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Studies on the Pollen Morphology in the Lythraceae[1]

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부처꽃科의 花粉形態에 關한 研究

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ABSTRACT

Pollen grains of 26 genera and 62 species of the Lythraceae were investigated by means of light microscopy. The result reveals that the family is divided into three pollen groups which are characterized by having a non-, 3- and 6-pseudocolpate aperture. The palynological study suggests a revision of the subfamilial division. Some taxonomic problems between the genera were discussed on the pollen morphology.

INTRODUCTION

The family Lythraceae is composed of about 26 genera, encompassing about 500 species. The family has been monographed once by Koehne (1903). In his treatment the 22 genera, recognized at that time, were grouped into two tribes, Lythreae and Nesaeae, based on the degree of completeness of the ovarian septa. His subdivision of the family, however, was disputed because the states of septa are variable and difficult to ascertain in many specimens (Graham, 1964).

Since Koehne's work, *Didiplis* and *Rhynchocalyx*, which were excluded from the Lythraceae by him, have been reassigned to the family (Webb, 1967; Sprague and Metcalfe, 1937), and three new genera have been described—*Alzatea* (Lourteig, 1965), *Capuronia* (Lourteig, 1960) and *Haitia* (Fedde, 1919). It has been indicated that there are many taxonomic confusions between genera (Koehne 1903; Cory, 1936; Webb, 1967; De Vos, 1971; Graham, 1977).

Pollen morphology is very useful in plant classification (Davis and Heywood, 1973). Innumerable studies have been made for most angiosperm families and genera (Erdtman, 1972; Tralau, 1974), including the lythraceous members (Coz Campos, 1964; Salgado-Labourau and Valio, 1964; Van Campo, 1964; Graham and Graham, 1967, 1971; Barth, 1971; Graham, 1977). Because there has been no broad study of the family since Koehne's work, the present study was initiated. This study aims primarily to evaluate Koehne's system, to resolve the taxonomic confusions and proposed

1) This study represents a major portion of a thesis (Lee, 1973) submitted in partial fulfillment of the requirements for a M.S. degree at Kent State University, Kent, Ohio, U.S.A.

2) The author thanks Drs. Alan and Shirley A. Graham for making available the pollen slides and giving a great deal of technical assistance during the course of this study. In preparation of the manuscript he had been indebted to Mrs. Linda Shane and Mr. Ralph MacGraw.

taxonmic problems, and to elucidate evolutionary trends among the genera on the basis of pollen morphology.

MATERIALS AND METHODS

The study was based on observations of pollen in the reference collections of Dr. Alan Graham in the Department of Biological Sciences, Kent State University, Kent, Ohio, U.S.A.

Pollen samples were obtained primarily from field collections of Dr. Shirley A. Graham and from vouchered materials from several herbaria (GH, K, MICH, and US). Slides were prepared by the KOH-acetolysis technique, or by the temporary lactic acid method described by Graham and Graham (1971), mounted in glycerin jelly, and sealed with diaphane. A few slides were obtained by exchange with other institutions (U.S. Geological Survey, Ohio State University, and Shell Oil Company). Photographs (Figs. 1-4) were taken with a Wild microscope and Nikon 35mm camera.

Terminology of Faegri and Iversen (1966) was adopted for the pollen description, however, Erdtman (1972) was also used when exceptionally needed.

POLLEN DESCRIPTIONS

All genera of the family except one are described here. *Tetrataxis* is apparently represented by only 3 herbarium sheets from Mauritius in the Paris Herbarium. *Alzatea* was not available but the descriptions of Lourteig (1965) were used. In the description, pollen characters at the generic level will be verbalized, whereas those of the species level will be summarized in Table 1.

Adenaria H., B. et K. (Fig. 1 : 1—3)

Pollen prolate-spheroidal; tricolporoidate, sometimes 4(5)-colporoidate; sometimes parasyncolpate, colpus long with costae and margo; pore margin indistinct; exine thin, sexine thicker than nexine, sometimes sexine becomes thicker to the poles, often slightly separated from nexine at poles; surface scabrate to rugulate.

Alzatea Lourt.

Pollen prolate to prolate-spheroidal; tricolporate; exo-aperture elongate narrower toward the equator, endoaperture little visible; surface finely reticulate.

Ammannia L. (Fig. 1 : 6—9)

Pollen prolate to prolate-spheroidal; tricolporate with 6 pseudocolpi; true colpi longer and broader than pseudocolpi, true colpi have distinct margo and costae, pore circular to elongate, pore margin distinct; sexine and nexine ±equally thick, often sexine becomes thicker or sometimes separated from nexine at poles; surface faintly rugulate or striate.

Capuronia Lourt. (Fig. 1 : 4, 5)

Pollen prolate to prolate-spheroidal; tricolporate; colpi long with indistinct costae, margo distinct; pore equatorially elongate, margin indistinct; sexine thicker than nexine; surface faintly scabrate.

Crenea Aubl. (Fig. 2 : 19—21)

Pollen prolate; tricolporate with 6 pseudocolpi; sometimes true colpi syncolpate, true colpi longer than pseudocolpi, pseudocolpi locate more closely to the true colpi; colpi margo and costae distinct; pore circular to elongate, margin faint; sexine and nexine equally thick or sexine slightly thicker than nexine; surface verrucate.

Cuphea P. Browne (Fig. 2 : 22—34)

Pollen oblate to peroblate, polar shape angular to semiangular; tricolporate; usually syncolpate, rarely biporate. When biporate, pores locate at poles and the equatorial pores are lacking; colpi with indistinct costae and slight to profound margo; pore circular or elongate, margin distinct, vestibulate and usually conspicuously protruding; exine thin; surface often striate, striae long and perpendicular or parallel to equator, sometimes irregularly striate or psilate.

Decodon J. F. Gmel. (Fig. 1 : 13—15)

Pollen perprolate to prolate; tricolporoidate; colpi with prominent margo and costae, pore margin indistinct; sexine slightly thicker than nexine, becomes thicker at polar regions; surface distinctly verrucate to rugulate.

Didiplis Raf. (Fig. 1 : 10—12)

Pollen prolate, polar shape intersemiangular; triporate, colpi hardly observable, might be recog-

Table 1. Pollen morphological data of Lythraceae

(1) Specific name	(2) Slide number	(3) Polar length (μm)	(4) Equatorial diameter (μm)	(5) Equatorial shape	(6) Polar shape	(7) Pore state	(8) Pore size(ExP μm)	(9) Pseudocolpus no. & state	(10) Anastomosis of true colpi	(11) Exine thickness (μm)	(12) Sculpture pattern
Adenaria											
floribunda	2564	18	13—15	prolate to prol-sphe-roid	circular to semiangu-lar	faint	?×3	absent	none	1.0	scabrate
floribunda	2505	23	18	prolate to prol-sphe-roid	circular to semiangu-lar	faint	?×1	absent	sometimes parasyncol-pate	1.5	scabrate—rugulate
Alzatea											
verticillata		21—16	16	prolate to prol-sphe-roid	semiangular	±distin-ct	?	absent	none	1.0	finely reticulate
Ammannia											
auriculata	8404	25—30	18—24	prolate to prol-sphe-roid	circular to semiangular	distinct	3	6 long	none	2.0	faintly striate
coccinea	5342	27—30	22—44	prolate to prol-sphe-roid	circular to semiangular	distinct	4'	6 long	none	2.0	faintly striate
latifolia	7044	27	23	prolate to prol-sphe-roid	circular to semiangular	distinct	4×3	6 long	none	1.5	rugulate
microcarpa	6572	27	24	prolate to prol-sphe-roid	circular to semiangular	±distin-ct	3×2	6 long	none	1.5	rugulate
pieureana	6568	27	24	prolate to prol-sphe-roid	circular	±distin-ct	2.5	6 long	none	2.0	psilate
Capuronia											
madagasca-riensis	13679	20	17	prolate to prol-sphe-roid	inter-semi-angular	distinct	3	6 long	none	1.5	faintly scabrate
Crenea											
maritima	7418	32—36	27	prolate	inter-semi-angular	±distin-ct	3	6 short	none	2.0	verrucate
surinamen-sis	6573	26	22	prolate	inter-semi-angular	±distin-ct	3	6 short	sometimes syncolpate	2.0	verrucate
Cuphea											
aperta	5545	12	27	peroblate	angular to semiangular	distinct	2×5	absent	syncol-pate	1.0	psilate
bombana-seae	5546	24	24	spherical	circular to semiangular	distinct	2.5×0.5	absent	none	1.5	rugulate
confertiflo-ra	5615	18	32	peroblate	angular	distinct	4×2	absent	syncol-pate	1.0	striate
cordata	5616	18	30	peroblate	semiangular	distinct	5×7	absent	parasyn-colpae	1.0	striate
melvilla	4058	20	36	peroblate	semiangular to angular	±distin-ct	?	absent	parasyn-colpate	1.0	striate
persistens	4059	42	29	prolate	angular	absent	polar-pore 7	absent	syncol-pate	1.0	striate
setosa	5643	19	25	peroblate	angular	distinct	5×7	absent	parasyn-colpate	1.0	striate

Table 1. (continued)

tetrapetala	5647	19	23	peroblate	angular	distinct	3	absent	none	1.0	striate
vesiculosa	2774	14	28	peroblate	angular	distinct	2×3	absent	none	1.0	striate
Decodon											
virticillatus	5661	30-36	20-27	perprolate to prolate	circular to semiangular	±distinct	?×6	absent	none	2.0	verrucate rugulate
Didiplis											
diandra	13707	14	11	prolate	inter-semiangular	distinct	2	absent	none	1.0	psilate
Diplusodon											
buxifolius	5658	72	60	prolate	semiangular	distinct	11.5×3.5	absent	none	5.0	areolate
hexander	7045	92-110	72-80	prolate	semiangular	distinct	15×8	absent	none	4.0	areolate
macrodon	7046	72-90	72	prolate-spheroidal	circular to semiangular	distinct	14.5×6.5	absent	none	5.0	areolate
strigosus	6585	90-110	70-90	prolate	circular to semiangular	distinct	18×14	absent	none	3.0	areolate
virgatus	6577	54-60	36-40	prolate	circular to semiangular	distinct	9×4	absent	none	1.5-3	scabrate-verrucate
Galpinia											
transvaalica	6586	23	18	prolate	hexagonal-semiangular	distinct	1.5×3	absent	none	2.0	scabrate
Ginoria											
americana	5663	32	27	prolate	intersemi-angular	distinct	3.5	6 long	none	1.5	scabrate
Grislea											
secunda	5662	23-27	18	perprolate	semiangular	faint	?	absent	none	1.0-2.5	psilate-scabrate
Haitia											
pulchra	5664	25-27	25-28	oblate-spheroidal	circular to semiangular	distinct	5×3	6 short	rarely syncolpate	2.0	verrucate-regulate
Heimia											
salicifolia	5680	32-38	33-36	spherical	circular to semiangular	distinct	4×2	absent	none	2.0	scabrate
Lafoensia											
pacari	2423	54-63	43-45	prolate	intersemi-angular	distinct	12×5	absent	none	2.0—3.0	verrucate
punicifolia	5346	72	50	prolate	intersemi-angular	distinct	14×10	absent	none	2.0	scabrate
Lagerstroemia											
calyculata	7844	31-37	26	prolate to prol-spheroid	circular	distinct	2-3	6 invaginated	none	2.0-3.0	finely verrucate
floribunda	7845	35-37	32	prolate	circular	distinct	3-5	6 invaginated	none	2.5-5.0	finely verrucate
flos-reginae	6576	37	32	prolate prol-spheroid	intersemi-angular	distinct	3	6 invaginated	none	1.5-3.0	scabrate
lanceolata	6570	32	25	prolate	circular	distinct	6×3	none	none	1.5-4.0	verrucate
ovalifolia	7848	40	32	prolate-spheroid	intersemi-angular	distinct	3	6 invaginated	none	3.5-5	verrucate rugulate
Lawsonia											
alba	7856	19	16	prolate prol-spheroid	intersemi-angular	distinct	2	6 invaginated	none	1.5	finely verrucate
inermis	2508	23	18	prolate prol-spheroid	intersemi-angular	distinct	2-3	6 invaginated	none	1.5	psilate

Table 1. (continued)

Lythrm											
acinifolium	13709	17 22	26 30	oblate-spheroid	semiangular	distinct	2	3 broad	none	1.5	rugulate
curtissii	13713	23	28	oblate	semiangular	distinct	2	3 broad	none	1.5	rugulate
hyssopofolia	4090	22	23	oblate-spheroid	semiangular	distinct	5×3	3 broad	none	1.5	rugulate
lanceolatum	13708	16-26	18-28	oblate	semiangular	distinct	1.5 or 3	3 broad	none	1.5	rugulate-striate
lineare	13711	22	20	prolate-spheroid	semiangular	distinct	3	3 broad	none	2.0	striate
salicaria	10463	24-30	20-25	prolate-spheroid	semiangular	distinct	3	3 broad	none	1-1.5	striate
Nesaea											
floribunda	6576	26-28	19-25	prolate to prol-spheroid	circular to intersemiangular	distinct	3	6 long	none	1.5	rugulate
lythroides	7043	26-28	25	prolate to prol-spheroid	circular	distinct	4×3	6 long	none	1.5	rugulate
Pemphis											
acidula	6578	57-67	54	prolate to prol-spheroid	semiangular	distinct	14×5	3 invaginated	none	2	scabrate rugulate
madagacariensis	6583	19-23	18	prolate to prol-spheroid	semiangular	±distinct	?	3 invaginated	rarely syncolpate	1.5	scabrate rugulate
Peplis											
portula	5657	20-21	22-25	oblate-spheroidal	circular to semiangular	distinct	3	3 broad	none	1.5	psilate
Physocalymma											
scaberrimum	6589	27	24-27	prolate-spheroidal	semiangular	±distinct	3	3 invaginated	none	1.5	scabrate
Pleurophora											
anomala	5651	27	28	oblate-spheroidal	semiangular	distinct	4×2	6 invaginated	none	1.5	finely verrucate
polyandra	5653	27	20	prolate	inter-semiangular	distinct	5×3	6 invaginated	none	1.0	psilate-scabrate
pungens	5654	24	17	prolate	hexagonal	distinct	1×2.5	6 invaginated	none	1.5	psilate-scabrate
saccocarpa	5655	24	24-27	oblate-spheroidal	semiangular	distinct	5×1	6 invaginated	none	1.0	verrucate-rugulate
Rhynchocalyx											
lawsonioides	10589	18	14	prolate	circular to semiangular	distinct	1.0	3 narrow	none	1.0	gemmate
Rotala											
densiflora	6574	22	17	prolate	intersemiangular	distinct	1.0	6 invaginated	none	1.0	scabrate
indica	6581	26	18	prolate	circular	distinct	1.0	absent	none	1.5	scabrate
ramosior	8046	19	14-17	prolate to prol-spheroid	circular to intersemiangular	distinct	2.5	6 invaginated	none	1.5	scabrate
rotundifolia	6567	24	18	prolate	circular	faint	?	absent	none	1.0	scabrate
Woodfordia											
floribunda	6584	22	14	prolate	circular to intersemiang.	faint	?	absent	none	1.0	psilate

nized by thinner wings of the pore to poles; pore elongate, margin distinct; exine thin, sexine thicker than nexine; surface psilate, the pore boundary granular.

Diplusodon Pohl. (Fig. 1 : 16—18)

Pollen prolate, sometimes prolate-spheroidal; tricolporate, colpi reduced and obscure, costae and margo indistinct; pore distinct, sometimes protruding; exine very thick (3-5μm), sexine slightly thicker than nexine, becomes thicker at polar regions; surface distinctly verrucate, verrucae become scarce at polar regions, often reticularly grooved (areolate).

Galpinia N.E. Brown (Fig. 2 : 35—37)

Pollen prolate; tricolporoidate; colpi with distinct margo and costae, costae with thin constriction at equator; pore margin distinct; exine 2μm thick, sexine and nexine ±equally thick, sexin becomes thicker at polar regions; surface scabrate.

Ginoria Jacq. (Fig. 3 : 38—40)

Pollen prolate to prolate-spheroidal; tricolporate with 6 pseudocolpi, true colpi with costae, longer and broader than pseudocolpi; pore distinct; exine 1.5μm thick; surface scabrate, colpus region granulate.

Grislea Loefl. (Fig. 3 : 41, 45)

Pollen perprolate; tricolporoidate; colpus with distinct costae and slight margo; pore indistinct; sexine and nexine equally thick, sexine becomes thicker at poles; surface psilate to scabrate.

Haitia Urb. (Fig. 3 : 42—44)

Pollen oblate-spheroidal; tricolporate with 6 pseudocolpi, true colpi slightly longer and broader than pseudocolpi; pore margin faint, pore equatorially elongate; exine 2μm thick; finely verrucate to rugulate.

Heimia Link. (Fig. 3 : 46—49)

Pollen spherical (prolate to oblate-spheroidal); tricolporate, colpi with distinct costae and slight margo; pore circular to equatorially elongate, margin distinct; exine 2μm; surface scabrate.

Lafoensia Vand. (Fig. 3 : 54—56)

Pollen prolate, equatorial shape circular to compressed oval; tricolporate, colpi with slight margo and costae; pore protruding, vesiculate, margin distinct, equatorially elongate; exine 2μm thick; surface scabrate to verrucate.

Lagerstroemia L. (Fig. 3 : 50—52).

Pollen prolate to prolate-spheroidal; tricolporate with 6 pseudocolpi or 6 invaginations where 6 pseudocolpi would be, usually colpi with conspicuous margo and slight costae; pore circular or sometimes longitudinally elongate, pore margin distinct; exine thick; surface distinctly scabrate, verrucate or finely rugulate.

Lawsonia L. (Fig. 4 : 59, 63, 67)

Pollen prolate to prolate-spheroidal; tricolporate with 6 pseudocolpi or undulations where pseudocolpi would be, colpi with slight margo, no costae; pore circular, sometimes equatorially elongate, pore margin distinct; exine 1.5μm thick, sexine thicker than nexine; surface psilate to faintly verrucate.

Lythrum L. (Fig. 3 : 53, 57, 58)

Pollen prolate to oblate-spheroidal; tricolporate with 3 pseudocolpi, true colpi broader and longer than pseudocolpi, true colpi with or without slight costae or margo; pore circular or longitudinally elongate, margin distinct; exine 1.5μm thick, sexine thicker than nexine; surface striate to rugulate, granular on the colpi.

Nesaea Comm. (Fig. 4 : 60, 64, 68)

Pollen prolate to prolate-spheroidal; tricolporate with 6 pseudocolpi, pseudocolpi shorter and narrower than true colpi, true colpi with or without slight margo and costae; pore circular or slightly longitudinally elongate, margin distinct, sometimes obscure; exine 1.5μm; surface scabrate or rugulate.

Pemphis Forst. (Fig. 4 : 61, 65, 69)

Pollen prolate to prolate-spheroidal; 3-4-colpor(oid)ate with 3 invaginations where 3 pseudocolpi would be, true colpi with slight margo and costae; pore longitudinally elongate, margin distinct or not; exine 1.5-2.0μm thick, sexine and nexine equally thick; surface scabrate to finely rugulate.

Peplis L. (Fig. 4 : 62, 66, 70)

Pollen oblate-spheroidal; tricolporate with 3 pseudocolpi, true colpi longer and narrower than pseudocolpi, colpi with slight costae and margo; pore circular, margin distinct; exine 1.5μm thick; surface psilate, colpus surface granular.

Physocalymma Pohl. (Fig. 4 : 71—73)

Pollen prolate-spheroidal; tricolporoidate, sometimes with 3 invaginations; colpi with slight costae and margo, costae constricted at equator; pore indistinct; exine 1.5μm thick; surface scabrate, colpus granulate.

Pleurophora Don. (Fig. 4 : 75—77)

Pollen prolate to oblate-spheroidal; tricolporate, sometimes with 6 invaginations; colpus with slight margo and costae; pore equatorially elongate, margin usually distinct, slightly vestibulate; exine 1.0—1.5μm thick, sexine and nexine ±equally thick, sometimes sexine becomes thicker at poles; surface finely verrucate to rugulate.

Rhynchocalyx Hook. (Fig. 4 : 74, 78, 79)

Pollen prolate; tricolporate with 3 pseudocolpi, true colpi and pseudocolpi more or less equally long and broad, true colpi with slight costae; pore circular, margin distinct; exine 1μm thick; surface gemmate.

Rotala L. (Fig. 4 : 80—82)

Pollen prolate to prolate-spheroidal; tricolporate, rarely with 6 invaginations, colpi with slight margo and costae; pore circular, margin distinct or diffused; exine thin; surface scabrate.

Woodfordia Salisb. (Fig. 4 : 83—85)

Pollen prolate; tricolporoidate, colpi with distinct costae and margo; pore margin indistinct; exine thin, sexine thicker than nexine, surface psilate.

POLLEN SLIDE NUMBERS AND COLLECTION DATA INVESTGATED

Adenaria floribunda H.B.K. #2564 Yungas 20, Panama, UM.

A. floribunda H.B.K. #2505 Yungas 374, Bolivia, UM.

Alzatea verticillata R. & P. Lourteig (1965).

Ammannia auriculata Willd. #8404 OSU exchange, Texas.

A. coccinea Rottboell #5342 Lundell 8047, Mexico, GH.

A. latifolia L. #7044 Cheesman & Wright 13111, St. Augustine, Kew.

A. microcarpa DC. #6572 No collection data.

A. prieureana Guill. et Perr. #6568 No collection data.

Capuronia madagascariensis Lourteig #13679 Güinet exchange.

Crenea maritima Aubl. #7418 Shell exchange.

C. surinamensis (L.f.) Koehne #6573 No collection data.

Cuphea aperta Koehne #5545 Corges 2078, Brazil, USNH.

C. bombanaseae Sprague #5546 Allard 21729, Argentina, USNH.

C. confertiflora St.-Hil. #5615 Schwindt 2966, Argentina, USNH.

C. cordata R. & P. #5616 Ferreyna 1743, Peru, USNH.

C. melvilla Lindl. #4058 Lindman 2093, Paraguay, GH.

C. persistens Koehne #4059 Sloruter 34391, Argentina, GH.

C. setosa Koehne #5643 Grant 9976, Columbia. USNH.

C. tetrapetala Koehne #5647 Haught 5386, USNH.

C. vesiculosa Koehne #2774 Graham 129, Mexico MICH.

Decodon verticillatus (L.) Ell. #5661 Holmes 163, Maryland, USNH.

Diplusodon buxifolius (Cham. et Schlechtd.) DC. #5658 Williams & Assis 6709, Brazil, USNH.

D. hexander DC. #7045 Airdel, Brazil, Kew.

D. macrodon Koehne #7046 Cardner 3752, Brazil, Kew.

D. strigosus Pohl #6585 Brazil, Kew.

D. virgatus Pohl #6577 Brazil, Kew.

Didiplis diandra (Nutt.) Wood #13707 Nicely 2409, Kentucky, UNC.

Galpinia transvaalica N.E. Brown #6586 Portuguese E. Afr., Kew.

Ginoria americana Griseb. #5663 Shafer 11201, Cuba, USNH.

Grislea secunda Loefl. #5662 Williams & Molina 23245, Honduras, USNH.

Haitia pulchra Ekm. et O.C. Schmidt #5664 Leonard & Leonard 13168, Haiti, USNH.

Heimia salicifolia (H.B.K.) Link #5680 Rzedowski 165, Morelos, USNH.

Lafoensia pacari St.-Hil. #2423 Morin 581, Paraguay, UM.

L. punicifolia DC. #5346 Allen 1066, Panama, GH.

Lagerstroemia calyculata S. Kurz #7844 Shell exchange, Indochina.

L. floribunda Jack #7845 Shell exchange, Burma.

L. flos-reginae Retz. #6576 No collection data.

L. lanceolata Wall. #6570 No collection data.

L. ovalifolia Teysm. et Binnend. #7848 No collection data.

Lawsonia alba Lam. #7856 Shell exchange, India.

L. inermis L. #2508 Sichenberger, UM.

Lythrum acinifolium (DC.) Koehne #13709 Graham 469, Mexico, MICH.

L. curtissi Fernald #13713 Graham 457, Florida, MICH.

L. hyssopifolia L. #4090 California, GH.

L. lanceolatum Ell. #13708 Demaree 65276, Ark., MICH.

L. lineare L. #13711 Graham, NC, MICH.

L. salicaria L. #10463 Denver exchange, Leopold, Switz.

Nesaea floribunda Sond. #6576 Mozambique, Kew.

N. lythroides Hiern #7043 Haarer 1344, Tanganyika, Kew.

Pemphis acidula Forst. #6578 Tokelau, Fakaops Is., Kew.

P. madagascariensis (Bak.) Koehne #6583 Madagascar, Kew.

Peplis portula L. #5657 Walas & Facik 549, Poland, USNH.

Physocalymma scaberrimum Pohl #6589 Bolivia, Kew.

Pleurophora anomala (St.-Hil.) Koehne #5651 Soer 91, Venez., USNH.

P. polyandra Hook. et Arn. #5653 Joseph 1399, Chile, USNH.

P. pungens Don #5654 Johnston 5216, Chile, USNH.

P. saccocarpa Koehne #5655 Schwarz 9919, Argentina, USNH.

Rhynchocalyx lawsonioides Hook. #10589 Strey 8080, Kew.

Rotala densiflora (Roth) Koehne #6574, India, Kew.

R. indica (Willd.) Koehne #6581 China, Kew.

R. ramosior (L.) Koehne #8046 OSU exchange, Columbia.

R. rotundifolia (Roxb.) Koehne #6576 W. China, Kew.

Woodfordia floribunda Salisb. #6584 India, Kew.

REMARKS OF POLLEN MORPHOLOGY WITHIN THE FAMILY

Pollen grains of all specimens investigated in this study are characteristically monad, isopolar and tricolporate. However, other pollen characters are variant and the family distinctly eurypalynous.

Grain size and exin thickness: Among the 26 genera and 62 species investigated, *Diplusodon hexander* has the largest pollen (cf. Fig. 1 : 16—18), while *Didiplis diandra* has the smallest (Fig. 1 : 10—12). The lengths of polar axis are 110 μm and 14 μm, respectively. The thickness of exine in these species also shows extremity, that is, 4 μm and 0.5 μm. Some large pollen can be found in *Lafoensia* (Fig. 3 : 54—56) and *Heimia* (Fig. 3 : 46—49); yet, in most of the genera the length of polar axis extends between 18 μm and 36 μm, and the exine thickness between 1.0 μm and 2.0 μm.

Grain shape: The shape of the grains varies from perprolate as in *Grislea secunda* (P/E=1.5, Fig. 3 : 45) to peroblate as in *Cuphea aperta* (P/E=0.4, Fig. 2 : 30). The most common shape ranges prolate to prolate-spheroidal. Usually *Cuphea* has peroblate to oblate pollen (Fig. 2 : 22—34) while few genera are oblate-spheroidal.

Sculpture pattern: The sculpture patterns of the family cover almost all types. The most common are scabrate or verrucate (to rugulate). There are few genera with other types. The pollen of *Woodfordia* and *Didiplis* are psilate (Fig. 3 : 83—85; 1 : 10—12), those of *Alzatea* finely reticulate, *Lythrum* striate (Fig. 3 : 57), and *Rhynchocalyx* gemmate (Fig. 4 : 78, 79). The pollen of *Diplusodon* is areolate in which areola possess verrucate or scabrate sculpturing (Fig. 1 : 18). The surface of *Cu-*

phea species is often peculiarly striate with long parallel striae arranged perpendicularly to the equator extending to colpi in *C. confertiflora* (Fig. 2 : 34). Parallel striae are also arranged horizontally to the equator in *C. melvilla* (Fig. 2 : 20) and *C. persistens* (Fig. 2 : 33).

Aperture: Pollen of the family is characterized by having a tricolporate aperture. In addition to the aperture, many genera possess one or two pseudocolpi between each pair of colpi with a total of 3 or 6 pseudocolpi per grain. A pollen grain, for example, has three pseudocolpi in *Lythrum* (Fig. 3 : 57) and *Peplis* (Fig. 4 : 62), while it has 6 in *Ammannia* (Fig. 1 : 7) and *Nesaea* (Fig. 4 : 64).

Pseudocolpi show a great variety of conspicuousness among the genera. Pseudocolpi of 6-pseudocolpate genera vary in length, whereas those of 3-pseudocolpate genera vary in width. On the other hand, the incipient state of both 3-and 6-pseudocolpi exhibits no distinct pseudocolpi but simple invaginations where pseudocolpi would exist (Fig. 4 : 71, 75).

The pseudocolpate genera can be arranged in the following order:

	(long)	(short)	(invaginated)
6-pseudocolpate genera	*Ammannia*	*Crenea*	*Lagerstroemia*
	Ginoria…………………	*Haitia*……………………	*Pleurophora*
	Nesaea	*Lawsonia*	*Rotala*
	(broad)	(slender)	(invaginated)
3-pseudocolpate genera	*Lythrum*………………	*Rhynchocalyx*……………	*Pemphis*
	Peplis		*Physocalymma*

In the non-pseudocolpate pollen of *Cuphea* and sometimes in those of *Adenaria*, colpi are anastomosed together at the poles (Fig. 2 : 28, 30, 34). Colpi of *Cuphea aperta*, *C. confertiflora* and *C. melvilla* simply meet at poles, whereas in *C. cordata* they form a triangle at the poles. A term "parasyncolpate" was used for this condition by Erdtman (1972). The diporate grains of *C. persistens* seems to have been derived from a syncolpate or parasyncolpate form; i.e. equatorial pores of colpi would have been disintegrated, whereas polar pores would have been differentiated from the syncolpate region.

With the exception of a few species of *Cuphea*, such as *C. persistens*, all pollen of the family has three pores and colpi. Pores are distinct in *Cuphea*, *Peplis*, *Diplusodon*, *Lafoensia*, *Heimia*, *Rotala* and most of the pseudocolpate genera. The rest of the family, however, does not possess distinct pores, i.e. their pollen is tricolporoidate. On the other hand, pores are sometimes distinct but often not in the same genus, e.g., *Pemphis* and, in the same species, *Physocalymma scaberrimum*. In *Cuphea vesiculosa* the pores are extremely protruding and vestibulate, and the shape in equatorial view is apiculate. Beside *Cuphea*, *Lafoensia* also has protruding pores; in the rest of the family, however, pores are slightly protruding or not protruding at all.

In many genera such as *Decodon*, *Alzatea*, *Grislea*, *Adenaria*, *Woodfordia*, and *Galpinia*, the colpi have distinct costae, while *Cuphea*, *Capuronia* and most genera with pseudocolpi either have no or very faint costae. In most species of *Diplusodon*, colpi are not distinct because of very coarse sculpture pattern and thick exine. The greatest reduction of colpi is observed in *Didiplis diandra* (Fig. 1 : 10—12). Since the colpi are hardly observable, the pollen of *D. diandra* appears triporate.

Pollen groups and evolutionary trends: Among the used pollen characters, the pseudocolpus is the most characteristic and typical. Pseudocolpus is rare among the angiosperms but common in the Lythraceae. As discussed above, many pollen characters parallel this feature. On the basis of this pollen study, it would be reasonable to conclude that the family be divided into non-, 3- and 6-pseudocolpate pollen groups.

Pseudocolpus would be a derived condition according to the assumption of ex-group comparison (Ross, 1974). As for the number of pseudocolpi, there seems to be no ancestor-descendent relationship between 3 and 6 because no transitional form exists. Therefore, 3- and 6-pseudocolpate groups are thought to have been independently originated from the ancestral stock with non-pseudocolpate pollen.

On the other hand, the tricolporate aperture has been derived from the tricolpate one (Muller, 1970). The colporoidate aperture in which the pore margin is faint, is transitional between colporate and colpate apertures. Thus the colporoidate aperture is believed to be a primitive condition within the family. In this regard, primitive genera may include *Adenaria*, *Decodon*, *Grislea* and *Woodfordia*.

Among the pseudocolpate as well as the non-pseudocolpate genera, pores of some genera exhibit a faint margin while the rest, a distinct margin. Then it is supposed that the pore margin would have been elaborated by a convergent evolution in the groups possessing different numbers of pseudocolpi. The existence of the pseudocolpus, typically in the Lythraceae, would readily reject the alternative assumption that the pseudocolpus would have been independently developed from both faintly and distinctly porate members, after the distinctly porate members were speciated from the faintly porate ancestors.

The proposed phylogenetic trends of the family based on the pollen morphology are summarized in Figure 5.

POLLEN KEY TO THE GENERA OF LYTHRACEAE

Using the morphology of pollen described above, a pollen key to the genera was constructed. The key is based on light microscopical observations of acetolyzed pollen grains. The quantitative values represent ranges, modes, or extreme measures.

Ⅰ. Pollen lacking pseudocolpi or invaginations
- A. Pore margin distinct
  - B. Shape peroblate to perprolate, usually syncolpate, pore slightly or consicuously protruding, surface parallel-striate or distinctly striate, rugulate, or psilate. ....*Cuphea*
  - BB. Shape oblate-spheroidal to perprolate, rarely syncolpate, pore rarely protruding, surface verrucate, scabrate, reticulate, psilate, areolate, or inconspicuously rugulate or striate.
    - C. Colpi lacking, size: P=14μm, E=11μm ....*Didiplis*
    - CC. Colpi present, size: P>19μm, E>14μm
      - D. P=70−110μm, E=36−90μm, surface areolate ....*Diplusodon*
      - DD. P<72μm, E<50μm, surface not areolate
        - E. P=52−72μm, E=43−50μm, pore protruding............*Lafoensia*
        - EE. P<38μm, E<36μm, pore not protruding
          - F. P=32−38μm, E=32−36μm, PV circular, semiangular or hexagonal, costae colpi distinct............*Heimia*
          - FF. P=19-26μm, E=14-19μm, PV circular to intersemiangular, costae colpi faint...*Rotala*
- AA. Pore margin indistinct
  - B. Costae colpi indistinct............*Capuronia*
  - BB. Costae colpi distinct
    - C. P=30−36μm, E=20−27μm, surface distinctly verrucate to rugulate............*Decodon*
    - CC. P<27μm, E<18μm, surface psilate, scabrate, faintly scabrate to rugulate, or reticulate
      - D. Surface reticulate............*Alzatea*
      - DD. Surface not reticulate
        - E. PV semiangular
          - F. Surface psilate to faintly scabrate, P/E=1.3−1.5............*Grislea*
          - FF. Surface scabrate to rugulate, P/E=1.0−1.3 ....*Adenaria*
        - EE. PV intersemiangular to hexagonal
          - F. Surface psilate, P/E=1.5, costae colpi prominent............*Woodfordia*
          - FF. Surface scabrate, P/E=1.2, costae colpi faint............*Galpinia*

Ⅱ. Pollen with pseudocolpi or invaginations
- A. Pseudocolpi or invaginations 6
  - B. Pseudocolpi distinct
    - C. Size small (P<25μm)............*Lawsonia*
    - CC. Size large (P>25μm)
      - D. Midridge twice broad as side-ridge ....*Crenea*
      - DD. Midridge ±equally broad
        - E. Colpus with slight margo, tiplinear, length shorter than 1/4 of radius in PV...*Haitia*

EE. Colpus with distint margo, tip acute, length longer than 3/4 of radius in PV
F. Colpus granular··················*Ginoria*
FF. Colpus not granular
G. Surface distinctly scabrate or rugulate·····························*Nesaea*
GG. Surface rugulate to striate ·······························*Ammannia*
BB. Pseudocolpi indistinct or invaginations only
C. Invaginations rare and slight·········*Rotala*
CC. Invaginations consistent
D. P> 30μm, exine 3–5μm, poles and midridges thicker than the rest part · *Lagerstroemia*
DD. P <30μm, exine 1.5μm, evenly thick ································· *Pleurophora*
AA. Pseudocolpi or invaginations 3
B. Pseudocolpi distinct
C. True and pseudocolpi similar in length and width, surface gemmate, colpi not granular, shape prolate·········*Rhynchocalyx*
CC. True and pseudocolpi dissimilar, surface striate or psilate, colpi granular, shape oblate
D. Pseudocolpi broader and shorter than true colpi, surface psilate ············*Peplis*
DD. Pseudocolpi narrower and longer than truecolpi, surface scabrate······*Lythrum*
BB. Pseudocolpi indistinct or invaginations only
C. PV semiangular, colpus finely granular, pore margin distinct, 4-colporate pollen not common··························· *Physocalymma*
CC. PV semiangular to circular, colpus not granular, pore margin not distinct, 4-colporate pollen common ················*Pemphis*

PALYNOLOGICAL COMMENTS ON TAXONOMY

The comparison of Koehne's classification of the Lythraceae with the number of pseudocolpi (Tab. 2) demonstrates that not only are the two tribes mixed with all three kinds of pollen, but also many small groups (Series) do not have the same type of pollen. The palynological results do not support Koehne's division of the family.

Taxonomic confusion between *Ammania* and *Rotala* (Rajagopal and Ramayya, 1969; Hara, 1977) is obviously resolved by pollen as well as by floral morphology (Koehne, 1885). *Ammannia* has prominent 6-pseudocolpate pollen, while *Rotala* never has 6-pseudocolpi, but rarely exhibits slight invaginations where 6-pseudocolpi would exist.

A taxonomic problem has been brought about in distinguishing *Nesaea* from *Ammannia* (Koehne, 1903). The close relationships between *Nesaea* and *Ammannia* are supported on the basis of pollen morphology, that is, the pollen of both genera have 6 distinct pseudocolpi. Differences between the two pollen types are slight, but some *Ammannia* pollen show distinctions, such as psilate or a faintly striate sculpture pattern, compared to the scabrate or rugulate condition in *Nesaea*.

Pollen morphology well resolves the confusion between *Nesaea* and *Heimia* (Cory, 1936). *Nesaea* shows a great difference from *Heimia*, that is, *Heimia* pollen never has the pseudocolpi which are prominent in *Nesaea*. The preceding result strongly support Graham's (1977) position on the distinctiveness of the two genera and the placement of *N. longipes*.

Although their pollen morphology also reveals close relationships between *Lythrum* and *Peplis* (Webb, 1967) by posession of distinct 3-pseudocolpi, even a most confusing species, *P. portula*, shows obvious differences from all species of *Lythrum*. The pollen of *P. portula* is oblate-spheroidal, its true colpi narrower and longer than pseudocolpi, and the surface psilate, while that of *Lythrum* is prolate to oblate-spheroidal, true colpi broader and longer than pseudocolpi, and the surface faintly rugulate to striate. Pollen data are not supportive of Webb's (1967) treatment based on the floral morphology.

Didiplis diandra has pollen which is quite distinct from that of all other genera in the family. Pollen grains show the smallest size, intersemiangular polar shape, triporate aperture, and psilate surface. Pollen morphology supports the position that the North American *Didiplis diandra* is distinct from *Peplis* with which *Didiplis* was combined (Koehne, 1903), and should be referred to the

Table 2. Koehne's classification associated with the number of pseudocolpi (in parenthesis)

Tribe Lythreae
- Subtribe 1. Lythrinae
  - Series I. *Rotala* (6), *Ammannia* (6), *Peplis* (3), *Lythrum* (3), *Woodfordia* (0), *Didiplis**(0)
  - Series II. *Cuphea* (0), *Pleurophora* (6)
- Subtribe 2. Diplusodontinae
  - Series I. *Galpinia* (0), *Pemphis* (3), *Diplusodon*(0), *Alzatea**(0)
  - Series II. *Physocalymma* (3), *Lafoensia* (0)

Tribe Nesaeeae
- Subtribe 1. Nesaeinae
  - Series I. *Crenea*(6)
  - Series II. *Nesaea* (6), *Capuronia**(0), *Heimia* (0), *Decodon* (0), *Grislea*(0), *Adenaria* (0)
  - Series III. *Tetrataxis* (?), *Ginoria* (6), *Haitia**(6)
- Subtribe 2. Lagerstroeminae
  - *Lagerstroemia* (6), *Lawsonia* (6), *Rhynchocalyx**(3)

* indicates genus included in the family after Koehne's work. Placement of the new genera follows the original authors' suggestions.

resurrected genus *Didiplis*, as suggested by Webb (1967), Graham (1975) and Wofford *et al* (1977). The suggestion that there is no delimitation between the two by De Vos (1971) is not supportive.

The new genus *Alzatea* was placed after *Diplusodon* and its pollen was described to be close to that of *Physocalymma* (Lourteig, 1965). The present study does not give the same result: *Alzatea* has non-pseudocolpate pollen with reticulate surface (Lourteig, 1965), whereas *Physocalymma* has 3-pseudocolpate pollen with scabrate surface. If her description of *Alzatea* is correct, the present study reveals that the pollen resembles that of *Grislea* or *Adenaria*. The assignment of *Alzatea* close to *Diplusodon* is definitely opposed by their pollen size, sculpture pattern, state of pore and colpus, etc.

The results of pollen morphological studies are nonsupportive of the placement of *Rhynchocalyx* near *Lawsonia* (Sprague and Metcalfe, 1937), they have different numbers of pseudocolpi (3 vs. 6) and pore state (indistinct to faint vs. distinct).

The close affinty of *Capuronia* to *Nesaea* suggested by Lourteig (1960) is also contradictory to this result, i.e. *Capuronia* does not have 6 pseudocolpi which are prominent in *Nesaea*.

摘　要

26屬 62種의 부처꽃科의 花粉을 光學顯微鏡으로 觀察한 結果 本科의 花粉은 0, 3, 또는 6個의 假溝口(pseudocolpi)를 갖는 세 그룹으로 나누어 짐을 알 수 있었다. 本 硏究는 부처꽃科의 科以下의 分類가 修正되어야 함을 暗示하고 있다. 花粉에 의한 屬의 檢索表가 作成되었고 屬間의 分類學的 問題點이 本 結果와 比較 考察되었다.

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Figure Caption

Fig. 1. 1—3, *Adenaria floribunda* ×1150 : 1, polar view (PV); 2, 3, equatorial view (EV). 4, 5, *Capuronia madagascariensis* ×1150: 4, PV; 5, EV. 6—9, *Ammannia coccinea* ×1000: 6, 7, PV; 8, 9, EV. 10—12, *Didiplis diandra* ×1000: 10, PV; 11, 12, EV. 13—15, *Decodon verticillatus* ×1000: 14, PV; 13, 15, EV. 16—18, *Diplusodon macrodon* ×750: 16, PV; 17, 18, EV.

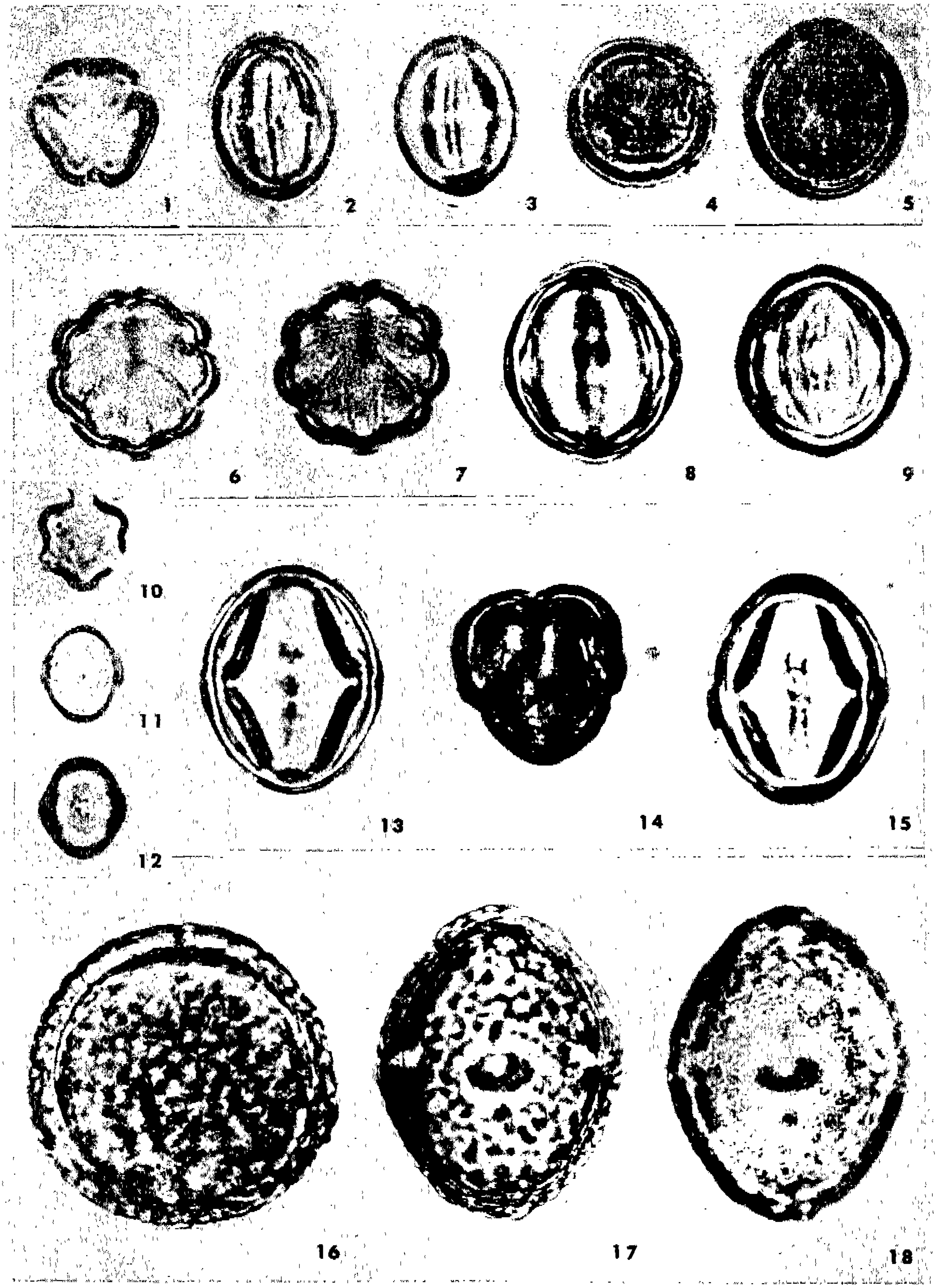
Fig. 2. 19—21, *Crenea surinamensis* ×1000: 19, PV; 20, 21, EV. 22, 25, *Cuphea vesticuligera* ×1150: 22, PV; 25, EV. 23, 26, 27, *C. cordata* ×1150: 23, PV; 26, 27, EV. 24, *C. utricularia* ×1150, PV. 28, *C. melvilla* ×1150, PV. 29, 33, *C. persistens* ×1150: 29, PV; 33, EV. 30, *C. aperta* ×1000, PV. 31, 32, *C. bombanaceae*: 31, PV; 32, EV. 34, *C. confertiflora* ×1000, PV. 35—37, *Galpinia transvaalica* ×1000. 35, PV; 36, 37, EV.

Fig. 3. 38—40, *Ginoria americana* ×1150: 38, PV; 39, 40, EV. 41, 45, *Grislea secunda* ×1150: 41, PV; 45, EV. 42—44, *Haitia pulchra* ×1150: 42, 43, PV; 44, EV. 46—49, *Heimia salicifolia* ×850: 46, 47, PV; 48, 49, EV. 50—52, *Lagerstroemia flos-reginae* ×1150: 50, PV; 51, 52, EV. 53, 57, 58, *Lythrum salicaria* ×1150: 53, 57, PV; 58, EV. 54—56, *Lafoensia pacari* ×750: 54, PV; 55, 56, EV.

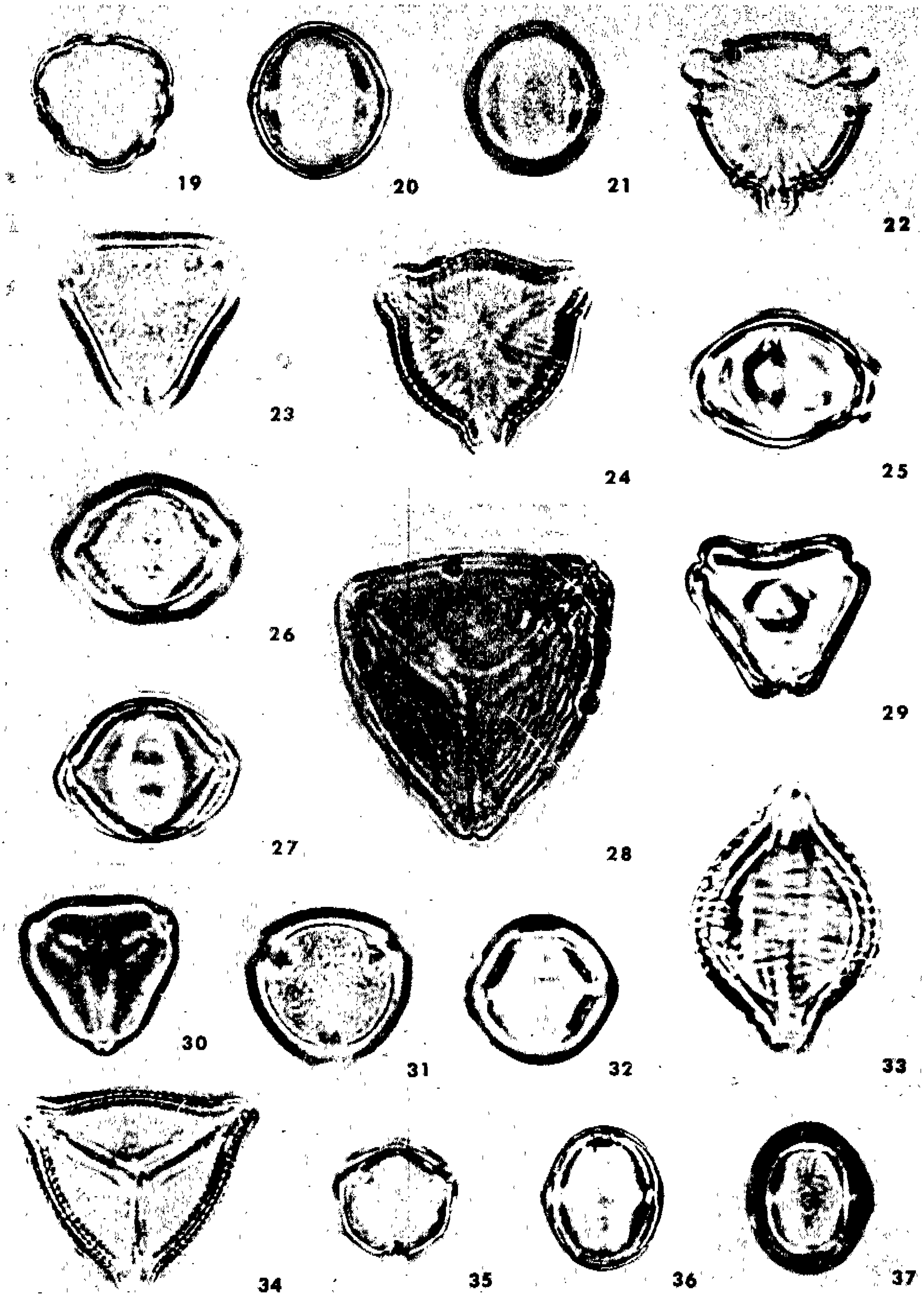
Fig. 4. 59, 63, 67, *Lawsonia inermis* ×1000: 59, PV; 63, 67, EV. 60, 64, 68, *Nesaea lythroides* ×1150: 60, 64, PV; 68, EV. 61, 65, 69, *Pemphis madagascariensis* ×1150: 61, PV; 65, 69, EV. 62, 66, 70, *Peplis portula* ×1150: 62, PV; 66, 70, EV. 71—73, *Physocalymma scaberrimum* ×1000: 71, PV; 72, 73, EV. 74, 78, 79, *Rhynchocalyx lawsonioides* ×1720: 74, PV; 78, 79, EV. 75—77, *Pleurophora polyandra* ×1150: 75, PV; 76, 77, EV. 80—82, *Rotala rotundifolia*: 80, ×1200, PV; 81, 82, ×1000, EV. 83—85, *Woodfordia floribunda* ×1000: 83, PV, 84, 85, EV.

Fig. 5. Pollen phylogeny of the Lythraceae. Pollen size relatively depicted. Evolutionary trends indicated by numbers and dotted lines: A……A, distinct pore; B……B, large grain size and granular surface; 1, six incipient pseudocolpi; 2, elongation of pseudocolpi; 3, three incipient pseudocolpi; 4, increase in pseudocolpus breath: 5,

elongate pseudocolpi and small grain size; 6, loss of colpi and small grain size; 7, parallel-striate surface and anastomosis of colpus tips; 8, development of two polar pores and loss of equatorial pores; 9, pore protrusion; 10, areolate surface and thick exine.



(Figure 1)



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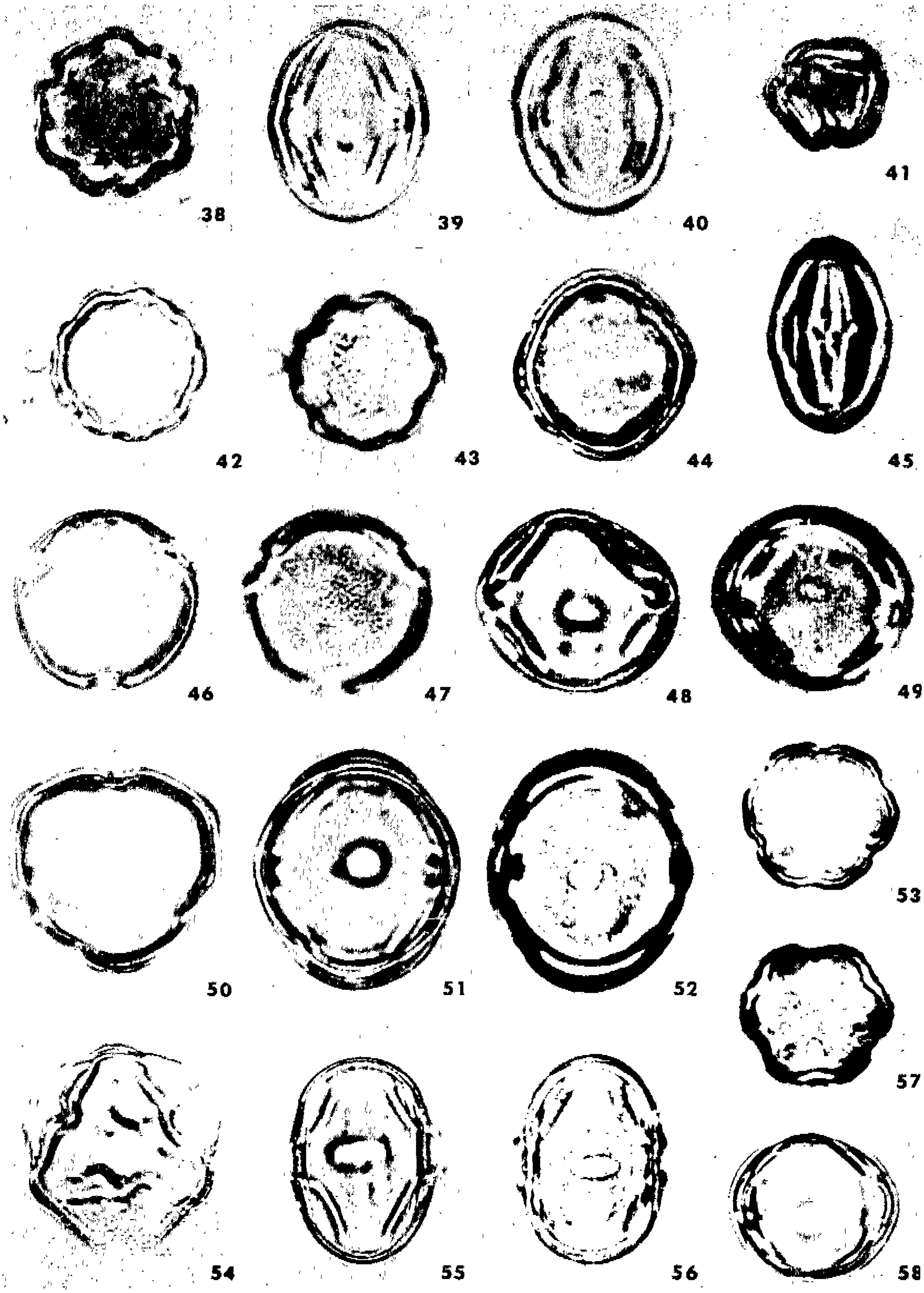

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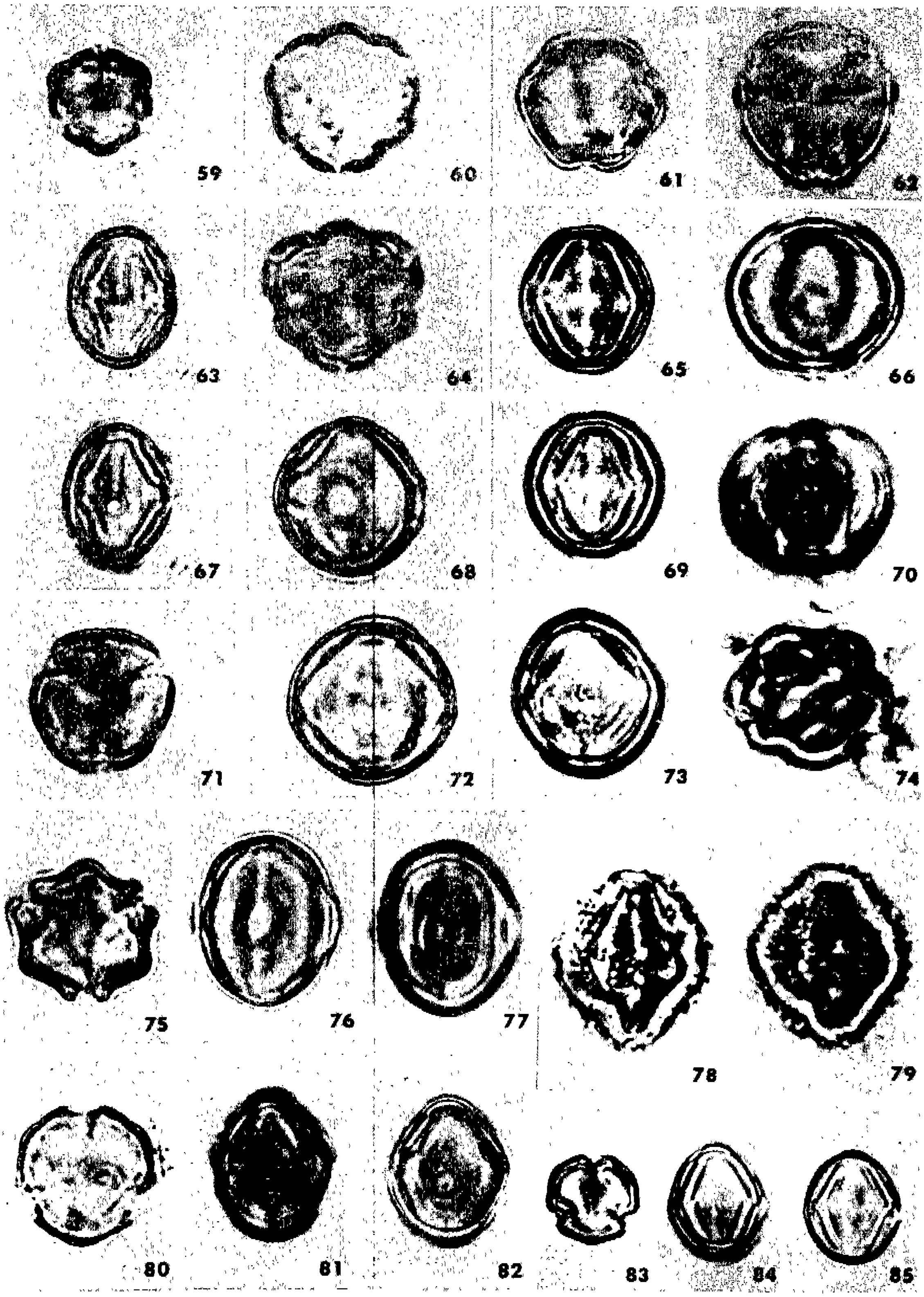
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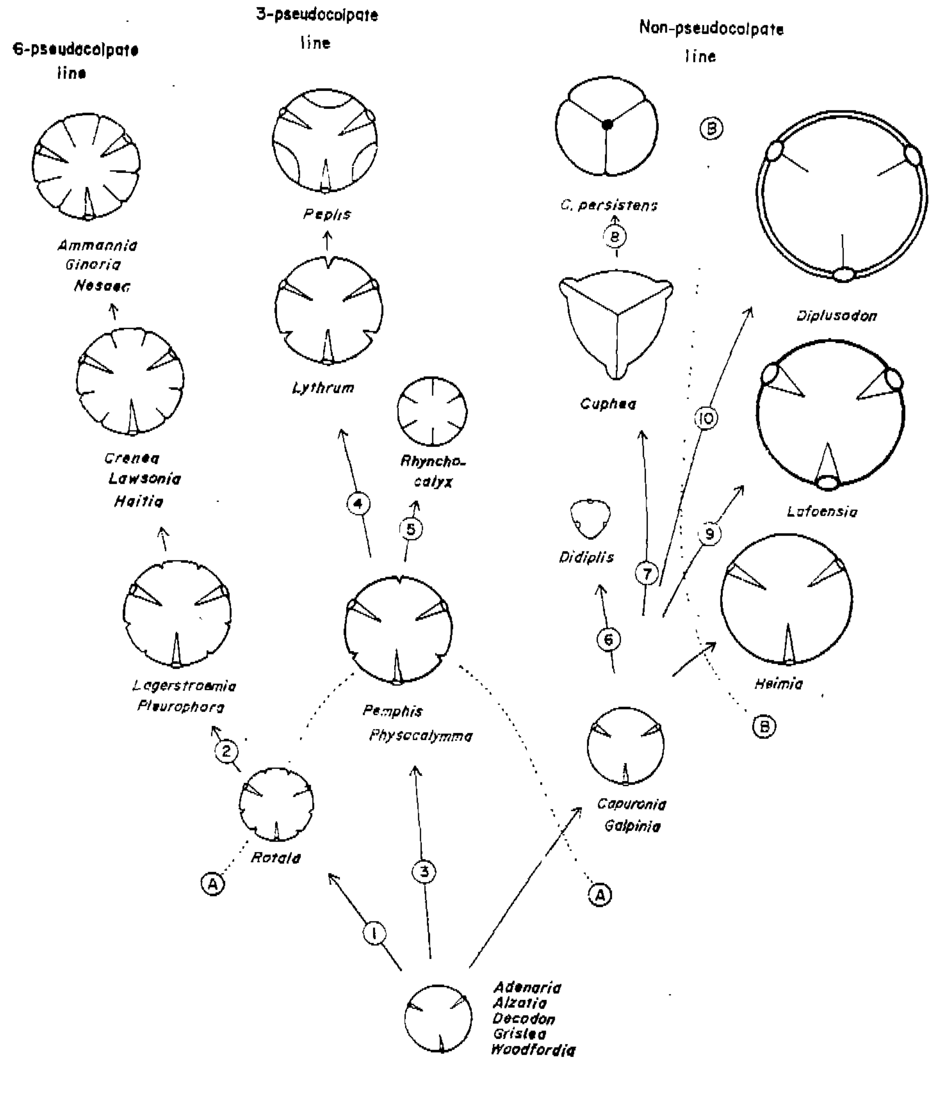
(Figure 4)



6-pseudocolpate line
3-pseudocolpate line
Non-pseudocolpate line
Ammannia
Ginoria
Nesaea
Peplis
C. persistens
Diplusodon
Lythrum
Cuphea
Crenea
Lawsonia
Haitia
Rhyncho-calyx
Lafoensia
Didiplis
Heimia
Lagerstroemia
Pleurophora
Pemphis
Physocalymma
Capuronia
Galpinia
Rotala
Adenaria
Alzatia
Decodon
Grislea
Woodfordia

(Figure 5)