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THE POLLEN MORPHOLOGY AND TAXONOMY OF LYSIMACHIA

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ABSTRACT. The pollen morphology of 98 species and varieties of *Lysimachia* (Primulaceae) has been investigated by light microscope, SEM and TEM. Ten major pollen-types and four sub-types are recognized on the basis of exine sculpture and stratification and overall shape and size of the grain. These pollen-types are examined in relation to the subgeneric classification of *Lysimachia* and are found to correspond closely to the major taxonomic groups, and to reinforce recent modifications in the classification. Pollen morphology is also shown to give valuable new insights into phylogeny within the genus.

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INTRODUCTION

The genus *Lysimachia* comprises some 180 species of perennial and annual herbs and is one of the largest in the Primulaceae. Although the

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centre of diversity of the genus occurs in South West China, its distribution extends throughout the temperate regions of the northern hemisphere and into the south east Asian tropics, with outlying members in South America, Africa and Australasia, so that it is represented in most of the principal land-masses of the globe.

The foundation of the modern subgeneric classification of *Lysimachia* was laid by Handel-Mazzetti (1928) in the course of his revision of the Chinese species. Significantly his 'new system' was the first to give due emphasis to floral structure, with special reference to the androecium. More recently, following an intensive reappraisal of the 122 Chinese species, Chen & Hu (1979) have recommended a number of modifications to this classification. The taxonomy of the genus in America has been examined by Ray (1956), who recognized 21 species, and also summarised the history of classification throughout *Lysimachia*.

In so large and widespread a genus, subgeneric classification is of considerable importance. Indeed some subgeneric elements have frequently been elevated to generic rank. Thus, for example, Nowicke & Skvarla (1977) refer to *Naumburgia* (*Lysimachia*) *thyrsiflora*. The emphasis on androecial characters in the current taxonomic treatments may imply strong selective pressures operating on these structures, which could also be reflected in the pollen morphology. Huynh (1970, 1971) exploited this possibility in a survey of 91 species of *Lysimachia*, in which he recognized eight pollen-types, four of which corresponded to four distinct subgenera. However, this exemplary survey was based solely on light microscope observations, but many of the potentially important exine characters are beyond the limits of resolution of this instrument.

Nowicke & Skvarla (1977) used both SEM and TEM sections in their general survey of Primulaceous pollen, but they were only able to examine four representatives of *Lysimachia*. Apart from the account of Erdtman (1972; Primulaceae, 337), who considered three *Lysimachia* spp. in his seminal light microscopic survey of Angiosperm pollen, the only other descriptions of pollen in this genus are found in local pollen floras, notably that of Taiwan by Huang (1972) who considered seven species, and in the treatment of Primulaceae for the *North West European Pollen Flora* (Punt et al., 1974) where seven species are assessed.

The recent suggestions of Chen & Hu (1979) for changes in the subgeneric classification based on gross morphology stimulated this study of *Lysimachia* pollen as a means of appraising their revision.

The present comparative survey is based on a detailed study of the exine using both the scanning and transmission electron microscopes, together with an examination of general pollen morphology in the light microscope.

MATERIALS & METHODS

Pollen was obtained from specimens in the herbaria of the Royal Botanic Garden Edinburgh (E), RBG Kew (K) and the South China Institute of Botany, Canton (IBSC). A list of the species investigated, with the provenance of the material is given in table 1.

TABLE 1

List of specimens examined and their pollen-types
[Following the classification of Handel-Mazzetti (1928) as modified by Chen & Hu (1979)]

Species	Pollen-type	Provenance
subgen. Idiophyton		
sect. Idiophyton		
L. insignis Hemsl.	1A	China: Yunnan, *Chang* 1481 (IBSC)
″	″	China: Yunnan, *Wang* 89014 (IBSC)
″	″	China: Guizhou, *Esquirol* 2120 (K)
″	″	China: Guizhou, *Guizhou Exped.* 919 (IBSC)
″	″	China: Guangxi, *Wang* (IBSC)
″	″	China: Guangxi, *Lungzhow Exped.* (IBSC)
″	″	China: Guangxi, *Da-Xian* (IBSC)
″	″	China: Guangxi, *Fang* (IBSC)
″	″	China: Guangxi, *Tien-E Exped.* (IBSC)
″	″	China: Guangxi, *Huang* (IBSC)
″	″	China: Guangxi, *Dong-Lan Exped.* (IBSC)
″	″	China: Guangxi, *De-Bao Exped.* (IBSC)
sect. Apodanthera		
ser. Evalves		
L. capillepis Hemsl.	1A	China: Hubei, *Chien* 6023 (E)
L. evalves Wall.	1A	Nepal: Arum Valley, *Stainton* 712 (E)
L. garrettii Fletcher	1A	Thailand: Doi Angka, *Garrett* 403 (E)
L. heterobotrys Chen & Hu	1A	China: Guangxi, *Chang & Wang* 4078 (IBSC)
L. microcarpa C. Y. Wu	1A	China: Yunnan, *Forrest* 18863 (E)
L. millietii Hand.-Mazz.	1A	China: Guizhou, *Cavalerie* 7757 (E)
L. naveillei Hand.-Mazz.	1A	China: Guizhou, *Esquirol* 722 (E)
L. saxicola Chen & Hu	1A	China: Guangxi, *Wang* 4098 (IBSC)
ser. Valvatae		
L. brachyandra Chen & Hu	1B	China: Guizhou, *Chang & Chang* 6107 (IBSC)
L. foenum-graecum Hance	1B	China: Yunnan, *Henry* 10643 (E)
L. interjacens Hu & Bennell	1B	Laos: Pu Bia, *Kerr* 21026! (K)
L. laxa Baudo	5	China: Yunnan, *Forrest* 12036 (E)
L. montana Bakh. f.	5	Java. *Lobb* 66 (E)
L. physaloides Wu & Chen	1B	China: Yunnan, *Yunnan Exped.* 926 (IBSC)
L. trichopoda Fr.	1B	China: Yunnan, *Hu* 1345 (IBSC)
L. wilsonii Hemsl.	1B	China: Sichuan, *Fang* 16770 (IBSC)
sect. Oppositifoliae		
L. cordifolia Hand.-Mazz.	5	China: Yunnan, *Yü* 16347 (E)
L. engleri Knuth	5	China: Yunnan, *Henry* 13025 (E)
subgen. Lysimachia		
sect. Lerouxia		
L. nemorum L.	8B	Spain: Santander, *Gibbs* 772 (E)
L. serpyllifolia Schreb.	8B	Greece: Crete, *Davis* 158 (E)
sect. Seleucia		
subsect. Steironema		
L. ciliata L.	6	USA: Bozeman, *Blankinship* 345 (E)
L. lanceolata Waeter	6	USA: Washington D.C., *Kearny* 1049 (E)

TABLE 1 (*contd*)

Species	Pollen-type	Provenance
L. quadriflora Sims	6	USA: Indiana, *Dean* 1319 (E)
L. tonsa Knuth	6	USA: Applachian region, *Ruth* 25 vii 1900 (E)
subsect. Verticillata		
L. quadrifolia L.	8A	USA: Carolina, *Bouford & Wood* 16074 (E)
L. terrestris BSP.	8A	USA: Minnesota, *Sheldon,* vii 1892 (E)
sect. Theopyxis		
L. sertulata Baudo	8A	Chile: Valdivia, *Buchtien* 6 i 1902 (E)
sect. Lysimachia		
L. davurica Ledeb.	8A	China: Yunnan, *Forrest* 22071 (E)
L. fraseri Duby	8A	USA: N. Carolina, *Biltmore* 6573 (E)
L. vulgaris L.	8A	Yugoslavia: N-E Ukinj, *Holliday* 325/77 (E)
sect. Nummularia		
L. alfredii Hance	7A	China: Hunan, *Wang* 325 (E)
L. christinae Hance	7A	China: Yunnan, *Rock* 6242 (E)
L. congestiflora Hemsl.	7A	China: Hunan, *Handel-Mazzetti* 12011 (E)
L. deltoidea Wight	7A	India: Madras, *Blegh* in 1855 (E)
L. deltoidea var. *cinerascens* Fr.	7B	China: Yunnan, *Rock* 2265 (E)
L. drymarifolia Fr.	7A	China: Yunnan, *Rock* 5044 (E)
L. eriosipetala Chen & Hu	7A	China: Sichuan, *Tu* 500 (IBSC)
L. esquirolii Bonati	7A	China: Guizhou, *Chang & Chang* 1363 (IBSC)
L. fordiana Oliv.	7A	China: Guangdong, *Kao* 80662 (IBSC)
L. franchetii Knuth	7A	China: Yunnan, *Forrest* 16680 (E)
L. fukienensis Hand.-Mazz.	7A	China: Jiangxi, *Wang* 328 (E)
L. grammica Hance	7B	China: Jiangsu, *Carles* 438 (E)
L. huitsunae Chien	3	China: Zhejiang, *Zheng* 8484 (IBSC)
L. hypericoides Hemsl.	7B	China: Sichuan, *Chang* 25266 (IBSC)
L. japonica Thunb.	7A	Japan: Hondo, *Okamoto* 1313 (E)
L. klattiana Hance	7A	China: Jiangsu, *Chiao* 2511 (E)
L. liui Chien	7A	China: *Fang* s.n. (IBSC)
L. longipes Hemsl.	7A	China: Zhejiang, *Ching* 1554 (E)
L. melampyroides Knuth	7A	China: Hunan, *Handel-Mazzetti* 12013 (E)
L. melampyroides var. *brunelloides* Chen & Hu	7B	China: Sichuan, *Wilson* 3789 (E)
L. nanchuanensis C. Y. Wu	7A	China: Sichuan, *Hsiung & Chow* 91923 (IBSC)
L. nummularia L.	7A	Sweden: Ostergötland, *Smith* 578 (E)
″	″	Czechoslovakia: Moravia, *Habetova* 29 iv 1969 (E)
L. omeiensis Hemsl.	3	China: Sichuan, *Fang* 2843 (E)
″	″	China: Yunnan, *Tsai* 52300 (E)
″	″	China: Yunnan, *Tsai* 52270 (E)
L. ophelioides Hemsl.	7B	China: Sichuan, *Lin* 1318 (IBSC)
L. paridiformis Fr.	7A	China: Hubei, *Wilson* 870 (E)
L. patungensis Hand.-Mazz.	7A	China: Guangdong, *Teng* 6216 (IBSC)
L. phyllocephala Hand.-Mazz.	7A	China: Yunnan, *Maire* 25/1913 (E)
L. pterantha Hemsl.	7A	China: Sichuan, *Yang* 58221 (IBSC)
L. punctata L.	7A	Greece: Pendalopon, *Mennega & Driehuis* s.n. (E)

TABLE 1 (*contd*)

Species	Pollen-type	Provenance
L. rubiginosa Hemsl.	7A	China: Hubei, *Wilson* 1559 (E)
L. sciadophylla Chen & Hu	7A	China: Hunan, *Lee* 342 (IBSC)
L. yingdeensis Chen & Hu	7A	China: Guangdong, *Tsang* 25205 (IBSC)
sect. Alternifoliae		
L. albescens Fr.	2	China: Yunnan, *Simon Ten* 298 (E)
L. alternifolia Wall.	5	Nepal: Maghang Khola, *Stainton* 822 (E)
L. fletcheri Hu & Bennell	9	Burma: Maymyo, *English* 131 (E)
"	"	Burma: Maymyo, *Lace* 5263 Holotype! (E)
L. peduncularis [Wall. ex] Kurz	1A	Burma: Maymyo, *Lace* 4339 (E)
sect. Rosulatae		
L. alpestris [Champ. ex] Benth.	1A	Hongkong: *Bodinier* 111 (E)
subgen. Palladia		
sect. Lubinia		
L. mauritiana Lam.	4B	China: Zhejiang, *Ching* 1927 (E)
sect. Spicatae		
L. barystachys Bunge	4A	China: Hubei, Schinder 163 (E)
L. clethroides Duby	4A	China: Sichuan, *Yü* 3235 (E)
L. fortunei Maxim.	4A	China: Zhejiang, *Ching* 1911 (E)
sect. Apochoris		
L. pentapetala Bunge	9	China: Shangdong, *Schinder* 537 (E)
sect. Chenopodiopsis		
L. chenopodioides Hook. f.	9	China: Yunnan, *Maire* 482/1913 (E)
L. reflexiloba Hand.-Mazz.	9	China: Sichuan, *Handel-Mazzetti* 7572 (E)
sect. Miltandrae		
L. auriculata Hemsl.	4A	China: Hubei, *Wilson* 781 (E)
L. circaeoides Hemsl.	4A	China: Hunan, *Handel-Mazzetti* 11927 (E)
L. heterogenea Klatt	4A	China: Zhejiang, *Ching,* 2107 (E)
L. stenosepala Hemsl.	4A	China: Hubei, *Wilson* 1217 (E)
sect. Ephemerum		
L. ephemerum L.	9	Spain: Del'andalousie, *Reverchon* 4 vii 1890 (E)
sect. Palladia		
L. atropurpurea L.	9	Bulgaria: *Ivanova* 1049 (E)
L. decurrens Forst. f	9	China: Guangdong, *Dalziel* s.n. (E)
L. likiangensis Forrest	9	China: Yunnan, *Rock* 4725 (E)
L. lobelioides Wall.	9	China: Yunnan, *Tsai* 53298 (E)
L. nutans Nees	9	S. Africa: E Cape, *Hilliard & Burtt* 10908 (E)
L. orbicularis Chen & Hu	9	China: Sichuan, *S-W Normol. Univ.* 12020 (IBSC)
L. platypetala Fr.	9	China: Yunnan, *Soulié* 1321 (E)
L. robusta Hand.-Mazz.	9	China: Yunnan, *Howell* 49 (E)
L. silvestrii Hand.-Mazz.	9	China: Kansu, *Hsia* 5363 (IBSC)
L. taliensis Bonati	9	China: Yunnan, *Forrest* 7126 (E)
L. violascens Fr.	9	China: Yunnan, *Forrest* 6133 (E)
sect. Candidae		
L. candida Lindl.	9	China: Jiangsu, *Steward* 1988 (E)
L. parvifolia Fr.	9	China: Yunnan, *Maire* 839 (E)
sect. Pumilae		
L. prolifera Klatt	9	China: Yunnan, *Forrest* 21639 (E)
L. pumila Fr.	9	China: Yunnan, *Forrest* 10005 (E)

TABLE 1 (*contd*)

Species	Pollen-type	Provenance
subgen. Heterostylandra		
L. crispidens Hemsl. (long style)	9	China: Sichuan, *Wang* 10273 (IBSC)
L. crispidens Hemsl. (short style)		China: Hubei, *Wilson* 9 (E)
subgen. Naumburgia		
L. thyrsiflora L.	8A	Sweden: Furskar, *Alm* 792 (E)
subgen. Sandwicensia		
L. hillebrandii [Hook. f. ex] A. Gray		
var. *helleri* Knuth	10	Hawaii: Kaui island, *Heller* 2614 (E)

For light microscopy anthers were dissected from flowers and acetolysed according to the method of Erdtman (1960), and the pollen mounted, unstained, in glycerine jelly. Observations were made using a Leitz Ortholux microscope. Measurements were based on 20 grains from each specimen and serve only as a rough indication of the size range of each species (including exine ornamentation). For scanning electron microscopy acetolysed pollen was rinsed in acetone and dried down on to glass cover slips attached to aluminium stubs (S. Blackmore, pers. comm.). Following sputter-coating with gold, restricted to 150A° to minimise artefacts (Leuenberger & Schill, 1975), the pollen was examined in an ageing Jeol JSM-2 SEM. For transmission electron microscopy pollen was suspended in 2% water agar, to facilitate handling, and fixed in 3% acrolein buffered in 0.05% sodium cacodylate for 2–12 hours at 4°C. Acrolein was found to achieve much better penetration of herbarium-dried grains than glutaraldehyde. Following postfixation in 1% buffered osmium tetroxide for 2 hours at 4°C, and dehydration in an ethanol series, the pollen was embedded in Spurr's low viscosity resin. Sections were cut on a Reichert OMU2 ultramicrotome and poststained in lead citrate and uranyl acetate, prior to examination with an AE1 EM6M TEM.

The viability of the pollen in certain collections was assessed by examining a sample of the grains, mounted in a drop of Alexander's stain (Alexander, 1969), with the light microscope.

Terminology for gross pollen morphology follows Erdtman (1972), and for detailed exine structure is modified after Hideux & Ferguson (1976).

GENERAL POLLEN MORPHOLOGY

General Morphology. The general form of pollen grains in *Lysimachia* is constant for almost all species. The grains are isopolar, tricolporate, small (smallest 13 × 9.5 μm in *L. capillepis*) to medium (largest 39 × 35 μm in *L. franchetii*). One small group of isolated species is exclusively tetracolporate (Fig. 84, 85), but grains with more than three colpi are occasionally found in other species (Fig. 9, 10, 58). The shape of the tricolporate grains ranges from prolate-spheroidal to prolate (P/E ratios 1.03–1.69), and the equatorial outline (amb) varies from triangular (e.g. Fig. 52) to circular (e.g. Fig. 42), circular-lobate (e.g. Fig. 74), and lobate-triangular (e.g. Fig. 8).

The ectoapertures (colpi) are long with tapering ends. Most grains are apocolporate, but these colpi occasionally meet at the poles (syncolporate) (e.g. Fig. 42), and are sometimes almost bridged or constricted at the equator by extensions of the mesocolpium (e.g. Fig. 13). The endoapertures (3) which occur at the equator beneath the ectoapertures, are mostly lalongate and vary from simple, short, dumbell-shaped (e.g. Fig. 24), to equatorially extended with diffuse or tapering ends. Sometimes these extensions turn longitudinally towards the poles, giving a characteristic H-shaped configuration (e.g. Fig. 25). In a number of species the endoapertures may meet laterally, producing a continuous equatorial band (zonorate) (e.g. Fig. 4, 69). Exceptional, small, circular, and somewhat indistinct endoapertures, barely extending beyond the colpus (colporoidate), are found in a limited group of species (Fig. 51).

Exine. The exine is ectexinous–endexinous, conforming to Type II as defined by Walker (1974). The endexine is homogeneous, non-lamellate, but of variable thickness. It is virtually absent from the region of the endoaperture (Fig. 48, 103), but usually greatly thickened adjacent to it, a condition clearly visible with the light microscope (e.g. Fig. 90). In the mesocolpium its thickness varies from 0.1 μm in *L. congestiflora* (Fig. 63) to nearly 0.5 μm in *L. ciliata* (Fig. 54).

The ectexine is generally three-layered, with a clearly differentiated foot layer. The middle columellar layer or interstitium (Walker & Walker, 1981), varies from well-developed columellae up to 0.4 μm in height in *L. congestiflora* (Fig. 63), to the almost negligible granular disjuncture above the foot layer detected in *L. capillepis* (Fig. 16). The overlaying tectum is imperforate in some species, in which the outer surface sculpturing ranges from smooth (psilate) to irregularly roughened (rugulate) (Fig. 11 cf. Fig. 12). The rest of the genus is characterised by possessing a tectum with varying degrees of perforation, from sparse scattered puncta (Fig. 34), to densely pitted (Fig. 46), to a true partial reticulum in which the lumina range from < 0.5 μm to > 3 μm (Fig. 60 cf. Fig. 94). It was found necessary to distinguish between the regular, densely-spaced puncta (sensu Praglowski & Punt, 1973) which constitute a true perforate tectum (e.g. Fig. 48, 50), and the sparse, irregular puncta, for which we propose the term 'subperforate' (e.g. Fig. 34, 38). The muri of the partial reticular grains are all simplicolumellate. Adjacent to the colpi the ectexine sometimes tapers away (Fig. 38) or the cleft of the endoaperture may be exaggerated by thickening of the foot layer (Fig. 15).

It is largely these characters of the ectexine, as revealed by combined use of the SEM and TEM in relation to the light microscope, which form the basis of our classification of pollen-types in *Lysimachia*. Distinction was made principally on tectum form, and the sculptural pattern it embodies, with subdivision according to size and shape of the grain, where these were clearly discrete.

POLLEN-TYPES

KEY TO POLLEN-TYPES

1a. Pollen grains tricolporate 2
1b. Pollen grains tetracolporate .... **(10) Hillebrandii-type**
2a. Tectum imperforate or subperforate.......... 3
2b. Tectum perforate or partial 8
3a. Tectum imperforate 4
3b. Tectum subperforate.......... 6
4a. Exine thin (< 1 μm), lacking columellar interstitium, pollen grains small 5
4b. Exine thicker (> 1 μm), with well-developed columellar interstitium, pollen grains medium .... **(2) Albescens-type**
5a. Pollen grains prolate to subprolate (P/E> 1.14) .. **(1A) Capillepis-type**
5b. Pollen grains prolate-spheroidal (P/E< 1.14)...... **(1B) Wilsonii-type**
6a. Tectum ornamented, rugulate–reticulate .... **(3) Omeiensis-type**
6b. Tectum smooth, with scattered puncta.......... 7
7a. Pollen grains prolate (P/E> 1.33) .... **(4A) Stenosepala-type**
7b. Pollen grains subprolate (P/E< 1.33).......... **(4B) Mauritiana-type**
8a. Tectum perforate (muri ⩾ lumina) 9
8b. Tectum partial (lumina< muri), reticulate 10
9a. Amb circular, endoaperture lalongate, distinct .... **(5) Laxa-type**
9b. Amb triangular, endoaperture circular, indistinct..... **(6) Ciliata-type**
10a. Pollen grains subprolate to prolate-spheroidal (P/E< 1.33) 11
10b. Pollen grains prolate (P/E> 1.33) .... **(9) Taliensis-type**
11a. Pollen grains medium-sized (> 24–28 × 23–26 μm) 12
11b. Pollen grains small-sized (19–26 × 16–22 μm).......... 13
12a. Tectum coarsely reticulate (lumina > 1.5 μm) . **(7A) Congestiflora-type**
12b. Tectum finely reticulate (lumina < 1 μm) ..... **(7B) Hypericoides-type**
13a. Tectum coarsely reticulate (lumina > 1.5 μm) ...... **(8A) Fraseri-type**
13b. Tectum finely reticulate (lumina < 1 μm) ...... **(8B) Serpyllifolia-type**

FIG. 1–17. Pollen-types 1A & 1B. **1.** *L. capillepis*, meridional view, LM. **2, 3,** *L. naveillei*: 2, meridional view with simple endoaperture, LM; 3, polar view, circular amb, LM. **4,** *L. alpestris,* meridional view, grain zonorate with endoaperture forming complete equatorial band, LM. **5, 6,** *L. foenum-graecum*: 5, meridional view, LM; 6, polar view, LM. **7–10,** *L. insignis*: 7, meridional view of normal grain (*Wang* 89014), LM; 8, polar view of normal tricolporate grain (*Wang* 89014), LM; 9, polar view of abnormal tetracolporate grain (*Guizhou Exped.* 919), LM; 10, polar view of abnormal 9-pantocolporate grain (*Esquirol* 2120), LM. **11,** *L. heterobotrys,* meridional view, ± smooth, complete tectum, SEM × c. 3,000. **12,** *L. saxicola,* meridional view, irregularly rugulose, complete tectum, SEM × c. 2,600. **13,** *L. brachyandra,* meridional view, finely rugulose, complete tectum, SEM × c. 2,400. **14,** *L. wilsonii,* meridional view, coarsely rugulose, complete tectum, SEM × c. 3,000. **15, 16,** *L. capillepis*: 15, TS grain showing ectoapertures, TEM × c. 6,000; 16, sporoderm section showing smooth, complete tectum and lack of a developed columellar interstitium, TEM × c. 40,000. **17,** *L. saxicola,* sporoderm section with irregularly rugulose, complete tectum, TEM × c. 40,000.

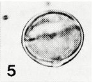
All light micrographs × 1,000. TEM micrograph abbreviations: C = interstitium; Eca = ectoaperture; E = endexine; Ena = endoaperture; F = foot layer; I = intine; T = tectum.


1


2


3


4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8


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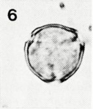
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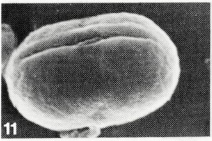
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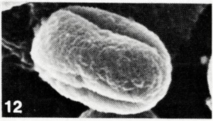
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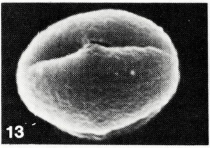
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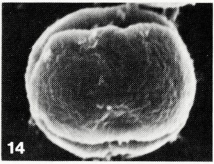
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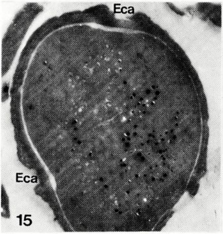

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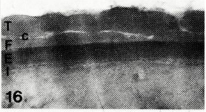

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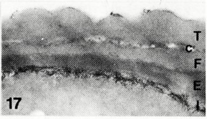

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ACCOUNT OF POLLEN-TYPES

1A: Capillepis-type (Fig. 1–4, 7–12, 15–17).

Pollen tricolporate, small, prolate to subprolate (P/E: 1.2–1.5) with broadly rounded poles, and circular amb (*L. naveillei,* Fig. 1–3), although the amb of *L. insignis* tends to be lobate-triangular (Fig. 8). Ectoapertures long, tapering, sometimes syncolporate. Endoapertures lalongate, showing continuous variation from short dumbell-shaped (*L. naveillei,* Fig. 2) through extended with tapering ends almost meeting (*L. millietii*), to a complete equatorial band (*L. alpestris*, Fig. 4; *L. heterobotrys*). Exine thin (< 1 μm) with a well-developed endexine. Ectexine lacking a columellar layer, there being only a minor granular interstitium between the foot layer and somewhat thicker, imperforate, tectum (Fig. 16, 17). The tectal surface varies from virtually smooth (*L. capillepis,* Fig. 16; *L. heterobotrys,* Fig. 11), to somewhat rugulose (*L. saxicola;* Fig. 12, 17). This sculpturing of the exine is sometimes discernible as a granular OL-pattern in the light microscope.

Eleven species:—

L. alpestris (16–18 × 11–13.5 μm)
L. capillepis (13–14 × 9.5–10.5 μm)
L. evalves (15–18 × 13–14 μm)
L. garrettii (14.5–16 × 12–14 μm)
L. heterobotrys (15–16 × 10–11 μm)
L. insignis (13.5–15 × 10–11.5 μm)
L. microcarpa (14–16 × 11.5–13.5 μm)
L. millietii (13–15 × 9–10.5 μm)
L. naveillei (16–16.5 × 12–13.5 μm)
L. peduncularis (16–18 × 11–14 μm)
L. saxicola (14–16 × 10–12.5 μm)

Note: a number of collections of *L. insignis* exhibited abnormal pollen characters (4–9 colpi and increased size (Fig. 7–10)). The significance of these is considered in the discussion.

1B: Wilsonii-type (Fig. 5, 6, 13–14).

This pollen-type differs from 1A only in the grains being more rounded, i.e. prolate-spheroidal (P/E 1.06–1.12) (Fig. 5, 6). The exine is thin, lacking a columellar interstitium and the tectum sculpturing is weakly rugulate, ranging from fine wrinkles in *L. brachyandra* (Fig. 13) to somewhat coarser in *L. wilsonii* (Fig. 14).

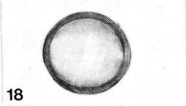
Six species:

L. brachyandra (16–17 × 14–15 μm)
L. foenum-graecum (15–16 × 13–15 μm)
**L. interjacens* (17–18 × 15–17 μm)
L. physaloides (14–15 × 13–13.5 μm)
L. trichopoda (17–20 × 15–16 μm)
L. wilsonii (14.5–16 × 12.5–14.5 μm)

* *Note*: *L. interjacens* is a new species discovered in the course of this study (Hu & Bennell, 1983).

FIG. 18–29. Pollen-types 2 & 3. **18–21,** *L. albescens*: 18, meridional view, LM; 19, polar view, circular amb, LM; 20, detail of exine sculpturing, showing fine rugulosity of complete tectum, SEM × c. 7,500; 21, sporoderm stratification with well-developed columellar interstitium, TEM × c. 15,000. **22–29,** *L. omeiensis*: 22, meridional view of normal grain (*Fang* 2843), LM; 23, polar view of normal grain (*Fang* 2843), LM; 24, meridional view of normal (short) grain (*Fang* 2843) with simple endoaperture, LM; 25, meridional views of abnormal (medium) grains (*Tsai* 52270), LM: a, with H-shaped endoaperture, b, with arms of endoaperture just meeting; 26, meridional views of abnormal (large) grains (*Tsai* 52300), LM: a, with simple broad lalongate endoaperature, b, zonorate grain with endoapertures linked into complete equatorial band; 27, detail of exine sculpturing showing microreticulate tectum, SEM × c. 6,500; 28, sporoderm stratification, with contorted subperforate tectum over distinct columellar interstitium, TEM × c. 16,000; 29, sporoderm stratification at endoaperture, TEM × c. 5,000.

All light micrographs × 1,000. TEM micrograph abbreviations: C = interstitium; Eca = ectoaperture; E = endexine; Ena = endoaperture; F = foot layer; I = intine; T = tectum.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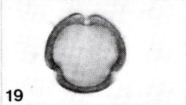
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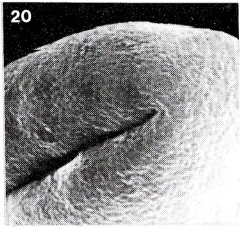
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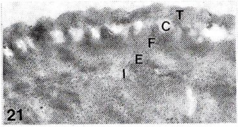
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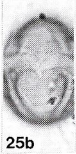
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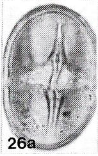
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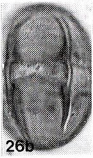
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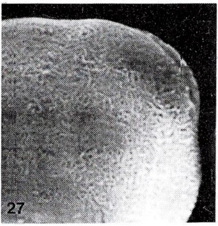
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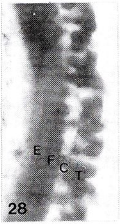
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2: Albescens-type (Fig. 18–21).

Pollen tricolporate, medium, prolate-spheroidal (P/E: 1.05–1.1) with circular amb. Ectoapertures long, tapering. Endoapertures lalongate, simple with diffuse ends. Exine up to 1.4 μm thick, with endexine thinner than conspicuous foot layer of ectexine (Fig. 21). There is a well-developed regular columellar interstitium surmounted by an imperforate tectum. The regular minute undulations of the tectum, where it overlays the intercolumellar spaces, contribute to the finely rugulate sculpturing of the grains in the SEM (Fig. 20). This distinctive morphology was only encountered in one species: *L. albescens* (20–23 × 19–22 μm)

3: Omeiensis-type (Fig. 22–29).

Pollen tricolporate, medium, subprolate to prolate-spheroidal (P/E: 1.1–1.2) with circular amb. Ectoapertures long and deep. Endoapertures variable, from simple, lalongate to complex, H-shaped, or as a continuous equatorial band in some grains. Exine 1.5 μm thick, with endexine thickness comparable to foot layer of ectexine. The latter features a distinct columellar interstitium, overlain by a complex rugulose-reticulate tectum, whose contorted profile is occasionally breached by perforations (Fig. 28, 29). The resulting sculpturing is revealed as a delicate microreticulum in the SEM (Fig. 27).

Two species:

L. huitsunae (28–31 × 25–26 μm)
L. omeiensis (23.5–26.5 × 20–22.5 μm)

Note: the pattern of variation in endoaperture character, with particular reference to *L. omeiensis,* is considered further in the discussion.

4A: Stenosepala-type (Fig. 30–34, 38, 39).

Pollen tricolporate, medium, prolate (P/E: 1.35–1.6) with circular amb. Ectoapertures long, tapering, occasionally syncolporate. Endoapertures lalongate, simple with diffuse ends, to complex H-shaped. Exine 1–1.5 μm thick, with well-developed endexine of similar thickness to foot layer, which itself is comparable to the smooth, subperforate tectum. The ectexine includes a thin columellar interstitium, clearly distinguished in *L. stenosepala* (Fig. 38), although less so in *L. fortunei* (Fig. 39). The sculpturing of this type of grain appears smooth, with occasional scattered puncta (Fig. 32, 34), which generate a faint dispersed OL-pattern in the light microscope.

Seven species:

L. auriculata (26–30 × 17–20 μm)
L. barystachys (29–31.5 × 20–24 μm)
L. circaeoides (24–27 × 16.5–19 μm)
L. clethroides (29–36.5 × 22–26 μm)
L. fortunei (22–24 × 15–16 μm)
L. heterogenea (27.5–31 × 18–22.5 μm)
L. stenosepala (30–33.5 × 17–19 μm)

4B: Mauritiana-type (Fig. 35–37).

This pollen differs from 4A in being subprolate (P/E: 1.23) with a more triangular amb (Fig. 35, 36). Furthermore the tectum in this species is somewhat more regularly punctate, giving an almost reticulate sculpturing, but with muri ≫ lumina (Fig. 37).

One species: *L. mauritiana* (26–30 × 20–22 μm)

5: Laxa-type (Fig. 40–50).

Pollen tricolporate, small to medium, subprolate to prolate (P/E

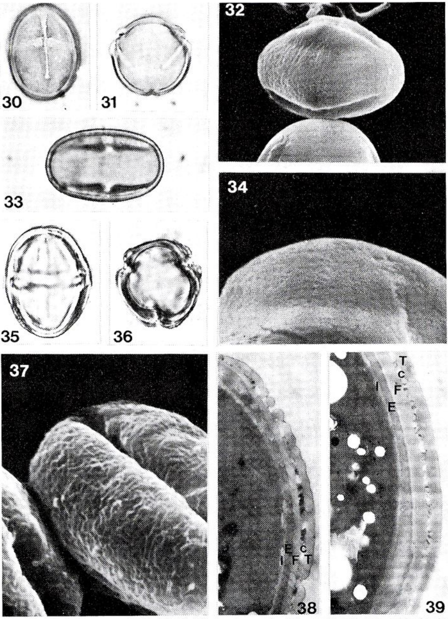

FIG. 30–39. Pollen-types 4A & 4B. **30–32**, *L. circaeoides*: 30, meridional view, with simple lalongate endoaperture, LM; 31, polar view, amb circular, LM; 32, meridional view, smooth, subperforate tectum, SEM × c. 1,600. **33, 34.** *L. stenosepala*: 33, meridional view, LM; 34, detail of exine sculpturing, showing sparsely scattered puncta of subperforate tectum, SEM × c. 4,800. **35–37**, *L. mauritiana*: 35, meridional view, LM; 36, polar view, amb triangular, LM; 37, detail of exine sculpturing, showing puncta in subperforate tectum, SEM × c. 2,500. **38**, *L. stenosepala*, sporoderm stratification featuring equal foot layer and subperforate tectum, with thin columellar interstitium. TEM × c. 8,000. **39**, *L. fortunei* sporoderm stratification, with smooth, barely subperforate tectum and thin columellar interstitium, TEM × c. 8,000.

All light micrographs × 1,000. TEM micrograph abbreviations: C = interstitium; Eca = ectoaperture; E = endexine, Ena = endoaperture; F = foot layer; I = intine; T = tectum.

1.23–1.38) with circular amb. Ectoapertures long, often syncolporate (e.g. Fig. 42). Endoapertures lalongate, characteristically complex H-shaped (e.g. Fig. 40). Exine 1–1.2 μm thick, with variable endexine, as thick as foot layer in *L. laxa* (Fig. 49), but much less developed in *L. engleri* (Fig. 50). The columellar interstitium, quite distinct in *L. laxa,* is similarly reduced in *L. engleri*. However the unifying character of these grains is the regularly and densely perforate tectum, which appears pitted or almost micro-reticulate in the SEM (Fig. 45–47), with a delicate OL-pattern as seen in the light microscope (Fig. 44).

Five species:

L. alternifolia (23–27 × 19–21 μm)
L. cordifolia (22–24.5 × 19–21 μm)
L. engleri (22–26 × 16–18.5 μm)
L. laxa (20–22 × 15–18.5 μm)
L. montana (21–24 × 17.5–20 μm)

6: Ciliata-type (Fig. 51–54).

Pollen tricolporoidate, small, prolate-spheroidal to subprolate (P/E: 1.1–1.3) with triangular amb (Fig. 52). Ectoapertures long, sometimes bridged at the equator, thus almost obscuring the characteristic small circular endoapertures (Fig. 51). Exine thin (c. 1 μm) consisting of a very well-developed endexine (Fig. 54), a thin foot layer, clear columellar interstitium, and overlaying smooth tectum. The regularly perforate nature of this outer layer generates a granular OL-pattern in the light microscope, and is seen as densely pitted in the SEM (Fig. 53).

Four species:

L. ciliata (21–22 × 19–21 μm)
L. lanceolata (20–23 × 16–20 μm)
L. quadriflora (21–23 × 17–18 μm)
L. tonsa (20–22 × 15–17 μm)

7A: Congestiflora-type (Fig. 55–64).

Pollen tricolporate, medium, prolate-spheroidal to subprolate (P/E: 1.05–1.25), with circular (Fig. 57) to almost triangular amb (Fig. 59). Ectoapertures long, frequently syncolporate. Endoapertures lalongate, simple, with diffuse ends, often extended to give a complete equatorial band. Exine 1.2–1.8 μm thick, with an endexine ranging from very thin (e.g. *L. congestiflora,* Fig. 63), to as thick as the foot layer (e.g. *L. japonica,* Fig. 64). The three layers of the ectexine are each well-developed, and more-or-less equal in thickness, with a smooth partial tectum supported

FIG. 40–54. Pollen-types 5 & 6. **40,** *L. laxa,* meridional view showing H-shaped endoaperture, LM. **41, 42,** *L. cordifolia*: 41, meridional view, LM; 42, polar view, syncolporate, LM. **43, 44,** *L. alternifolia*: 43, meridional view, optical section, LM; 44, meridional view, high focus, showing granular OL pattern, LM. **45,** *L. laxa*, detail of exine sculpturing, showing densely perforate tectum, SEM × c. 5,500. **46,** *L. alternifolia,* meridional view, densely pitted, perforate tectum, SEM × c. 2,000. **47,** *L. engleri*, meridional view, perforate tectum, SEM × c. 1,700. **48, 49,** *L. laxa*: 48, oblique LS grain, with endoaperture, TEM × c. 4,000; 49, sporoderm stratification, perforate tectum and thin columellar interstitium, TEM × c. 20,000. **50,** *L. engleri*, sporoderm stratification, regularly perforate tectum, very short, thick columellae and prominent foot layer, TEM × c. 20,000. **51–53,** *L. quadriflora*: 51, meridional view, grain colporoidate, with small indistinct circular endoaperture, LM; 52, polar view, amb triangular, LM; 53, detail of exine sculpturing, regularly perforate, SEM × c. 4,000. **54,** *L. ciliata*, sporoderm stratification, thick endexine, thin foot layer, distinct columellae and smooth, perforate tectum, TEM × c. 20,000.

All light micrographs × 1,000. TEM micrograph abbreviations: C = interstitium; Eca = ectoaperture; E = endexine; Ena = endoaperture; F = foot layer; I = intine; T = tectum.


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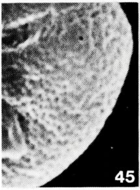
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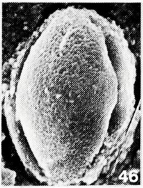
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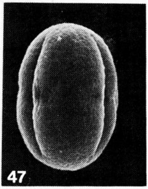
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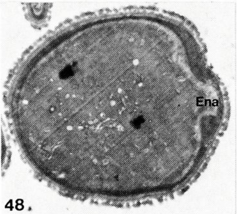

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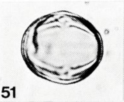
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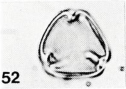
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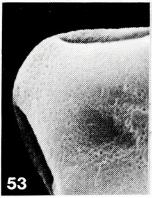
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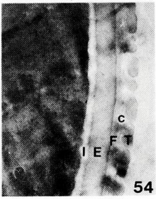

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by wide-spaced columellae. Under the light microscope the resultant reticulum is revealed as simplicolumellate. The large lumina of the reticulum (> 1.5 μm) is clearly revealed in the SEM (Fig. 60–62), although the thickness of the muri varies from quite narrow in *L. congestiflora* (Fig. 60), outlining regular isodiametric lumina, to thicker in *L. nummularia* (Fig. 61), and similarly thick, but outlining irregular lumina, in *L. japonica* (Fig. 62).

Twenty-five species:

L. alfredii (27–32 × 26–29.5 μm)
L. christinae (29.5–32 × 27–31 μm)
L. congestiflora (30–36 × 26.5–29 μm)
L. deltoidea (31–38 × 28–31 μm)
L. drymarifolia (25–31 × 21–24 μm)
L. eriosipetala (32–36 × 27–29 μm)
L. esquirolii (33–35 × 29–31 μm)
L. fordiana (31–33 × 27–29 μm)
L. franchetii (33–39 × 31–35 μm)
L. fukienensis (28–35 × 24–27 μm)
L. japonica (31–33 × 24–25 μm)
L. klattiana (26.5–30 × 23.5–25.5 μm)
L. liui (31–34.5 × 26–29.5 μm)
L. longipes (24–27.5 × 23–25) μm)
L. melampyroides (30–36.5 × 26– 31.5) μm)
L. nanchuanensis (27–29 × 24–25 μm)
L. nummularia (27–32 × 22–25.5 μm)
L. paridiformis (29.5–31.5 × 26–30 μm)
L. patungensis (28–30 × 25–27 μm)
L. phyllocephala (28.5–36 × 28–33 μm)
L. pterantha (28–29 × 24–25 μm)
L. punctata (29–32 × 27–28.5 μm)
L. rubiginosa (26.5–29.5 × 23.5–27.5 μm)
L. sciadophylla (34–36 × 31–32 μm)
L. yingdeensis (32–36 × 26–30 μm)

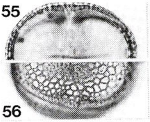
Note: A few unusual tetracolporate grains (Fig. 58) were observed in *L. nummularia* (up to 20% in one collection).

7B: Hypericoides-type (Fig. 65–70).

This pollen-type is distinguished from 7A by much finer reticulate surface sculpturing, with lumina usually < 1 μm. The more delicate OL-pattern is quite clear, even in the light microscope (Fig. 65, 67, 68), but the finely partial-reticulate form of the tectum is best revealed in the SEM (Fig. 69, 70). The amb of this pollen-type tends to be more circular-lobate (Fig. 66), such equatorial profiles displaying the distinctly thick exine. Endoapertures forming complete equatorial bands which are quite common in this group, are very apparent in the light microscope (Fig. 68).

Fig. 55–70. Pollen-types 7A & 7B. **55–57,** *L. congestiflora*: 55, meridional view, low focus, LM; 56, meridional view, high focus, showing clear reticulum, LM; 57, polar view, syncolporate, LM. **58,** *L. nummularia,* abnormal tetracolporate grain in polar view, LM. **59,** *L. melampyroides*, polar view, syncolporate, with coarse reticulum, LM. **60,** *L. congestiflora* detail of exine sculpturing, showing reticulate, partial tectum, SEM × c. 5,000. **61,** *L. nummularia,* meridional view, reticulum with thick muri, SEM × c. 1,200. **62,** *L. japonica*, meridional view, irregular reticulum with thick muri, SEM × c. 1,200. **63,** *L. congestiflora,* sporoderm stratification, thin endexine and three ± equal layers of endexine, with partial tectum, TEM × c. 10,000. **64,** *L. japonica,* sporoderm stratification; partial tectum, distinct columellae, foot layer, and endexine TEM × c. 10,000. **65, 66,** *L. melampyroides* var. *brunnelloides*: 65, meridional view, high focus, showing fine reticulum, LM; 66, polar view, amb lobate, with thick exine, LM. **67,** *L. deltoidea* var. *cinerascens,* polar view, with dark OL pattern of fine reticulum, LM. **68,** *L. grammica*, meridional view, with clear equatorial band (zonorate), LM. **69,** *L. melampyroides* var. *brunnelloides,* meridional view, with fine reticulum, SEM × c. 1,400. **70.** *L. hypericoides*, detail of exine sculpturing, microreticulate partial tectum, SEM × c. 3,200.

All light micrographs × 1,000. TEM micrograph abbreviations: C = interstitium; Eca = ectoaperture; E = endexine, Ena = endoaperture; F = foot layer; I = intine; T = tectum.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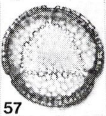
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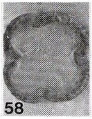
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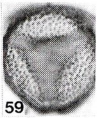
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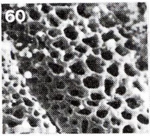
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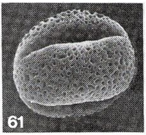
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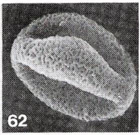
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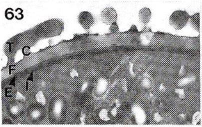
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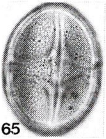
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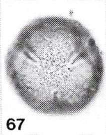
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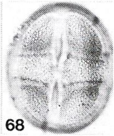
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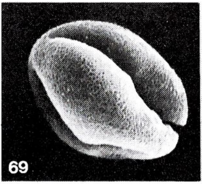
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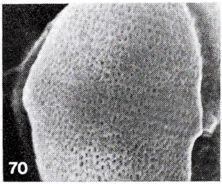
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Five species:

L. deltoidea
  var. *cinerascens* (29–34 × 25–28 μm)
L. grammica (34–38 × 29–32 μm)
L. hypericoides (25–27 × 20–22.5 μm)
L. melampyroides
  var. *brunnelloides* (28–36 × 25–28 μm)
L. ophelioides (25–26 × 24–25 μm)

8A: Fraseri-type (Fig. 71–77).

Pollen tricolporate, small, prolate-spheroidal to subprolate, (P/E: 1.1–1.25) with circular-lobate amb. Ectoapertures long, narrow, sometimes bridged at the equator (Fig. 76, 77), and occasionally syncolporate. Endoapertures lalongate, simple, with diffuse ends. Exine 1–1.4 μm thick, similar in structure to type 7A, with a partial tectum. The clear reticular sculpturing, with slightly thickened muri, features wide lumina (> 1.5 μm) in the mesocolpium and apocolpium (Fig. 75, 76), reducing progressively towards the colpus and forming more or less distinct colpus margins in some species (e.g. *L. fraseri*, Fig. 77).

Seven species:

L. davurica (19–22 × 17.5–19.5 μm)
L. fraseri (21–23 × 19–21 μm)
L. quadrifolia (22–24 × 19–21 μm)
L. sertulata (23–25.5 × 19–21.5 μm)
L. terrestris (22–25 × 19–22 μm)
L. thyrsiflora (20–23 × 16.5–18 μm)
L. vulgaris (22–24 × 19–22 μm)

Note: An account of exine stratification relevant to this pollen-type was given by Nowicke & Skvarla (1977) for *L. thyrsiflora* which showed a smooth, partial tectum and well-developed columellar and foot layers, the latter slightly thinner than the tectum. Beneath these ectexine layers, a moderately thick endexine was observed.

8B: Serpyllifolia-type (Fig. 78–82).

This pollen-type differs from 8A in the smaller dimensions of its exine sculpturing (8B is to 8A as 7B is to 7A). These species are characterised by a fine regular reticulum, featuring small lumina (< 1 μm diameter), which can be distinguished in both the light microscope (Fig. 79), and the SEM (Fig. 81, 82). The amb of these grains tends to be more circular (Fig. 80).

Two species:

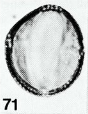
L. nemorum (19–22 × 16–17 μm)
L. serpyllifolia (20–24 × 17.5–21 μm)

9: Taliensis-type (Fig. 87–104).

Pollen tricolporate, small to medium, prolate (P/E: 1.34–1.70) with circular to lobate amb (Fig. 89, 96). Ectoapertures long, tapering, sometimes syncolporate. Endoapertures lalongate, simple to complex

FIG. 71–86. Pollen-types 8A, 8B & 10. **71, 72,** *L. sertulata*: 71, meridional view, LM; 72, polar view, amb lobate, LM. **73–75,** *L. thyrsiflora*: 73, meridional view, LM; 74, polar view, amb lobate, LM; 75, polar view, high focus, showing coarse reticulum, LM. **76,** *L sertulata,* meridional view, reticulate partial tectum, colpi bridged at equator, SEM × c. 1,700. **77,** *L. fraseri*, detail of exine sculpturing, tectum almost complete at margins of colpi, SEM × c. 2,000. **78–81,** *L. serpyllifolia*: 78, meridional view, LM; 79, meridional view, with very fine OL pattern, LM; 80, polar view, amb circular, LM; 81, meridional view, microreticulate partial tectum, SEM × c. 2,200. **82,** *L. nemorum*, detail of exine sculpturing, fine reticulum, SEM × c. 2,500. **83–86,** *L. hillebrandii*: 83, meridional view, LM; 84, polar view, tetracolporate, with thick exine, LM; 85, polar view, exine thinner, LM; 86, detail of exine sculpturing, showing scattered puncta in smooth tectum, SEM × c. 2,100.

All light micrographs × 1,000.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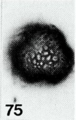
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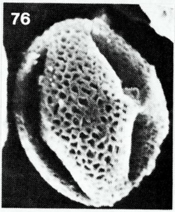
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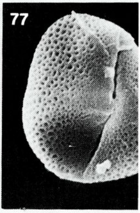
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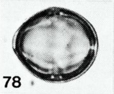
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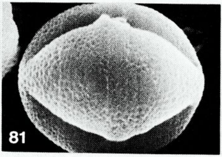
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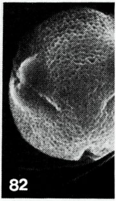
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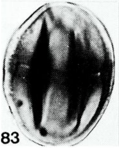
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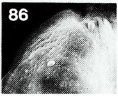
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H-shaped. Exine 1.3–1.8 μm thick, with endexine usually slightly thinner than foot layer, but much thickened beneath the colpus, at either side of the endoaperture (Fig. 102, 103). This character is also clearly discernible under the light microscope (Fig. 90). The columellar interstitium of the ectexine is only poorly-developed, so that the partial tectum arises almost directly from a foot layer of equal thickness (Fig. 104). The resulting reticular sculpturing ranges from the clear wide lumina of *L. lobelioides* (Fig. 87) and *L. nutans* (Fig. 99), to the smaller lumina of *L. chenopodioides* (Fig. 91), and the regular micro-reticulum of *L. crispidens* (Fig. 100) and *L. fletcheri* (Fig. 94). The former species, which is heterostylous, is classified here on the basis of pollen from the long-styled form (Fig. 95, 96). The grains of the short-styled form exhibit a similar sculpturing, but are smaller and tend to be subprolate (Fig. 97, 98).

Unlike pollen-types 7 and 8, which naturally segregate into two discrete subgroups with large, clear reticulum, and small, fine reticulum respectively, the species of this pollen-type form an indivisible continuum from large to small reticulum, and range from medium (e.g. *L. lobelioides,* Fig. 87), to quite small grains (e.g. *L. atropurpurea,* Fig. 92).

Twenty-one species:

L. atropurpurea (22–25 × 13.5–17 μm)
L. candida (25–30 × 17–18.5 μm)
L. chenopodioides (26–28.5 × 19–22 μm)
L. crispidens
  long style (26–29 × 19.5–21 μm)
  short style (16–17.5 × 14–16 μm)
L. decurrens (26–29 × 17.5–19 μm)
L. ephemerum (27–28.5 × 16–20 μm)
**L. fletcheri* (23–25 × 15–17 μm)
L. likiangensis (29–36 × 18–22 μm)
L. lobelioides (32–40 × 20–23 μm)
L. nutans (34–37.5 × 24–28.5 μm)
L. orbicularis (27–30 × 17–19.5 μm)
L. parvifolia (26.5–29 × 18.5–20.5 μm)
L. pentapetala (23.5–24.5 × 15–17.5 μm)
L. platypetala (25–28 × 18–21 μm)
L. prolifera (29–33 × 19–21 μm)
L. pumila (32–36 × 20–26 μm)
L. reflexiloba (31–33 × 20–25 μm)
L. robusta (26–28 × 17–20 μm)
L. silvestrii (25–29 × 19–20 μm)
L. taliensis (22–27 × 16–18 μm)
L. violascens (25.5–28.5 × 17.5–21 μm)

* *Note*: *L. fletcheri* is a new species distinguished by Hu & Bennell (1983) in the course of this study.

10: Hillebrandii-type (Fig. 83–86).

Pollen tetracolporate, medium, subprolate, to prolate (P/E: 1.2–1.6),

FIG. 87–104. Pollen-type 9. **87**, *L. lobelioides*, meridional view, coarse reticulum, LM. **88, 89**, *L. nutans*: 88, meridional view, LM; 89, polar view, LM. **90**, *L. violascens*, meridional view, low focus, showing thickened endexine above and below endoaperture, LM. **91**, *L. chenopodioides*, meridional view, with OL pattern of fine reticulum, LM. **92**, *L. atropurpurea*, meridional view, LM. **93**, *L. lobelioides*, detail of exine sculpturing, showing thick muri of irregularly reticulate, partial tectum, SEM × c. 1,900. **94**, *L. fletcheri*, detail of exine sculpturing, microreticulate tectum, SEM × c. 3,000. **95, 96**, *L. crispidens* (long-styled form): 95, meridional view, LM; 96, polar view, LM. **97, 98**, *L. crispidens* (short-styled form): 97, meridional view, LM; 98, polar view, LM. **99**, *L. nutans*, meridional view, regular reticulum with large lumina, SEM × c. 1,000. **100**, *L. crispidens*, meridional view, fine microreticulum with very small lumina, SEM × c. 1,300. **101–104**, *L. taliensis*: 101, meridional view, exine sculpturing featuring reticulate, partial tectum, SEM × c. 1,800; 102, oblique TS, endexine thickened beneath colpus, TEM × c. 5,000; 103, sporoderm stratification at endoaperture, with thickened endexine, TEM × c. 10,000; 104, sporoderm stratification, partial tectum, thin columellar interstitium, TEM × c. 24,000.

All light micrographs × 1,000. TEM micrograph abbreviations: C = interstitium; Eca = ectoaperture; E = endexine; Ena = endoaperture; F = foot layer; I = intine; T = tectum.


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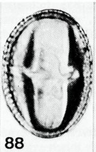
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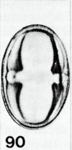
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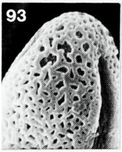
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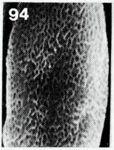
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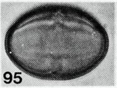
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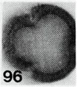
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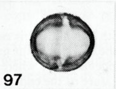
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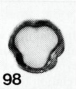
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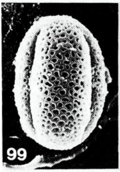
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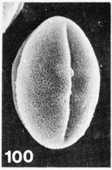
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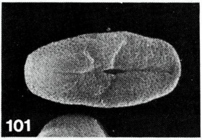
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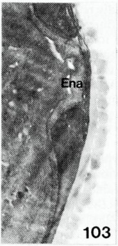

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104

very variable, with rectangular amb (Fig. 84, 85). Ectoapertures long, deeply cleft. Endoapertures lalongate, simple, usually connected as an equatorial band. Exine thick (> 2 μm), stratification not studied, but sexine-nexine clearly distinguished and of more-or-less equal thickness in the light microscope (Fig. 84). The surface sculpturing is revealed in the SEM to consist of irregularly-scattered perforations in an otherwise smooth tectum (Fig. 86).

One species: *L. hillebrandii* (24–36 × 20–32 μm)

Note: This species and its Hawaiian relatives were examined more extensively by Huynh (1970), who reported much variability within collections, including heteropolar and 3- and 5-colporate grains. However this isolated group of species were clearly discriminated by their generally 4-colporate form.

DISCUSSION

In common with Huynh, in his earlier survey of the genus (1970, 1971), we also found shape and size of the grains of value in discriminating the pollen-types in *Lysimachia*. But, whereas Huynh considered these characters in relation to a feature of the endexine, namely the endoaperture (i.e. the zone from which this sporoderm layer is virtually absent), in our survey the emphasis has been shifted, by the use of electron microscopes with their improved resolution, to characters of the ectexine. The nature of the endoaperture is seen to be highly variable, both within and between different collections of the same species. With the exception of the very distinctive colporoidate aperture of the Ciliata pollen-type, endoaperture character was not found helpful in establishing a pollen classification within *Lysimachia*. In contrast, the tectum form and consequent surface sculpturing of the grains is remarkably constant for each species. However, throughout the genus the tectum shows continuous variation from imperforate to broadly reticulate (partial), with a spectrum of punctate and microreticulate intermediate forms. The boundaries between subperforate and perforate, and to a lesser extent between perforate and partial are sometimes difficult to interpret, particularly in cases where the distribution of perforations, or the diameter of the lumina in relation to muri, varies across the mescolpium.

POLLEN-TYPES AND THEIR TAXONOMIC SIGNIFICANCE

The ten pollen-types and four sub-types derived from assessment of tectum form in relation to grain size and shape (P/E ratio) each comprise groups of species (Table 1) which correspond closely to the subgenera and their sections within *Lysimachia,* as modified by Chen & Hu (1979) after Handel-Mazzetti (1928). This relationship is presented in Table 2 (p. 448), to which the major characters of flower colour and androecial structure, upon which these classifications are based, have been added.

Subgenus Idiophyton Hand.-Mazz. amplif. Chen & Hu

Section Idiophyton. This entire subgenus is characterised by yellow flowers with large basifixed anthers, but as originally conceived by Handel-Mazzetti (1928) included only *L. insignis,* which was retained by Chen & Hu (1979) in its own section. A range of morphology was encountered in different collections of this species (see discussion of pollen variability within species, p. 452), but normal grains conformed to Type 1A.

Section Apodanthera Hand.-Mazz. Handel-Mazzetti established this section within subgenus *Lysimachia*. Its subsequent removal to subgenus *Idiophyton* by Chen & Hu (1979) is strongly supported by the dominance of pollen-type 1, which it shares with *L. insignis*. It is also noteworthy that the subdivision of pollen-type 1 into A and B, exactly mirrors the division of the section into series *Evalves* and *Valvatae* respectively. The value of the separate series has sometimes been questioned, but the longer, narrower anther and shorter filament of the woody-stemmed *Evalves* produces distinctly subprolate grains (1A), whereas the broader anther with a relatively longer filament in the herbaceous *Valvatae* produces more rounded, prolate-spheroidal grains (1B).

The species *L. laxa* and *L. montana* are exceptional in being pollen-type 5, but this, perhaps, relates to the distinct method of opening of the anther by a slit, in contrast to all other members of the section in which the anther opens by a terminal pore. In this respect they constitute a link to section *Oppositifoliae*. The distinct pollen morphology of these two species also correlates with their geographical isolation in Java and Sumatra as southern outposts of this subgenus.

Section Oppositifoliae Hand.-Mazz. The two species examined, from the total complement of four described in this section, also have pollen of type 5, and, significantly, their anthers also open by short slits, reinforcing the relationship with *L. laxa* and *L. montana.*

Subgenus Lysimachia Hand.-Mazz.

This is the largest subgenus and is characterised by yellow flowers, rarely white, with filaments equal to, or longer than the versatile anthers.

Section Lysimachia. This section contains only four species, of which we have examined three. In spite of their wide and different distributions, each restricted to a separate continent (*L. vulgaris* native to Europe and extending eastwards to Turkestan, *L. davurica* indigenous to East Asia, and *L. fraseri* restricted to North America) the similar pollen-type, all 8A, emphasises their unity as a section.

Section Lerouxia (Mérat.) Endl. As originally conceived by Handel-Mazzetti (1928) this included four subsections, but their correspondence to varied pollen-types suggests that such a combination is unnatural. Thus, subsections *Hypericoideae* and *Ophelioideae* have pollen of type 7B, whereas, subsection *Godinella* conforms to type 8B, and subsection *Peduncularis* type 1A. The last was transferred to section *Alternifoliae* by Chen & Hu (1979), who also reduced *Ophelioideae* and *Hypericoideae* to

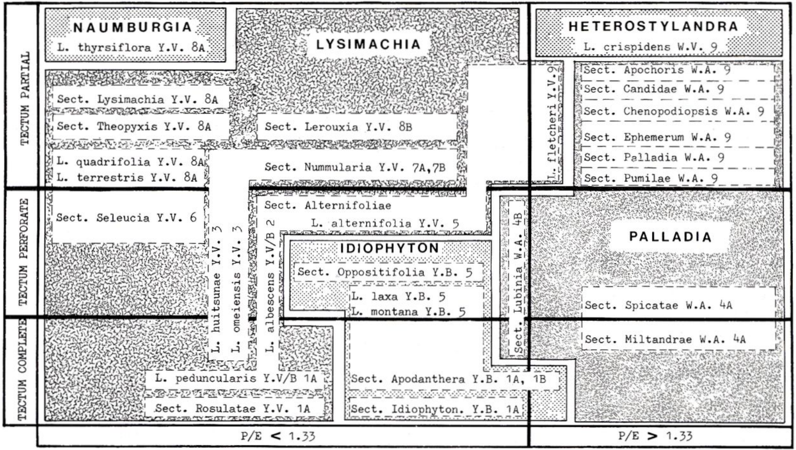


TABLE 2. Interrelationship of subgenera and sections of Lysimachia (according to Chen & Hu (1979) modified after Handel-Mazzetti (1928)), based on pollen morphology. (Y: Fl. yellow; W: fl. white to pink; A: filament adnate halfway up corolla; V: filament adnate at corolla base, anther versatile; B: filament adnate at corolla base, anther basifixed. 1–10: pollen-types. — — — —: Sections; ————: Subgenera; where sectional and subgeneric boxes cross major divisions of the table their constituent species exhibit an appropriate range of pollen morphologies.)

series in section *Nummularia*. Certainly the broadly reticulate, medium-sized pollen of e.g. *L. longipes* (*Ophelioideae*) clearly belongs to type 7, and supports this decision. Thus section *Lerouxia,* as now recognized, contains only subsection *Godinella* from Handel-Mazzetti's original concept. The two species studied from this section (*L. nemorum, L. serpyllifolia*) both conform to pollen-type 8B, which proved to be peculiar to this taxonomic group.

Section Nummularia (Gilib.) Klatt. Twenty-three species, covering all of the eleven series recognized in this, the largest section in the genus, were studied. With only two exceptions, all species have reticulate pollen of type 7. The subdivision into pollen-types 7A and 7B, on the basis of the size of this reticulum, although clearly discrete, shows no taxonomic correlation. However this distinction perhaps casts some doubt on the decision of Chen & Hu (1979) to redesignate *L. deltoidea* var. *brunnelloides* as a variety of *L. melampyroides,* for its delicate microreticulate tectum (Fig. 65, 69) more closely resembles that of *L. deltoidea* var. *cinerascens* (Fig. 67; pollen-type 7B) than *L. melampyroides* with its large clear reticulum (Fig. 59; pollen-type 7A).

The two distinct species *L. omeiensis* and *L. huitsunae* are of the unusual pollen-type 3, characterised by a complex rugose-microreticulate subperforate tectum. However, their affinity in terms of pollen morphology reinforces Chen & Hu's decision (1979) to remove the latter species from subgenus *Palladia,* to which it had previously been assigned, chiefly because of its white flower colour, and place it in series *Hypericoideae* section *Nummularia* alongside *L. omeiensis,* on the evidence of general morphology.

Section Theopyxis (Griseb.) Pax. Only one of the four species in this grouping of Central and South American species with distinctive umbellate inflorescences was examined. Its pollen conformed to type 8A, as for section *Lysimachia*. This is the only other section of subgenus *Lysimachia* in which white flower colour occurs. The separate occurrence of this character, in taxonomically and geographically distinct taxa outside the subgenus *Palladia,* emphasises that flower colour alone is an inadequate criterion for infrageneric classification.

Section Seleucia (Bigelow) Hand.-Mazz. All eleven species in this section are indigenous to North America. Four of the six species examined, all from subsection *Steironema,* have the quite distinct pollen-type 6, with its triangular amb and unique (for the genus) colporoidate aperture structure. Considered in relation to its equally distinctive flower structure, characterised by the possession of a set of sterile filaments (staminodes) attached to the corolla on the same ring as the whorl of anther-bearing stamens, it seems reasonable to follow Ray (1956) in treating this group of species as a separate subgenus.

The two remaining species investigated, *L. quadrifolia* and *L. terrestris,* both belong in subsection *Verticillatae,* whose species lack staminodes, and are of pollen-type 8A, similar to sections *Lysimachia* and *Theopyxis*. Undoubtedly the *Verticillatae* should be excluded from subgenus *Seleucia,* and retained as a section of subgenus *Lysimachia,* as Ray (1956) also proposed.

Section Rosulatae Knuth. This section contains only two species, both endemic to South China. In spite of gross differences in flower structure, Handel-Mazzetti included it as a section of subgenus *Lysimachiopsis,* allying it to the Hawaiian species with tetracolporate pollen. Examination of *L. alpestris* revealed it to be tricolporate, of pollen-type 1A, thereby expressing affinities with subgenus *Idiophyton*. Significantly, on the basis of flower structure, Chen & Hu (1979) confidently assigned this section to subgenus *Lysimachia,* with the qualification that it could be derived directly from section *Apodanthera* of subgenus *Idiophyton.* The pollen evidence strongly supports this treatment. In his assessment of this section Huynh (1970) found it necessary to define a distinct pollen-type for *L. alpestris* on the basis of the clear equatorial band and apparent central thickening of its endoaperture. However this character is also apparent in *L. heterobotrys* of section *Apodanthera,* whose pollen and general morphology are very close to *L. alpestris.* Consequently our studies do not support Huynh's (1970) erection of a new subgenus, *Nullicaulis,* to accommodate the species of section *Rosulatae.*

Section Alternifoliae Knuth. emend. Hand.-Mazz. This section now comprises four species, including the newly-described *L. fletcheri* (Hu & Bennell, 1983), all of which are confined to the adjacent regions of North India, Burma and South West China. This isolated section has often been considered an intermediate group linking the major subgenera *Idiophyton, Lysimachia* and *Palladia.* The diverse pollen-types encountered form a morphological series and support this hypothesis (Table 3). It should be noted that a progressive change from basifixed to versatile anther attachment, and from filaments of more or less the same length as the anthers, to longer than the anthers, is paralleled by increasing perforation of the tectum. In addition, it is noteworthy that pollen-type 5 (*L. alternifolia*) also occurs in subgenus *Idiophyton* (section *Oppositifolia*) and the two distinct species from section *Apodanthera* (Table 2). Furthermore pollen-type 9 (*L. fletcheri*) is also representative of a large proportion of subgenus *Palladia,* thus emphasising the intermediate status of this section.

Subgenus Palladia (Moench) Hand.-Mazz.

This subgenus is characterised by white flowers with filaments adnate halfway up the corolla-tube and includes two major pollen-types. All species of sections *Pumilae, Candidae, Palladia, Chenopodiopsis, Ephemerum* and *Apochoris* examined conformed to pollen-type 9, elsewhere reported only for *L. fletcheri* of subgenus *Lysimachia* section *Alternifoliae.* Within these six sections the species are mostly indigenous to Asia, with some occurring in Europe and Africa, but their taxonomic affinity is confirmed by their pollen morphology. All of their constituent species have strongly prolate pollen, with the exception of *L. nutans,* an isolated South African representative whose grains tend towards subprolate.

TABLE 3

Morphological series of anther and pollen characters in subgenus Lysimachia, section Alternifoliae

	albescens →	**peduncularis** →	**alternifolia** →	**fletcheri**
anther	± basifixed	intermediate	versatile	versatile
filament length	≑ anther	≑ anther	> anther	> anther
tectum	imperforate	imperforate	perforate	partial
pollen-type	2	1	5	9

The remaining sections of the genus all have pollen-type 4, within which two subtypes are recognized.

Section Spicatae Knuth & *section Miltandrae* Hand.-Mazz. These sections comprise a total of eight species, of which we have examined seven, and all have pollen of type 4A. Section *Miltandrae* features a red gland at the tip of the anther, according to which distinctive character Chen & Hu (1979) moved *L. circaeoides* from section *Palladia* (*Coxia*) where it had been placed by Handel-Mazzetti (1928), into section *Miltandrae.* The unifying pollen morphology, also type 4A, supports this transfer.

Section Lubinia (Comm.) Klatt. This section has only one species, the widely-dispersed *L. mauritiana,* which ranges across the Indian and Pacific Oceans from Mauritius to Hawaii, and has diagnostically rather large, upright anthers. Its pollen is also somewhat individual, being similar to sections *Miltandrae* and *Spicatae* in size but distinguished as pollen-type 4B by its more regularly perforate tectum, and its prolate shape.

Subgenus Heterostylandra (Hand.-Mazz.) Chen & Hu

This subgenus was erected by Chen & Hu (1979) to accommodate *L. crispidens,* a species of unclear affinity with dimorphic, long-tubed flowers — a feature encountered nowhere else in the genus. The long- and short-styled flower morphs were shown to correspond to the occurrence of dimorphic pollen grains, as found in some other members of the Primulaceae. The long-styled flowers produce somewhat larger grains of pollen-type 9, as in much of subgenus *Palladia,* whereas pollen from the short-styled flowers would properly be assigned to type 8B, as found in section *Lerouxia* of subgenus *Lysimachia,* because of the smaller, more subprolate grains.

Subgenus Naumburgia (Moench) Hand.-Mazz. *L. thyrsiflora,* the only species in this monotypic subgenus, is a widespread species occurring in North America, Europe and Asia, and is characterised by distinctive 6–7-merous flowers. It is of uncertain affinity, and has been treated by some authors as a separate genus. In North America it is reputed to be a parent, with *L. terrestris,* of the hybrid *L.* × *commixta,* although this has never been verified by experiment. The pollen conforms to type 8A, the same as section *Verticillatae* of subgenus *Lysimachia* to which the other putative parent belongs. The similarity of the pollen morphology reinforces the possible close relationship of these species, and supports retention of *Naumburgia* as a subgenus only.

Subgenus Sandwicensia Huynh (= *Lysimachiopsis* (Heller) Hand.-Mazz. nom. illegit.)

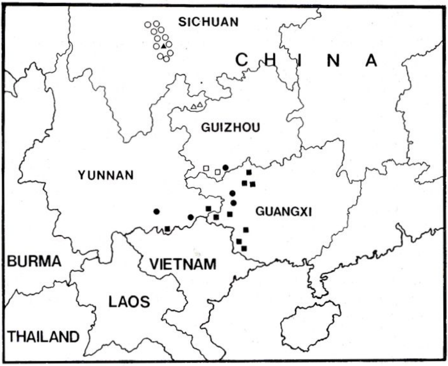
This subgenus embodies approximately nine, quite distinctive, red-flowered, 6–9-merous species, endemic to the Hawaiian Islands. The pollen of this isolated group is similarly distinctive, being tetracolporate and of its own type, 10. Although only one species, *L. hillebrandii,* was examined, Huynh's survey (1970) included a further six species, which all exhibited the characteristic tetracolporate pollen morphology.

POLLEN VARIABILITY WITHIN SPECIES

A variation in pollen morphology was exhibited in different collections of two species endemic to South West China, *L. insignis* and *L. omeiensis*. It showed some geographical correlation, and in this respect differed from the variation noted within collections of other species (e.g. occasional tetracolporate pollen grains in *L. nummularia,* and a small proportion of abortive, collapsed pollen grains in many species).

L. omeiensis. Three collections were examined, and found to constitute a morphological series. Although the exine pattern was consistently a complex microreticulum (Fig. 27), with increasing size of the pollen grains the endoapertures tended to lengthen around the equator of the grain. Thus, the endoapertures of the 'normal', short (23.5–26.5 × 20–22.5 μm) pollen grains (*Fang* 2843) are all simple, lalongate (Fig. 24). Those of the medium pollen grains (28.5–30 × 24–25 μm) (*Tsai* 52270) range from similarly lalongate to complex with extended arms forming an H-shape (Fig. 25a), which in some pollen grains just meet (Fig. 25b). The long grains (34–39 × 25–27 μm) (*Tsai* 52300) are characterised chiefly by endoapertures linked as an equatorial band (zonorate) (Fig. 26b), although in some grains shorter, lalongate endoapertures do occur (Fig. 26a). This variability in endoaperture, both within and between collections of a species, undermines the undue emphasis placed on this character by Huynh (1970) in his earlier palynological survey of *Lysimachia.* Reference to Map 1 reveals that the normal pollen collection derives from the type locality, Mount Omei, at the centre of distribution of this restricted species, whereas both abnormal forms are from adjacent outlying populations in North East Yunnan.

L. insignis. This species was treated by Huynh as a distinct and very unusual pollen-type (Huynh 1970, p. 277) based upon examination of one specimen: *Esquirol* 2120. The pollen of this collection, which we have re-examined, is clearly abnormal, the grains being large and irregular, and varying from 6–9-pantocolporate (Fig. 33), although virtually all exhibited normal cytoplasmic contents. However from our study of a further eleven specimens, *L. insignis* clearly conforms to pollen-type 1A, in common with section *Apodanthera* of subgenus *Idiophyton*, with 'normal' tricolporate pollen grains of small size (e.g. *Chang* 1481), and a smooth, thin exine. Amongst these other collections some had a high proportion of collapsed and aborted pollen grains lacking cytoplasmic contents (e.g. *Fang* s.n.), and



MAP 1. Distribution of *L. omeiensis* and *L. insignis*. *L. omeiensis*: ▲, normal pollen; △, abnormal pollen; ○, all other collections (not examined). *L. insignis*: ■, normal pollen; □, abnormal pollen; ●, all other collections (not examined).

one specimen (*Guizhou Expedn*. 919), which was intermediate in both size and colpus number (4) (Fig. 9) between the normal and the 9-pantocolporate pollen, featured grains with collapsed, seemingly non-functional cytoplasmic contents. This variation again correlates with the restricted distribution of the species (Map 1). Collections are known from three provinces, but the abnormal pollen derives from adjacent populations at the northern end of the distribution in Guizhou.

In both *L. omeiensis* and *L. insignis* the abnormal pollen-morphs seem to relate to the limit of distribution of the species. At the edge of its range, a species may be under stress, or attempting to exploit new habitats. In these circumstances polyploidy is often encountered (Stebbins, 1972). Although the specimens examined were not separable morphologically, the increasing grain size and colpus number in the pollen of *L. insignis* might correlate with increasing ploidy levels. Similar variation in aperture number and grain size with ploidy level have already been described in the Primulaceae for *Trientalis europaea* (Punt et al., 1974). The recent intensive study of abnormalities of pollen morphology in *Rapanea* (Myrsinaceae) by Vasanthy & Pocock (1981) is of relevance (it should be noted that *L. insignis*, is a possible primitive link from *Lysimachia* to the Myrsinaceae — see discussion of phylogeny). Vasanthy & Pocock concluded that the variation was probably the result of cytological anomalies. No chromosome numbers are available for *L. insignis,* but a polyploid series can be detected in other members of subgenus *Idiophyton* (e.g. *L. laxa* 2n = 20; *L. evalves* 2n = 30; *L. sikokiana* 2n = 60, Kurosawa, 1971). Clearly the karyology of *L. insignis* across its geographic range merits further investigation.

The abnormal pollen observed in *L. omeiensis* is less likely to correspond to a polyploid series, but may reflect other karyological changes, perhaps as the result of meiotic malfunctions. Such variation in pollen morphology has been encountered on a number of occasions and is reviewed briefly by Ferguson (1980) in his account of pollen abnormalities in *Ceratonia siliqua.* In this species macromorphological variation is also observed and it is suggested that the range of pollen-types may reflect a phylogenetic trend for increasing specialisation. Similar assessment of percentage pollen fertility and abnormality from a broader sample of collections will be necessary, in order to determine whether such an explanation is relevant to *L. omeiensis.*

POLLEN-TYPES AND THEIR EVOLUTIONARY SIGNIFICANCE

From the distribution of pollen-types in relation to the accepted subgeneric classification, outlined diagrammatically in Table 2, a series of major trends in pollen morphology can be discerned. If progressive increase of pollen grain size and exine complexity as an evolutionary tendency, as suggested originally by Wodehouse (1935) and subsequently demonstrated in many taxonomic groups, e.g. Dichapetalaceae (Punt, 1975) and Umbelliferae (Cerceau-Larrival, 1971), is accepted, it is possible to trace various evolutionary lines within the genus.

Handel-Mazzetti (1928) considered subgenus *Idiophyton,* and *L. insignis,* in particular, to be the most primitive element in the genus. Pollen morphology supports this notion, the species possessing small pollen grains, with a smooth, imperforate, only partially-differentiated (i.e. lacking a columellar interstitium) ectexine. Within section *Apodanthera* of this subgenus there may be a trend from psilate to a more rugulose tectum, as observed in some species. It is noteworthy that all species of *Lysimachia* with pollen characterised by an imperforate tectum also possess a large basifixed anther on a short filament, which is generally considered to be a primitive form.

From this thin, barely-ornamented exine structure, trends involving increasing perforation of the tectum and progressive elaboration of a columellar interstitium within the ectexine, can be discerned. A detailed examination of the patterns of exine evolution in *Lysimachia* as revealed by thin section and SEM studies will be the subject of a separate paper. However such general trends are of importance in assessing the crucial status of section *Alternifoliae* (subgenus *Lysimachia*) within the genus. Its central position between the major subgenera is reflected in the diverse but related pollen-types represented in its four constituent species (Table 2), in which a progressive differentiation of the exine, in relation to androecial character, has been outlined (Table 3). The possible evolutionary links between the subgenera, recognized within *Lysimachia,* are outlined in Table 4, (numbers refer to the succeeding text).

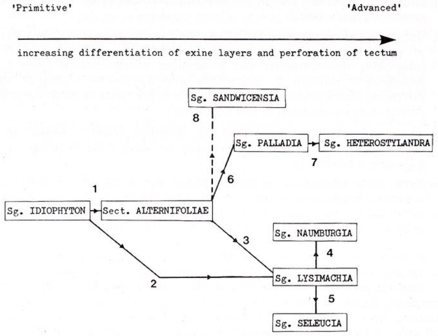


TABLE 4. Possible evolutionary trends in Lysimachia, suggested by pollen morphology. (Numbers refer to text below).

1. Pollen morphology suggests that section *Alternifoliae* (of subgenus *Lysimachia*) can be derived from section *Apodanthera* of the primitive subgenus *Idiophyton* through *L. peduncularis,* with which it shares pollen-type 1A.
2. On the same basis subgenus *Lysimachia* is linked to *Idiophyton* via *L. alpestris,* whose small, non-ornamented grains also conform to pollen type 1A.
3. A further link to the largest subgenus, *Lysimachia,* can be traced via *L. albescens* in section *Alternifoliae,* whose imperforate but rugose tectum and well-developed columellae (Fig. 21) show some similarities to *L. omeiensis* (Fig. 28) in section *Nummularia.* In this context it may be relevant that *L. christinae*, also within section *Nummularia,* appears morphologically almost indistinguishable from *L. albescens*, differing only in the critical character of anther attachment (basifixed in *L. albescens,* versatile in *L. christinae*).
4. From subgenus *Lysimachia* the link to subgenus *Naumburgia* is obvious. Thus *L. thyrsiflora* shares pollen-type 8A with sections *Lysimachia, Theopyxis* and *Verticillatae,* including *L. terrestris* (with which it is purported to hybridise).
5. Less clear pollen characters associate subgenus *Seleucia* with subgenus *Lysimachia*: but although the former is clearly segregated from the other American species in section *Verticillatae,* on account of its triangular-

ambed, colporoidate pollen, the size and exine characters of these two groups are quite similar.

6. Subgenus *Palladia* may be linked to subgenus *Idiophyton* via the range of pollen types exhibited in section *Alternifoliae* (Table 3). The progressive differentiation and perforation of the tectum from *L. peduncularis* through *L. alternifolia* and *L. fletcheri,* coupled to increasing pollen grain size, leads naturally to the range of perforate and partial tecta encountered in this subgenus.
7. The more tenuous relationships of subgenus *Heterostylandra* (*L. crispidens*) to subgenus *Palladia,* with part of which it shares pollen-type 9, is only a possibility.
8. Even more speculative is the suggested derivation of the isolated subgenus *Sandwicensia* from section *Alternifoliae* through the partly sympatric *L. mauritiana* (in subgenus *Palladia*), whose subperforate tectum and thick wall are also found in the Hawaiian species.

It it of interest that the general trends of exine stratification and sculpture, which correlate with increasing pollen grain size, diverge from section *Alternifoliae* along two separate lines, one to the prolate-spheroidal grains of the rest of subgenus *Lysimachia* (e.g. *L. congestiflora,* Fig. 56), and the other to the strongly prolate grains of subgenus *Palladia* (e.g. *L. taliensis,* Fig. 101). Furthermore, this divergence and the overall links between the major subgenera correspond to the change from large anthers, basifixed to short filaments and attached to the corolla base, in subgenus *Idiophyton,* via the intermediate forms described in section *Alternifoliae* (see Table 3), to small versatile anthers, with long filaments attached to the corolla base, in subgenus *Lysimachia,* and to small versatile anthers, adnate halfway up the corolla-tube, in subgenus *Palladia.*

Probably the most advanced element in the genus is represented by *L. crispidens*, the only species to exhibit heterostyly. The associated pollen dimorphism is considered a character of the more advanced members of the Primulaceae (Spanowsky, 1962). In general *Lysimachia* is accepted as the most primitive genus in the Primulaceae, with possible affinities to the Myrsinaceous genera *Ardisia* and *Maesa.* Huang (1972) in the *Pollen Flora of Taiwan* described several species from the latter genera, and their small, tricolporate form, with a smooth to roughened, thin exine, corresponds closely to the 'primitive' pollen-type of *Lysimachia* subgenus *Idiophyton* and lends credence to this affinity.

The widest range of pollen morphology is encountered in China, where only pollen-type 6 (of the North American subgenus *Seleucia*) and pollen-type 10 (of the Hawaiian subgenus *Sandwicensia*) are lacking, thus confirming this area as the centre of diversity of the genus.

CONCLUSIONS

The pollen of *Lysimachia* is shown to be quite heterogeneous, but the 14 pollen-types recognized echo many of the taxonomic subdivisions in the genus, and support the modifications of Handel-Mazzetti's system (1928) made by Chen & Hu (1979). The distinction of subgenus *Seleucia,* excluding section *Verticillatae,* as suggested by Ray (1956), is also supported.

The isolation of *L. alpestris* in a separate subgenus, as proposed by Huynh (1970), is shown to be based on a variable pollen character and is rejected. The pollen of *L. insignis,* defined as a unique pollen-type by Huynh (1970) is re-examined and shown to be based on an abnormal collection. Variation of pollen in this species and *L. omeiensis* is correlated with their respective distributions.

Pollen morphology reflects the accepted evolutionary trends within the genus, its changes in size and exine structure correlating with that of the form of the androecium. Species of section *Alternifoliae* in subgenus *Lysimachia* are intermediate links between the primitive subgenus *Idiophyton* and the more advanced sections of *Lysimachia,* and subgenus *Palladia.*

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