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PALYNOLOGY AND SYSTEMATICS OF THE LYTHRACEAE. II. GENERA HAITIA THROUGH PEPLIS[1]

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ABSTRACT

Pollen morphology for 12 genera of the Lythraceae is described, using light microscopy (LM), scanning (SEM) and transmission electron microscopy (TEM). The genera surveyed are *Haitia, Heimia, Hionanthera, Lafoensia, Lagerstroemia, Lawsonia, Lythrum, Nesaea, Orias* (= *Lagerstroemia*), *Pehria, Pemphis,* and *Peplis.* Among results of taxonomic significance are 1) the similarity of pollen between *Haitia* and *Ginoria,* suggesting that future classifications reflect a close relationship between these genera, 2) a comparable similarity in pollen between *Pehria* and *Adenaria,* 3) the distinction of *Hionanthera* pollen from that of *Ammannia,* 4) an exine similar in certain ultrastructural characteristics between *Orias* and some species of *Lagerstroemia,* although in general aspect they appear quite different, 5) that within the *Didiplis-Lythrum-Peplis* complex, there are three palynologically distinct groups, with *Didiplis* standing apart from the somewhat more similar, but nevertheless, distinct *Lythrum* and *Peplis,* and 6) that considerable differences exist between pollen of *Pemphis acidula* and *Pemphis madagascariensis,* supporting removal of the latter species to a new genus. This pollen survey is part of a multidisciplinary effort to clarify generic limits in the Lythraceae, and evaluate relationships within the family and among families of the Myrtales.

IN AN EARLIER paper (Graham et al., 1985) the results of a pollen survey were presented for ten genera of the Lythraceae—*Adenaria, Ammannia, Capuronia, Crenea, Cuphea, Decodon, Didiplis, Diplusodon, Galpinia,* and *Ginoria,* as well as *Alzatea,* subsequently given family status (Alzateaceae; Graham, 1984). The purpose of the survey is to contribute palynological data to an on-going multidisciplinary assessment of the taxonomy and relationships of genera presently listed for the family, and included here, specifically, for the purpose of pollen description. Interest in the systematics of the Lythraceae has increased because of recent recognition of its key evolutionary position in the order Myrtales (Dahlgren and Thorne, 1984), and because of intense efforts to develop *Cuphea* into a new oil-seed crop plant (see J. Amer. Oil Chemists' Soc. [JAOCS] 62(1), 1985).

In this paper pollen morphology is described for 12 genera: *Haitia* Urban (2 species), *Heimia* Link (2), *Hionanthera* Fernandes & Diniz (4), *Lafoensia* Vand. (10), *Lagerstroemia* L. (53), *Lawsonia* L. (1), *Lythrum* L. (35), *Nesaea* Comm. ex Juss. (50), *Orias* Dode (1; = *Lagerstroemia*), *Pehria* Sprague (1), *Pemphis* J. R. & G. Forst. (2), and *Peplis* L. (3). The pollen is illustrated with SEM and TEM, and also with LM for stratigraphic palynologists working with pollen as plant microfossils. General conclusions are deferred to the final (third) paper in the series, but results of taxonomic interest are briefly summarized here for the 12 genera surveyed. Other introductory information about the family and the survey is provided in the initial paper (Graham et al., 1985).

MATERIALS AND METHODS—as described in Graham et al. (1985).

RESULTS—In the initial paper of the series it was noted that ektexine bridges are probably more common than suggested by the descriptions because these structures frequently separate when the grains expand. We would also add that slight differences in size are not regarded as significant because some pollen samples were collected from living greenhouse material, others came from herbarium specimens

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of different ages, and the grains were in glycerine jelly mounting medium for varying lengths of time. All these factors are known to affect pollen size, and this feature was not used to distinguish pollen unless the differences were great and consistent among several collections; these exceptions are noted in the text. There can be some range in pollen shape, and the categories prolate, spherical and oblate, together with the P/E (polar/equatorial dimensions) ratios and the PI (Polar Index), are general characterizations. It should also be noted that the distinction between scabrate and finely verrucate is whether the sculpture elements are 1 μm or less vs. just slightly larger than 1 μm. More useful in pollen sculpture in the Lythraceae are the categories 1) scabrate/finely verrucate, 2) distinctly verrucate, and 3) striate. Finally, the difference between pseudocolpi absent and pseudocolpi faint is sometimes difficult to discern, even utilizing LM and SEM. Usually this distinction can be made when the grains are observed in polar view, but very subtle, vaguely defined zones of varying wall thickness or granulation could represent pseudocolpi among individual species of the genera surveyed. (See further discussion under *Decodon* in Graham et al., 1985.) Clear and obvious pseudocolpi, numbering three or six (or more in the rare tetracolporate grains) are common in the Lythraceae and can be used as a taxonomic characteristic.

Haitia (Fig. 1, 2, 32, 62)—A rare, showy-flowered, ditypic genus of small shrubs endemic to Hispaniola. Six-merous flowers 10 mm long are borne on long pedicels either singly or in 2–6-flowered racemes. The floral tube bears an unusual broad encircling flange (epicalyx) at the base of the calyx lobes. The rose-purple petals are among the largest in the family, 16–20 mm long and nearly as wide, while stamens number a high 34–38. The ovary is 6-locular with minute, elongate, bilaterally compressed seeds similar to those of *Crenea, Ginoria,* and *Tetrataxis. Haitia* is most closely related to and perhaps derived from *Ginoria.* Some 6-merous species of *Ginoria* approach *Haitia* in high stamen number and development of accessory flanges on the floral tube. Surprisingly, the wood anatomy of *Haitia* is not similar to that of *Ginoria* and shows no special relationship to any other genus in the family (Baas, 1986).

Description: Pollen oblate-spheroidal, amb circular (lobate due to colpi/pseudocolpi); tricolporate with 6 pseudocolpi (heterocolpate), colpi meridionally elongated, equatorially arranged, equidistant, straight, ca. 18 μm long, extending within 5–6 μm of pole (PI 0.2), P/E 0.9, margin entire, undulating, tapering to acute apex, colpus membrane minutely granular (SEM), pseudocolpi shorter (12–14 μm), otherwise like colpi, pore circular to slightly elongated equatorially, diameter ca. 2–3 μm, situated at midpoint of colpus, margin entire, faint annulus; wall 2–2.5 μm thick, scabrate; tectate; 23–27 P × 25–29 E μm.

In SEM, *Haitia buchii* and *H. pulchra* (Fig. 32) both have well-developed pseudocolpi and a scabrate tectum. In TEM the tectum of *Haitia buchii* (Fig. 62) is thick, sometimes with large perforations; the columellae are thick, becoming slightly granular distally, and the foot layer is about twice as thick as the endexine, except near the apertures where the endexine predominates.

The relationship between *Haitia* and *Ginoria,* suggested by vegetative and floral morphology, is reinforced by the close similarity in pollen. Both have six pseudocolpi, a scabrate sculpture pattern, and are similar in other quantitative features (cf. Fig. 1, 2, 32, 62 with Graham et al., 1985, fig. 25, 26, 50–54, 76, 77). Pollen evidence supports a close affinity between *Ginoria* and *Haitia.*

Heimia (Fig. 3, 4, 33, 63)—A New World genus of two or possibly three closely related species occurring along river margins and ditches from Texas to Argentina. The species are small shrubs with solitary, axillary, campanulate flowers and deep yellow petals. The flowers are mostly 6-merous with 12 stamens and a 3–6-loculicidally dehiscent capsule enclosing many elongated obpyramidal seeds. A haploid number of 8, base number for the family, has been counted for two species (Graham, 1966, 1971). It is the only genus of Lythraceae characterized by deep yellow petals, although in a few genera of the family (*Diplusodon, Lafoensia, Cuphea, Nesaea*) there are species with cream-yellow petals that become yellow on drying. *Heimia* shares similar floral morphology with several genera, including *Decodon, Ginoria,* and *Nesaea,* as well as *Pemphis madagascariensis* (Graham, 1977; Tobe, in preparation). Prior to Koehne's (1903) monograph, *Heimia* was generally regarded as a subgenus or section of *Nesaea* (Bentham and Hooker, 1867; Baillon, 1877), but was subsequently accepted as a distinct genus following Koehne's treatment.

Other features of *Heimia* relate it to diverse genera in the family. Similar seed morphology occurs in *Didiplis, Lythrum, Pehria,* and *Woodfordia* (Graham and Tobe, in preparation). Anatomically, the vessel elements are specialized by the presence of spiral thickenings, a characteristic also found in the seem-

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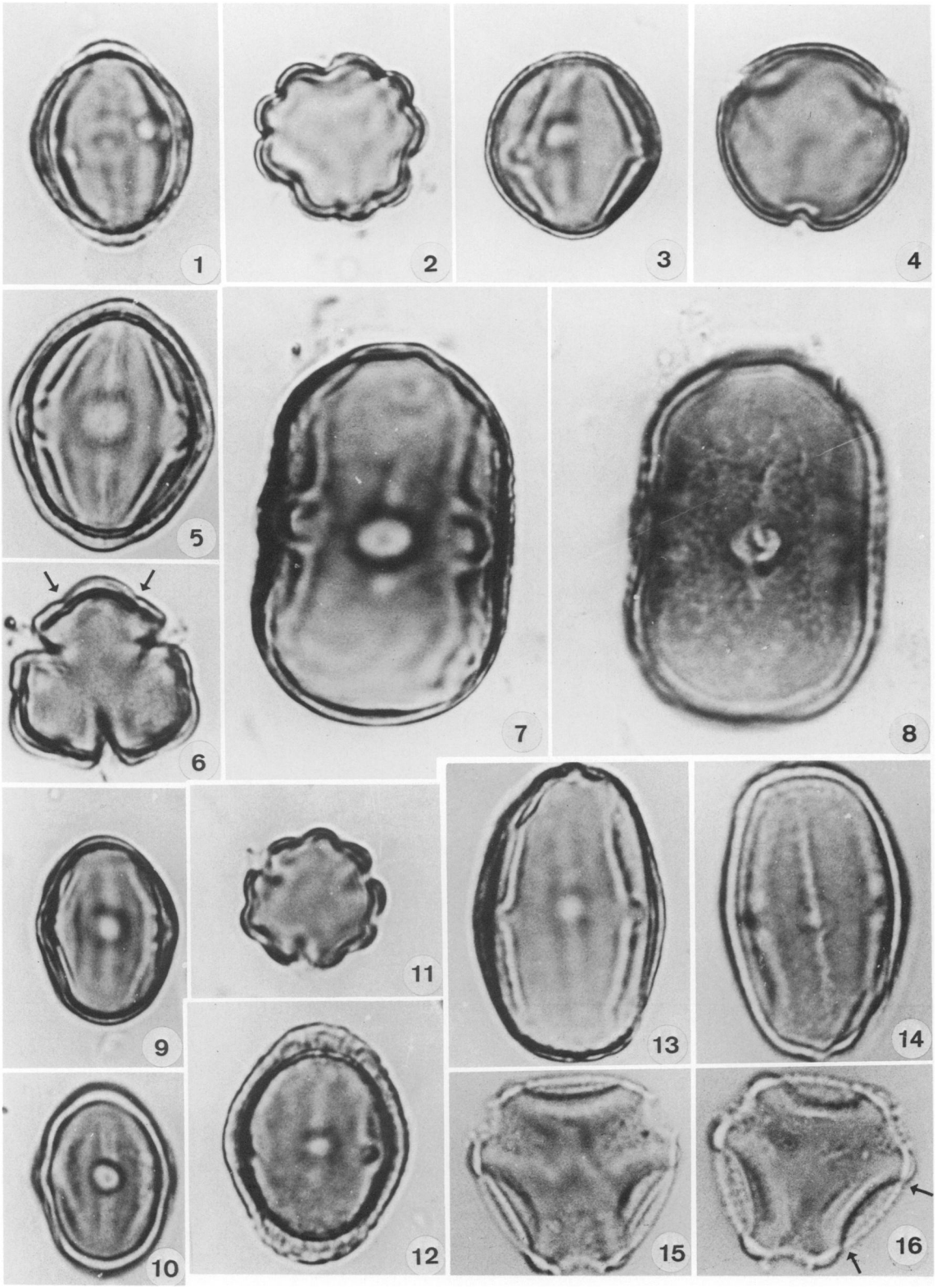


Fig. 1–16. LM of Lythraceae pollen. All taken at ×400 magnification. **1, 2.** *Haitia pulchra.* **3, 4.** *Heimia salicifolia.* **5, 6.** *Hionanthera torrei.* Note pseudocolpi at arrows. **7, 8.** *Lafoensia punicifolia.* **9–11.** *Lawsonia inermis.* **12.** *Lagerstroemia glabra,* thick-walled form. **13, 14.** *Lagerstroemia glabra,* thin-walled form. **15, 16.** *Peplis portula.* Note broad pseudocolpus between arrows.

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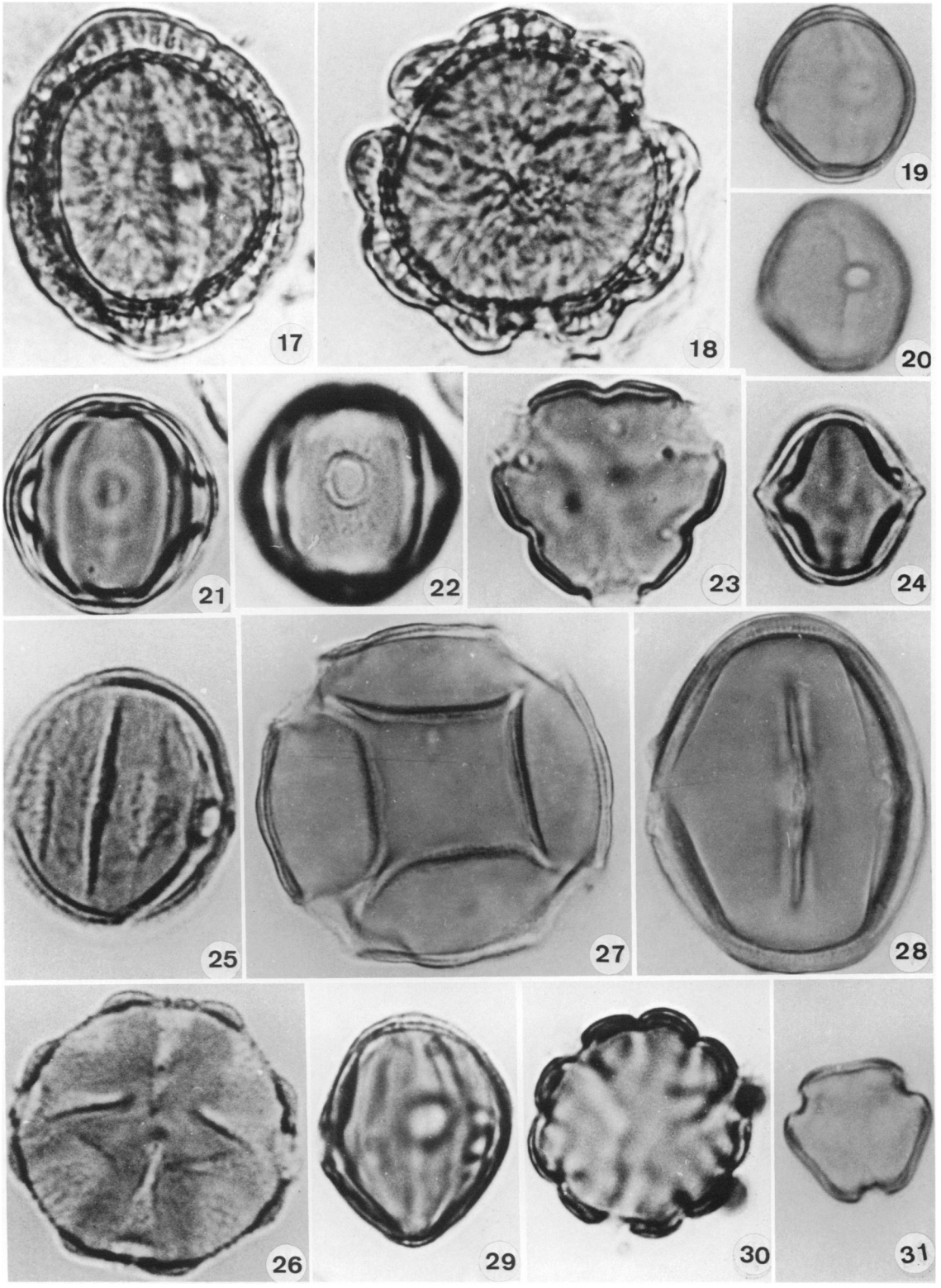


Fig. 17–31. LM of Lythraceae pollen. All taken at ×400 magnification. **17, 18.** *Lagerstroemia ovalifolia.* **19, 20.** *Orias excelsa.* **21–23.** *Lythrum salicaria.* **24.** *Pehria compacta.* **25, 26.** *Lythrum borysthenicum.* **27, 28.** *Pemphis acidula.* **29, 30.** *Nesaea radicans.* **31.** *Pemphis madagascariensis.*

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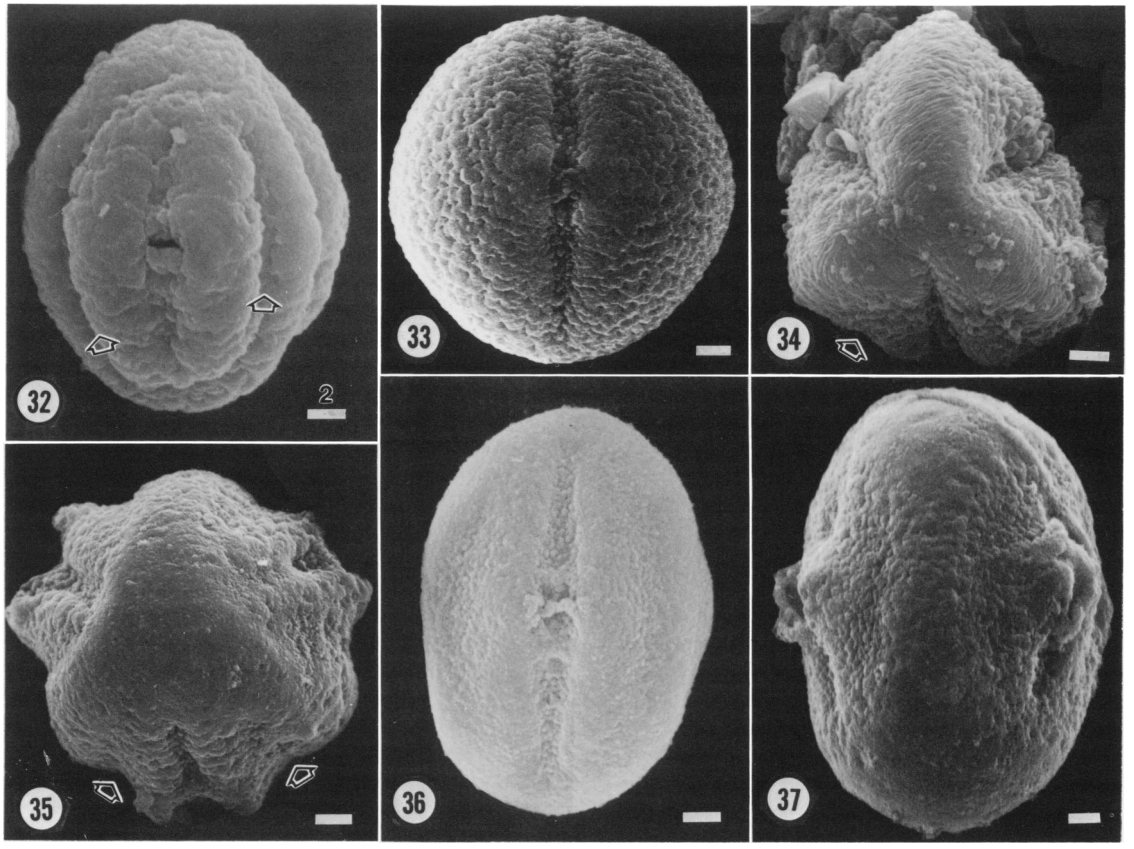


Fig. 32–37. SEM of Lythraceae pollen. **32.** *Haitia pulchra,* equatorial view. Arrows point to pseudocolpi. ×2,800. **33.** *Heimia salicifolia,* equatorial view. ×3,000. **34.** *Hionanthera mossambicensis,* polar view. Arrow points to indentation of pseudocolpi. ×3,000. **35.** *Lafoensia replicata,* polar view. Arrows point to indentation of pseudocolpi. ×3,000. **36.** *L. nummulariifolia,* equatorial view. ×3,000. **37.** *L. punicifolia,* equatorial view. ×3,000. Scales equal 2 μm.

ingly unrelated *Pleurophora* and in *Nesaea.* A second specialized anatomical feature in *Heimia,* presence of vascular tracheids, is also seen in *Woodfordia* (Baas and Zweypfenning, 1979; Baas, 1986).

Description: Pollen prolate to prolate-spheroidal, amb circular; tricolporate, colpi meridionally elongated, equatorially arranged, equidistant, straight, ca. 12 μm long, extending within 3–4 μm of pole (PI 0.12), P/E 1.3, margin entire, sides parallel, apices rounded, costae colpi, granular membrane, pore circular to slightly elongated equatorially, diameter ca. 3 μm, situated at midpoint of colpus, margin entire, annulus ca. 1 μm wide; wall 1.5–2.5 μm thick, scabrate; tectate; 20–30 P × 15–25 E μm.

In SEM, *Heimia myrtifolia* and *H. salicifolia* (Fig. 33) lack pseudocolpi and have a similar verrucate/rugulose tectum. In TEM the tectum of *Heimia salicifolia* (Fig. 63) has an undulate outer and smooth inner surface, and may be perforate; the columellae are elongate and unbranched. The foot layer and endexine are equally thick except near colpi, where the endexine becomes granular and slightly thicker.

Hionanthera (Fig. 5, 6, 34, 64)—This is a genus of four species of slender, hydrophilous herbs endemic to southeastern Africa. It was described (Fernandes and Diniz, 1955) as intermediate between *Ammannia* and *Rotala,* but differing from either in its much larger seeds (1–1.75 mm long × 0.5–1 mm wide) and persistent petals. Cook (1974) regarded *Hionanthera* and *Ammannia* as congeneric, but Panigrahi (1976) maintained the separation of the genera, based in part on pollen data, i.e., the lack of pseudocolpi in *Hionanthera* (but see below), the consistent presence of six pseudocolpi in *Ammannia,* and the occasional (variable) presence of three pseudocolpi in *Rotala.* Anatomical distinctions are also given by Panigrahi, but these are overlapping or incompletely compared and thus difficult to assess. The size of the seed in two of the four species

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(*H. mossambicensis, H. graminea*) as recorded in the protologues is greater than that of *Ammannia,* which ranges to 1 mm in length. The third species, *H. torrei,* is described with seed 1 mm long, which is within the range of *Ammannia,* and the fourth, *H. garciae,* is described by Fernandes and Diniz (1955) as seed unseen. However, Panigrahi (1976) described the seed of the latter as 1,480 μm long, and both viewed the same collection (*Garcia 790*). Seed number is more clear. No more than five seeds per capsule are recorded for any species of *Hionanthera,* a condition unknown in either *Ammannia* or *Rotala,* where seeds are generally numerous. If the combination of features described for *Hionanthera* is maintained upon closer scrutiny of additional material, i.e., persistent petals, nectariferous ring present, large seeds with no more than five per capsule, and distinctive pollen, the genus would have a firm basis for recognition.

Description: Pollen prolate to prolate-spheroidal, amb circular to more lobate in some species due to slight mesocolpial ridge; tricolporate with 6 faint pseudocolpi (heterocolpate), colpi meridionally elongated, equatorially arranged, equidistant, straight, ca. 16 μm long, extending within 4–5 μm of pole (PI 0.16), P/E 1.1, margin entire, sides parallel, apices rounded, narrow costae colpi ca. 2 μm wide, granular membrane, pseudocolpi short (12–14 μm), otherwise like colpi, pore circular, diameter ca. 3–4 μm, situated at midpoint of colpus, margin entire, annulus; wall 2–2.5 μm thick, finely striate, striae arranged parallel to colpi bordering apertures, at right angles to colpi in mesocolpial region; tectate; 27–29 P × 23–25 E μm.

In SEM, *Hionanthera mossambicensis* (Fig. 34) has faint pseudocolpi and a finely striate tectum except near the apertures where the striae are more distinct, even disrupted. In TEM of *H. garciae* (Fig. 64) a slightly oblique cross section through the mesocolpium indicates that the meridional ridges are formed by a greatly increased foot layer and more elongate columellae; nearer the colpi, however, the foot layer becomes very reduced, even absent, and the columellae are also highly reduced. Over the meridional ridge the tectum is very thin, consisting of striae underlain by a thin continuous layer that becomes much thicker near the colpi. The endexine is relatively uniform in thickness, except near the colpi where it becomes slightly thicker and granular. The thinning of the ektexine on each side of the ridge indicates pseudocolpi. Most of the striae have been cut at right angles to their long axis and appear beaded. The occasional doubling of striae may reflect the disrupted pattern shown in SEM (Fig. 34).

Panigrahi (1976) states that the pollen of *Hionanthera garciae* lacks pseudocolpi. We have examined four species, including *H. garciae,* and all have 6 pseudocolpi, although some are very faint and difficult to observe. They are represented by very slight elongated thinnings of the exine and are not readily apparent in equatorial view. In polar view, however, they are usually evident as indentations in the exine, one on each side of the mesocolpial ridge (viz., between the mesocolpial ridge and the colpus; Fig. 6).

Although the pollen of *Hionanthera* (Fig. 5, 6, 34, 64) does have 6 pseudocolpi, they are poorly developed in contrast to *Ammannia* (Graham et al., 1985: fig. 9–11, 29–32, 58; Patel, Skvarla and Raven, 1984, fig. 2A–B). Both genera have species with striate sculpture, but the striae in *Ammannia* are a single layer clearly attached to a thin uniform tectal layer, whereas in *Hionanthera* the striae in some areas form a double layer, and the layer beneath varies widely in thickness. *Ammannia* and *Hionanthera* share similar structure of the meridional ridges, thick foot layer, elongate columellae, and thin tectum. The decision to maintain *Hionanthera* as a genus requires further study, but the pollen of *Hionanthera* is considered distinct from that of *Ammannia.*

Lafoensia (Fig. 7, 8, 35–37, 65, 66)—This genus includes approximately 10 species of small shrubs to tall trees distributed from tropical South America north to southern Mexico, growing along the margins of gallery forests and on drier open sites. Key generic characters include leaves with an apical nectariferous pore, large (to 3 cm) fleshy or leathery, actinomorphic, 8–16-merous flowers which ultimately fall away from the capsule, showy yellowish white petals, 16–32 mm long, exserted stamens and woody capsules enclosing layers of large seeds (to 3 cm long) that are encircled by a thin wing. The flowers are among the largest in the family and unusual in lacking purple-toned petals. Three species of *Lafoensia* are reported to be bat-pollinated—*L. pacari, L. glyptocarpa,* and *L. punicifolia* (Vogel, 1958; Sazima and Sazima, 1975, 1977). *Lafoensia* shares two apomorphic features, foliar apical nectariferous pores that also occur only in *Galpinia* and *Capuronia,* and spiral seed coat hairs found in *Woodfordia, Pleurophora,* and *Cuphea.* In wood anatomy, characters are neither primitive nor advanced within the family, and anatomically *Lafoensia* is at a level of advancement with *Tetrataxis, Ginoria, Pehria, Galpinia,* and *Ca-*

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puronia (Baas and Zweypfenning, 1979). The genus displays the base chromosome number of the family $x = 8$, in the count of $2n = 16$ in *Lafoensia nummulariifolia* (Tobe, Raven and Graham, 1986).

Description: Pollen prolate to subprolate, amb circular (slightly lobate due to protruding pores, mesocolpial ridges, and pseudocolpi); tricolporate with 6 pseudocolpi (heterocolpate), colpi reduced in some species, meridionally elongated, equatorially arranged, equidistant, ca. 35–40 μm long, extending within 4–5 μm of pole (PI 0.10), P/E 1.2, margin entire to slightly diffuse, minutely dentate, tapering to acute apex, costae colpi ca. 1.5 μm wide, granular membrane, pseudocolpi slightly shorter (30–35 μm), otherwise like colpi, pores conspicuous, relatively large (diameter 8–10 μm), situated at midpoint of colpus, margin entire, protruding, narrow annulus ca. 1 μm wide; wall 1.5–2.5 μm thick, scabrate to finely verrucate, becoming psilate-punctate along equatorial zone of mesocolpial ridge and psilate at poles; tectate; 45–55 P × 35–45 E μm.

Four species of *Lafoensia* were examined in SEM: *L. nummulariifolia* (Fig. 36), *L. punicifolia* (Fig. 37), *L. replicata* (Fig. 35), and *L. pacari* (not illustrated). All species examined have pseudocolpi, best illustrated in polar view (Fig. 35). The tectum is almost psilate along the mesocolpial ridges and at the poles, but becomes scabrate on the borders of the apertures. In *L. pacari,* the coarsely scabrate sculpture extends to some degree onto the ridges and poles.

In TEM, the thin polar exine of *Lafoensia punicifolia* (Fig. 65) consists of a complete tectum, reduced columellae and foot layer, and very thin endexine. Near the equator the endexine becomes much thicker, the tectum is also thicker but perforate, and columellae more distinct. The meridional ridges are formed by an increase in the foot layer and elongation of the columellae. Our TEM observations of this species (see also Patel et al., 1984) are in agreement with those of Muller (1981).

In contrast to *Lafoensia punicifolia* (Fig. 65), the thick polar exine of *L. replicata* (Fig. 66) consists of a thick non-perforate tectum, well-developed, elongate and sometimes branched columellae, a thick foot layer, and a very thin endexine. However, nearer the pores the foot layer is highly reduced, the columellae are smaller and unbranched, and the tectum is slightly thinner than at the poles and perforate. The very electron dense endexine becomes the predominant layer. It is finely granular at the pore margin. Muller (1981) noted that the columellae are coarser and longer over the polar areas in *L. nummulariifolia,* whereas in *L. punicifolia* they are distinct but very short.

The exine structure is thin-walled in *L. nummulariifolia* and *L. punicifolia,* thicker-walled in *L. pacari,* and thick-walled in *L. replicata.* Differences in thickness of the wall are probably not attributable to evolution from dimorphic stamen types such as occur in *Lagerstroemia.* In *Lafoensia* both epipetalous and episepalous stamens are present in a single whorl, each arising individually, and all are of equal length. No evidence of stamen dimorphism is found in the genus.

Coz Campos (1964) and Muller (1981) noted that *Lafoensia punicifolia* had no colpate ectoapertures and his SEMs (pl. VII, fig. 1–2) support this contention. However, the specimen (*Breedlove 40657* (MO) Mexico) examined and illustrated in SEM in this study (Fig. 37) and in an earlier one (Patel et al., 1985, fig. 3D–E), does show colpate ectoapertures. In five additional collections (Table 1) examined in LM only, elongated, meridionally-oriented thinnings above and below the pores are clearly evident (Fig. 7, 8). The SEMs do show colpate ectoapertures, and *L. punicifolia,* like all other species of *Lafoensia* examined, is tricolporate.

There is some variation in pollen morphology among the species examined. The pollen of *L. pacari* differs slightly in being more prolate-spheroidal, with smaller less conspicuous pores, and with an exine slightly thicker in relation to the size of the grain. The pollen is of the same basic type, however, and shows only minor quantitative differences.

Lagerstroemia (Fig. 12–14, 17, 18, 38–42, 67)—Fifty-three species of small to large forest trees native to the Asian tropics comprise *Lagerstroemia.* The genus is well known in warmer climates of the Old and New World by the widely planted ornamentals, *L. indica* (crepe myrtle) and *L. speciosa.* Leaves are more or less alternate, apparently secondarily so, since in the Lythraceae they are typically opposite and often decussate. Inflorescences include simple racemes, compound cymes, and large lateral or terminal panicles. Flowers are 5–8-merous, with coriaceous floral tubes which may be furrowed or winged, and showy, long-clawed, rose-purple to white petals. Stamens are mostly numerous, up to 200, occasionally as few as 15 (*L. subcostata*), and in many species, including *L. indica,* are dimorphic. In *L. indica* the episepalous ones are longer and fewer in number, have thicker filaments, red anthers, and are attached singly. Epipetalous ones are shorter and more numerous, have thinner fil-

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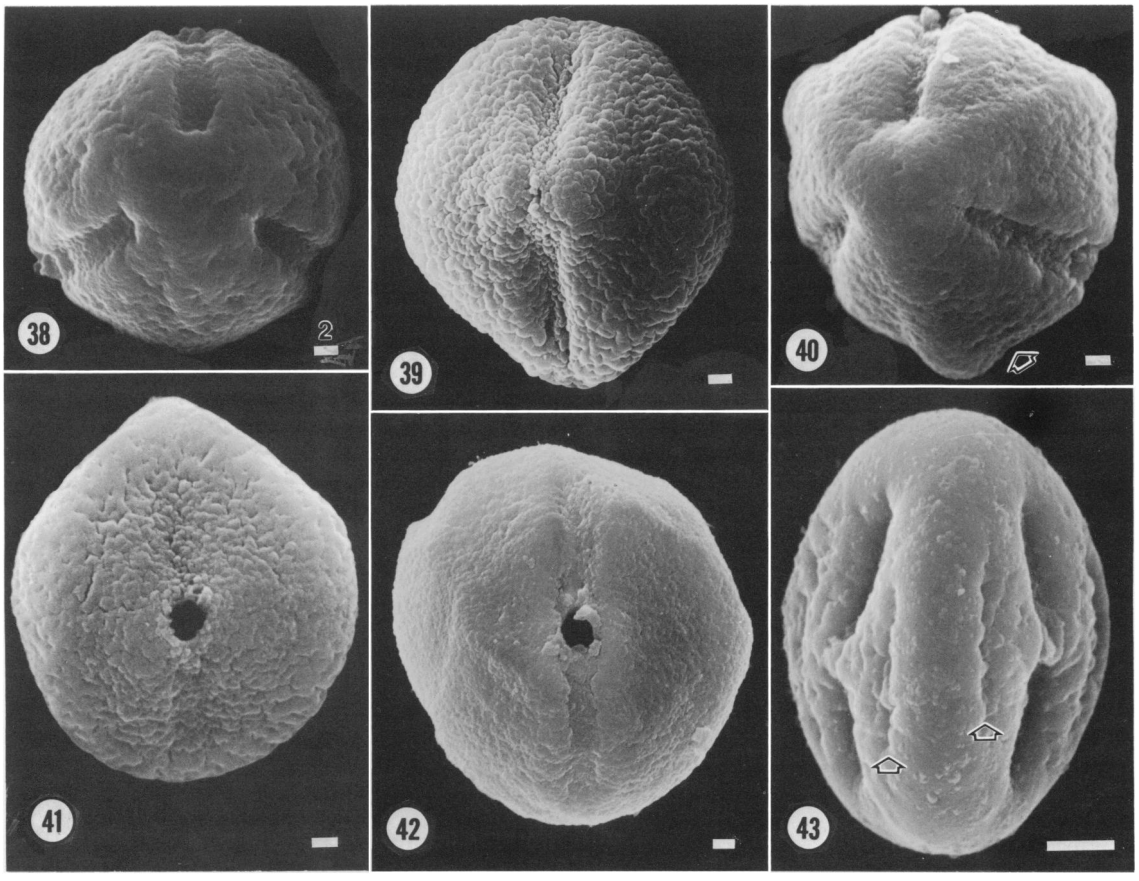


Fig. 38–43. SEM of Lythraceae pollen. **38.** *Lagerstroemia calyculata,* polar view. ×2,000. **39.** *L. floribunda,* equatorial view. ×1,835. **40.** *L. speciosa,* slightly oblique polar view. Note mesocolpial ridges. Arrow points to indentation of a pseudocolpus. ×2,000. **41.** *L. indica,* equatorial view. ×1,835. **42.** *L. tomentosa,* equatorial view. ×1,835. **43.** *Lawsonia inermis,* equatorial view. Arrows point to pseudocolpi. ×5,700. Scales equal 2 μm.

aments, yellow anthers, and are clustered basally. Both red and yellow anthers are fertile, but the pollen of the yellow ones is reportedly more moist allowing it to be better gathered by insects (Harris, 1909, 1914). Nectaries are absent in the genus (Tobe, in preparation). Seeds are unilaterally winged with revolute cotyledons, unique apomorphies in the family. Results of wood anatomical studies suggest *Lagerstroemia* is the most advanced genus in the family, combining advanced character states of crystalliferous fibers, abundant parenchyma, and homogeneous rays (Baas and Zweypfenning, 1979). Koehne (1885) regarded the genus as most closely related to *Lawsonia,* an alliance supported by wood anatomy and floral morphology (Tobe, in preparation; see pollen discussion under *Lawsonia*). Chromosome numbers in the genus range from $2n = 16$ to $n = 60$, and indicate that most species are high polyploids (Tobe et al., 1986). The genus is represented by fossil leaf impressions from the lower Eocene Deccan flora of India (Graham and Graham, 1971).

Description: Pollen prolate to prolate-spheroidal, amb circular to lobate (due to prominent mesocolpial ridges); tricolporate with 6 pseudocolpi (heterocolpate), ranging from faint, poorly defined, linear zones paralleling the colpi, to more definite and obvious pseudocolpi, colpi meridionally elongated, equatorially arranged, equidistant, straight, ca. 20–30 μm long, extending within 8–12 μm of pole (PI 0.3), P/E 1.4, margin dentate, tapering to acute apex, costae colpi 1.5–2.5 μm wide, granular membrane, pseudocolpi shorter (15 μm), otherwise like colpi, pore prominent, circular to slightly oval, diameter 3–4 μm, situated at midpoint of colpus, margin entire, annulus 1–2 μm wide; pollen dimorphic in some species, in short stamens pollen wall thick, 2–4 (–7) μm at mesocolpial ridge and at poles (polar cap), 1–3 μm nearer colpus, 1.5–2 μm along colpus, scabrate to finely verrucate, becoming scabrate-

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punctate (viz., a more solid tectum) along mesocolpial ridge, distinct columellae evident in most species and prominent in several, especially at poles, in long anthers pollen thinner-walled; tectate; 35–55 P × 25–40 E μm.

Six species were examined in SEM: *Lagerstroemia calyculata* (Fig. 38), *L. balansae, L. floribunda* (Fig. 39), *L. indica* (Fig. 41), *L. speciosa* (Fig. 40), and *L. tomentosa* (Fig. 42). Pseudocolpi are poorly developed (Fig. 40 arrow, Fig. 38) in some species. The tectum can be almost psilate at the poles and mesocolpial ridges (Fig. 40–41) while scabrate near the apertures (Fig. 41). In *L. indica* (Fig. 41) and *L. floribunda* (Fig. 39) the tectum is verrucate. In TEM the tectum of *L. indica* (Fig. 67) is incomplete near the pores; the columellae are numerous, elongate and finely granular distally; the foot layer is thin, and the endexine is thick, becoming even thicker at the pores. The meridional ridges are formed by elongated columellae, and a slightly thicker tectum and foot layer. Muller (1981) also found granular columellae in some species of *Lagerstroemia* (pl. IV, fig. 2–4).

In our preparations of *Lagerstroemia glabra* (Fig. 12–14), *L. indica,* and *L. parviflora,* a thicker-walled, coarsely sculptured, prolate-spheroidal form, and a thinner-walled, finely sculptured, and more prolate form occurred together. Single-anther lactic acid preparations showed that the thicker-walled pollen is produced by the smaller anthers with shorter filaments, while the thinner-walled pollen is produced by the larger anthers with longer filaments. Muller (1981), who designated the thinner-walled form as type A, and the thicker-walled form as type B, found this condition in *L. ovalifolia, L. piriformis,* and *L. tomentosa,* as well as *L. indica.* TEM of both pollen types of *L. indica* (Sanders 176; see Table 1) indicated that their exines are structurally similar, i.e., the thicker walled type is due to enhancement of all units—foot layer, columellae, and tectum. However, in *L. ovalifolia* Muller (1981, pl. III) found that the difference between the thick and thin-walled types was due primarily to the better development of the columellae layer in the former. In *L. speciosa* the stamens are monomorphic and there is little or no pollen dimorphism. The same is true for *L. floribunda* which has subequal stamens (Muller, 1981).

There is some variation in pollen morphology (Fig. 38–42) within this genus of 53 species apart from dimorphism associated with long and short stamens. In *Lagerstroemia indica* (Fig. 41) the ectoapertures are poorly defined, whereas in *L. calyculata* (Fig. 38) and *L. speciosa* (Fig. 40) they are well differentiated, but with blunt polar margins in the former species and pointed in the latter. In *L. floribunda* (Fig. 39) the tectum is scabrate-verrucate, in *L. tomentosa* (Fig. 42) it appears to be finely granular, in *L. calyculata* (Fig. 38) and *L. speciosa* it is mostly psilate, and in *L. indica* (Fig. 41) it is psilate on the ridges and poles, and finely verrucate near the apertures. Even with these variations, however, the pollen of *Lagerstroemia* is a recognizable type that can be characterized as prolate to prolate-spheroidal, tricolporate with six pseudocolpi, albeit very faint ones in some species, and with mostly prominent mesocopial ridges. Species with dimorphic pollen have a thicker-walled form in which individual columellae are distinct in optical section and a moderately verrucate tectum, and a thinner-walled form with very reduced columellae and a scabrate to finely verrucate tectum. For a comparison of the thinner- and thicker-walled forms in SEM, see Muller (1981, pl. III). In another plate (IV, Fig. 2–4) he illustrates in TEM the exines of a thick-walled form of *L. tomentosa* and two species with monomorphic pollen, *L. speciosa* and *L. floribunda,* all of which have granular columellae. (See *Orias* for further discussion of variation in *Lagerstroemia.*)

Lawsonia (Fig. 9–11, 43, 68)—A monotypic genus, possibly of African origin, but widely cultivated for centures throughout the Old World tropics and subtropics as a source of the red dye henna and for its fragrant showy inflorescences. *Lawsonia inermis* is a shrub with multi-flowered panicles of 3–5 mm long, white-petaled, 4-merous flowers. Eight stamens appear in pairs opposite the sepals. The capsule is indehiscent with non-winged pyramidal seeds that are thickened internally by a spongy float tissue. Floral morphology and anatomy place *Lawsonia* closest to, but less advanced than *Lagerstroemia,* and similar to, but more advanced than the more generalized genus *Ginoria.* Haploid chromosome numbers of 12, 15, and 16 occur in the genus (Tobe et al., 1986).

Description: Pollen prolate, amb circular (slightly lobate due to moderate mesocolpial ridges); tricolporate with 6 pseudocolpi (heterocolpate), colpi meridionally elongated, equatorially arranged, equidistant, straight, ca. 11–13 μm long, extending within 3–4 μm of pole (PI 0.18), P/E 1.3, margin entire (minutely dentate at SEM magnification), sides parallel, apices rounded, narrow costae colpi ca. 1.5 μm wide, pseudocolpi shorter (8–10 μm), distinctly granular, otherwise like colpi, pore circular to

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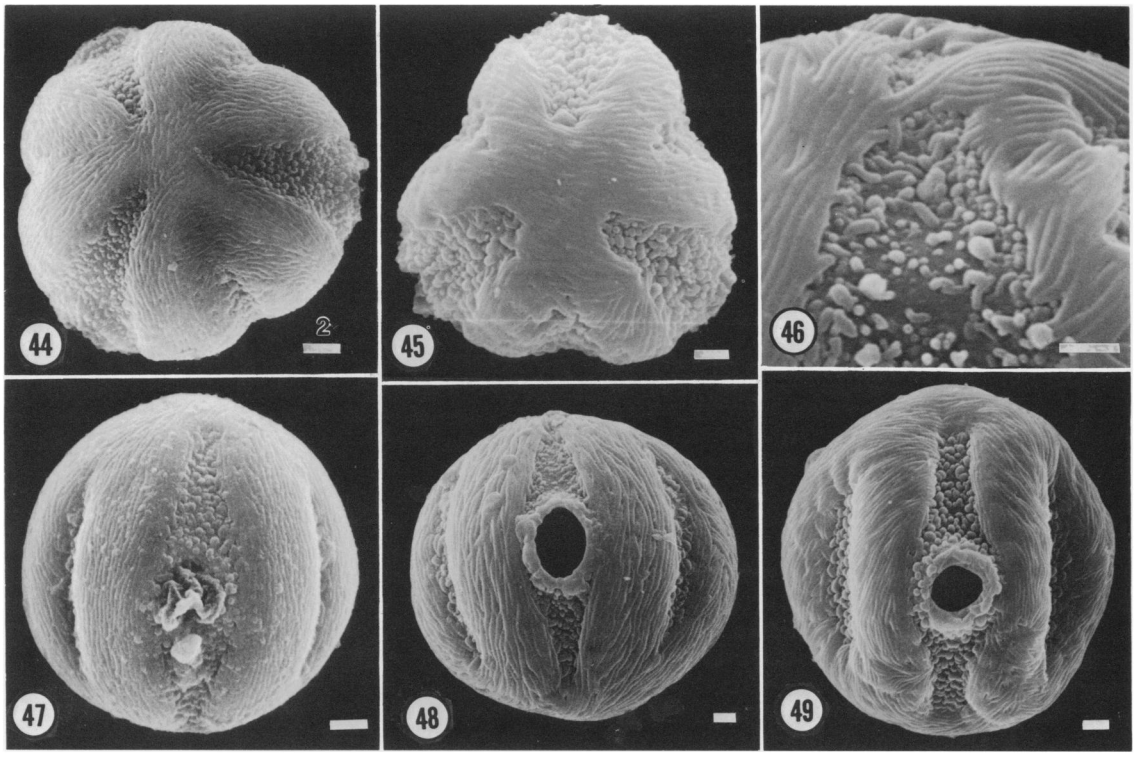


Fig. 44–49. SEM of *Lythrum* pollen. **44.** *L. salicaria,* polar view. Note wide granular colpi on all Lythrums. ×2,960. **45, 46.** *L. anceps.* **45.** Polar view. ×3,070. **46.** Tectum. ×5,000. **47.** *L. californicum,* equatorial view. ×3,140. **48.** *L. lineare,* equatorial view. ×1,800. **49.** *L. rotundifolium,* equatorial view. ×2,040. Scales equal 2 μm.

slightly elongated equatorially, diameter 2–3 μm, situated at midpoint of colpus, margin entire, narrow annulus ca. 1 μm wide; wall 1–1.5 μm thick, psilate; tectate; 20–25 P × 15–17 E μm.

Lawsonia inermis (Fig. 43) has well-delimited pseudocolpi and a generally psilate tectum except near the apertures where it is faintly verrucate/rugulose or coarsely granular. In TEM (Fig. 68) only sections cut parallel to the polar axis were observed. The thicker polar exine consists of a continuous tectum, elongate columellae that are slightly granular distally, a thick foot layer, and thin endexine. Near the equator the electron dense endexine becomes the predominant layer, with both columellae and foot layer very reduced, and the tectum less so. Although wood anatomy and floral morphology suggest an alliance between *Lawsonia* and *Lagerstroemia,* the pollen of *Lawsonia* does not match monomorphic types or dimorphic forms in *Lagerstroemia.* Pollen of both genera have six pseudocolpi (faint in some species of *Lagerstroemia*) and granular columellae, but otherwise are distinct. That of *Lawsonia* is smaller and more uniformly psilate than that of *Lagerstroemia.* Pollen morphology does not suggest a close relationship between *Lawsonia* and *Lagerstroemia.*

Lythrum (Fig. 21–23, 44–49, 69, 70)—Lythrum is a genus of primarily Eurasian and North American distribution, represented by about 35 species. It it best known by the European *L. salicaria,* loosestrife, a trimorphic species whose pollination and breeding mechanisms were the basis for the first extensive account of heterostyly (Darwin, 1865, 1877). Generic limits are not entirely clear. The species encompass a wide range of floral forms from those with floral tubes longer than wide and having conspicuous petals, to those with floral tubes wider than long with minute petals. The latter have been variously included in *Didiplis, Lythrum,* and *Peplis.* The most recent study merges *Peplis* with *Lythrum,* and maintains *Didiplis* as a monotypic North American genus (Webb, 1967). The contribution of pollen morphology to the question of relationships among these genera is discussed under the treatment of *Peplis.*

Lythrum sensu stricto consists of herbs or subshrubs of aquatic or marshy habitats, with (4-) 6-merous flowers borne singly or paired in

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the leaf axils, and a septicidal, 2–4-valved capsule. The base chromosome number is 5, with haploid numbers of 5, 10, 15, 25, and 30 reported (Tobe et al., 1986). The wood anatomical pattern of *Lythrum* is typical of several genera of small herbaceous perennials, including *Ammannia, Nesaea, Crenea,* and the shrubby *Adenaria,* and is juvenilistic in nature (Baas and Zweypfenning, 1979).

Most species of *Lythrum* are homostylous or distylous. Five species are tristylous: *L. junceum, L. maculatum, L. salicaria, L. thymifolia,* and *L. virgatum.* The North American species, comprising subsect. *Pythagorea* of sect. *Euhyssopifolia,* are all distylous with a haploid chromosome number of 10, and are probably monophyletic. The distylous condition in this section is considered derived from a tristylous one through loss of the short-style form (Ornduff, 1979). As a rule, in heterostylous species the longest stamens produce the largest pollen, the shortest produce the smallest, and the larger pollen contains a greater amount of starch (Ganders, 1979). This heterostylous syndrome is present in *Lythrum* pollen (Schoch-Bodmer, 1940; Dulberger, 1970; Ornduff, 1979). Other pollen features (aperture, shape, sculpture patterns) are similar among the various floral forms.

Description: Pollen oblate-spheroidal to prolate-spheroidal, amb circular to lobate; tricolporate with 3 pseudocolpi (heterocolpate), colpi meridionally elongated, equatorially arranged, equidistant, straight, ca. 18–26 μm long, extending within 3–5 μm of pole (PI 0.10), P/E 0.5, margin entire, tapering to acute apex, narrow costate colpi ca. 1–1.5 μm wide, granular membrane, pseudocolpi shorter (14–20 μm), otherwise like colpi, pore circular, relatively large and conspicuous (diameter 2.5–4 μm), situated at midpoint of colpus, margin entire, annulus ca. 1 μm wide, slightly protruding with granulations frequently evident on flanks of annulus; wall 1.5 μm, striate, striae arranged parallel to colpi (viz., pole to pole); tectate; 18–26 to 40–48 μm.

The pollen of *Lythrum* (Fig. 44–49) is uniform and can be distinguished by the three prominent granular pseudocolpi alternating with the three apertures, in which the colpi are also granular. The tectum is finely striate with the long axis of the striae mostly parallel to the polar axis. In TEM of *L. californicum* (Fig. 69) the exine consists of a thick tectum, sometimes with perforations, the outer margin undulate, the inner more smooth. Columellae are short and unbranched, and the foot layer is very thick. The endexine becomes thicker near the colpi and pseudocolpi, with the inner part becoming granular. The exine structure of *L. lineare* (Fig. 70) is similar. The slightly thicker, better defined foot layer shown in the illustration reflects the area sectioned (the mesocolpium).

In our preparations of *Lythrum borysthenicum* (Table 1) the aperture number is variable, frequently four with four pseudocolpi (Fig. 25, 26). An increase in aperture number can be associated with polyploidy. (See, for example, the increase in apertures in polyploid *Fuchsia* in Nowicke et al., 1984.) Polyploidy may account for tetracolporate pollen in this species, as well. In *Lythrum* the base number is 5, while *L. borysthenicum* is a hexaploid with $n = 15$ (Tobe et al., 1986). *Lythrum salicaria* ($n = 15$, 25, 30), however, has tricolporate pollen, so polyploidy is not always reflected in increased number of apertures in this genus. *Lythrum borysthenicum* has been treated as *Peplis erecta* Req. ex Moris and its status is considered in the treatment of *Peplis.*

Nesaea (Fig. 29, 30, 50–55, 71)—The genus consists of approximately 50 species of annual and perennial herbs. The majority of the species are African, but three occur disjunctly as endemics in northern Mexico and adjacent Texas. Floral morphology varies extensively, with flowers superficially similar to those of several other genera, e.g., *Ammannia, Crenea, Heimia,* and *Rotala. Nesaea* is as much recognized by lack of unique features as by a well-defined generic circumscription. Generally plants are less than 50 cm tall, the flowers are less than 5 mm long, actinomorphic, 4–8-merous, and mostly homomorphic. Distylous and possibly tristylous species are reported to occur, but have not been investigated. The capsule dehiscence is unusual, being at first circumscissile, then irregularly dehiscent below the initial opening. Only two chromosome numbers, $2n =$ ca. 50 and 60, have been reported (Tobe et al., 1986). Wood anatomy is that typical of the perennial herbs and shrubs of the family, generally lacking highly specialized features. The exception is the faint spiral thickenings of the vessels, known elsewhere in the family only in *Heimia. Nesaea* was regarded by Koehne (1903, p. 20) as "probably the oldest genus of the whole order" and he portrays the genus as central in the family, giving rise to four major evolutionary lines, including direct evolution to *Ammannia* (Koehne, 1885, p. 32).

Description: Pollen prolate to prolate-spheroidal, amb circular (lobate due to mesocolpial ridges and pseudocolpi); tricolporate with 6 pseudocolpi (heterocolpate), colpi meridionally elongated, equatorially arranged, equi-

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TABLE 1. *List of specimens examined. Species names follow the generally accepted generic treatments. Names in parentheses are those under which the herbarium specimen is presently filed, when they differ from the accepted epithet*

Species	Collection	Location	Figures
Haitia buchii Urban	Ekman 5676 TEX	Haiti	
	Ekman H5942 K	Haiti	62
H. pulchra Ekman and Schmidt	Leonard and Leonard 13168 US	Haiti	1, 2, 32
Heimia myrtifolia Cham. and Schlecht.	Smith and Reitz 10078 US	Brazil	
H. salicifolia Link	S. Graham 141 MICH	Mexico	
	S. Graham 141 KE	Mexico	63
	Runyon 575 US	Texas	3, 4, 33
	Rzedowski 165 US	Mexico	
Hionanthera garciae Fernandes and Diniz	Biegel s.n. COI	Zimbabwe	64
H. graminea Fernandes and Diniz	Torre 715 COI	Mozambique	
H. mossambicensis Fernandes and Diniz	Biegel 1022 KE	Zimbabwe	
	Biegel 1022 SRGH	Zimbabwe	34
H. torrei Fernandes and Diniz	Torre 1212 COI	Mozambique	5, 6
Lafoensia nummulariifolia St. Hil.	Dusen 15977 US	Brazil	
	S. Graham 912 MICH	Brazil	36
	Hatschbach 5087 US	Brazil	
L. pacari St. Hil.	Morin 581 MICH	Paraguay	
	Tax. Class Univ. de Brasilia No. 423 MO	Brazil	
L. punicifolia DC	Allen 1066 GH	Panama	
	Breedlove 40657 CAS	Mexico	
	Breedlove 40657 MO	Mexico	37, 65
	Calderon 1251 US	El Salvador	7, 8
	Dwyer 7131 MO	Panama	
	Foster 1389 MO	Panama	
	Hinton et al. 10822 US	Mexico	
L. replicata Pohl ssp. *adenophylla* Koehne	Irwin et al. 31929 US	Brazil	35, 66
L. vandelliana Cham. and Schlecht.	Dusen 15915 US	Brazil	
Lagerstroemia balansae Koehne	Dee 707 US	Thailand	
L. calyculata Kurz	Kerr 21305 K	Laos	
L. calyculata Kurz (*L. angustifolia* Pierre ex Laness.)	Dee 344 US	Thailand	38
L. floribunda Jack	Collins 1395 US	Thailand	
	Larsen et al. 32169 MO	Thailand	
	Larsen et al. 32169 US	Thailand	39
L. glabra (Koehne) Koehne (*L. microcarpa* Wight)	Saldanha and Ramamoorthy HFP 1676 US	India	12–14
L. indica L.	S. Graham s.n. Cult.	Texas	41
	S. Graham 502 KE	Texas	
	Rehder 2885 MICH	China	
	Sanders 176 OKL	Oklahoma	67
L. lanceolata Wall.	Ritchie 177 K	India	
L. loudonii Teijsm. and Binn.	Witt 14 K	Thailand	
L. ovalifolia Teijsm. and Binn.	Shell Oil exchange s.n., s. c.	Sumatra	17, 18
L. parviflora Roxb.	Gamble 544A K	India	
L. speciosa (L.) Pers.	Cuatrecasas 19672 US	Colombia	
L. speciosa (L.) Pers. (*L. flos-reginae* Retz.)	Franck 1114 US	Malaya	40
	Lace s.n. K	Burma	
L. tomentosa Presl	Gillis 11905 MO	Florida	42
Lawsonia inermis L. (*L. alba* Lam.)	R. Graham 232 US	Kenya	43
L. inermis L.	Bally B12595 K	Kenya	68
	King 447 TEX	Mexico	9–11
Lythrum alatum var. *alatum* Pursh	S. Graham 483 MICH	Ohio	
L. alatum var. *lanceolatum* Rothrock (*L. lanceolatum* Ell.)	Demaree 6527b KE	Arkansas	
L. anceps Makino	Togasi TNS, NO. 1578 US	Japan	45, 46
L. borysthenicum (Schrank) Litv.	Lonachevsky s.n. 6-1911 TCD	USSR	25, 26
	Ferguson and Natzio s.n. 13-6-1963 TCD	Greece	
L. borysthenicum (Schrank) Litv. (*Peplis erecta* Req. ex Moris)	Sandwith 6150 K	Spain	

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TABLE 1. *Continued*

Species	Collection	Location	Figures
L. californicum S. Wats.	S. Graham 701 KE	Texas	69
	S. Graham 701 MICH	Texas	47
	Young 93 GH	Texas	
L. curtissii Fern.	S. Graham 457 MICH	Florida	
L. hyssopifolia L.	Ferguson and Natzio s.n. 29-5-1963 TCD	Italy	
	Ferguson and Natzio s.n. 13-6-1963 TCD	Greece	
L. junceum Banks and Sol.	Brimmott and Ernst s.n. TCD	Portugal	
L. lineare L.	Fernald and Long 12747 US	Virginia	48, 70
	S. Graham 441 MICH	N. Carolina	
	Killip 13390 US	New Jersey	
	Nicolson 1790 US	N. Carolina	
L. ovalifolium Koehne	Kincaid and Johnston 54628 TEX	Texas	
L. rotundifolium Hochst. ex A. Rich.	Burger 2673 US	Ethiopia	
	Greenway and Kanuri 14840 MO	Kenya	49
L. salicaria L.	Larsen et al. s.n. 6-8-1969 TCD	Germany	
	Mazzer s.n. 7-68 KE	Michigan	21–23, 44
L. thesioides M. Bieb.	s. c., s.n. TCD	France	
L. thymifolia L.	Borel s.n. TCD	France	
L. tribracteatum Salzm. ex Sprengel	Savi s.n. TCD	Italy	
L. virgatum L.	Paun et al. s.n. 8-7-1970 TCD	Romania	
L. vulneraria Schrank	S. Graham 50 MICH	Mexico	
Nesaea cordata Hiern	Hambler 742 MO	Nigeria	
	Chase 2902 MO	Mozambique	
N. erecta Guill. and Perr.	Stubbings 3 MO	Nigeria	53
N. floribunda Sonder	Robyns 20075 US	S. Africa	50, 71
N. heptamera Hiern	Argus 2433 MO	Zambia	
	Pawek 5695 MO	Malawi	
	Robinson 3943 K	Zimbabwe	
N. lanceolata Koehne	Fosberg 51275 US	India	54
N. longipes A. Gray	Correll and Ogden 28220 TEX	Texas	51
	Palmer 72 MO	Mexico	
	Palmer 13561 A	Mexico	
	Warnock 843 US	Texas	
N. lythroides Hiern	Haarer 1344 K	Tanganyika	
N. pringlei Rose	Pringle 6758 MO	Mexico	
N. radicans Guill. and Perr.	De Cary s.n., 1931 US	Malagasy Republic	29, 30
	Lehase 2902 MO	Portuguese E. Africa	55
	Richards 25819 MO	Tanzania	
N. rigida Koehne	Plower 1499 MO	Zimbabwe	
N. sagittifolia Koehne	Scheepers 1474 MO	S. Africa	
	Werdermann and Oberdieck 2058 US	Namibia	52
N. schinzii Koehne	Best 395 MO	Zimbabwe	
N. stuhlmannii Koehne	Drummer 1934 MO	Kenya	
N. triflora (L.f.) Kunth	Schlieben 10782 MO	Mauritius	
Orias excelsa Dode	Farges s.n. P	China	19, 20
	Farges 1398 P	China	56, 72
Pehria compacta (Rusby) Sprague	Williams 10364 US	Venezuela	73
	Williams and Molina R. 23245 US	Honduras	
	Wiliams et al. 23319 TEX	Nicaragua	24, 60
Pemphis acidula Forst.	Canfield 475 US	Micronesia	59
	Fosberg and Stoddart 45805 MO	Phoenix Island	
	Frazier 1106 MO	Kenya	
	Kibuya 1204 K	Kenya	
	Kibuwa 1240 MO	Kenya	
	Raulerson 3464 MO	Guam	74
	Stoddart 7143 MO	Amirante Is.	
	Stoddart 14425 MO	Australia	
	Stoddart 14511 MO	Australia	
	von Mueller 3 K	Micronesia	27, 28

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TABLE 1. *Continued*

Species	Collection	Location	Figures
P. madagascariensis (Baker) Koehne	D'Arcy and Rakotozafy 15317 MO	Malagasy Republic	57, 58
	Lam and Meeuse 5430 K	Malagasy Republic	31
Peplis alternifolia M. Bieb.	Tzelev and Petchenyuk s.n. 1983 KE	USSR	
P. portula L.	Blake 6321 TEX	Scotland	15, 16, 61
	Howell 18566 US	California	
	Montezuma s.n. KE	Portugal	75
	Pederson and Dellgaard s.n. 6-26-1969 TCD	Denmark	
	Walas and Facik 549 US	Poland	

distant, straight, ca. 24–28 μm long, extending within 3–6 μm of pole (PI 0.11), P/E 1.2, margin entire to minutely dentate, gradually tapering to acute apex (pseudocolpi) to frequently more rounded (colpi), narrow costae colpi ca. 1.5 μm wide, membrane sparsely to more distinctly granular, pseudocolpi slightly shorter (18–22 μm), otherwise like colpi; pore circular, relatively large and conspicuous (diameter 3.5–4.5 μm), situated at midpoint of colpus, margin entire, narrow annulus ca. 1 μm wide; wall 1.5 μm thick, slightly thicker in mesocolpial region, forming faint ridges that fuse at poles (giving a trichotomous aspect in polar view of some species), striate, striae generally arranged parallel to colpi or occasionally irregularly oriented; tectate; 26–38 P × 20–32 E μm.

Seven species of *Nesaea* were examined in SEM: *N. erecta* (Fig. 53), *N. floribunda* (Fig. 50), *N. heptamera, N. lanceolata* (Fig. 54), *N. longipes* (Fig. 51), *N. radicans* (Fig. 55), and *N. sagittifolia* (Fig. 52). With the exception of *N. lanceolata* (Fig. 54), the pollen has well-defined pseudocolpi with pronounced mesocolpial ridges, and striate tecta—characteristics that are also found in *Ammannia* (Graham et al., 1985, fig. 29–32). In *N. floribunda* (Fig. 71) the tectum consists of striae underlain by a thin layer that may be discontinuous near the apertures; columellae are unbranched and sometimes very thick; the foot layer is moderately thick in the mesocolpium but very reduced near the apertures; the endexine is thin in the mesocolpium but thicker near colpi and pseudocolpi, and granular near the endoapertures.

There is a group of small, herbaceous, primarily African genera—*Ammannia, Nesaea, Rotala*—that form a related complex in the Lythraceae. Also, *Decodon, Heimia,* and *Nesaea* were historically placed together (as *Nesaea*). These alliances are evaluated in the next paper after the pollen of *Rotala* has been described.

Orias (Fig. 19, 20, 56, 72)—Orias excelsa was first described as a monotypic genus of large trees from eastern Sichuan, China, belonging to subtribe *Lagerstroemiinae* and related morphologically to both *Lagerstroemia* and *Lawsonia* (Dode, 1909). The genus is characterized by large terminal racemes to 30 cm in length, composed of minute, white, fragrant flowers. Flowers of the type specimen are 5–6-merous with only 5 or 6 episepalous stamens, compared to both episepalous and epipetalous stamens in other *Lagerstroemia.* However, new material studied by Tobe reveals "two to six (or five) epipetalous stamens in addition to the six (or five) episepalous stamens" (Tobe, personal communication to Raven, 1986). The loculicidal capsule contains two winged seeds in each of four locules. The seeds are identical to those of *Lagerstroemia* in being unilaterally winged with revolute cotyledons, a combination of characters not known elsewhere in the family. Anatomically, wood anatomy of *Orias* strongly resembles *Lagerstroemia subcostata* (Baas, 1986) and thus also supports treatment of *Orias* as a species of *Lagerstroemia. Orias* was compared to *L. yangii* Chun, by Chun (see Lee and Lau, 1983), who concluded *Orias excelsa* to be synonymous with *L. yangii.* The new combination, *Lagerstroemia excelsa* (Dode) Chun ex Lee & Lau, has recently been made (Lee and Lau, 1983).

Description: Pollen prolate to prolate-spheroidal, amb circular (faint, poorly-developed mesocolpial ridges occasionally evident); tricolporate, colpi meridionally elongated, equatorially arranged, equidistant, straight, ca. 18 μm long, extending within 3 μm of pole (PI 0.13), PE 1.1, margin entire, gradually tapering to acute apex, narrow costae colpi ca. 1–1.5

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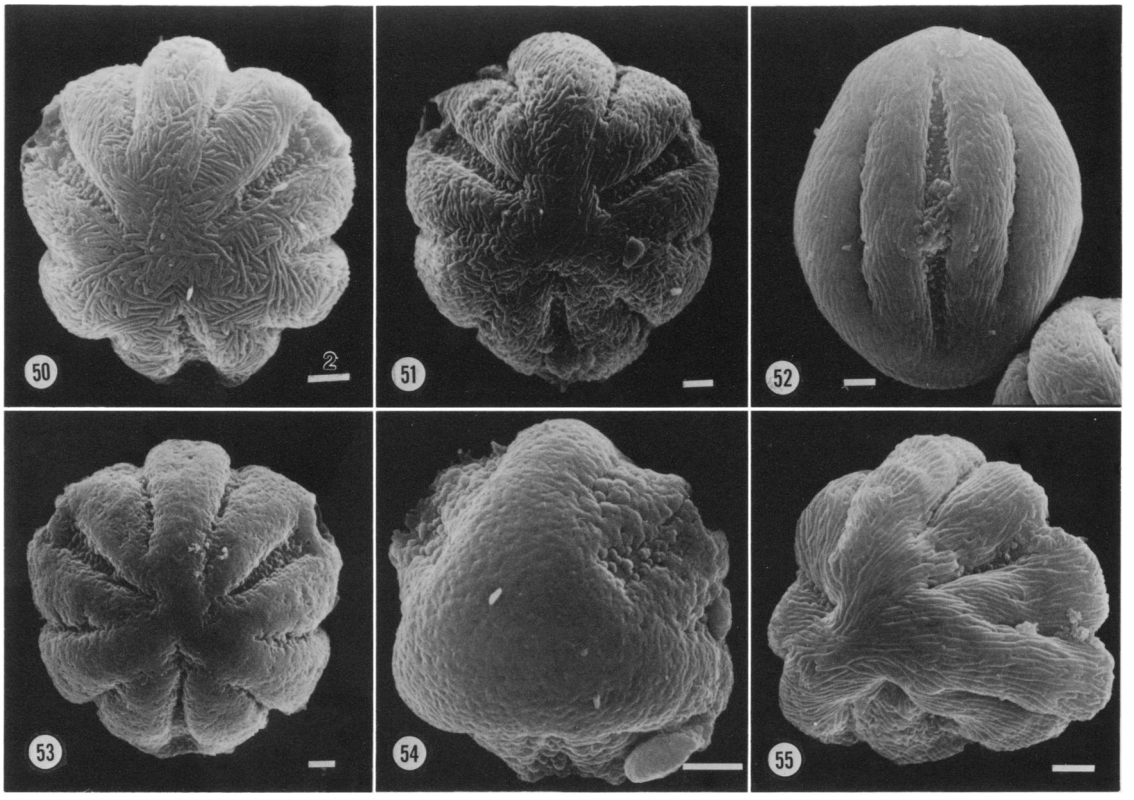


Fig. 50–55. SEM of *Nesaea* pollen. **50.** *N. floribunda,* polar view. Note prominent pseudocolpi in all Nesaeas except possibly Fig. 54. ×3,400. **51.** *N. longipes,* polar view. ×2,750. **52.** *N. sagittifolia,* equatorial view. ×3,330. **53.** *N. erecta,* polar view. ×2,600. **54.** *N. lanceolata,* polar view. ×5,500. **55.** *N. radicans,* oblique polar view. ×3,700. Scales equal 2 μm.

μm, membrane minutely granular (SEM), pore circular, relatively conspicuous, diameter 2 μm, situated at midpoint of colpus, margin entire, narrow annulus ca. 1 μm or less; wall 1.5–2 μm thick, psilate (LM; faintly scabrate SEM), very slight separation of ektexine from endexine occasionally evident at poles; tectate; 24–28 P × 20–24 E μm.

In SEM, the pollen of *Orias excelsa* (Fig. 56) has an irregularly scabrate tectum and appears to lack pseudocolpi. In TEM (Fig. 72) the exine of *O. excelsa* has a slightly perforate tectum, uniformly thick, as is the endexine and to a lesser extent, even the foot layer. The columellae are distinctive—elongate, numerous, and finely granular distally, matching those in some *Lagerstroemia* (Muller, 1981). A similar condition in the Polygonaceae, described as a granular inner surface of the tectum (Nowicke and Skvarla, 1977), reflected there close taxonomic relationship. Slightly granular columellae were found in *Haitia* (Fig. 62) and *Lawsonia* (Fig. 68).

Pollen of *Orias* differs from that of *Lagerstroemia* species studied to date (Table 1) by the lack of prominent meridional ridges, absence of well-defined pseudocolpi, and by its smaller size (24–28 × 20–24 μm vs. 35–55 × 25–40 μm). However, both share a restricted characteristic, that of numerous and elongate columellae that are distinctly granular near the tectum. Unilaterally winged seeds with revolute cotyledons, found only in these two genera and their very similar wood anatomy support reduction of *Orias excelsa* to a species of *Lagerstroemia.* Small flower size places *Lagerstroemia excelsa* in sect. *Adambea,* subsect. *Microcarpium,* with close affinities to *L. subcostata* (Furtado and Srisuko, 1969).

Pehria (Fig. 24, 60, 73)—Pehria is a monotypic genus of shrubs occurring in seasonally dry woods, along roadsides and riverbanks in northern Colombia, Venezuela, Panama, Nicaragua, and Honduras. Red-purple, cyathiform, 4-merous flowers with small red petals

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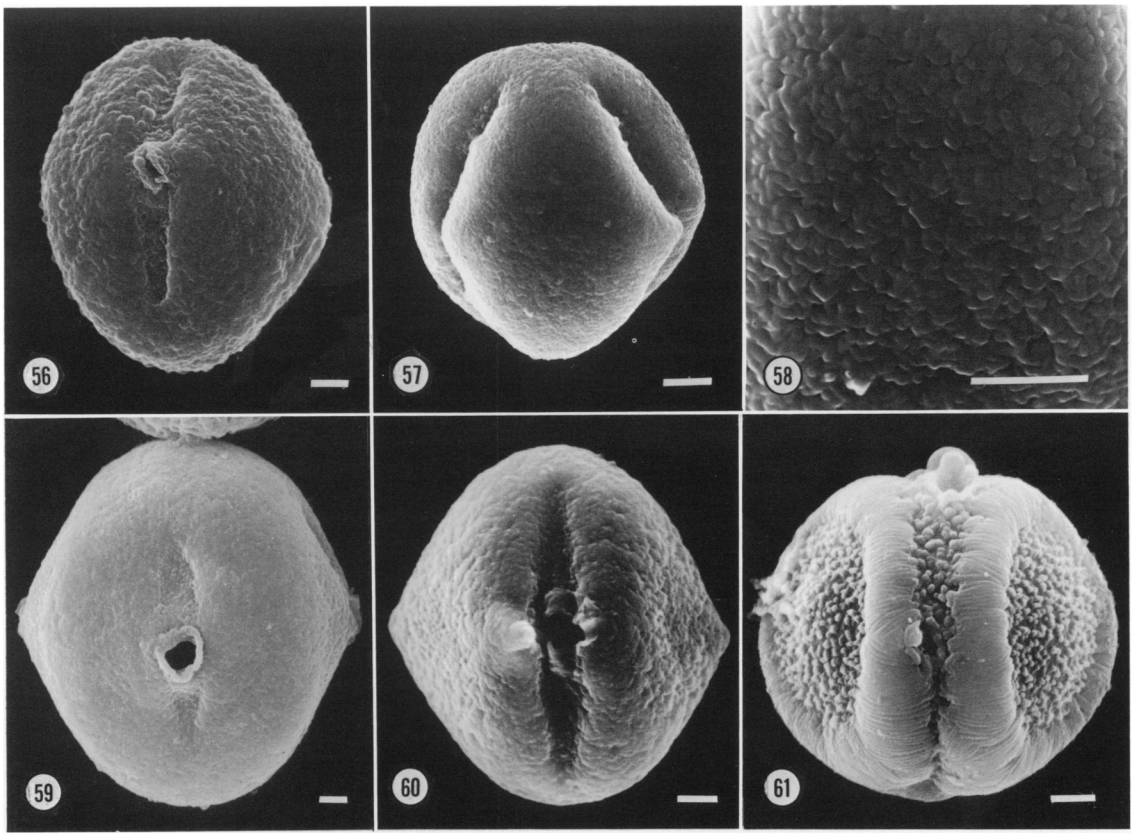


Fig. 56–61. SEM of Lythraceae pollen. **56.** *Orias excelsa,* equatorial view. ×3,000. **57, 58.** *Pemphis madagascariensis.* **57.** Oblique equatorial view. ×4,000. **58.** Tectum. ×10,000. **59.** *P. acidula,* equatorial view. ×3,375. **60.** *Pehria compacta,* equatorial view. ×2,125. **61.** *Peplis portula,* equatorial view. ×3,970. Scales equal 2 μm.

are borne in short axillary panicles along the leafy branches. The circumscissile, irregularly dehiscent capsules enclose elongate, planoconvex seeds. Floral and vegetative surfaces, including the petals, are dotted with bulbous, glandular hairs filled with an orange viscous fluid that darkens on desiccation. The same glands appear on *Adenaria* and *Pemphis madagascariensis.* Similiar, but apically stalked, glandular hairs appear in *Woodfordia* (Shome, Mehrotra and Sharma, 1981) and *Adenaria.* Anatomically, *Pehria* is linked to *Ginoria* by the presence in both of crystalliferous fibers, similar ray types, and paratracheal parenchyma. The chromosome number has been determined as $2n = 32$ (Tobe et al., 1986). Closest relationship, based on totality of commonly held apomorphies, is with *Adenaria,* another monotypic genus of northern South America, Central America, and Mexico. Besides the unusual glandular trichomes, both genera have leafy axillary inflorescences, and conspicuously stipitate ovaries.

Description: Pollen prolate, amb circular to oval-triangular, tricolporate, colpi meridionally elongated, equatorially arranged, equidistant, straight, ca. 14–16 μm long, extending within 3–4 μm of pole (PI 0.17), P/E 1.4, mar-

→

Fig. 62–68. TEM of Lythraceae pollen. **62.** *Haitia buchii.* Section through mesocolpium between a colpus and pseudocolpus. Note that columellae are slightly granular distally. **63.** *Heimia salicifolia.* Section through mesocolpium. **64.** *Hionanthera garciae.* Section of entire mesocolpium. Note variation of different layers: only the endexine is uniform in thickness; meridional ridge is formed by greatly increased foot layer and elongated columellae. Indentation (arrow) may represent a pseudocolpus. Arrowheads mark areas where striae are two-layered. **65.** *Lafoensia punicifolia.* Longitudinal section of entire grain. **66.** *L. replicata.* Longitudinal section passing through endoaperture. Polar exine consists of a thick, complete tectum, well-developed sometimes branched columellae, thick foot layer, and very thin endexine. Near the endoaperture the very electron dense endexine becomes massive with a concomitant reduction in foot layer

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and columellae. Note finely granular endexine and flecks of ektexine that cover the barely visible aperture membrane. **67.** *Lagerstroemia indica.* Section of a meridional ridge. Note elongate columellae and coarse granules (pollen is from a short stamen). **68.** *Lawsonia inermis.* Section through pole. Note shift of predominance between foot layer and endexine. Scales equal 1 μm.

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gin entire, sides parallel to gradually tapering to rounded apex, narrow costae colpi ca. 1 μm wide, ektexine bridge occasionally evident over pore on some specimens, pores circular, diameter 1.5 μm, situated at midpoint of colpus, margin entire; wall 1.5 μm thick, psilate (LM; minutely scabrate SEM), scabrae becoming more dense bordering colpi forming faint margo, columellae slightly longer (wall thicker) and more distinct at poles; tectate; 22–28 P × 16–18 E μm.

In SEM, *Pehria compacta* (Fig. 60) appears to lack pseudocolpi, but in polar view there are slight intercolpar concavities. In TEM, a cross section through an entire mesocolpium (Fig. 73) illustrates the different exine structure in the concavity: large, irregular elements of ektexine are either directly underlain by a uniformly thick endexine, or in between there may be very short columellae and a thin foot layer. At the margins of this concavity, however, the exine consists of a very thick, continuous tectum, small columellae, thin foot layer, and a thickened endexine.

The pollen of *Pehria* is very similar to that of *Adenaria* (Graham et al., 1985, fig. 1–3, 27, 55) in size (22–28 × 16–18 μm vs. 18–22 × 16–20 μm), shape (prolate vs. more prolate-spheroidal), apertures (tricolporate), sculpture (scabrate), and in the lack of pseudocolpi. In TEM *Pehria* and *Adenaria* compare well with each other, but the latter has better defined tectum, columellae, and foot layer in the mesocolpia than the former. Differences include larger and more distinct columellae at the poles, and a slightly more coarse sculpture pattern in *Pehria* (viz., the scabrae are a little larger). Nonetheless, it is clear that *Pehria* and *Adenaria* belong to the same pollen group, supporting a relationship suggested by commonly held apomorphies.

Pemphis (Fig. 27, 28, 31, 57–59, 74)—This genus consists of two highly disparate species of the Old World, *Pemphis acidula* and *P. madagascariensis.* The former is a common member of strand floras from the coast of east Africa to islands of the South Pacific. It bears solitary, axillary, 6-merous flowers with small, erect calyx lobes and white petals. Capsule dehiscence is circumscissile and the numerous seeds are surrounded by a thick, aerenchymatous tissue. Chromosome number is $2n = 32$ (Lewis, 1975). On the basis of its unique wood anatomy, *P. acidula* is without close relationship to any other genus (Graham et al., 1986). The flowers of *Pemphis acidula* are distylous, but incompletely so, with evidence that the species has evolved toward distyly from a tristylous condition by loss of the mid-styled form, in contrast to certain *Lythrum* species where distyly has evolved from tristyly by loss of the short-styled form (Lewis and Rao, 1971; Lewis, 1975; Gill and Kyauka, 1977; Ornduff, 1979). In preparations made for this study, pollen was found to be highly infertile (ca. 1% as indicated by counts of 200 grains stained 24 hours in cotton blue-lacto phenol) in both mid and low anthers in four of five long-styled collections surveyed; in the fifth, it was 29% fertile. Aborted mid-anther pollen is to be expected as the mid-style form is eliminated (Mulcahy, 1964), but in these cases little viable pollen was produced by any anther of the long-styled form. Pollen of the short-styled form averaged 69% fertility in the three collections studied, varying widely from 50 to 91%. A trend toward dioecy in these populations is suggested by the data. In Lewis and Rao's (1971) study, pollen size was largest in high anthers, intermediate in mid-anthers and smallest in low anthers, although the differentials between high-mid and mid-low were not great. There appear to be no significant morphological differences accompanying size differences in the pollen.

The second species, *Pemphis madagascariensis,* differs from *P. acidula* in a number of important ways. In *P. madagascariensis* the flowers and leaves are gland-dotted (as in *Pehria* and *Adenaria*); the floral tubes lack the vestiture and furrowing of *P. acidula*; and they have large, reflexed lobes and display rose-purple petals and long-exserted, homomorphic stamens and style. Stamens are biseriate, with one stamen in front of each petal and two in front of each sepal.

Description (Pemphis acidula): Pollen prolate to prolate-spheroidal, amb square; tetracolporate with 8 faint pseudocolpi (occasionally tricolporate with six pseudocolpi), colpi meridionally elongated, equatorially arranged, equidistant, straight, 25–35 μm long, extending within 8–10 μm of pole (PI 0.16), P/E 1.2, margin entire, gradually tapering to slightly rounded to acute apex, costae colpi 1.5–2 μm wide, ektexine bridge frequently evident over pore, pseudocolpi represented by slightly increased granulation in equatorial mesocolpial region, two on each side of slight mesocolpial ridge, shorter than colpi (ca. 14–18 μm), otherwise like colpi, pore circular, diameter 10–14 μm, situated at midpoint of colpus, margin entire, narrow annulus; wall 2 μm thick to 3–3.5 μm in mesocolpial region reflecting slight mesocolpial ridge, psilate to faintly scabrate; tectate; 40–55(–67) P × 30–40(–54) E μm.

Description (Pemphis madagascariensis): Pollen prolate-spheroidal, amb oval-triangular

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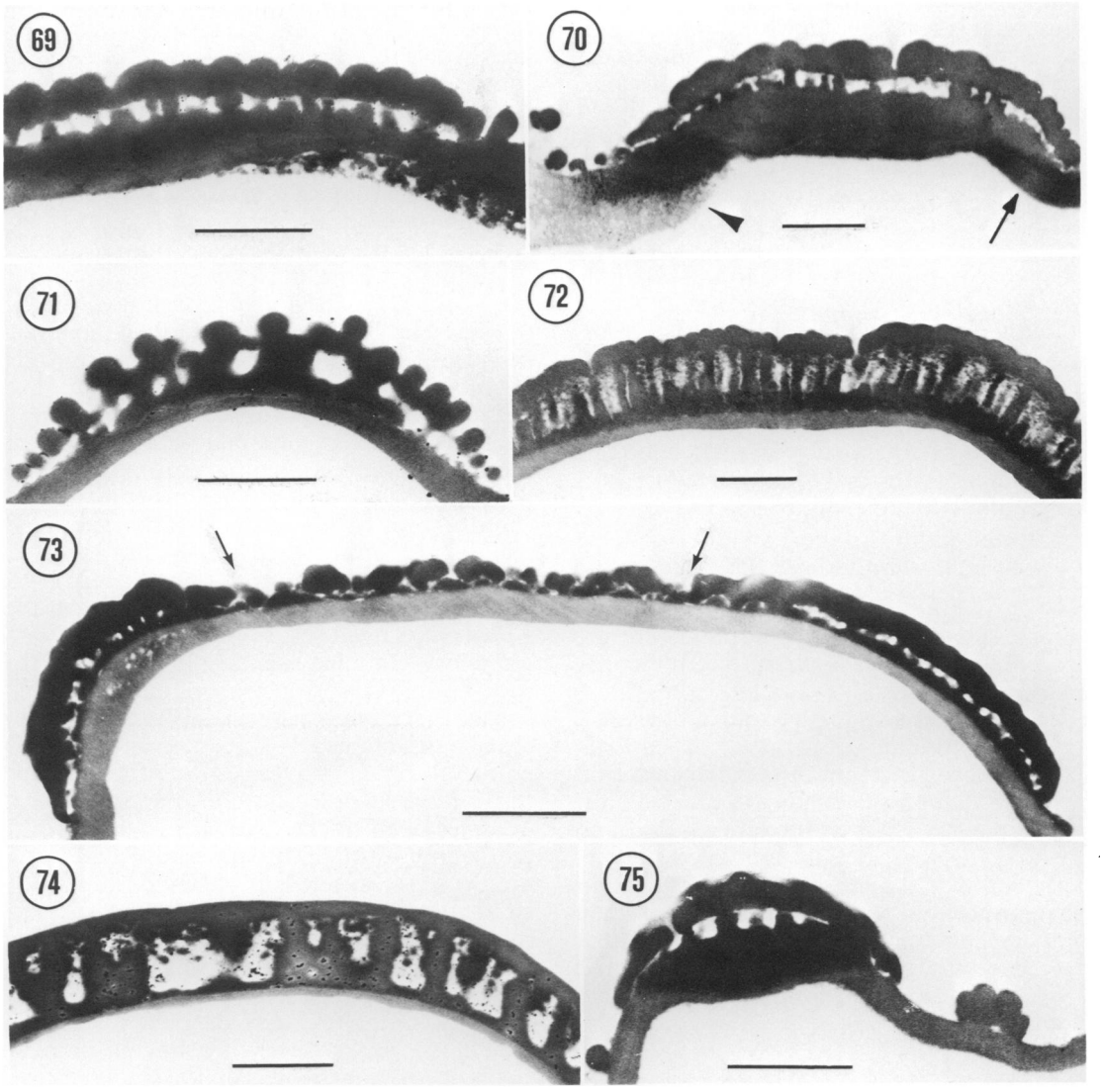


Fig. 69–75. TEM of Lythraceae pollen. **69.** *Lythrum californicum.* Section of mesocolpium near an endoaperture. Note short, thick columellae. **70.** *L. lineare.* Section through mesocolpium. Note shift of predominance between foot layer and endexine below colpus (arrowhead) and pseudocolpus (arrow), respectively. **71.** *Nesaea floribunda.* Section through part of mesocolpium. **72.** *Orias excelsa.* Section through mesocolpium. Columellae are numerous, elongate, and distally granular. Foot layer and endexine are equally and uniformly thick. **73.** *Pehria compacta.* Section of mesocolpium. Central part (between arrows) may represent an intercolpar concavity. **74.** *Pemphis acidula.* Section of center of mesocopium. Note thick, branched columellae and granular material in between. **75.** *Peplis portula.* Section of exine between intercolpar concavity (to right) and colpus (to left). Note that here the foot layer is very electron dense, as are the short columellae. Scales equal 1 μm.

to nearly spherical, rarely square reflecting occasional tetracolporate grain; tricolporate with 3 faint pseudocolpi, colpi meridionally elongated, equatorially arranged, equidistant, straight, 10–16 μm long, extending within 3 μm of pole (PI 0.16), P/E 1.3, tapering to acute apex, narrow costae colpi ca. 1 μm wide, ektexine bridge frequently evident over pore, pseudocolpi represented by slightly increased granulation in equatorial mesocolpial region, shorter than colpi (7–9 μm), otherwise like colpi, pore circular, diameter 2.5–3 μm, situated at midpoint of colpus, margin entire; wall 1.5 μm thick, faintly scabrate; tectate; 19–26 P × 14–20 E μm.

Pemphis acidula (Fig. 59) is tetracolporate, without pseudocolpi, with an almost psilate tectum; *P. madagascariensis* (Fig. 57, 58) is

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tricolporate, with 3 faint pseudocolpi, with a tectum that is scabrate but with a uniform configuration. In the mesocolpium of *Pemphis acidula* (Fig. 74) the tectum is thin, the columellae thick, branched, and with granules in the intercolumellar spaces. Both foot layer and endexine are very thin. Toward the mesocolpial margins (not illustrated here) the tectum is slightly thicker, columellae are unbranched, short, and without granules in the intercolumellar spaces; the foot layer is thinner than the endexine.

To determine if tetracolporate pollen was a consistent feature of *Pemphis acidula,* samples were taken from floral forms of the following collections:

Frazier 1106; (long style)
Kibuwa 1240; (short style)
Stoddart 7143; (long style)
Stoddart 14511; (short style)
Fosberg & Stoddart 54805; (long style)
Stoddart 14425; (short style)

Single-flower lactic acid mounts were prepared for each floral form among the collections. In all, the pollen was tetracolporate in both the long-style and short-style flowers.

The very different pollen type of *P. madagascariensis* suggests that the inclusion of this species in *Pemphis* expands the generic limits to a degree greater than for other lythraceous genera (*Cuphea* excepted). A detailed study recently completed has concluded that differing pollen morphology, together with numerous floral morphological and vegetative differences, necessitates removal of this species from *Pemphis* and the designation of a new genus (Graham et al., 1986).

Peplis (Fig. 15, 16, 61, 75)—This is a genus of small aquatic herbs whose taxonomic boundaries are presently in question. Considered by Koehne (1903) to consist of three species, it has most recently been treated as a congener of *Lythrum* (Webb, 1967). Two western Eurasian species, *P. portula* (*Lythrum portula* (L.) Webb) and *P. alternifolia* Bieb. (*L. volgense* Webb) are 6-merous, with a base chromosome number of $x = 5$. A third species, *P. diandra* DC., with 4-merous flowers and $x = 8$ (Tobe et al., 1986) is now generally recognized as the monotypic American genus *Didiplis diandra* (DC.). Wood (Graham et al., 1985, fig. 22, 41, 71). According to Webb (1967), there is no significant difference in floral tube shape, stamen and petal number or size, or capsule dehiscence between the European *Peplis* and certain species of *Lythrum,* especially *L. borysthenicum* Litv. (also regarded as *Peplis erecta* Req. ex Moris). However, nectaries are lacking in *P. portula, P. alternifolia,* and *L. borysthenicum,* and present in *Lythrum* sensu stricto (Tobe, in preparation). Studies in floral anatomy show *P. portula, L. borysthenicum,* and *Didiplis* distinct with respect to placental vascularization, with *Didiplis* and *L. borysthenicum* more similar to each other than to *P. portula.* Both *Didiplis* and *P. portula* vascularization patterns, however, may be derived by reduction from the *L. borysthenicum* type (DeVos, 1971). The pollen morphology of *Peplis* (based on *P. portula*) is described separately because it, like *Didiplis,* is distinct from *Lythrum.*

Description: Pollen oblate-spheroidal, amb oval-triangular, tricolporate with 3 conspicuous pseudocolpi (intercolpar concavity, see Patel et al., 1984; heterocolpate), colpi meridionally elongated, equatorially arranged, equidistant, straight, ca. 12–14 μm long, extending within ca. 3 μm of pole (PI 0.15), P/E 0.8, margin slightly diffuse, sides nearly parallel with rounded apices, colpus membrane conspicuously granular, pseudocolpi large, oval (ca. 9 × 4 μm), occupying most of equatorial mesocolpial region, conspicuously granular, pore circular, diameter 2.5–3.5 μm, situated at midpoint of colpus, pore margin entire, annulus ca. 1 μm wide, outer annulus margin lobate to irregular; wall thickest (ca. 1 μm) in mesocolpial region, thinner at colpi and pseudocolpi, mesocolpia restricted to bands 2–3 μm wide, striate, striae oriented transversely across mesocolpial bands, more randomly oriented clusters of striae toward poles; tectate; 15–17 P × 19–21 E μm.

Peplis portula (Fig. 61) has pollen with large oval intercolpar concavities having granular elements similar to those on the ectoapertures. As a result of the large concavities, the striate tectum, on which the striae are oriented transversely (i.e., parallel to the equatorial axis) is limited to the poles and a narrow band on each side of the apertures. In TEM (Fig. 75) the tectum is complete and the columellae are short, thick and unbranched. The foot layer is massive and very electron dense, and the endexine very thin. The intercolpar concavities appear to consist of an endexine layer with granular elements. Pollen of *P. alternifolia,* observed in LM and SEM, is comparable to that of *P. portula.*

Pollen of *Peplis portula* and *P. alternifolia* is similar to that of *Lythrum*: tricolporate with 3 pseudocolpi, striate mesocolpial areas, and granular colpi. However, in *Peplis* the mesocolpial striations are oriented at right angles to the colpus, and the pseudocolpi are oval with

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broad apices. Grains of *Peplis* further differ from *Lythrum* in size and, to a lesser degree, in shape. The diameter of *Peplis* pollen (15–17 μm) approaches that of the smallest grains of *Lythrum* (18–26(–40) μm) and the shape is less prolate than in *Lythrum*. The exine of the mesocolpia is similar in *Peplis* and *Lythrum*, with a very thick foot layer, short and simple columellae, a thick tectum, and a very thin endexine.

Pollen of *Lythrum borysthenicum* (*Peplis erecta*; Fig. 25, 26) is more similar to typical *Lythrum* pollen than to *Peplis*, in its size, striations generally parallel to the polar axis, and presence of narrow pseudocolpi with acute apices. On the basis of pollen characters, this species would be regarded as a *Lythrum* (see additional comments under discussion of *Lythrum*).

The genus *Didiplis* (*Peplis diandra*), as reported earlier (Graham et al., 1985), differs substantially from both *Peplis* and *Lythrum* pollen types in lacking pseudocolpi and/or intercolpar concavities. Further, in *Didiplis* (Graham et al., 1985, fig. 41) the triangular shape in polar view is due to the prominent mesocolpial ridges, whereas in *Peplis* (Fig. 61) the triangular shape in polar view is due to the restriction of the tectum to narrow bands on each side of the three colpi. Recognition of *Didiplis* as a monotypic genus, rather than a member of *Peplis* or *Lythrum* is supported by its distinctive pollen morphology.

Species examined in the *Peplis-Lythrum* complex (Table 1) belong in one of two pollen groups: 1) small grains with transverse mesocolpial striations and oval pseudocolpi with rounded apices, including *P. portula* and *P. alternifolia*, and 2) larger, more prolate grains with mesocolpial striations mostly parallel to the colpus, and more linear pseudocolpi with acute apices, including *L. borysthenicum* and all other *Lythrum* examined. How these pollen categories ultimately are reflected in a revised classification of the group will depend upon a synthesis of information from all sources. On the basis of pollen data, *Peplis portula* and *P. alternifolia* comprise a taxonomic unit distinct from *Lythrum* sensu stricto.

DISCUSSION—A summary of general conclusions will be deferred until the study is complete, but results of taxonomic interest can be presented for six groups of genera included in this part of the survey. First, pollen evidence suggests a close relationship between *Haitia* and *Ginoria*. Similarly, *Pehria* and *Adenaria* clearly belong to the same pollen group. The status of *Hionanthera* is still under review, but there are differences between the pollen of *Hionanthera* and *Ammannia*. It is noteworthy that the pollen of *Ammannia*, excluding *Hionanthera*, is similar among the eight species surveyed. A complex of morphological features supports the inclusion of *Orias* in *Lagerstroemia*. The pollen has a different aspect in LM and SEM, but does share certain ultrastructural characteristics. The contribution of pollen data to understanding relationships in the *Peplis-Lythrum* complex is that 1) the pollen of *Lythrum* sensu stricto is relatively uniform among the species examined, and 2) pollen of *Peplis portula* and *P. alternifolia* differs sufficiently from that of *Lythrum*, including *L. borysthenicum*, to support treatment of *Peplis* as a separate genus. Finally, the pollen of *Pemphis acidula* is different from that of *P. madagascariensis*, and this difference was one reason for removing *P. madagascariensis* from *Pemphis* to a new genus (*Koehneria*; S. Graham et al., 1986). The concluding paper of this study will treat the genera *Physocalymma, Pleurophora, Rotala, Tetrataxis* and *Woodfordia*, and present a summary of palynological results relevant to the systematics of the Lythraceae.

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