COMPARATIVE POLLEN MORPHOLOLOGY OF THE CORNACEAE AND ALLIES

by

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INTRODUCTION

In the previous paper(13) the phylogenetic relationships of the family Cornaceae and its allies were discussed from the viewpoint of wood anatomy. In order to supplement the results of anatomical data, pollen grains from the representative species are also examined and reported in this paper.

It is a well established fact that studies of the comparative pollen morphology may yield sets of data useful in the field of plant classification. Investigations have now progressed to initiate extensive studies of specific families or groups. Citations to extent studies will be found in Wodehouse(20, 21) and Erdtman(7).

Considerable differences exist in the classification of the family Cornaceae and its allied families by various taxonomists. A brief revision of the different systems of classifications of the Cornaceae and its allies was given in the previous paper(13). This study of pollen in the Cornaceae and its allies is pursued to aid in arriving at a more natural arrangement of the families and genera studied.

MATERIALS AND METHODS

Pollen specimens for this investigation were largely obtained from herbarium specimens from the herbarium of the National Taiwan University, the herbarium of the Botanical Institute of Academica Sinica, and the United States National Herbarium. These specimens are listed with the descriptions of the pollens and are indicated by the abbreviations NTU, AS, and USNH respectively. Besides the species and varieties described below, a number of species of the Araliaceae and Caprifoliaceae were also studied in detail for comparison.

In mounting the pollens, the wholly grown anthers were placed in a drop of lactic acid (ca. 85%) on a slide. After dissecting out the pollens, debris were removed followed by the addition of lactic acid and cover-glass, and the covers were sealed with the paraffin-bee wax.

All observations were made with an apochromatic oil emmersion objective (95 x, N. A. 1.25) and a compensating ocular (10 x). Records were the average of 20 suitably oriented grains for each species or variety with an ocular micrometer. All drawings were made with the aid of camera lucida. Only portion of the surfaces are represented.

DESCRIPTION OF POLLENS

1. GARRYACEAE LINDL.

Garrya Dougl.

G. longifolia Rose—G. B. Hinton (USNH), Mexico—Figs. 38 a, b.

Grains tricolpate, elliptical to oval in outline, 30.6×35.7 μ; exine striated; furrows short and tapering, broad, unequally spaced, one lying at the top of the grain, the other two making an angle about 30 degrees with the long axis of the grain and lying at the opposite side, germinal apertures indistinct; furrow membranes smooth.

2. NYSSACEAE ENDL.

Camptotheca Dcne.

C. acuminata Baill.—W. T. Tsang 27824 (USNH), Kwangsi, China—Figs. 39 a, b.

Grains tricolpate, triangular in outline, 33.2×41.1 μ; exine granular, granules distinct; furrows long and tapering, broad, at the angles, reaching principally toward their centers, each provided with a distinct germinal aperture, elliptical or irregular in outline; furrow membranes nearly smooth, pores bulging out as if having ruptured the furrow membrane.

Nyssa L.

N. sylvatica March—D. Demarec 14951 (USNH), Arkansas, U. S. A.—Figs. 42 a, b.

Identical to the above mentioned species but larger, 40.8×45.9 μ.

Davidia Baill.

D. involucrata Baill.—Y. Tsiang 7717 (AS), Kweichow, China—Figs. 40 a, b.

Grains tricolpate, elliptical to oval in outline, 33.2×38.3 μ; exine granular, granules distinct; furrows long and tapering, broad, equally spaced and crossing the long axis of the grain, each provided with a distinct germinal aperture, elliptical in outline and with the long axis parallel to the furrow; furrow membranes nearly smooth, pores bulging out as if having ruptured the furrow membrane.

D. involucrata Baill. var. *Vilmoriniana* (Dode) Wang—W. P. Fang 6088 (USNH), Szechuan, China—Figs. 41 a, b.

Similar to the grains of the above species but smaller, 29.9×33.2 μ.

3. CORNACEAE LINK.

Mastixia Blume

M. philippenensis Wang.—M. R. Edano (AS), Philippenes—Figs. 37 a, b.

Quite similar to the grains of *Nyssa sylvatica* but the furrows broader and moderately long, germinal apertures spherical in outline, pores often expanded, 25.9×56.1 μ in size.

Cornus L.

C. controversa Hemsl.—F. T. Wang 20376 (NTU), Szechuan, China—Figs. 23 a, b.

Grains tricolpate; elliptical, sometimes oval in outline, 30.6×38.3 μ; exine finely granular; furrows long and rather narrow, equally spaced and parallel to the long axis of the grain, each provided with a germinal aperture, elliptical in outline and with the long axis parallel to that of the furrow, furrow membranes smooth, pores bulging out.

C. Monbeigii Hemsl.—C. W. Wang 63603 (NTU), Yunnan, China—Figs. 29 a, b.

Similar to the grains of the above species but larger, 51.7×66.7 μ.

C. longipetiolata Hay.—S. Sasaki (NUT), Taiwan, China—Figs. 27 a, b.

Grains spherical to oval in outline, 38.3×40.8 μ, furrows broad; other characters identical to the grains of *C. controversa.*

C. oblonga Wall.—C. W. Wang 70446 (NTU), Yunnan, China—Figs. 30 a, b.

Grains of this species differ from the grains of *C. controversa* in having furrows crossing to the long axis of the grain and being broader, germinal apertures rectangular in outline and with the long axis parallel to that of the furrow, and rather small in size, 26.9×31.8 μ.

C. mas L.—Masamune (NTU), France—Figs. 28 a, b.

Grains tricolpate, spherical to oval in outline, 25.5×26.4 μ; exine granular; furrows long and tapering, rather broad, almost reaching from pole to pole, equally spaced and crossing the long axis of the grain, each provided a germinal aperture, elliptical in outline and with the long axis parallel to that of the furrow, furrow membranes smooth, pores not readily bulging out.

C. chinensis Wang.—C. W. Wang 71742 (NTU), Yunnan, China—Figs. 22 a, b.

Identical to the grains of the above species, but with the germinal apertures spherical in outline.

C. canadensis L.—Y. Kudo 135 (NTU), Kimofuri, Japan—Figs. 21 a, b.

Grains tricolpate, elliptical to oval in outline, 28.1×33.1 μ; exine finely granular; furrows moderately long, broad, equally spaced and parallel to the long axis of the grain, each provided with a germinal aperture, oval in outline, furrow membranes smooth, pores bulging out as if having ruptured the furrow membranes.

C. suecica L.—Y. Kudo 3074 (NTU), Kushiro, Japan—Figs. 31 a, b.

Identical to the above species but spherical to oval in outline, 25.5×25.9 μ.

C. florida L.—E. J. Palmer 5079 (USNH), Columbia—Figs. 24 a, b.

Grains spherical to oval in outline, 38.0×38.3 μ; exine finely granular to nearly smooth; other characters identical to the grains of *C. controversa.*

C. kousa Buerger—S. Hibino (NTU), Taiwan, China—Figs. 26 a, b.

Grains identical to the grains of *C. controversa*, 28.1×30.6 μ, furrows moderately long and crossing the long axis of the grain, and germinal pores bulging out as if having ruptured the furrow membrane.

C. hongkongensis Hemsl.—C. Wang 2068 (NTU), Kwangtung, China—Figs. 25 a b.

Similar to the grains of the above species, 25.5×29.3 μ.

Corokia A. Cunn.

C. buddleoides A. Cunn.—A. W. Anderson 225 (USNH), New Zealand—Figs. 32 a, b.

Grains tricolpate, spherical to oval in outline, 28.1 μ; exine granular; furrows very long and tapering, rather broad, reaching from pole to pole, equally spaced and parallel to the long axis of the grain, each provided with a germinal aperture, irregular in outline and with the long axis parallel to that of the furrow, furrow membranes nearly smooth, pores small and bulging out.

Aucuba Thunb.

A. chinensis Benth.—E. H. Wilson 2047 (USNH), Hupeh, China—Figs. 19 a, b.

Grains tricolpate, oval in outline, 46.2×51.0 μ; exine reticulate, reticuli irregular in outline, rather fine; furrows long and tapering, broad, reaching from pole to pole, equally spaced and crossing the long axis of the grain, each provided with a germinal aperture, spherical in outline, rather indistinct; furrow membranes smooth, pores bulging out.

A. japonica Thunb.—R. Yohü 363 (NTU), Japan—Figs. 20 a, b.

Similar to the grains of the above memtioned species, but rather spherical in outline, 49.7×50.8 μ, and the reticuli very fine.

Griselinia Forst.

G. jodinifolia (Griseb.) Taub.—C. Buchtien (USNH), Valfivia, Chile—Figs. 33a, b.

Grains tricolpate, oval to elliptical in outline, 22.8×25.4 μ; exine granular; furrows long and tapering, reaching from pole to pole, equally spaced and crossing the long axis of the grain, each provided with a germinal aperture, oval to irregular in outline; furrow membranes smooth to slightly flecked, pores bulging out.

G. lucida Forst.—T. Kirk 341 (USNH), New Zealand—Figs. 34 a, b.

Identical to the grains of the above species, but the furrows parallel to the long axis of the grain.

4. HELWINGIACEAE ENDL.

Helwingia Willd.

H. himalaica Hook. f. et Thom.—Hand.-Maz. 6081 (USNH), Yunnan, China—Figs. 36 a, b.

Grains tricolpate, elliptical in outline, 22.5×30.1 μ; exine finely granular; furrows long and tapering, broad, equally spaced, crossing the long axis of the grain, each provided with a germinal aperture, spherical to oval in outline; furrow membranes smooth, pores bulging out as if having ruptured the furrow membrane.

H. chinensis Batalin—C. W. Wang 20434 (NTU), Yunnan, China—Figs. 35 a, b.

Identical to the above mentioned species, but rather small in size, 20.4×25.5 μ, and the furrow membranes flecked.

5. ALANGIACEAE LINDL.

Alangium Lem.

A. Handelii Schiff.—C. Wang 37007 (NTU), Kwangtung, China—Figs. 2 a, b.

Grains tricolpate, oval to elliptical in outline, 74.0×84.0 μ, exine reticulate, reticuli irregular in outline and becoming finer toward the poles and the furrows; furrows long and tapering, rather broad, equally spaced and crossing the long axis of the grain, each provided with a distinct but rather small germinal aperture, elliptical in outline and with the long axis crossing that of the furrow; furrow membranes smooth.

A. chinensis Rehd.—T. M. Tsui 355 (USNH), Kwangtung, China; P. S. Ten 506 (USNH), Yunnan, China—Figs. 1 a, b.

Grains oval in outline, 67.0×82.0 μ; reticuli fine; furrows very short, germinal apertures spherical in outline; other characters identical to the above mentioned species.

A. premnifolium Ohwi—Kaneshiro-Tetsmo 692 (NTU), Liukiu—Figs. 4 a, b.

Similar to the grains of *A. Handelii* but larger, 77.0×87.0 μ, reticuli polygonal in outline, and the germinal apertures larger in size.

A. platanifolium Harms—S. K. Lau 24240 (NTU), Kwangtung, China—Figs. 3 a, b.

Identical to the grains of *A. Handelii*, but with wave-like reticuli, furrows rather short, and with the germinal apertures spherical in outline.

6. TORRICELLIACEAE HU

Torricellia DC.

T. tilifolia DC.—C. W. Wang 72484 (NTU), Yunnan, China—Figs. 43 a, b.

Grains tricolpate, spherical in outline, 28.1 μ; exine smooth; furrows short and tapering, broad, equally spaced and meridionally arranged, each provided with a distinct germinal aperture, spherical in outline; furrow membranes smooth, pores bulging out.

DISCUSSION

As summarized in the previous paper(13), the family Cornaceae and its allies show phylogenetically very complicated assemblage of plants from the viewpoint of anatomical structures and no scheme of classifications already proposed corresponds very closely with that which could be made out from the study of wood structures. Data obtained from this investigation of the pollen grains of the family and its allies coincide closely to the above conclusions and deserve to be considered by taxonomists.

The pollen grains of the Cornaceae as studied in this investigation vary from spherical to elliptical, very rarely triangular, in outline. The size of the grains ranges from approximately 25 μ to over 50 μ. All the grains are tricolpate, *i.e.*, there are three meridionally arranged furrows. The elliptical grains have the furrows either parallel to the long axis of the grain or crossing to it. The furrows are broad, long and tapering, but never reaching to the poles. The furrow membranes are smooth, very rarely irregular. The germinal apertures lie in the furrows and are chiefly spherical in outline and smooth. The germinal pores are commonly bulging out. Noticeable spines or papillae are not present. The exines are distinctly granular to nearly smooth, rarely reticulate. The reticuli are very fine and irregular in outline.

In wood structure, as well as in external morphology, the Cornaceae resembles

closely the Caprifoliaceae. The grains of *Cornus* can be compared with the typical Caprifoliaceous grains like *Sambucus* and *Viburnum*. They show great similarities in having three meridionally arranged furrows which are broad, long and tapering, and each provided with a germinal aperture, spherical in outline and not extending out of the furrow membrane.

The grains of the latter two genera, however, differ from that of the former one in the extremely spherical shape, in rather small size, and in the reticulate-pitted exines.

The floral structure of the Cornaceae shows closest resemblance to that of the Araliaceae. A study of the pollen morphology of the Araliaceae reveals that they form a divergent group of plants. This finding coincides to that of the previous investigation(13). The grains of the Araliaceae studied vary from very small to rather large, with nearly smooth, granular, reticulate, to striated exines. The furrows are either very long and narrow or rather short and broad. Yet the grains of the Araliaceae are chiefly rhomboidal in outline. The furrows are either very long and narrow or short and broad and largely unequally spaced. The germinal apertures are mainly irregular in outline. The grains of *Cornus* of the Cornaceae are similar to that of the *Schefflera* of the Araliaceae in having three equally spaced furrows which are rather long and with the granular and spineless exines However, the grains of *Schefflera* are more or less rhomboidal in outline and the furrows are rather narrow.

The phylogenetic order of the Garryaceae is an interesting subject to taxonomists. Formerly it was included in the Cornaceae and later created as a distinct family and placed in Monochlamydeae. As reported by Li and Chao(13) and Metcalfe and Chalk(14), the wood structure of the Garryaceae bears some similarities to that of the Cornaceae. From the cytological point of view, Darlington and Ammal(5) imply that *Garrya* should probably be returned to the Cornaceae. The pollen grains of the Garryaceae differ from that of the Cornaceae in having distinctly granular, with the tendency to be striated, exines. The furrows are short and unequally spaced. Both the germinal apertures and pores are not well developed.

The wood structure of the Nyssaceae shows to resemble closely to the Cornaceae. They are both included in the same order Cornales by Rickett(16), but generally the Nyssaceae are placed in the order Myrtiflorae. The grains of the Nyssaceae bear some dis-similarities to that of the Cornaceae. The former, as compared with the latter, are midium-sized to large and triangular to elliptical in outline. The exines are distinctly granular. The furrows are rather short and broad, lying at the angles when the grains are triangular in outline, and crossing the long axis of the grain when the grain is elliptical in shape. Germinal apertures are mainly irregular in outline and often extended out of the furrow membranes. The germinal pores are highly developed and bulge out as if having ruptured the furrow membranes.

The Nyssaceae are divided by Wangerin(18) into 2 subfamilies: Davidioideae and Nyssoideae. The two genera *Camptotheca* and *Nyssa* are closely associated and form the subfamily Nyssoideae. The wood structure also shows sharp difference between these

two subfamilies, yet no significant difference in the pollen morphology between these two subfamilies could be particularly mentioned.

The phylogenetic position of the genus *Helwingia* is very interested to taxonomists. Its wood structure exhibits close relationships with *Schefflera* of the Araliaceae, although it is also similar to that of *Cornus* of the Cornaceae. Its pollen morphology shows instead of great resemblance to *Cornus* rather than to *Schefflera*. The grains of this genus are elliptical in outline with finely granular exines. The furrows are long and broad, equally spaced, not reaching from pole to pole, and each provided with a distinct germinal aperture which is oval in shape. Germinal pores bulge out. The mild characters in wood structure and pollen morphology, as well as external morphology, of the genus *Helwingia* between the Cornaceae and Aaliaceae may represent it as a link between these two families.

The grains of the monotypic family Torricelliaceae created by Hu(12) are extremely spherical in shape and medium-sized as compared with that of the Cornaceae and of the Araliaceae. The furrows are short and the exines are extremely smooth.

The wood structure of *Mastixia* shows the most primitive one among the Cornaceous genera(31) and is closely to resemble that of the Nyssaceae. The pollen morphology of this genus also indicates some peculiarities among the genera of the Cornaceae. The grains are triangular in shape and with distinct granular exines. The germinal furrows are rather short and the germinal pores are highly developed. It is interested to note that the pollens of this genus resemble those of *Camptotheca* and *Nyssa* of the Nyssaceae. The presence of secretory canals in pith of *Mastixia* gives it a unique position within the family. It is suggested that *Mastixia* may represent a link between the Cornaceae and Nyssaceae rather than a link between the Cornaceae and Araliaceae as proposed by others, because the pollen morphology and wood structure between the former two families are very similar.

The grains of *Cornus* studied range from 25 μ to more than 60 μ in diameter. The grains of the Chinese species *C. Monbeigii* are the largest, which also differ from the others of the complex in having narrow germinal furrows. They are commonly oval to elliptical in shape. The exines are finely granular to nearly smooth. The germinal furrows are rather long and broad, equally spaced, and, except *C. kousa*, *C. hongkongensis*, and *C. oblonga*, parallel to the long axis of the grain. The germinal apertures are, except *C. oblonga*, spherical in outline. The furrow membranes are smooth and the germinal pores are well developed.

A study of the pollen morphology of *Cornus* reveals that they form a homogenous group of plants. No distinct features are present which could be used to divide these species into several distinct genera. The only difference is in size which is, nevertheless, not a distinct feature of the pollen grains, as it is not only more or less variable within a single species. Here it should be mentioned that the mountainous species *C. oblonga* exhibits peculiarity both in wood structure and pollen morphology. This species is also considered to be doubtful in its position by taxonomists.

The grains of the genus *Corokia* show affinity with *Cornus*. In comparison with the latter, the grains of *Corokia* are rather small in size and strictly spherical in shape. The exines are distinctly granular and the germinal apertures are irregular in outline.

The genus *Aucuba*, together with the genus *Cornus*, is included in the tribe Corneae as in Wangerin's system(18). However, Nakai(15) suggested to form another tribe Aucubeae for *Aucuba*. Both the wood structure and pollen morphology strongly support Nakai's suggestion, as the pollens of this genus are wholly different from that of *Cornus*. The grains of this genus are oval in shape and rather large. The exines are extremely reticulate. The germinal apertures are confined to the germinal furrows.

The grains of *Griselinia* resemble the grains of *Cornus*. However, the former are rather small in size and oval in shape. The exines are distinctly granular and the germinal apertures are elliptical to irregular in outline.

SUMMARY

1. The Cornaceae are closely related to the Araliaceae as indicated by their pollen morphology and wood structure as well as floral characters. *Helwingia* may represent as a link between these two families.

2. As indicated by their pollen morphology and wood structure, *Camptotheca* and *Nyssa* of the Nyssaceae and *Mastixia* of the Cornaceae show close relationships and the latter may represent as a link between these two families.

3. *Cornus* resembles *Viburnum* and *Sambucus* of the Caprifoliaceae in both pollen morphology and floral structure.

4. The establishment of separate families, Garryaceae for *Garrya*, Alangiaceae for *Alangium*, Nyssaceae for *Camptotheca*, *Nyssa*, and *Davidia*, and Torricelliaceae for *Torricellia* seems reasonable.

5. *Cornus* includes species generally similar in their pollen morphology and wood structure. It seems not necessary for their generic segregation. However, the species *C. oblonga* and *C. Monbeigii* are distinct in both pollen morphology and wood structure from the most members of the complex.

6. *Aucuba* is rather different from *Cornus* in both pollen morphology and wood structure. It is desirable to establish a separate tribe Aucubeae instead of being included in the Corneae.

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EXPLANATION OF PLATES

All the figures in Plates I–IV are drawings of pollen grains which were made at the same magification, approximately 800×. Only portions of the surfaces are represented.

a—lateral view b—polar view

Plate I

1. Alangium chinensis Rehd.
2. A. Handelli Schiff.
3. A. platanifolium Harms.
4. A. premnifolium Okwi.
5. Acanthopanax trifoliatus (L.) Merr.
6. Aralia bipinnata Blanco
7. A. elata Seem. var. canascens Nak.

Plate II

8. Aralidium punnatifidum Miq.
9. Diplopanax stachyanthus Hand.-Maz.
10. Hedera nepalensis K. Koch var. sinensis (Tobl.) Rehd.
11. Schefflera Delavayi (Fr.) Harms.
12. S. elleptifoliola Merr.
13. Abelia aschermmina (Graebn.) Rehd.
14. Lonicera ligustrina Wall.
15. Sambucus Buergeriana Blume var. Miqueli Nek.
16. S. javanica Blume.
17. Viburnum Hanceanum Maxim.
18. V. tomemtosum Thunb.
19. Aucuba chinensis Benth.
20. A. japonica Thunb.

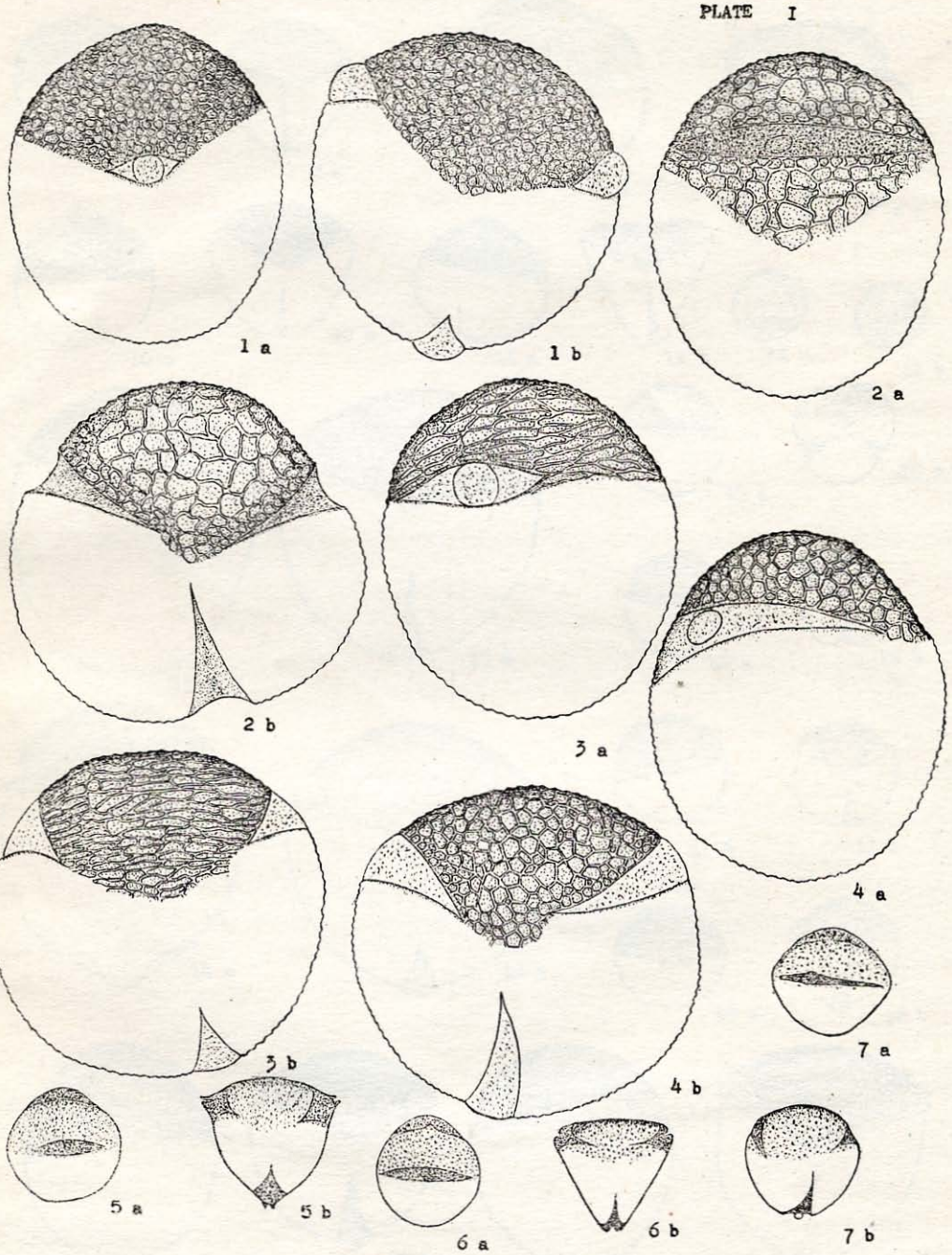
Plate III

21. Cornus canadensis L.
22. C. chinensis Wang.
23. C. controversa Hemsl.
24. C. florida L.
25. C. hongkongensis Hemsl.
26. C. kousa Buerger.
27. C. longipetiolata Hay.
28. C. mas L.
29. C. Monbeigii Hemsl.
30. C. oblonga Wall.
31. C. auesica L.
32. Corokia buddleioides A. Cunn.
33. Griselinia jodinifolia (Griseb.) Taub.
34. G. lucida Forst.
35. Helwingia chinensis Batal.
36. H. himalaica Hook. f. et Thoms.

Plate IV

37. Mastixia philippenensis Wang.
38. Garrya longifolia Rose.
39. Camptotheca acuminata Dcne.
40. Davidia involucrata Baill.
41. D. involucrata Baill. var. Vilmoriniana (Dcne) Wang.
42. Nyssa sylvatica Marsh.
43. Torricellia tilifolia DC.

PLATE I



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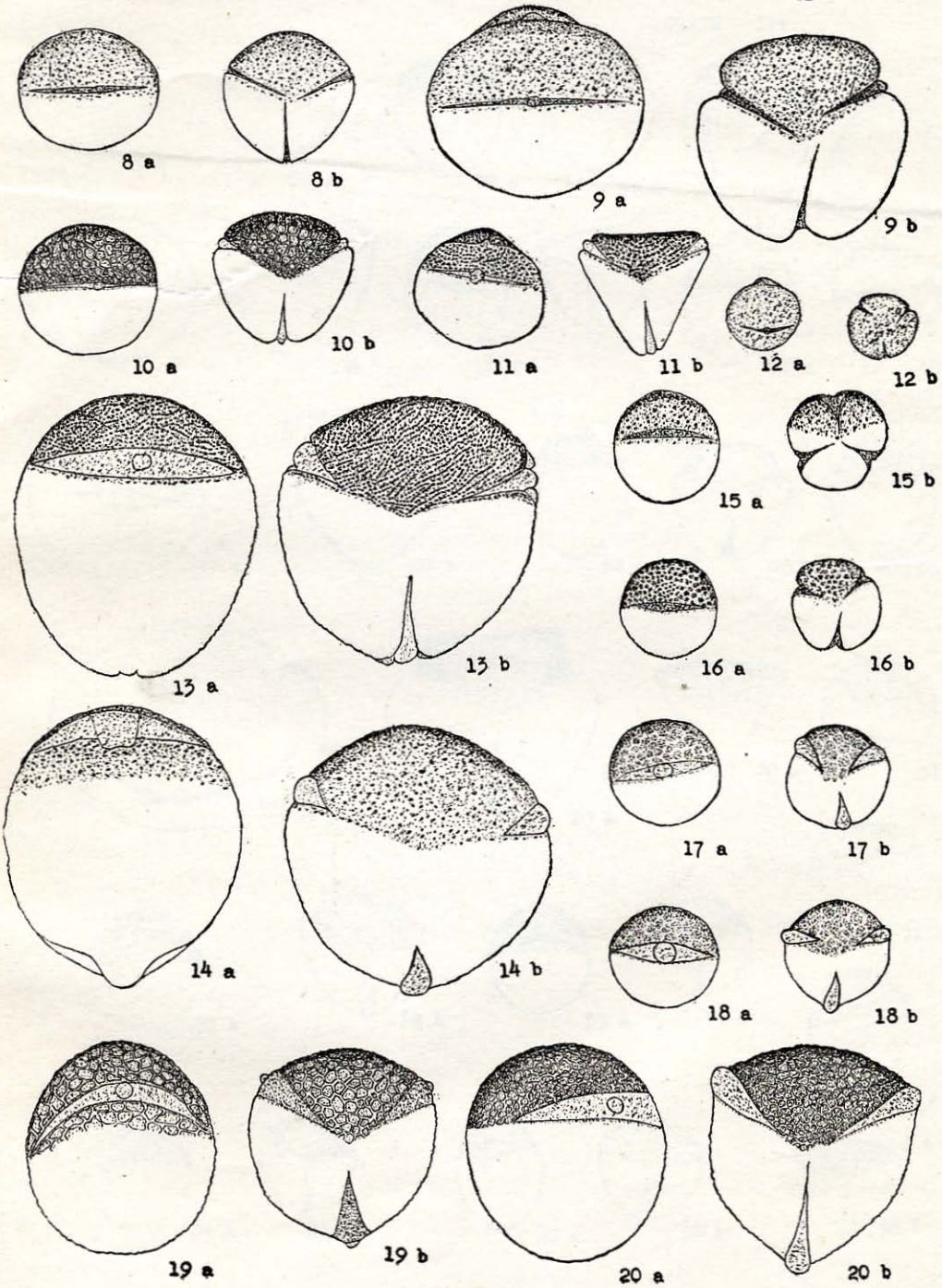
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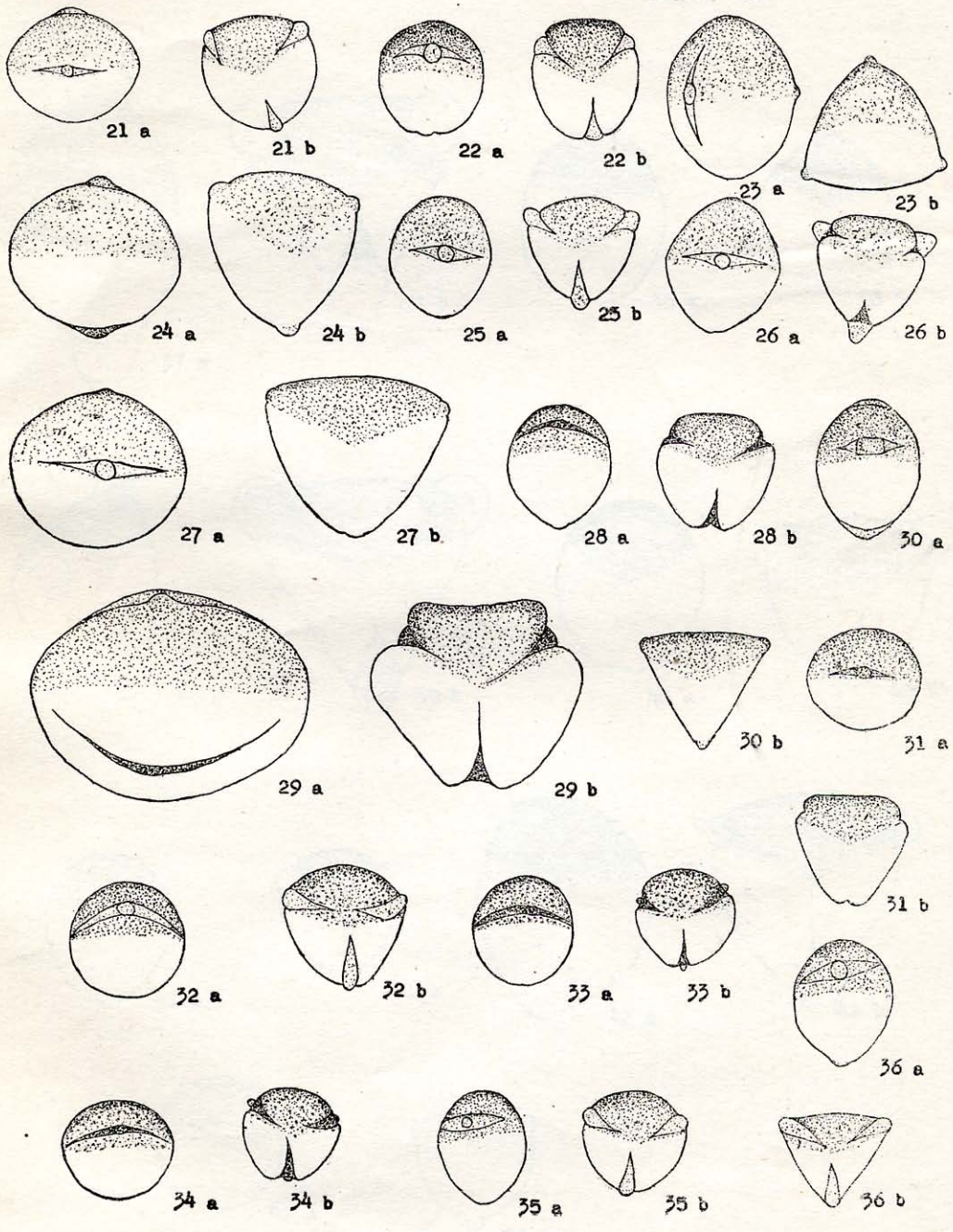
PLATE III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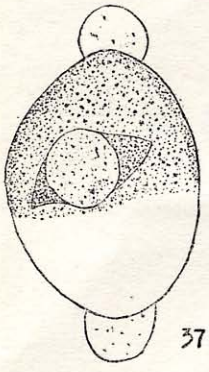
36 b

PLATE IV



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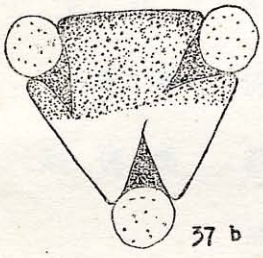
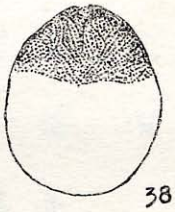


37 b



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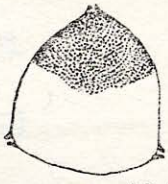

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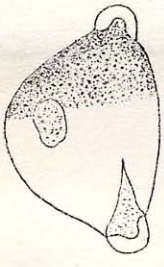

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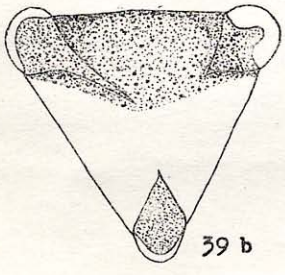

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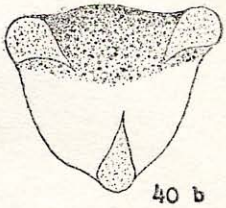

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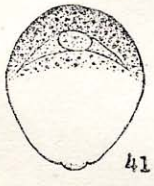

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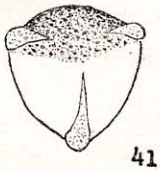

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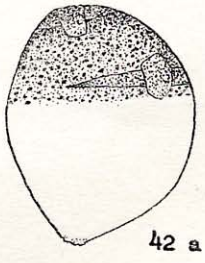

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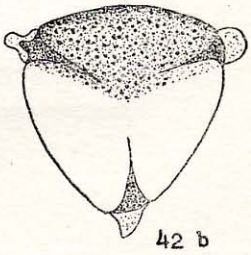

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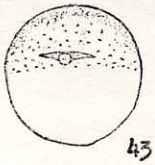

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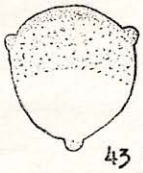

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