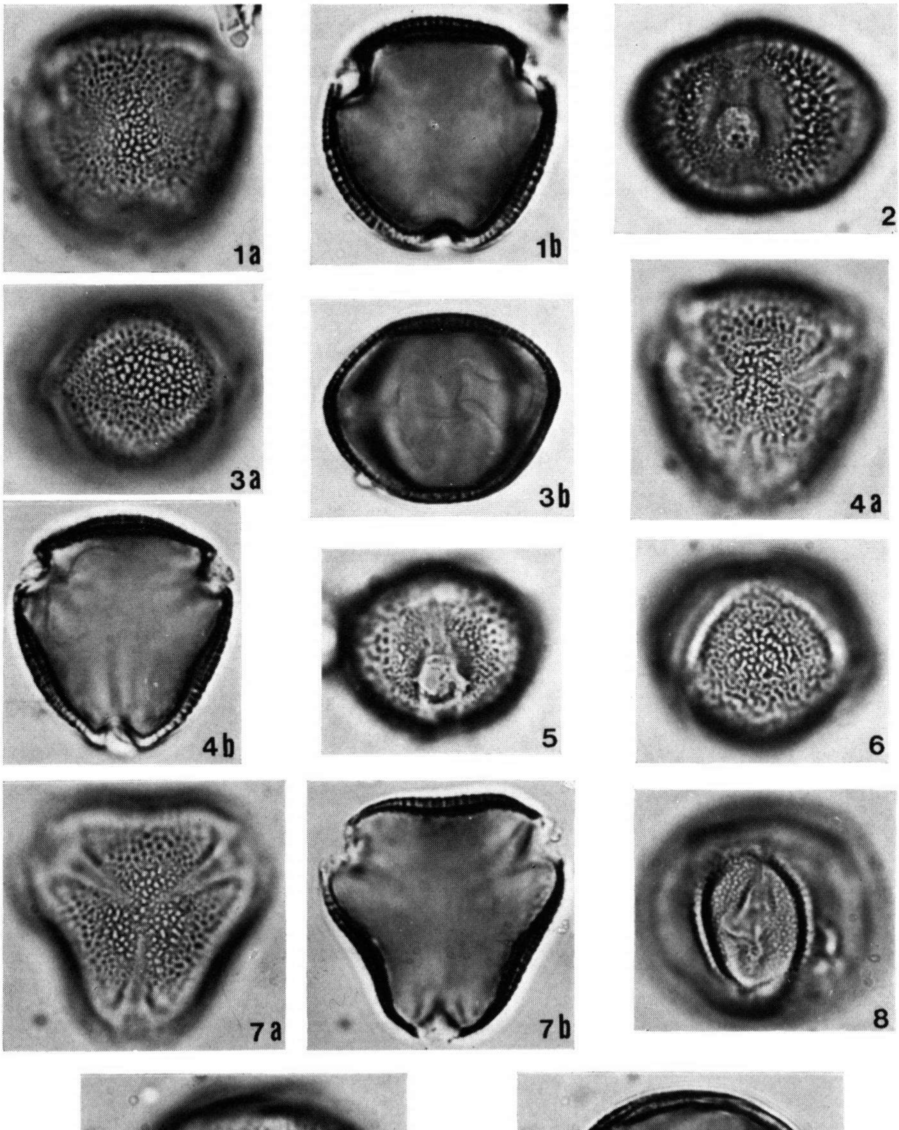

Plate XIX. Fig. 1—3: *L. senegalensis 'rubra' (Koelz 24693)*. — Fig. 4—6: *L. senegalensis 'montana' (NBFD A 2946)*. — Fig. 7—9: *L. senegalensis 'paucijuga' (Alvins 638)*. All 1000 ×.

decreasing in length towards apertures (fig. 1 E), arranged in a reticulate pattern in single (Pl. XII: 6 b) or double rows (Pl. XIV: 8 b), spacing variable. Tectum reticulate, variably developed, lumina of variable shape, in finely reticulate grains generally isodiametric (Pl. XIII; 7), rarely irregularly and narrowly elongated (Pl. XIII: 1, 3), in coarsely reticulate grains isodiametric or irregularly angular (Pl. XIV: 8 a), from 1 to 3 μ in diameter, generally coarser on mesocolpia and often so on poles, rather abruptly decreasing in coarseness near apertures which are often bordered by a narrow smooth zone (Pl. XII: 9), muri in finely reticulate grains $< 0.5\ \mu$ high, in coarsely reticulate ones 2—3 μ high, generally highest on mesocolpia, gradually decreasing towards apertures, generally broadened at base (fig 1 E; Pl. XIV: 6; Pl. XV: 2) and fused with the reticulately arranged columellae, tops crested, sometimes twisted, forked and interconnected, forming locally an upper subreticulate tectum (fig. 1 E; Pl. XV: 1) or striately arranged creating a regulate-striate pattern (Pl. XIII: 3), in some coarsely reticulate grains interrupted with dead ends terminating in interconnected lumina (Pl. XII: 3, 6 b; Pl. XIV: 3).

Comments. The considerable variability in the pollen grains of this species is mainly expressed in the ektexine structure. In general each sample has a characteristic sculptural pattern, but it is difficult to separate types, since transitions are frequent. It has been attempted, in table 1, to classify the samples investigated according to type and coarseness of the reticulate pattern.

Table 1. Variation in coarseness of reticulate sculpture in Lepisanthes fruticosa.

reticulate sculptural pattern				
fine lumina up to 1 μ		medium coarse lumina up to 2 μ	coarse lumina up to 3 μ	
lumina curvilinear	lumina isodiametric			retirugate
Nicholson 48511, Borneo	*Squires 850*, Vietnam: '*erythrocalyx*'	*Eberhardt 2636*, Vietnam	*Edaño 26847*, Philippines	*SF 3933*, Thailand
	Pierre 1283, Vietnam	*Murdoch 86*, Mal. Pen.	*Lopez 41389*, Philippines	
	Zimmerman 112, Thailand	*Clemens 27612*, Borneo: '*glandulosa*'	*Merrill 3660*, Philippines	
	SF 18759, Mal. Pen.	*BNB 5917*, Borneo	*PNH 14388*, Philippines	
	Ridley 6948, Mal. Pen.	*Kostermans 7329*, Borneo: '*erythrocalyx*'	*Quisumbing 8066*, Philippines	
	BNB 3245, Borneo	*Wood 1784*, Borneo	*Ramos 39744*, Philippines	
	Pingkun 8844, Borneo: '*glandulosa*'	*Curran 19325*, Philippines		
	S. 25182, Borneo: '*glandulosa*'	*Curran 5820*, Philippines		
		Rachmad 372, Celebes		

From this table the following conclusions may be drawn:

1. The races '*erythrocalyx*' and '*glandulosa*', tentatively separated by Leenhouts from the typical '*fruticosa*', cannot be distinguished on pollen characters, since they fall entirely within the variability of the latter form.
2. The coarsest reticulate sculpture is restricted to the Philippines.
3. Single samples from Borneo and Thailand show deviating sculptural types.

section **Anomotophora**

Lepisanthes alata (Bl.) Leenh. — **Pl. XV: 6—9.**

Material studied. Malay Pen.: *Wood SF 23118.* —Java: *Teysmann s.n.; Zollinger 3456;* cult. *H. Bog. XII. B. IX. 51:* cult. *H. Bog. XII. B. IX. 127.* — Borneo: *Alston 13229; Clemens 21509; Main 1896; SAN 31620.*

Pollen grains spherical, P/E 1.00, equatorial outline circular or slightly rounded-triangular, tricolporate. Size: P 22 (24.9) 30 μ, E 22 (24.9) 31 μ. Ektoapertures distinct (Pl. XV: 6), 12 (19.6) 26 μ long, E/c 1.27, up to 4 μ wide at equator, tapering towards poles, slightly costate. Endoapertures irregular-circular, occasionally elliptical and elongated in polar direction, 3 (3.9) 6 μ. Total wall thickness 1.0 μ on poles, 1,4 μ on mesocolpia, 0.9 μ near apertures. Endexine 0.5 μ thick, slightly thickened alongside ektoapertures. Columellae up to 0.5 μ in diameter, circular-elliptical in cross section, up to 1 μ long, shorter and less distinct near apertures, arranged in a reticulate pattern, in single rows (Pl. XV: 8 a, 9). Tectum reticulate, lumina variable in shape, irregularly isodiametric especially on poles (Pl. XV: 8 a), more uniform towards apertures (Pl. XV: 6), variable in size, up to 2 μ in diameter on poles, 1.5 μ on mesocolpia, 0.5 μ near apertures, muri < 0.5 μ wide, < 0.5 μ high, exceptionally broadened.

Comment. The pollen of this species shows little variability, except that in *SAN 31620* pollen dimorphism was noted, 90 % of the grains being normal and 10 % showing a ruguloreticulate sculpture with locally broadened muri, forming an irregular tectate-verrucate pattern.

subgenus ERIOGLOSSUM

Lepisanthes membranifolia (Radlk.) Radlk. — **Pl. XVI: 1, 2.**

Material studied. New Guinea: *Beccari PP 317.*

Pollen grains oblate, P/E 0.67, equatorial outline rounded triangular to semi-lobate, tricolporate. Size: P 19 (19.5) 20 μ, E 25 (29.3) 32 μ. Ektoapertures indistinct, 6 (8.4) 11 μ long, E/c 3.48, 1 μ wide at equator, sides parallel. Endoapertures circular, 3 (3.6) 4 μ, indistinctly annulate. Total wall thickness 0.5 μ on poles, 1.0 μ on mesocolpia, 0.5 μ near apertures. Endexine indistinct, probably < 0.5 μ thick, possibly slightly thicker around endoapertures. Ektexine undifferentiated, surface smooth.

Comment. Since the pollen of this species is only known from one specimen, it is difficult to be sure whether the very thin structureless wall and the narrow indistinct ektoapertures are really characteristic.

Lepisanthes rubiginosa (Roxb.) Leenh. — **Pl. XVI: 3—10.**

Material studied. Malay Pen.: *Henderson SF 38966; Ridley s.n.* — Sumatra: *Lörzing 15864.* — Java: *Backer 76; Blume s.n.; Popta 843/203.* — Madura: *Coert 780; de Vriese s.n.* — Borneo: *Kanis BNB 4759.* — Palawan: *Edaño PNH 14184; Elmer 12917.* — Philippines: *Ramos B.S. 46362.* — Celebes: *Forman 329.* — Ceram: *de Vriese & Teysmann s.n.*

Pollen grains oblate, P/E 0.74, equatorial outline rounded triangular to semi-lobate, tricolporate. Size: P 13 (19.9) 26 μ, E 22 (26.9) 33 μ. Ektoapertures fairly distinct (Pl. XVI: 9) or indistinct (Pl. XVI: 4, 6), 6 (9.6) 14 μ long, E/c 2.80, up to 5 μ wide at equator, sides parallel or tapering. Endoapertures fairly distinct (Pl. XVI: 4, 6) circular, 2 (3.3) 5 μ, rarely faintly annulate. Total wall thickness 1.2 μ on poles, 1.3 μ on mesocolpia, 1.2 μ near apertures. Endexine 0.5 μ thick. Columellae absent, very indistinct, or fine and distinct (Pl. XVI: 3 a, 7), < 0.5 μ in diameter, < 0.5 μ long. Tectum smooth (Pl. XVI: 4), very finely reticulate or pitted with lumina < 0.5 μ (Pl. XVI: 8) or, rarely, rugulate-corrugated (Pl. XVI: 10a), thickness < 0.5 μ.

Comment. The majority of the samples investigated show thinwalled, smooth pollen grains, but the Philippine and Celebes samples deviate in several respects. *Ramos BS 46362* is thus characterized by rather long ektoapertures and elliptical, polarly elongated endoapertures, *Forman 329* by a fairly thick corrugated-rugulate ektexine which makes the impression of being too wide for the endexine.

subgenus APHANIA

Lepisanthes mixta Leenh. — **Pl. XVII: 1—6.**

Material studied. New Guinea: *Aet 679.*

Pollen grains spherical-suboblate, P/E 0.93, equatorial outline circular, tricolporate. Size: P 20 (21) 22 μ, E 19 (21.4) 23 μ. Ektoapertures indistinct (Pl. XVII: 2, 3), 9 (11.2) 15 μ long, E/c 1.91, 1—2 μ wide at equator, sides parallel. Endoapertures circular (Pl. XVII: 3), 3 (3.5) 4 μ, slightly annulate. Total wall thickness 0.8 μ on poles, 1 μ on mesocolpia, 1.3 μ near apertures. Endexine < 0.5 μ thick, slightly thickened near apertures. Columellae very indistinct, < 0.5 μ in diameter, < 0.5 μ long, arranged in a reticulate pattern. Tectum reticulate, lumina very variable in size and shape (Pl. XVII: 6 a), isodiametric or elliptical, rounded or subangular, up to 2 μ in diameter on mesocolpia, up to 1 μ on poles, rather abruptly decreasing in size close to the ektoapertures, muri up to 0.5 μ in width, 0.5 μ high, fused with single rows of reticulately arranged columellae.

Lepisanthes senegalensis (Poir.) Leenh. — **Pl. XVII: 7—9; Pl. XVIII; Pl. XIX.**

Material studied. Senegal: *Leprieur s.n.; Vigneron 1388.* — Togo: *Warnecke 383.* — Kenya: *Scheffler 344.* — Tanganyika: *Tanner 1094.* — Sikkim: *Hooker s.n.* — Assam: *Koelz 24693; Koelz 27251.* — E. Pakistan: *King's coll. 265.* — Burma: *Lace 4665.* — Thailand: *Zimmerman 108.* — Laos: *Thorel 2676.* — Malay Pen.: *Alvins 638.* — Java: *v. Borssum Waalkes 676; Koorders 29076; Kostermans Unesco 1; Vincent 4695;* cult. *H. Bog. III. J. 66.* — Borneo: *Patrick SAN 39801; Wood NBFD A 2946.* — Philippines: *Edaño PNH 15358.* — New Guinea: *Brass 8363; Brass 24258; Brass 24404; Darbyshire 670; Hoogland 4691.*

Pollen grains very variable in shape, subprolate to oblate, P/E 0.68 (0.94) 1.27, equatorial outline circular to rounded triangular, tricolporate, rarely tetra- or dicolporate. Size: P 18 (23.6) 31 μ, E 19 (25.1) 35 μ. Ektoapertures distinct (Pl. XVII: 8, 11 b; Pl. XVIII: 3 a), 12 (20.3) 29 μ long, E/c 0.95 (1.24) 2.15, exceptionally syncolpate, 2—3 μ wide at equator, sides parallel or slightly tapering, in subprolate grains especially often inwardly folded (Pl. XVII: 7 b). Endoapertures distinct (Pl. XVII: 8; Pl. XIX: 2) or indistinct (Pl. XVIII: 4; Pl. XIX: 8), irregularly shaped, circular or elliptical and elongated in polar direction, 1 (3.9) 9 μ. Total wall thickness 1.1 μ on poles, 2—3 μ on mesocolpia, 1.0 μ near apertures, sometimes, however, remarkably uniform (Pl. XVIII: 5 b). Endexine 0.5 μ thick. Columellae only distinct in more coarsely reticulate grains (Pl. XVIII: 3 a, 6), < 0.5 μ in diameter, < 0.5 μ long, arranged in a reticulate pattern. Tectum uniformly finely reticulate (Pl. XVIII: 3 a; Pl. XIX: 7 a) or with a mosaic like distribution of reticulate and rugulate areas (Pl. XVII: 11 b; Pl. XVIII: 1 b), lumina isodiametric-elliptical, occasionally irregularly aligned (Pl. XIX: 6), rather uniform in size and shape, slightly coarser on mesocolpia, finer towards apertures (Pl. XVII: 11 a), muri variably developed, width between < 0.5 and 1 μ, in some samples conspicuously irregularly broadened at base or partly fused, creating a verrucate rugulate pattern, 0.5—1 μ high, lowest near apertures.

Comments. The pollen of this species appears to exhibit a clinal variability pattern in shape and sculpture. In order to demonstrate this, the samples investigated are in table 2 divided into four geographically separated groups and the shape, expressed as the ratio P/E, the relative length of the ektoapertures (E/c), the maximum lumen size, and the type of mural development are given.

Table 2. Clinal variation in shape, relative length of ektoapertures and sculptural type in Lepisanthes senegalensis.

ratio P/E

	individual measurements													mean
Africa						1	5	7	2		3	2	2	1.07
Cont. Asia			2	1	3	5	6	8	2	1	2	1		0.97
W. Malesia	1	2		8	7	4	2							0.85
New Guinea				5	1	4	3	2	2	3	2			0.98
	0.65 0.69	0.70 0.74	0.75 0.79	0.80 0.84	0.85 0.89	0.90 0.94	0.95 0.99	1.00 1.04	1.05 1.09	1.10 1.14	1.15 1.19	1.20 1.24	1.25 1.29	

ratio E/length ektoapertures

	individual measurements													mean
Africa	3	4	10	5		2	1	1						1.17
Cont. Asia	1	4	7	11	5	7	2	2	1	1	1		1	1.33
W. Malesia		4	10	7	6	4		1						1.23
New Guinea		2	8	5	5	4	3	2	2		1			1.33
	0.90 0.99	1.00 1.09	1.10 1.19	1.20 1.29	1.30 1.39	1.40 1.49	1.50 1.59	1.60 1.69	1.70 1.79	1.80 1.89	1.90 1.99	2.00 2.09	2.10 2.19	

	maximal lumen size, individual samples			development of muri, individual samples	
Africa	2	3	5	1	4
Cont. Asia	2	3	2	5	2
W. Malesia		3	3	4	1
New Guinea	1	1	3	5	
	< 0.5 μ	0.5 μ	1 μ	normal	broadened

These data show that the African samples stand apart by their spherical-subprolate shape, long ektoapertures, large lumen size, and conspicuously broadened muri and reticulate-rugulate sculptural pattern. They show little variability and will in the next chapter be distinguished as a separate pollen type.

The samples from continental Asia are more variable in all parameters and differ, on the average, in their more spherical shape, shorter colpi, smaller lumen size, and mostly normally developed muri.

The West Malesian samples, including those from the Malay Peninsula, are also relatively homogeneous and differ from the two preceding groups in their suboblate shape and shorter ektoapertures.

So far there exist thus clear indications for a West-East trend in shape and sculpture.

However, the New Guinea samples do not continue this trend, since they come closest to the samples from continental Asia, although they appear to have a less variable, coarser sculpture. An additional characteristic of these samples is the regular presence in low percentages of tetracolporate, dicolporate, and syncolpate grains, which have not yet been recorded from the other areas.

The dimorphism observed in African samples of *L. senegalensis* (= *Aphania senegalensis*) by Merville (1965) is not pronounced in the more extensive material available for the present study and it appears likely that all transitions between rugulate-reticulate and reticulate grains are present.

IV. POLLEN TYPES

In order to clarify the relationships within the genus *Lepisanthes*, it was attempted to distinguish pollen types, characterized by significant combinations of morphological features. Although some types could be rather clearly demarcated, between others transitions occur and their delimitation is to some extent arbitrary. From the following diagnoses it will become clear on which morphological features the types are established. The numerical data are based on the minima, averages, and maxima of all the mean values of the forms included. The types are named after a representative taxon.

1. Schizolepis type

Shape oblate, P/E 0.67 (0.72) 0.76, E 26.9 (28.0) 28.2 μ, equatorial outline rounded triangular to semi-lobate, ektoapertures mostly indistinct, very short and rather narrow, E/c 2.80 (3.12) 3.70, endoapertures wider than ektoapertures, often annulate, wall very thin, not thickened on mesocolpia, ektexine structureless or indistinctly differentiated into a faint layer of columellae and tectum, surface mostly smooth, rarely faintly finely reticulate or foveolate.

This type is found in the following 'races' of *L. tetraphylla: schizolepis, 46,* and in *L. simplicifolia, L. membranifolia,* and *L. rubiginosa.*

2. Montana type

Shape spherical-suboblate, P/E 0.78 (0.89) 0.95, E 24.2 (30.1) 36.1 μ, equatorial outline circular, ektoapertures rather distinct, short and broad, E/c 1.40 (1.73) 2.24, endoapertures distinct, wider than ektoapertures, often annulate with thickened endexine, wall not thickened on mesocolpia, columellae generally distinct, tectum smooth or finely perforate-reticulate, lumen size < 0.5 μ. This type occurs in the following 'races' of *L. tetraphylla: angustifolia, cuneata, deficiens, heterolepis B, hirta, lamponga, langbianensis, longifolia, montana, petiolaris, 21, 33, 35, 37, 39,* and in *L. falcata.*

3. Browniana type

Shape spherical-suboblate, P/E 0.86 (0.90) 0.98, E 21.3 (30.2) 38.0 μ, equatorial outline circular, ektoapertures rather distinct, short and broad, E/c 1.17 (1.64) 2.04, endoapertures wider than ektoapertures, rarely annulate, wall not thickened on mesocolpia, columellae rather distinct, tectum reticulate, lumina uniformly 0.5—1 μ in diameter.

This type is found in the following 'races' of *L. tetraphylla: basicardia, browniana, poilanei, scortechinii, pallens, heterolepis A*, and in *L. banaensis* and *L. ferruginea.*

4. Tetraphylla type A

Shape spherical-suboblate, P/E 0.86 (0.90) 0.93, E 21.6 (24.1) 26.5 μ, equatorial outline subtriangular, ektoapertures distinct, long, narrow, F/c 1.14 (1.22) 1.23, endoapertures indistinct, often developed as a bridge-like equatorial constriction of the ektoapertures, wall distinctly thickened on mesocolpia, columellae mostly absent or very indistinct, rarely distinct, tectum smooth or finely reticulate, lumina up to 0.5 μ in diameter, finer towards apertures.

This type occurs in the following 'races' of *L. tetraphylla: assamica, mekongensis, siamensis, tetraphylla, tonkinensis*, and in *L. andamanica.*

5. Tetraphylla type B

Shape spherical-suboblate, E 24.0 μ, ektoapertures absent, endoapertures circular, 3—4 in number, columellae indistinct, tectum finely reticulate. This type is similar in all respects except apertures to the preceding one and probably represents a genetic variant in which the development of the ektoapertures has been suppressed. It only occurs in a small percentage in one sample of *L tetraphylla 'tetraphylla'.*

6. Amoena type

Shape spherical, P/E 0.88 (0.94) 0.98, E 24.0 (26.0) 28.0 μ, equatorial outline rounded triangular, ektoapertures distinct, long, narrow, occasionally costate, E/c 1.23 (1.29) 1.39, endoapertures distinct or indistinct, not wider than ektoapertures, irregularly shaped, often elongated in polar direction, wall considerably thickened on mesocolpia, columellae mostly indistinct, when distinct arranged in a reticulate pattern, tectum finely reticulate, lumina 0.5—1 μ in diameter, coarsest on mesocolpia and poles.

This type is found in *L. amoena, L. divaricata, L. multijuga*, and in the following 'races' of *L. senegalensis: danura, montana, rubra*, and *paucijuga.*

7. Kinabaluensis type

Shape spherical, P/E 0.99, E 25 (30.7) 33 μ, equatorial outline circular, ektoapertures distinct, rather wide, costate, E/c 1.38, endoapertures rather indistinct, wall thickened on mesocolpia, thinner alongside costae, columellae indistinct, tectum finely reticulate, alternating with verrucate-echinate sculpture.

This type only occurs in *L. kinabaluensis.*

8. Mixta type

Shape spherical-suboblate, P/E 0.93, E 19 (21.4) 23 μ, equatorial outline circular, ektoapertures indistinct, E/c 1.91 endoapertures distinct, slightly annulate, wider than ektoapertures, wall hardly thickened on mesocolpia, columellae indistinct, arranged in a reticulate pattern, tectum reticulate, lumina up to 2 μ in diameter.

This type only occurs in *L. mixta.*

9. Senegalensis type

Shape spherical-subprolate, P/E 0.95 (1.07) 1.23, E 20 (24.2) 28 μ, equatorial outline circular, ektoapertures distinct, frequently inwardly folded, long, narrow, costate, E/c 0.90 (1.17) 1.60, endoapertures rather distinct, generally elongated in polar direction, as wide as ektoapertures, wall distinctly thickened on mesocolpia, columellae rather distinct, arranged in a reticulate pattern, tectum reticulate, lumina up to 1 μ in diameter, muri conspicuously irregularly broadened and thickened.

This type is found in *L. senegalensis sensu stricto* from Africa.

10. Fruticosa type

Shape spherical, P/E 0.96 (0.98) 1.00, E 24.9 (28.0) 30.0 μ, equatorial outline circular or rounded triangular, ektoapertures distinct, rather wide, occasionally costate, E/c 1.26 (1.29) 1.34, endoapertures rather distinct, as wide as colpi, irregularly shaped, wall thickness variable, hardly thickened on mesocolpia, columellae rather distinct, arranged in a reticulate pattern in single or double rows, tectum rather coarsely reticulate, lumina 2—3 μ in diameter.

This type occurs in *L. alata, L. bengalan*, and *L. fruticosa.*

Before proceeding to a discussion of these pollen types it must be stated that they are hardly comparable to those described by Merville (1965) for the *Sapindaceae* as a whole. She has not utilized exine structure and sculpture for her subdivision, attaching much weight to endexinal folds, a feature here considered, for the genus *Lepisanthes* at least, to be of doubtful significance. The best correspondence is between her *laccodiscus type* and the *montana type* described here. The other types recognized in *Lepisanthes* can probably be accomodated in her *lychnodiscus type*. It is worth mentioning in this connection that nothing equivalent to the *schizolepis type* has been encountered by Merville, who also did not attempt to interprete the morphological relations between her types. For *Lepisanthes* it appears possible to arrive at some tentative ideas on these relations, which are summarized on fig. 2. Here the types are arranged according to the two most significant morphological features, the complexity of the ektexine sculpture and the relative length of the ektoapertures. In this scheme central types and peripheral types can be distinguished, the connecting lines denoting possible morphological trends.

The *tetraphylla A, montana*, and *amoena types* are central, the remaining ones peripheral, while the *tetraphylla B type* actually departs from the schema because of the lack of ektoapertures.

In studying this scheme it is important to remember that not all types are equally well demarcated. The *montana* and *schizolepis types* are well separated from each other, but between the *montana* and *browniana type* and between the *montana* and the *tetraphylla A type* transitions occur. The *amoena type* is transitional between the *tetraphylla A* and *fruticosa types.*

From this general relationship and from the diagnoses of the types presented earlier, the following specific morphological trends can now be deduced:

I. shape
  a) P/E: oblate — spherical — subprolate
  b) equatorial outline: lobate — rounded triangular — circular
II. ektoapertures
  a) relative length: short — medium — long
III. endoapertures
  a) size: large, wider than ektoapertures — medium, as wide as ektoapertures — small, indistinct.

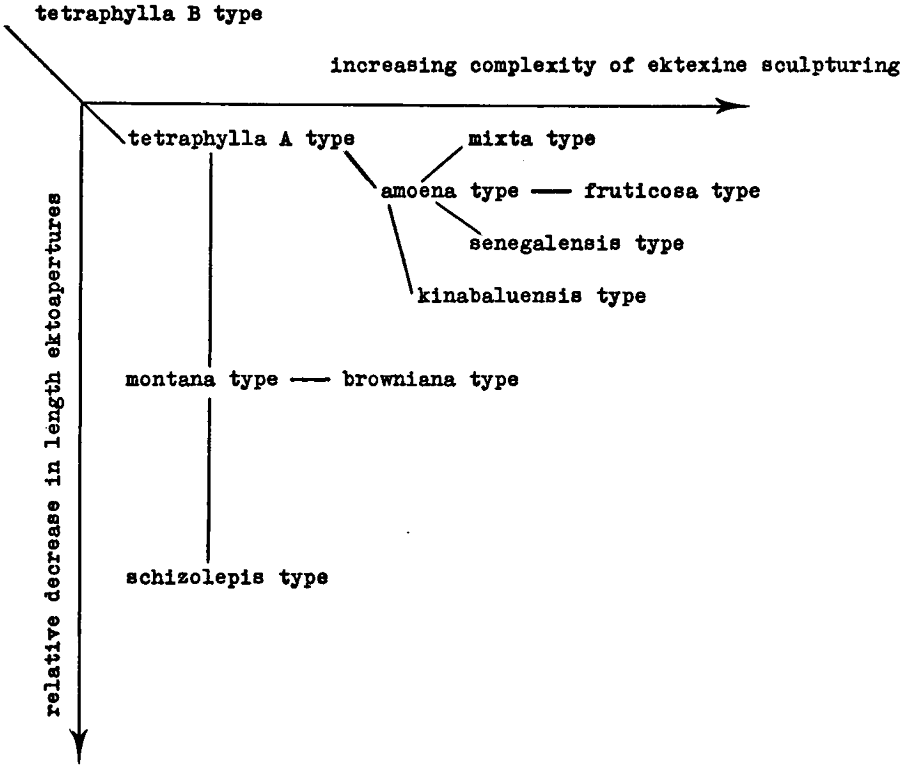

Fig. 2. Pollenmorphological trends in the genus Lepisanthes

b) border: annulate — costate on polar sides only — not bordered by thickened exine.

IV. wall thickness: uniformly thin — uniformly medium thin, — thickened on mesocolpia.

V. ektexine
  a) radial differentiation: very thin, structureless — differentiated into layer of columellae and tectum.
  b) columellae: absent — indistinct — distinct
  c) arrangement of columellae: scattered — reticulate pattern
  d) tectum: closed — perforate — finely reticulate — coarsely reticulate
  e) lumina: small, even in size — large but finer near ektoapertures
  f) muri: simple, rather low — thickened at base, rather high.

To a large degree these trends are intercorrelated and the resulting general relationships are shown on fig. 2. Thus it is possible to consider the oblate-lobate, thin walled *schizolepis type* with reduced ektoapertures and the spherical, heavily sculptured *fruticosa type* with long, distinct ektoapertures and reduced endoapertures as opposing extremes of a general trend. The *tetraphylla B, kinabaluensis, senegalensis,* and *mixta types* represent sidebranches which have not led to further development in a new direction.

In order to make the morphological evidence summarized above useful for interpretation of natural relationships it is now necessary to consider the problem of the direction of the postulated trends, or, more simply stated, which condition is primitive and which advanced.

Without further evidence, it could equally well be argued that the *schizolepis type* or the central *montana type* represents the primitive condition in *Lepisanthes.*

The arguments which can be advanced to approach these problems will now be briefly reviewed. The most significant data would, of course, result from a fossil record for *Lepisanthes* pollen, but, unfortunately, this has not yet been established. A functional interpretation of the various structural trends as expressed in the pollen types can also produce valuable leads. In this respect the *schizolepis type* may be interpreted as a pollen type in which the harmomegathic stresses are mainly absorbed by the thin, flexible wall, reduction of volume being accomplished by shortening of the equatorial axis and increase in lobateness. The *tetraphylla A, amoena, fruticosa,* and especially the *senegalensis type,* in contrast, accomodate volume changes mainly by meridional folding of the ektoapertures. The *montana type* appears, in this respect, to be less specialized and may be closer to the original type, although the functional significance of the annulate thickenings of the endoaperture is not clear. Which environmental factors have influenced the evolution of these pollen types is, however, unknown, except for the suggestion that the development of the *tetraphylla A type* may have been connected with a more seasonal climate. One could also compare the trends established in *Lepisanthes* with those present in other Sapindaceous genera, but for this purpose only the paper by Merville is available in which, as pointed out earlier, pollen types are recognized in a different way, while any discussion of morphological trends is lacking. The present author will continue his studies of Sapindaceous genera, however, and it is expected that later results will allow a more general discussion of pollenmorphological trends in the family.

Rather more is known from other Angiosperm families and van Campo (1966) has formulated several rules, according to which it is possible to determine the direction of certain pollenmorphological trends. For the present study it is of importance that small size, lack of ornamentation, and the presence of colpate apertures are considered by her to denote primitiveness. Similar considerations derive from a study of fossil Angiosperm pollen development in general (Muller, 1970) and, especially, larger size, complicated apertures, and increased structural and sculptural differentiation are likely to be advanced conditions.

Nevertheless it must be stressed that it is dangerous to apply such general rules without taking into account the possibility of reversals of evolutionary trends as well as of parallel convergent developments.

A further important criterion is the geographical distribution of the pollen types. Thus it is possible to state, for example, that, within the species *L. tetraphylla,* the *schizolepis pollen type* is probably derived, since it occurs isolated at the periphery of the total geographic area occupied by the species. Similarly, the *kinabaluensis type* is probably derived, because it is found only in one endemic species from Mt. Kinabalu.

Finally, one can always base oneself on the opinion of the taxonomist as to which forms are primitive and which advanced, but this, of course, entails the grave danger of circular reasoning.

A critical comparison of all available lines of evidence is thus necessary and in the next chapter a synthesis of pollen morphological and taxonomical evidence will be attempted.

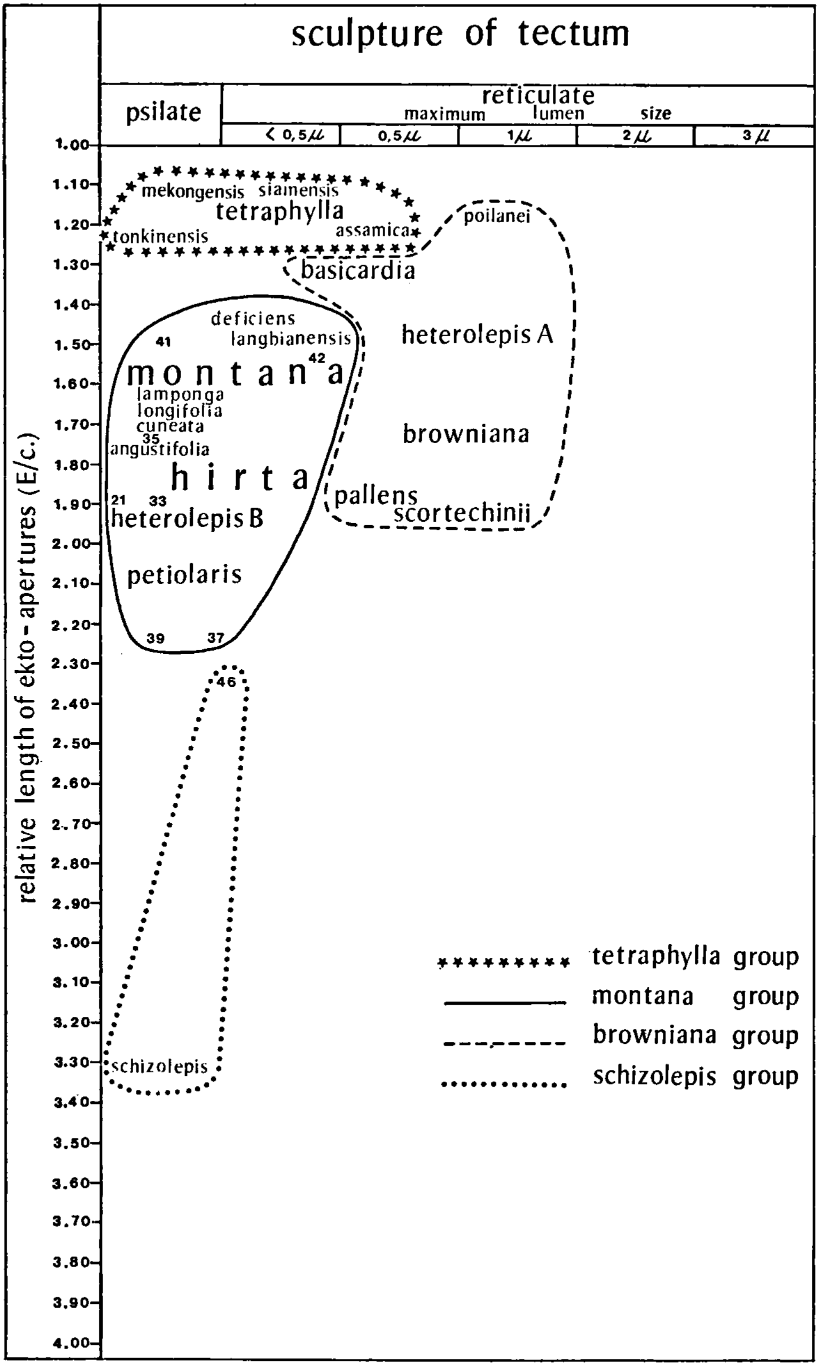

Fig. 3. Relation between relative length of ektoapertures, sculpture of tectum, and palynological grouping of races in *Lepisanthes tetraphylla*.

V. POLLEN MORPHOLOGY AND TAXONOMY

The pollenmorphological subdivision as expressed in the pollen types recognized in the previous chapter, will now be tested against Leenhouts's taxonomic framework. For this purpose the taxa studied will be discussed in his sequence, followed by a summary of the relationships within the genus as a whole and illustrated by a number of diagrams (fig. 3—6).

I. Section **Lepisanthes**

Lepisanthes andamanica

The pollen of this species, which, according to Leenhouts, is hardly more than a derived form out of the *L. tetraphylla* complex, is of the *tetraphylla A type* and shows a striking resemblance to that of *L. tetraphylla 'tetraphylla'*. Leenhouts's opinion that *L. andamanica* seems to be nearest related to *L. tetraphylla 'lamponga'* is not supported by the palynological evidence.

Lepisanthes tetraphylla

As shown on fig. 3, the races of this species can be grouped according to their pollen type. The distribution of these groups is shown on fig. 4.

a. *'Tetraphylla' group: 'tetraphylla', 'assamica', 'siamensis', 'mekongensis', 'tonkinensis'.*

Although the group as a whole shows little variability, the relatively isolated taxonomic position of *'assamica'* is still expressed in a deviating, shallowly foveolate sculpture. *'Siamensis'*, on the other hand, shows much resemblance to *'mekongensis'* and Leenhouts's opinion that the latter also is a relatively isolated form is not supported by its pollenmorphology.

b. *'Montana' group: 'deficiens', 'langbianensis', 'longifolia', 'hirta', 'cuneata', 'montana', 'lamponga', 'angustifolia', '21', '33', '35', 'petiolaris', '41', '42', 'heterolepis' B, '27', '39'.*

This group, which appears to be well demarcated against the *'tetraphylla' group*, shows slightly more variability as can be seen from fig. 3. This is not only expressed in the differences between individual races, but also in the greater variability in some of the more widespread ones. In *'montana'* clinal variation even appears to exist, since the samples from the Malay Peninsula, Sumatra, and Borneo are uniformly psilate while those from Java vary between perforate and finely reticulate. The pollen of *'42'*, which macromorphologically is closely allied to *'schizolepis'*, differs clearly in shape and relative length of ekto-apertures. The resemblances, mentioned by Leenhouts, of *'39'* to *'46'* and *'tetraphylla'* are only confirmed for the former, since the relative length of the ekto-aperture comes close to that of *'46'*.

c. *'Browniana' group: 'basicardia', 'browniana', 'poilanei', 'scortechinii', 'pallens', 'heterolepis' A.*

The *'browniana' group* is not sharply delimited against the *'montana' group*, but is rather distinct from the *'tetraphylla'* and especially from the *'schizolepis' group*. According to Leenhouts *'pallens'* from Timor is distinctly allied to *'angustifolia'*, *'montana'*, and *'tonkinensis'*. Its pollen is close to the perforate forms of *'montana'* from Java, as is also clear from its position on the graph. With *'tonkinensis'* from N. Vietnam, which belongs to the *'tetraphylla' group*, no pollenmorphological relations are indicated.

d. *'Schizolepis' group: 'schizolepis', '46'.*

This group represents an extreme in pollen morphological development and is, in consequence, rather well demarcated although *'46'* still shows a certain amount of structural differentiation in the wall, approaching in this respect the *'montana' group.*

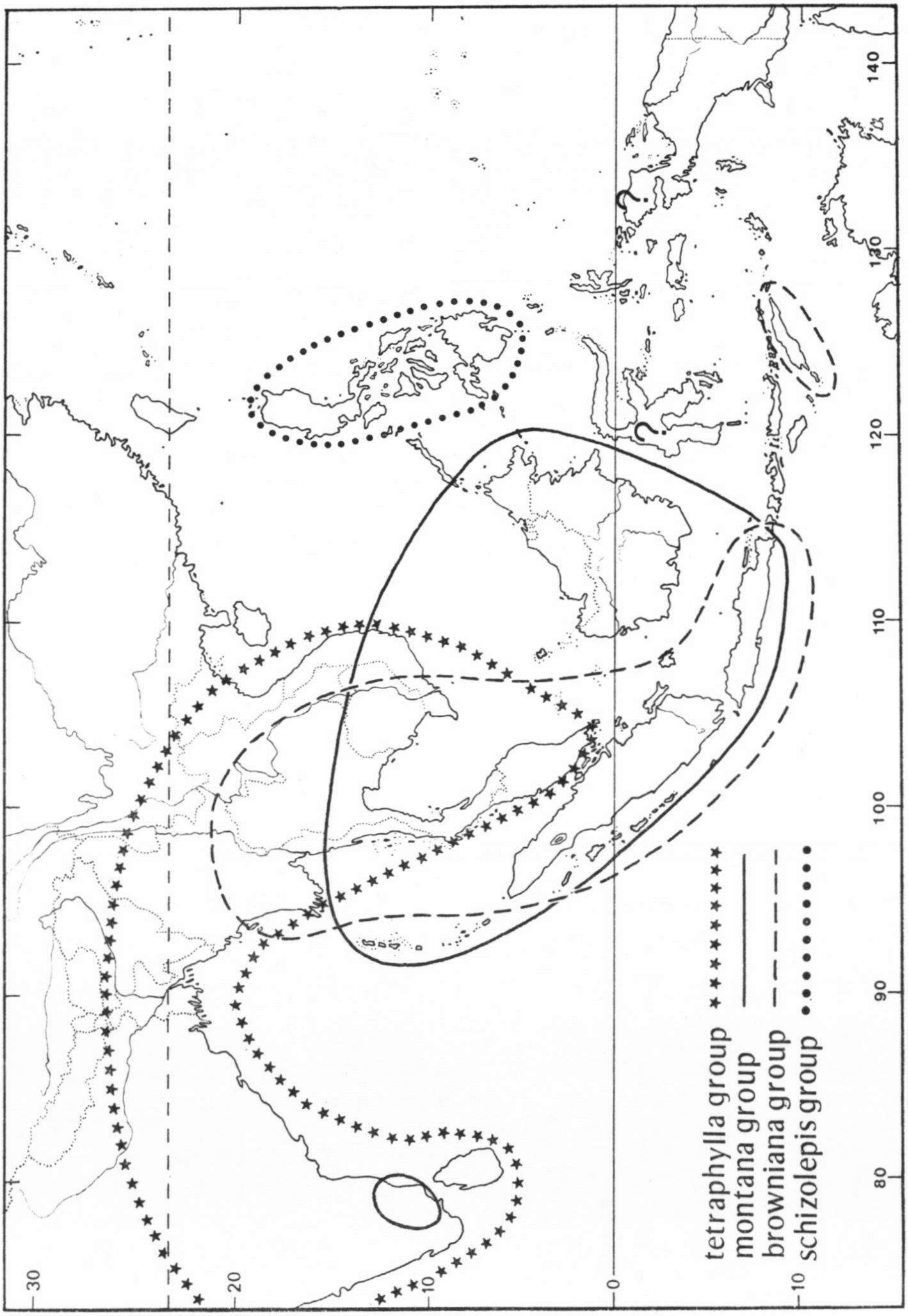

Fig. 4. Distribution of palynological groups of races in *Lepisanthes tetraphylla.*

For an interpretation of relationships within the species *L. tetraphylla*, the general rules formulated in the preceding chapter should be applied. Much weight will be attached first of all to the geographical distribution of the palynological groups as shown on fig. 4. The *'tetraphylla' group* is found on Ceylon and in continental Asia, including the Malay Peninsula. The *'montana' group* is concentrated in the southeasternmost part of Asia, the Andamans, and the Larger Sunda Islands, while an isolated occurrence is present in the southeastern part of the Deccan Peninsula. The *'browniana' group* has roughly the same distribution, but is absent from India and Borneo and has an isolated occurrence on Timor. The *'schizolepis' group* is restricted to the Philippines. This distribution pattern clearly shows a concentration of variability in the SE. corner of continental Asia and decreasing variability in the more peripheral areas.

If this evidence is now combined with the interpretation of the pollenmorphological trends as discussed in the preceding chapter and outlined on figs. 2 and 3, it will be obvious that the *'montana' group* occupies a central position, both geographically and morphologically, while the *'tetraphylla.* and *'schizolepis' groups* might represent the endproducts of opposing pollenmorphological trends which are also geographically peripheral. The *'browniana' group*, on the other hand, is linked by many transitions to the *'montana' group*. It is further of interest to note that the *'montana' group* appears to be largely restricted to the everwet part of the range of the species, while the *'tetraphylla' group* occupies mainly areas with a seasonal climate. This could suggest a selective influence of the climate on pollen type.

However, as stated at length in the preceding chapter, it is at present not yet possible to decide, on strictly pollenmorphological grounds, which group shows the most primitive pollen type, but when the data presented here are compared with Leenhouts's systematic interpretation of the interrelationships within this complex species, a pattern emerges which offers a reasonable hypothesis as to its phylogeny. According to Leenhouts *'montana'* is the most primitive form, which, moreover, can hardly be separated from *'cuneata'* and *'lamponga'*. Since these forms all posses the *'montana' pollen type* it would appear a reasonable assumption that this is also a primitive pollen type. On the other hand the races with exclusively derived macromorphological characters are arranged at the borders of the area and this can be interpreted as a diverging development, culminating in continental Asia in the *'tetraphylla' type*, and in the Philippines in the *'schizolepis' type*. Within the *'browniana' group* the races *'browniana'*, *'heterolepis'*, and *'pallens'* are considered by Leenhouts to be *'montana'* derivatives, which is supported by pollenmorphology.

Summarizing the above considerations the following tentative picture of pollen evolution in relation to general affinities within the *L. tetraphylla* complex can be sketched. The ancestral pollen type, as retained by the *'montana' group*, was a medium-sized, suboblate grain with medium-short ektoapertures and a rather distinct endoaperture. The wall was of uniform thickness, with endexine, layer of columellae, and a psilate or perforate tectum. The area of origin may have been the everwet part of West Malesia. The single occurrence in S. India may be either a relict station or indicate independent origin. From this ancestral group the *'browniana' type* evolved by increased sculptural development of the tectum, coupled with a slight increase in size. This probably has taken place independently several times over much of the area occupied by the *'montana' group*, but not in Borneo.

On this island a different trend may have originated leading via the pollen found in the races *'petiolaris'*, *37*, and *39*, by shortening of the ektoapertures, reduction of ektexine development, and a change towards an oblate, lobate triangular shape to the *'schizolepis'* *type* which has apparently evolved in relative isolation in the Philippines. As already pointed out before, race *46*, comes closest to the *'montana' group*, while race *'schizolepis'* forms an extreme development.

The *'tetraphylla' group* overlaps geographically with the *'montana' group* in the Malay Peninsula and SE. Asia and its pollen type may have originated from the *'montana' type* via transitional forms like the pollen of *'langbianensis'* by increase of the length of the ektoapertures, reduction of endoapertures, and decrease in size. The possibility that this process may have been influenced by climatic factors is suggested.

II. Section **Hebecoccus**

Pollenmorphologically, this section encompasses slightly less variation than section *Lepisanthes*, the *'tetraphylla' type* being lacking. A further difference is that, in contrast to the situation in section *Lepisanthes*, in *Hebecoccus* the transitional forms are absent. This could be in agreement with Leenhouts's view that section *Hebecoccus* is older than section *Lepisanthes* and has at present a relict distribution. Because of this, it is of course more difficult to discuss the relationship between the pollen types and the systematic affinities within the section. However, it would appear that trends similar to those established for section *Lepisanthes* are present. This is best demonstrated by the striking resemblance between the pollen of *L. simplicifolia* and that of *L. tetraphylla 'schizolepis'*. It is significant that the latter has evolved in isolation in the Philippines, while the former did so in Ceylon, which suggests an independent origin of this extreme pollen type. It would evidently be erroneous to assume a close systematic affinity of these two taxa, belonging to two different sections, on the basis of their pollen characters alone. This case nicely illustrates the danger present in equating too closely pollen morphological similarity with close affinity. It is here rather the parallel independent realization of an evolutionary trend, based on a closely comparable potential for genetic variability, which is a measure of affinity between the two sections.

III. Section **Otophora**

In this section the pollen of *L. amoena*, *L. divaricata*, and *L. multijuga* is of the same type and virtually indistinguishable from each other, while that of *L. kinabaluensis*, although of the same general shape and aperture configuration, shows a more specialized exine sculpture and forms a type of its own. This specialized character of the pollen of *L. kinabaluensis*, an endemic from Mt. Kinabalu and one of the few species of *Lepisanthes* which appears immediately recognizable by its unique pollentype, supports Leenhouts's opinion based on macromorphological evidence, that the species is a derived one.

IV. Section **Pseudotophora**

Lepisanthes bengalan

The pollen of this species, a restricted endemic from E. Borneo, falls within the range of variability of *L. fruticosa*, thus only the *fruticosa type* occurs in this section. Since this is obviously a derived type, showing no close connection with the pollen types present in subgenus *Lepisanthes*, palynology thus supports Leenhouts's decision to include *L. bengalan* in section *Pseudotophora*, despite some superficial resemblance to the former subgenus.

Lepisanthes fruticosa

It would appear that the difficulties experienced by Leenhouts in defining infraspecific taxa in this species are also evident in the rather wide, continuous variability of the pollen grain sculpture. The only significant exception is formed by the Philippine samples, which can be clearly separated and which suggest that here a genetically rather homogenous population has developed in relative isolation. Leenhouts also comments on the lack of indications for race formation in the Philippines, due to a wide but continuous variability. In this area the trend towards increased coarseness of the reticulate ornamentation culminates and this is clearly a derived condition.

V. Section **Anomotophora**

The fact that the pollen of the only species examined, *L. alata*, is indistinguishable from certain Bornean samples of *L. fruticosa*, notably *Kostermans 7329* assigned to the *'erythrocalyx' group*, confirms Leenhouts's opinion of a close affinity with the latter species, as well as his suggestion that the development of this section has mainly taken place in Borneo.

VI. Subgenus ERIOGLOSSUM

The pollen of the two species belonging to this subgenus, *L. membranifolia* from New Guinea and *L. rubiginosa* which has a much wider distribution from N. India, over the whole of Malesia to NW. Australia, is very similar and uniform. For the latter species this agrees with the exceptionally narrow range of variation in macromorphological characters (Leenhouts, l.c., p. 39). *Erioglossum* is thus both macromorphologically and palynologically a natural and well defined unit. As regards its affinities, the similarity of its pollen with that of *L. simplicifolia* and *L. tetraphylla 'schizolepis'*, both included in the *'schizolepis' pollen type*, at once indicates taxonomic affinity with the subgenus *Lepisanthes*. This has been expressed on fig. 6 by placing *Erioglossum* next to *Lepisanthes*. The question which of the two sections of *Lepisanthes* is closest allied to *Erioglossum* is more difficult to answer, since it again raises the problem of possible independent origin of this specialized pollen type, already touched upon earlier under *Hebecoccus*. Leenhouts is in favor of affinity to the latter section, but the only species known to posses the same pollen type is restricted to Ceylon, outside the range of *Erioglossum*. Unfortunately, the pollen of *L. erecta*, the nearest relative of *L. simplicifolia*, and distributed from Ceylon to Burma, was not available. Within section *Lepisanthes*, *L. tetraphylla 'schizolepis'* and *'46'*, both from the Philippines, come closest. Palynological evidence is thus not yet complete enough to permit more than speculations on this point.

The parallelism, mentioned by Leenhouts, between the subgenera *Erioglossum* and *Aphania* is not expressed in their pollenmorphology, which has taken widely diverging courses in its evolution.

VII. Subgenus APHANIA

Lepisanthes mixta

The intermediate position of this species, as evident on macromorphological characters, is also expressed in its pollen morphology, since it shows a unique combination of a coarsely reticulate tectum, such as is typical for subgenus *Otophora*, and a reduced ektoaperture, as generally found in subgenus *Lepisanthes* (Fig. 5). This has led to the recognition of a special pollen type.

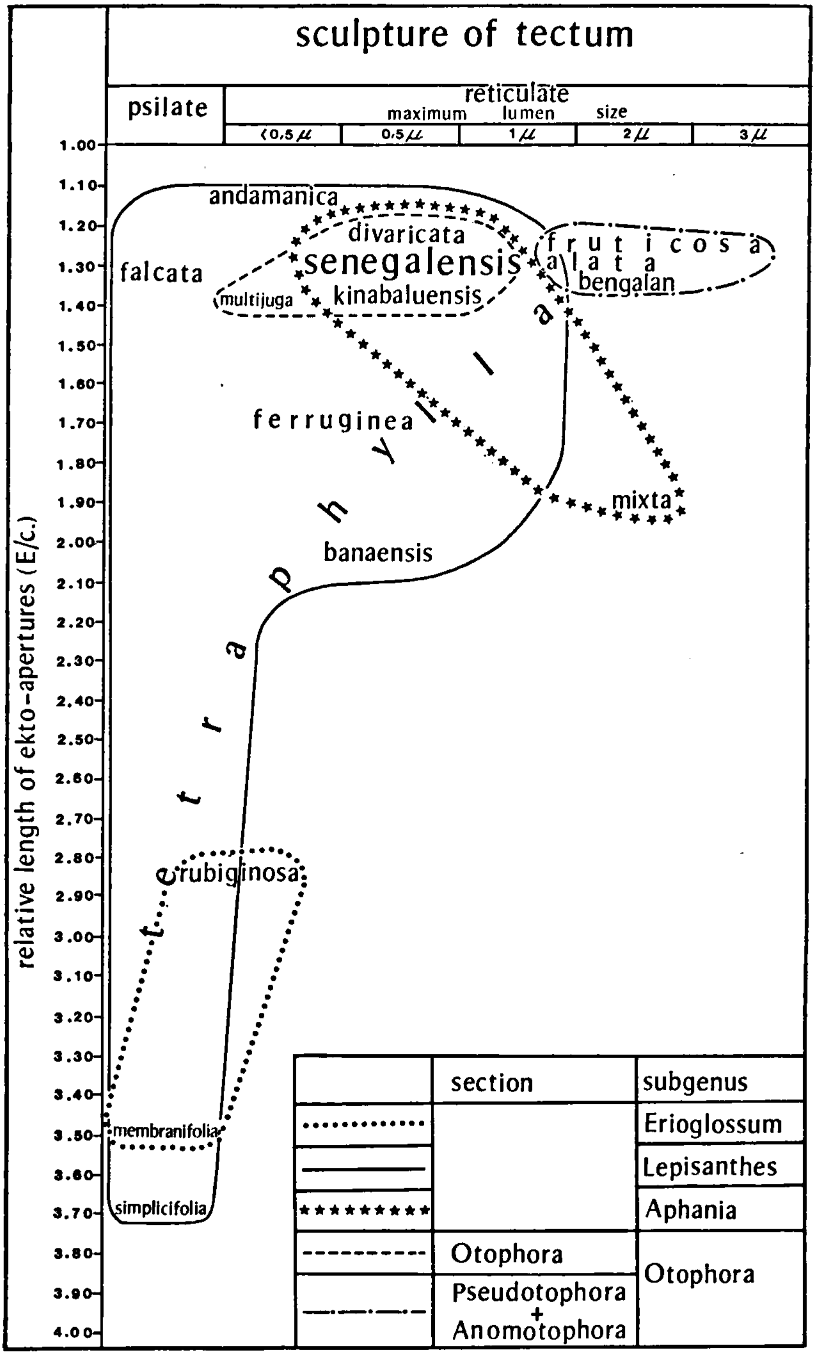

Fig. 5. Relation between relative length of ektoapertures, sculpture of tectum, and taxonomic subdivision in the genus *Lepisanthes*.

Lepisanthes senegalensis

When the pollenmorphological variability pattern of this species is compared with Leenhouts's macromorphological observations, the results appear comparable. His inability to delimit infraspecific taxa is reflected in the overlapping pollenmorphological variability, although a certain clinal pattern appears to be present, with the African samples showing such distinctive pollen that a separate type, the *'senegalensis' type* could be established, agreeing more or less with *'senegalensis' sensu stricto.* This pollen type again is undoubtedly a derived form.

It is further of interest that the West Malesian samples of *L. senegalensis* are very similar to those of *L. amoena* occupying the same area, which could suggest a relationship between subgenus *Aphania* and subgenus *Otophora* section *Otophora.*

Summary of relationships

If the total available pollen evidence as summarized on figs. 5 and 6 is now compared with Leenhouts's major subdivision of the genus *Lepisanthes*, it can first of all be stated that the subgenera *Lepisanthes* and *Erioglossum* on one hand and *Otophora* and *Aphania* on the other are also demarcated palynologically. The first two have retained a less evolved, but more variable pollen morphology, while the latter two show more narrowly specialized, derived pollen types. The transition between these two major groups may have been via forms similar to the *'tetraphylla' group* of *L. tetraphylla* and *L. amoena.* The subgenera *Otophora* and *Aphania* are more evolved macromorphologically than subgenus *Lepisanthes*, which view is thus supported by the pollen evidence.

For subgenus *Erioglossum* palynology appears to be more positive about its affinity than macromorphology, since the pollen characters clearly indicate affinity to subgenus *Lepisanthes.*

Subgenus *Otophora* may, according to Leenhouts, have been derived from subgenus *Lepisanthes* via a form near *L. bengalan*, but the pollenmorphological evidence rather suggests a derivation via section *Otophora* from subgenus *Lepisanthes*, probably from the *'tetraphylla' group* of *L. tetraphylla.*

The sections *Anomotophora* and *Pseudotophora* of subgenus *Otophora* are pollenmorphologically closely allied, and both can be derived from section *Otophora* which has less specialized pollen grains. This is entirely in accord with the taxonomic conclusions of Leenhouts.

Both macromorphology and palynology suggest that subgenus *Aphania* can be derived from subgenus *Otophora* section *Otophora.* This is based on the similarities between the fruits in *Aphania* and those present in *L. kinabaluensis* and *L. multijuga* and on the resemblance between the pollen of *L. senegalensis* and that of *L. amoena.* A direct derivation via *L. mixta* from subgenus *Lepisanthes*, as might perhaps be suggested by the latter's position on fig. 5, appears less probable and is anyhow not indicated by macromorphology.

The ancestral home of the genus is thought by Leenhouts to have been West Malesia and this is supported by the fact that here the largest pollenmorphological variability is present. From this central area diverging development took place, the results of which are clearly expressed both in pollen morphology and macromorphology. Of special interest in this respect is the situation in the Philippines where *L. tetraphylla* and *L. fruticosa* have evolved rather distinct pollen forms. This suggests a relative degree of isolation, after the initial colonization, probably from the direction of Borneo. Also the single species which has reached Africa, *L. senegalensis*, shows in its pollenmorphology clearly the influence of isolation, while on Borneo the endemic species of Mt. Kinabalu has similarly given rise to a special pollentype.

subgenus	Erioglossum	Lepisanthes		Aphania	Otophora		
section		Hebecoccus	Lepisanthes		Otophora	Pseudotophora	Anomotophora
1. schizolepis type	X	X	X				
2. montana type		X	X				
3. browniana type		X	X				
4. tetraphylla type A			X				
5. tetraphylla type B			X				
6. amoena type				X	X		
7. kinabaluensis type					X		
8. mixta type				X			
9. senegalensis type				X			
10. fruticosa type						X	X

Fig. 6. Pollen types and taxonomic subdivision in the genus Lepisanthes.

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