

KOEHNERIA, A NEW GENUS OF LYTHRACEAE FROM MADAGASCAR¹

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ABSTRACT

The new monotypic genus *Koehneria* is described, based on *Pemphis madagascariensis*, one of two species of the lythraceous genus *Pemphis*. It is distinguished from *Pemphis acidula* and other members of the Lythraceae by a combination of characters including: glandular trichomes, strongly reflexed calyx lobes, doubled episepalous stamens, a conspicuous ovary stipe, elongated inner epidermal cells of the ovary wall, septifragal capsule dehiscence, 3-pseudocolpate pollen, and wood with septate fibers, scanty parenchyma, and erect ray cells. Morphological, palynological, and anatomical comparison of *Koehneria* is made to the Old World genera *Pemphis*, *Lagerstroemia*, *Woodfordia*, and the New World genera *Adenaria* and *Pehria*. The last three genera share with *Koehneria* a three-character synapomorphy absent from *Pemphis* and *Lagerstroemia* and all other genera of the family. A common ancestral origin is postulated for *Koehneria*, *Woodfordia*, *Adenaria*, and *Pehria*, but subsequent extensive morphological divergence, together with wide geographic dispersal and extinction of intervening forms, limits understanding of more specific inter-generic relationships.

Among the 15 monotypic or ditypic genera of the family Lythraceae is the Old World genus *Pemphis*, whose two species have long been regarded as highly disparate (Koehne, 1901). *Pemphis acidula* Forster, the type of the genus, is a well-known, widely-distributed species of strand and dune habitats occurring on the east African coast and eastward on islands throughout the Indian and western Pacific Oceans. *Pemphis madagascariensis* (Baker) Koehne, in contrast, is an endemic of semiarid savannahs of the southern half of Madagascar. Recently, new collections of *P. madagascariensis* became available for study, allowing the question of the species' generic status and its affinities to other members of the family to be reassessed from a more extensive data base.

Pemphis madagascariensis was originally described as a *Lagerstroemia* from south-central Madagascar in 1881 (Baker, 1881, 1882). At that time, only flowering material, without fruits, was known. Koehne's monograph of *Lagerstroemia*, which followed soon after, included the species, although it was noted that authentic material had not been seen by the author (Koehne, 1883). In

1896, a second species of *Pemphis*, *P. punctata* Drake, was described from the same general geographical area as *L. madagascariensis* and was distinguished from *P. acidula* by the presence of punctae on the leaves, buds, and ovaries and by the long-exserted stamens and style. Koehne, in monographing the family Lythraceae, remarked that he had yet to see a single flower of *Lagerstroemia madagascariensis* (18 years after his treatment of *Lagerstroemia*) and noted in the same work that *P. punctata* was quite different from *P. acidula* although they shared the same inflorescence type (Koehne, 1901). In completing the monograph of the Lythraceae, Koehne finally was able to study material of this taxon from Kew, which included important features of the seed, undescribed until then, and as a result he transferred *Lagerstroemia madagascariensis* to *Pemphis*, citing *P. punctata* in synonymy (Koehne, 1903).

The generic position of *Pemphis madagascariensis* has depended exclusively on inflorescence and floral morphological features observed at the turn of the century. This study presents detailed floral morphological and anatomical features, leaf

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and wood anatomical characteristics, and pollen morphology for *P. madagascariensis*, and provides comparison to *P. acidula* and other putative allies. The unique circumscription of *P. madagascariensis* described here supports its treatment as a new genus of the Lythraceae.

MATERIALS AND METHODS

Observations on floral and seed morphology and floral anatomy of *Pemphis madagascariensis* were based on FAA-preserved material (*D'Arcy & Rakotozafy 15317*, MO; *Dorr et al. 3923, 3933*, MO), supplemented by dry materials from herbarium specimens (TAN and MO). Anatomical observations of flowers were made using microtome sections prepared following a standard paraffin method; scanning electron-microscopic observations were made according to standard techniques using a JSM-25S (JEOL) microscope.

The following additional fixed materials were compared: *Adenaria floribunda* H.B.K., *Knapp & Schmalzel 5208* (MO); *Pehria compacta* (Rusby) Sprague, *Berry 4006, 4028* (VEN); *Pemphis acidula* Forster, *Raulerson s.n. in 1982* (MO); *Woodfordia fruticosa* Kurz, *Dice & Musial s.n. in 1983* (MO), *Nasir s.n. in 1983* (MO), and *Bird s.n. in 1983* (MO).

For leaf anatomical descriptions of *Pemphis madagascariensis*, material of *R. Decary 8940* (L) and *L. Bernardi 11181* (L) was studied. For leaf-anatomical comparisons, data scattered in the literature and summarized by Solereder (1899, 1908), Metcalfe and Chalk (1950) and Napp-Zinn (1973, 1974) were complemented with original observations for *Adenaria*, *Pehria*, *Lagerstroemia*, and *Woodfordia* in order to contribute to an assessment of the affinities of this new genus. Sections of other genera represented in the Rijksherbarium slide collection (*Ginoria*, *Lawsonia*, *Lafoensia*, and *Physocalymma*) were also included in the comparison. For wood anatomy, twigs of *P. madagascariensis* 3 and 4.5 mm in diameter were studied from the collection *D'Arcy & Rakotozafy 15317* (MO) and ca. 12 mm diameter from *Dorr et al. 3923, 3933* (MO). The paper by Baas and Zweypfenning (1979) served as a source of comparative data, complemented by sections of twig material of *Pemphis* and *Lagerstroemia*.

Light microscope and scanning electron microscope (SEM) comparisons of pollen of *Pemphis madagascariensis* were made with pollen of all genera of the Lythraceae utilizing the pollen

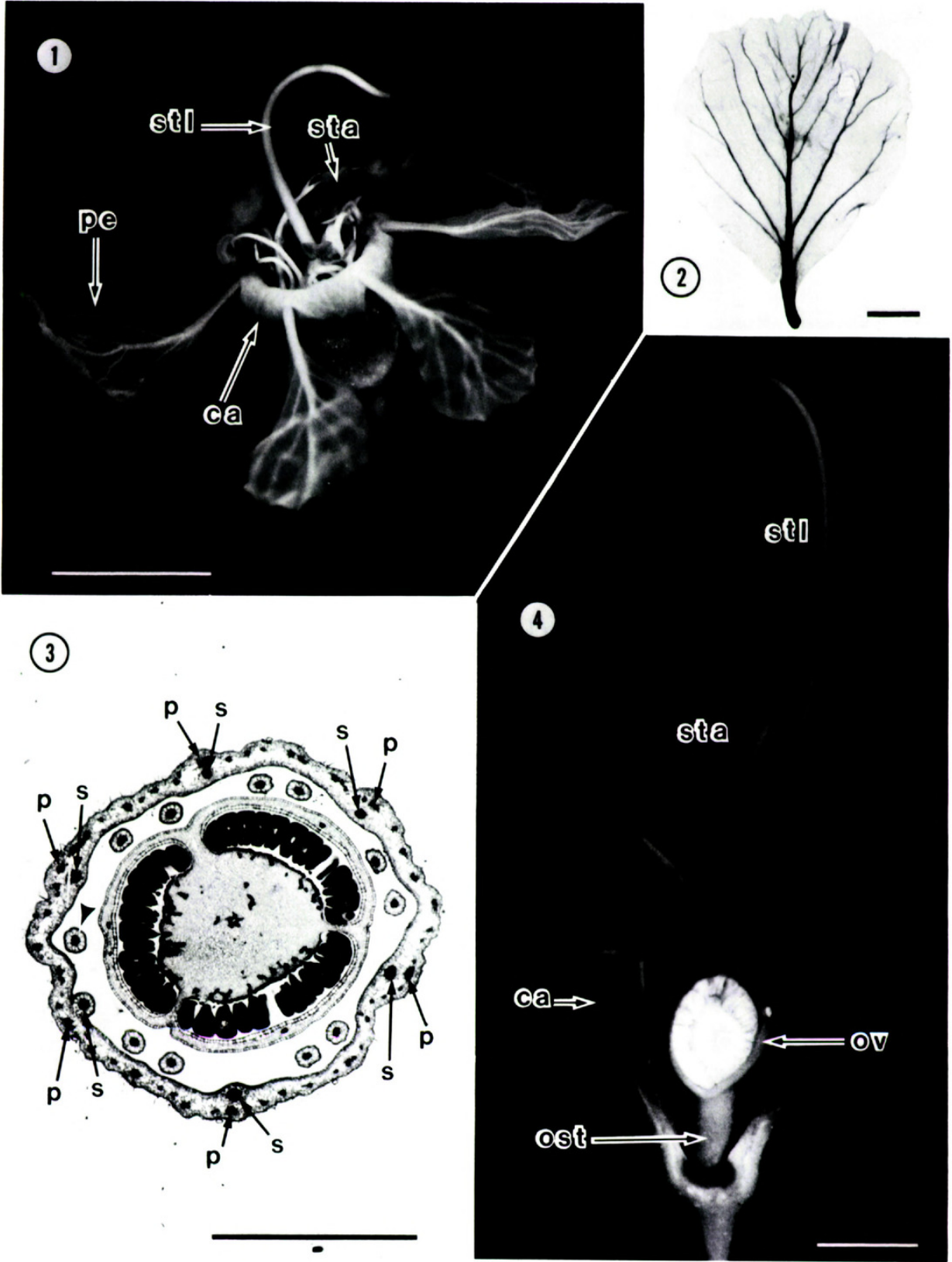
collections of A. Graham, Kent State University. A Cambridge Stereoscan SEM 100 was employed for pollen and leaf trichome photos.

FLORAL MORPHOLOGY

Flowers are homomorphic, actinomorphic, perfect, and basically 6-merous (Fig. 1). The floral tube is campanulate, and the length from the base to the tip of the calyx lobes is 4.5–8.5 mm. The calyx lobes are six in number, deltoid, and strongly reflexed (Figs. 1, 4). A conspicuous appendage (the epicalyx) is present at the sinus between adjacent lobes and its length varies from 0.0 to 2.0 mm. There are six petals opposite the appendages. These are widely obovate with a short claw, 5.5–10.0 mm long and 4.0–7 mm wide (Fig. 2). The venation of the petals is simple, with a thick midvein present in the center, and four or five secondary veins. There are no anastomoses between the secondary veins (Fig. 2).

The androecial position is perigynous. The stamens are commonly 18 in number (occasionally fewer or more) of which 12 (10–14) are opposite the sepals, and 6 opposite the petals. Episepalous stamens are inserted at nearly two-fifths the height of the floral tube, and epipetalous stamens at a slightly higher level (Fig. 3). The episepalous stamens are generally paired; in Figure 3 ten of the 11 episepalous stamens are paired, the single remaining one is indicated by an arrow. The paired stamens seem to have been derived by early splitting of the stamen meristem (chorisis), an occurrence common in several Lythraceous genera such as *Lagerstroemia*, *Crenea*, *Lawsonia*, *Nesaea*, *Heimia*, and *Ginoria* (Tobe et al., in prep.). Rarely, additional stamens are produced by splitting of a filament 1–2 mm above the point of insertion to form two stamens. Filaments of the episepalous stamens are 10–11 mm long, somewhat longer than those of the epipetalous stamens, which are 7–8 mm long. Exsertion of episepalous and epipetalous stamens approximately equals the length of the floral tube (Fig. 4).

The ovary is superior and globose, with a conspicuous stipe, 1.0–1.2 mm long (Figs. 4, 7). Presence of a comparable ovary stipe is seen elsewhere in the family only in *Adenaria* and *Pehria*. The style is narrow, slightly exceeding the stamens, and 7–15 mm long. It tapers to a punctiform stigma. The capsule is globose, and the mode of dehiscence is probably septifragal marginicidal. Although sometimes incomplete, dehiscence occurs from the top of the capsule by



FIGURES 1-4. *Koehneria madagascariensis*.—1. Flower.—2. Petal cleared with 8% KOH.—3. Transverse section (TS) of flower. Note that, while TSs of filaments of episepalous stamens appear as paired small circles, TSs of filaments of epipetalous stamens do not appear yet at this level. An arrow indicates a non-paired, single episepalous stamen.—4. Lateral view of dissected flower. Abbreviations: ca, calyx lobe; pe, petal; sta, stamen; stl, style; p, vascular bundle to a petal; s, vascular bundle to a stamen; ost, ovary stipe; ov, ovary. Scale equals 5 mm for Figure 1; 1 mm for Figure 2; 2 mm for Figures 3 and 4.

two or three longitudinal lines along the ovary septa to approximately half the length of the capsule. The seeds are more or less conical with the chalazal part broadest (Fig. 9). They are small, 1.2–1.3 mm long and 0.9–1.0 mm wide. The seed coat surface is almost smooth, without specializations such as the inverted epidermal hairs found in a number of lythraceous genera.

FLORAL ANATOMY

In anatomical section nectariferous tissue may be seen forming a narrow ring at the base of the floral tube surrounding the ovary (Fig. 7). Cells of the tissue are densely cytoplasmic, making the tissue easily recognizable in thin section because of its high stainability.

The number of locules (or constituent carpels) of the ovary is often three (Fig. 3), not always two as has been described (Koehne, 1903). The ovary wall is thin and four to five cells thick with inner epidermal cells of the wall showing remarkable radial enlargement (Fig. 8).

TRICHOMES

Two types of trichomes occur in the species, one a simple unicellular falcate hair, the other multicellular, globose, and glandular. The unicellular hairs form a very dense cover on the abaxial leaf surface (Fig. 12) and a sparser one on the adaxial side. Glands are also more abundant and larger on the abaxial than on the adaxial surface. Both types are abundant on leaves, young branches, pedicels, and the outer surface of the floral tube (Figs. 5, 6, 12). Both types also occur on the upper half of the ovary, although the glandular hairs are most abundant (Fig. 6; see also Fig. 8). Unicellular trichomes are 90–180 μm long; glandular trichomes are 70–130 μm in diameter. There is no size difference between glandular trichomes on the flower surface and those on the ovary surface.

LEAF ANATOMY

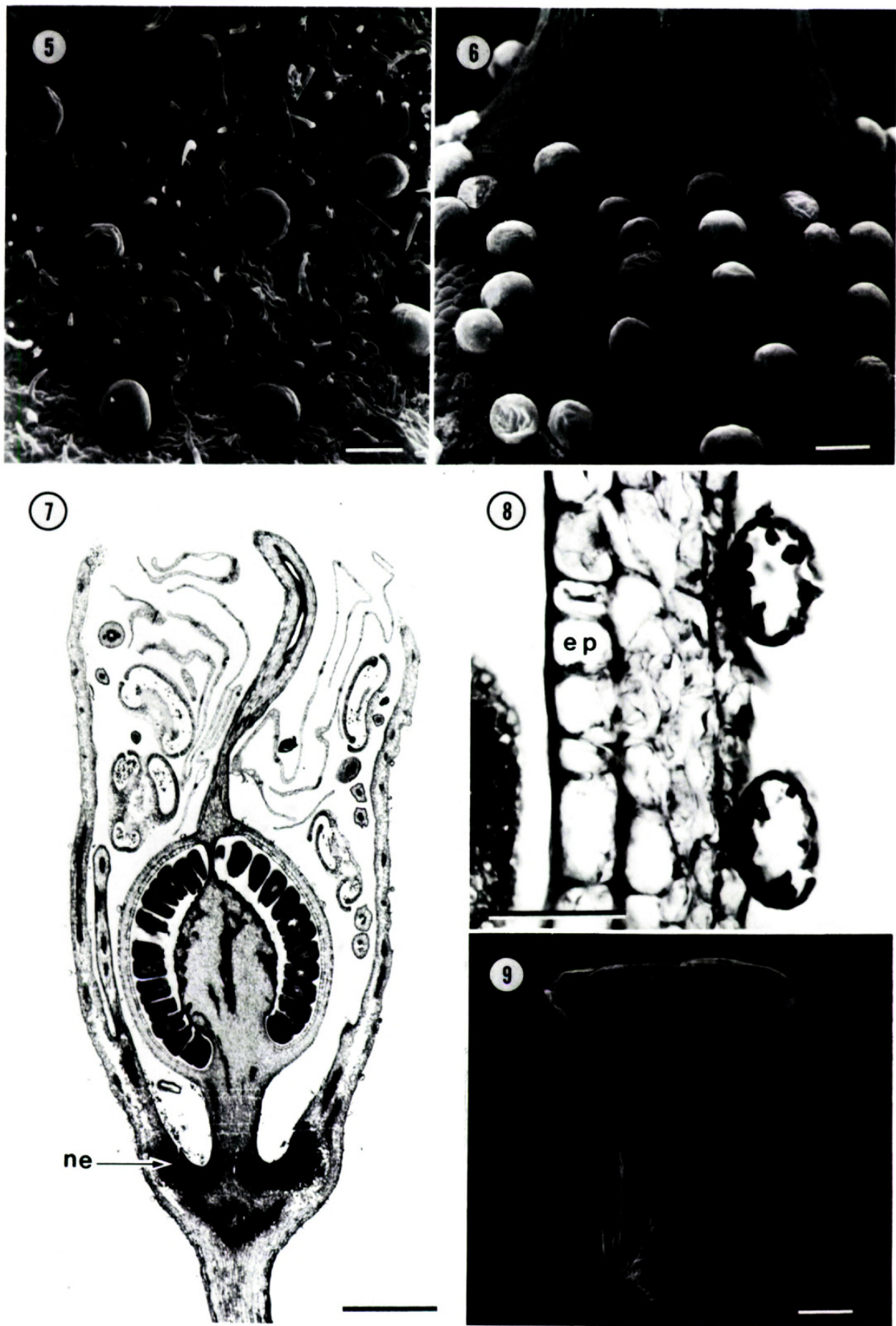
In surface view the leaves have an indumentum of unicellular hairs and globular, multicellular glands (dark dots as seen with a hand lens) (Figs. 12, 13). The unicellular hairs are proximally broad and slender and thick-walled distally (Fig. 14). The glands on the abaxial surface are 100–130 μm in diameter, on the adaxial surface 70–90 μm . They are sessile, with a very short multiseriate base, and composed of one (locally

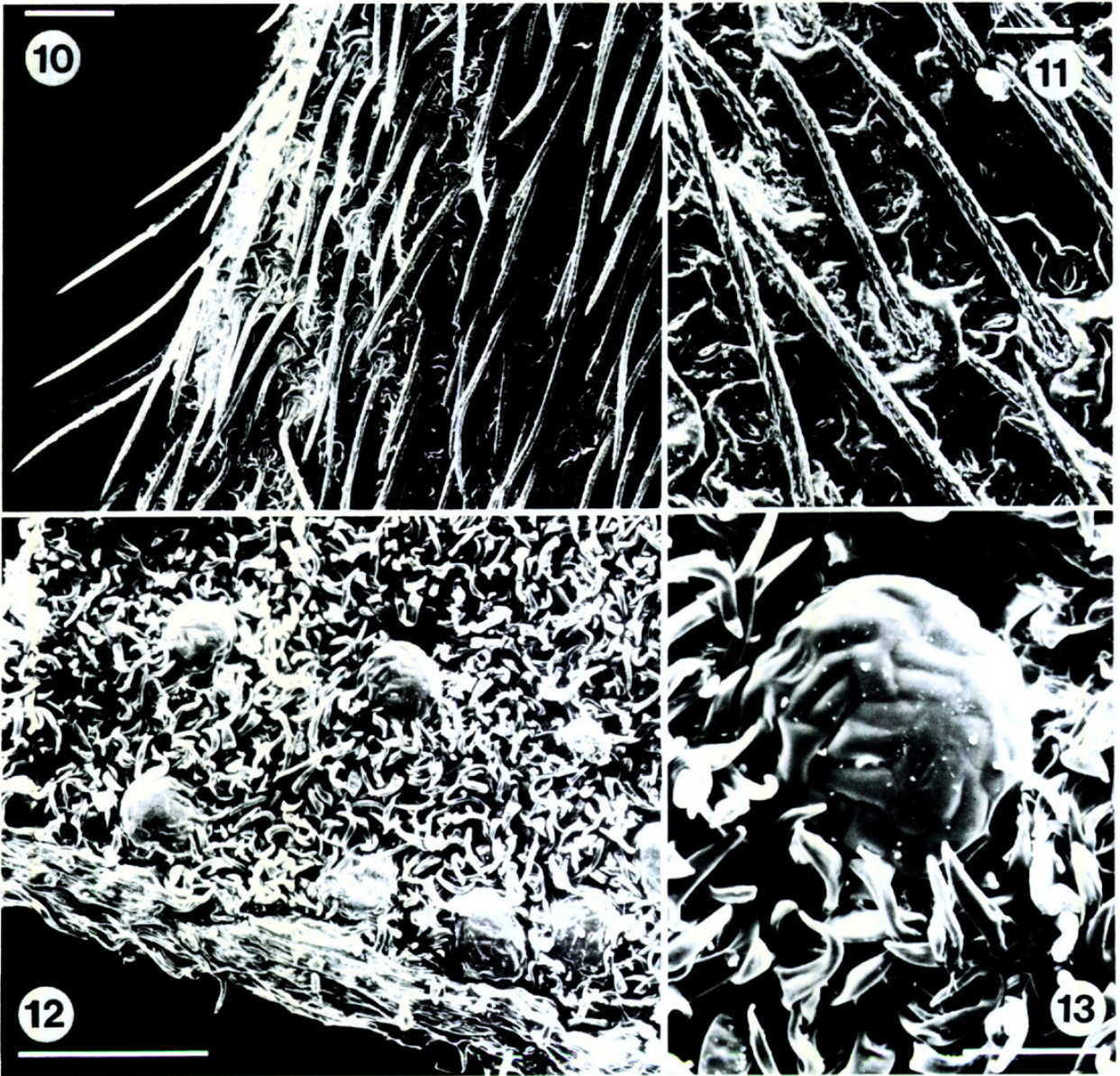
two) layers of cells enclosing a large cavity with more or less granular contents (Fig. 15; the structure of mature glands suggests a lysigenous or schizolysigenous development of these cavities). Epidermal cells have straight to curved anticlinal walls. Stomata are confined to the abaxial surface, anomocytic to cyclocytic, and the guard cell pairs are (18–)20(–22) μm wide, (22–)24(–26) μm long.

In transverse section the lamina is dorsiventral, ca. 170–200 μm thick; the cuticle is 1 μm thick or less. Epidermal cells are almost all with convex periclinal walls and mucilaginous, although sometimes with periclinal division walls and then only the inner daughter cell mucilaginous. The stomata are slightly raised but well protected by dense hair cover; inner and outer cuticular ledges are fairly well developed. A hypodermis is absent. The mesophyll is composed of one layer of tall palisade cells and spongy tissue. The midrib is provided with a single, bi-collateral vascular bundle, linked through a collenchymatous bundle sheath extension to the upper epidermis and by a parenchymatous to collenchymatous ground tissue to the lower epidermis, without supporting sclerenchyma. Minor veins are mostly embedded in the mesophyll; vascular bundles of the major lateral veins are vertically transcurrent through parenchymatous to collenchymatous bundle sheath extensions. Crystals are present as druses in the vicinity of vascular bundles.

WOOD ANATOMY

Growth rings are faint to distinct. Vessels are diffuse or wood is semi-ring-porous in some of the growth increments. Vessels number ca. 150–200 per sq. mm, ca. 25–45% are solitary, the remainder in radial multiples of 2–4(–7) or more rarely in small clusters, round to oval, the tangential diam. (20–)40(–60) μm , the radial diam. up to 70 μm , the walls 3–4 μm thick. Vessel member length is (180–)360(–420) μm . Perforations are simple in oblique to nearly horizontal end walls. Inter-vessel pits are crowded, alternate, vestured, round to polygonal, 3–5 μm , with slit-like apertures. Vessel-ray pits are similar but half-bordered. The fibers are (370–)580(–770) μm long, with walls medium to very thick, sometimes weakly gelatinous, with simple to minutely bordered pits confined to the radial walls, septate. Parenchyma was not seen. Rays are mainly uniseriate, partly with low biseriate portions, al-





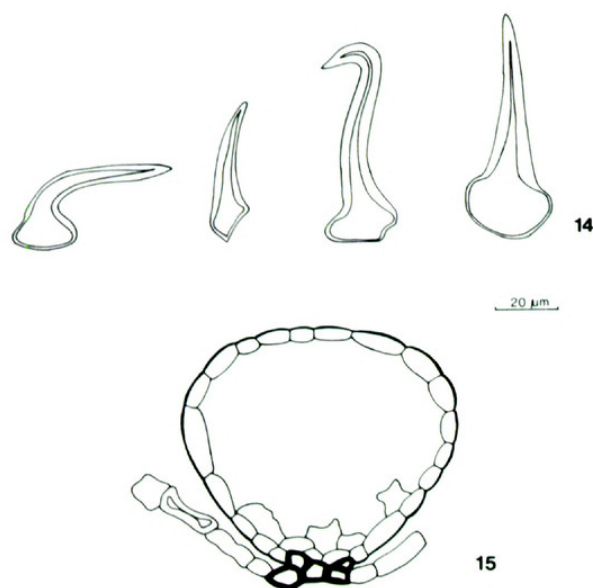
FIGURES 10–13. Scanning electron micrographs of lower leaf surfaces of *Pemphis acidula* [Cramer 4935 (MO)] and *Koehneria madagascariensis* [D'Arcy & Rakotozafy 15317 (MO)].—10. Sericeous lower leaf surface of *P. acidula*.—11. Enlargement of unicellular trichomes of *P. acidula*.—12. Tomentose lower leaf surface of *K. madagascariensis*.—13. Enlargement of multicellular, globose, glandular trichome, surrounded by unicellular, non-glandular trichomes of *K. madagascariensis*. Scale equals 200 μm for Figures 10 and 12; 50 μm for Figures 11 and 13.

most entirely composed of upright cells, central cells sometimes square to weakly procumbent (this ray type would probably develop into heterogeneous type I in a more mature stem). Cry-

stals were not observed. Many fibers with dark-staining contents (probably living fibers) are present (Figs. 16, 17).

Additional stem characters are: Phloem de-

FIGURES 5–9. *Koehneria madagascariensis*.—5. Scanning electron micrograph of trichomes on the outer surface of the floral tube.—6. Scanning electron micrograph of trichomes on the surface of the upper half of the ovary.—7. Longitudinal section (LS) of flower.—8. LS of ovary wall.—9. Scanning electron micrograph of nearly mature seed [see specimens examined, Réserves Naturelles 2689 (TAN)]. Abbreviations: ne, nectariferous tissue; ep, inner epidermal cell. Scale equals 100 μm for Figures 5, 6, 8, and 9; 1 mm for Figure 7.



FIGURES 14, 15. Camera lucida drawings of leaf trichomes of *Koehneria madagascariensis*.—14. Unicellular trichomes; three trichomes on the left from lower epidermis and one on the right from upper epidermis.—15. Multicellular, glandular trichome from lower leaf surface. Scale equals 20 μ m.

void of sclerenchymatous elements; secondary phloem with narrow bands of crystalliferous cells containing druses; interxylary phloem well-developed; pith with nests of thick-walled sclereids.

POLLEN MORPHOLOGY

The pollen is prolate-spheroidal and tricolporate with three faint pseudocolpi (Figs. 18–20, 24). The colpi are meridionally elongated, equatorially arranged, equidistant, straight, 10–16 μ m long, extending to within 3 μ m of the pole and tapering to an acute apex; costae colpi are narrow, ca. 1 μ m wide. The exine is faintly scabrate, tectate with an ectexine bridge frequently present over the pore; pseudocolpi are shorter than the colpi (7–9 μ m) and represented by thinned mesocolpal regions with increased granulation of the exine (Fig. 19). The poles are circular, located at the midpoint of the colpus, 2.5–3 μ m in diam. The grain size is 22–26 μ m long (P) \times 16–20 μ m wide (E) at the equator.

RELATIONSHIP TO *PEMPHIS ACIDULA*

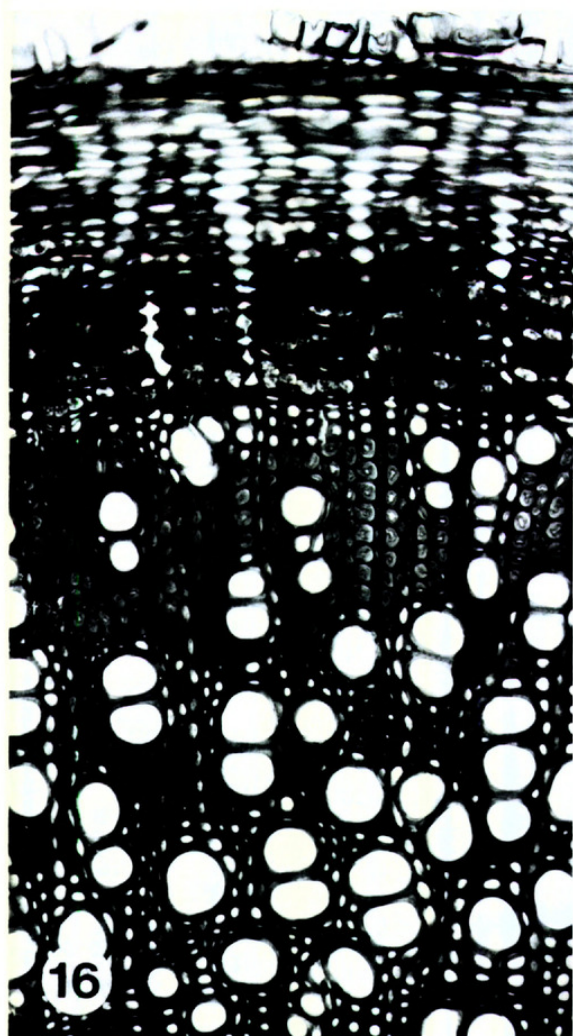
The great difference between the two species currently assigned to *Pemphis* is apparent in comparative summaries of their reproductive and anatomical characters (Tables 1, 2). The most striking floral features of *P. madagascariensis* are the distinctive glandular trichomes and conspic-

uous ovary stipe, both of which are lacking in *P. acidula*. In addition, the combination of septifragal marginicidal capsule dehiscence, doubled condition of episepalous stamens and bilevel stamen insertion, strongly reflexed calyx lobes, restricted stigma development, limited basal production of nectariferous tissue, and the specialized elongated inner epidermal cells of the ovary wall clearly set *P. madagascariensis* apart from *P. acidula*. In contrast, *P. acidula* has circumscissile capsule dehiscence, single stamens inserted at one level, erect calyx lobes, bilobed stigma, nectariferous tissue lining the floral tube to the level of stamen insertion, and specialized tanniferous cells in the upper one-third of the ovary that harden in association with its circumscissile dehiscence mode. The morphology of the flower in *P. acidula* is related to its distylic condition (Lewis, 1975; Gill & Kyauka, 1977). The flowers of *P. madagascariensis* are homomorphic. The seeds are similar but much smaller in *P. madagascariensis* than in *P. acidula*.

The difference in vestiture between the two taxa is another indicator of their disparity. Both are well adapted to xerophytic habitats, but the trichome complements are entirely different. In *Pemphis madagascariensis* a mixture of sessile, globose, glandular hairs and unicellular, falcate, non-glandular hairs occurs (Figs. 12, 13). In *P. acidula* the dense sericeous indument is composed entirely of long, straight, thick-walled, unicellular hairs ringed by a basal collar of the thickened epidermal cell wall (Figs. 10, 11).

Pollen differences between the two species are as great as between any two genera in the family. The pollen of *Pemphis madagascariensis* is tricolporate with three faint pseudocolpi, one to each mesocolpal area, and the exine is faintly scabrate (Figs. 18–20, 24). The pollen of *P. acidula* is twice as large and is consistently tetracolporate (ca. 1% tricolporate) with eight faint pseudocolpi, two to each mesocolpal area. The exine is characteristically psilate to faintly scabrate (Figs. 21–23).

From the summary of important anatomical attributes (Table 2), it is clear here again that *Pemphis madagascariensis* and *P. acidula* show many striking and significant differences. The anatomical characterization of *P. acidula*, particularly, stands out from all Lythraceae, including *P. madagascariensis*, by its conspicuous vasicentric xylem parenchyma, and by other anatomical features (Baas & Zweypfenning, 1979). Only a few of these can be interpreted as spe-



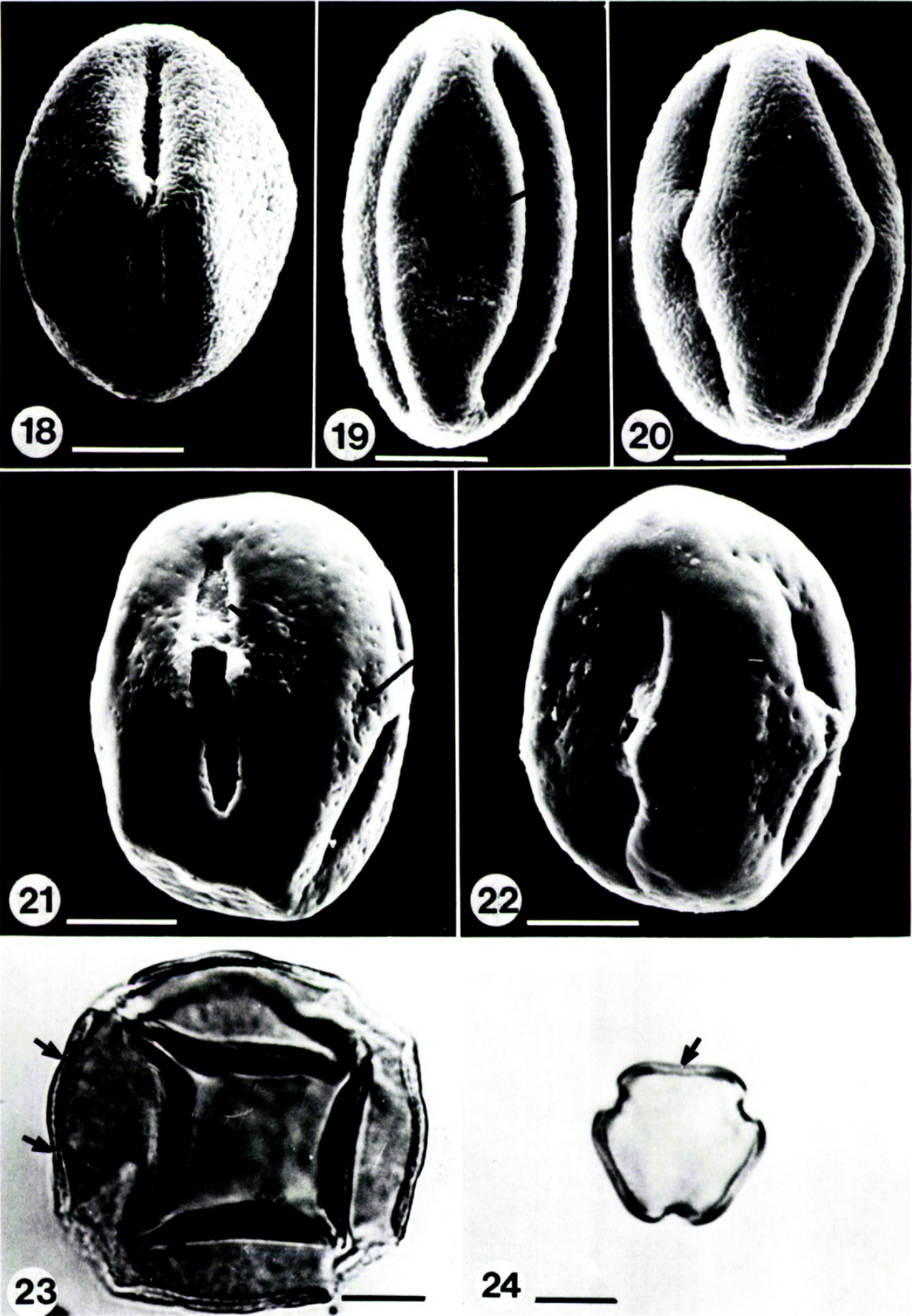
FIGURES 16, 17. Stem anatomical sections of *Koehneria madagascariensis*.—16. Transverse section of stem showing cork, cortex, phloem and secondary xylem, $\times 135$.—17. Radial longitudinal section through the secondary xylem showing septate fibers (left) and narrow vessel elements (right), $\times 540$.

cializations related to its xerophytic habit (thick isobilateral leaves with stomata on both sides; cf. Kienholz, 1926). Vegetative anatomy unambiguously supports separation of the two taxa.

Features shared by *Pemphis madagascariensis* and *P. acidula*, such as actinomorphic flowers and diplostemonous stamens with long episealous filaments, are common to most genera of the Lythraceae. The generalized nature of these characters does not negate their inclusion in this comparison but does invalidate their usefulness as indicators of phylogenetic relationship. All evidence suggests there is no direct relationship between *P. madagascariensis* and *P. acidula*. Support for removal of the former from the genus *Pemphis* is well founded on all grounds investigated. The new generic name, *Koehneria*, is henceforth used in this discussion in place of *Pemphis madagascariensis*.

RELATIONSHIP TO *LAGERSTROEMIA*

The original disposition of *Koehneria* as a species of *Lagerstroemia* appears to have been made through ignorance of the definitive characters of *Lagerstroemia* or incomplete knowledge of the fruiting condition of *Koehneria*. *Lagerstroemia* uniquely has unilaterally winged seeds with a pyramidal seed body and revolute cotyledons. In addition, its inflorescences are multi-flowered racemes or panicles, the ovary is sessile, and the capsule is loculicidally dehiscent. In *Koehneria* the seeds lack wings and have straight cotyledons, the flowers are mostly solitary and axillary, the ovary is stipitate, and the capsule is septifragally dehiscent. Metcalfe and Chalk (1950) recorded glandular trichomes for *Lagerstroemia*, but this is apparently based on *L. madagascariensis*. Furtado and Srisuko (1969)



loosely applied the terms "dotted" and "gland-dotted" to the leaves of a number of *Lagerstroemia* species, but glands were not found on herbarium specimens at Leiden of some of those species. Both Koehne (1903) and Furtado and Srisuko (1969) indicated that *L. ovalifolia* Teysm. & Binnend. has leaves that are black-punctulate beneath, and thus they might bear glands comparable to those of *Koehneria*. Examination of leaves of this species from four countries, however, revealed no glandular trichomes but instead numerous large subepidermal secretory cavities. These are especially abundant on the lower leaf surface and macroscopically appear as dark, not black, punctae after specimens are dried. Glandular trichomes of the *Koehneria* type probably are absent from all *Lagerstroemia*.

Similarities in wood anatomical characteristics of *Lagerstroemia* and *Koehneria* (Table 2) are plesiomorphic in nature, whereas the numerous wood anatomical features in which they differ are clearly apomorphic and indicate that sizable phylogenetic distance separates the two entities. Pollen features of each, likewise, indicate only their distant common ancestral origin; they suggest no close relationship between the taxa. *Lagerstroemia* is the only genus of Lythraceae with a center of speciation in southeastern Asia. No native species are found either in Africa or Madagascar. The species closest to Madagascar occur 4,000 miles to the northeast in Indonesia. From all evidence, there is no close phylogenetic affinity between the two genera and Koehne was unquestionably correct in removing *Koehneria* from *Lagerstroemia*.

RELATIONSHIPS TO OTHER LYTHRACEAE

Koehneria is unique in the Lythraceae in possessing the following suite of apomorphies: sol-

itary, axillary, 6-merous flowers with strongly reflexed lobes; 18 stamens, of which 12 appear as pairs on the six sepals; a conspicuous elongate ovary stipe; elongate inner epidermal cells of the ovary; a septifragally dehiscent capsule; and globose, glandular trichomes on vegetative and floral parts. Among all other members of the family, the genus bears closest resemblance to the New World genera *Adenaria* and *Pehria*, and the Afro-Asian genus *Woodfordia*, by the appearance in all of the unusual globose glandular trichomes, an ovary stipe, and enlarged inner epidermal cells of the ovary wall (Table 3). These synapomorphies are unknown elsewhere in the Lythraceae and point to close common origin of the genera. Two other lythraceous genera, the zygomorphic New World *Pleurophora* and some species of the New World *Lafoensia*, possess a similar ovary stipe but lack other specialized characters that would ally *Koehneria* with this group. The stipe is regarded as having evolved independently in these taxa. In *Woodfordia* the ovary stipe is much less developed than in the other genera. In some specimens it appears to be absent; the nectariferous tissue then is fused directly to the base of the ovary. In other specimens, a very short stipe, free from the surrounding nectary, is discernible.

Some variation exists in the glandular trichomes as well. In *Woodfordia* and *Adenaria* a canalicular apical extension may develop on some glandular trichomes. This form was first observed in *Woodfordia* (Shome et al., 1981) and now is also noted in *Adenaria*. The necked form is restricted in *Woodfordia* to the outer surface of the floral tube and pedicel (Fig. 27); the stems and leaves bear the globose form (Figs. 25, 26). In *Adenaria* necked glandular trichomes, identical in appearance to those of *Woodfordia*, are seen sparsely mixed with globose forms on the ovary only on specimens from southeastern

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FIGURES 18–24. Pollen of *Koehneria madagascariensis* and *Pemphis acidula*. — 18. Scanning electron micrograph of *K. madagascariensis*, equatorial view of a colpus with ectexine bridge. — 19. Scanning electron micrograph of *K. madagascariensis*, equatorial view of slightly collapsed grain emphasizing location of pseudocolpus (indicated by arrow). — 20. Scanning electron micrograph of *K. madagascariensis*, equatorial view of fully expanded grain, faint pseudocolpus flanked by colpi. — 21. Scanning electron micrograph of *P. acidula*, equatorial view showing pore, colpus, and two faint pseudocolpi (indicated by arrows). — 22. Scanning electron micrograph of *P. acidula*, equatorial view, the mesocolpal area at the center of the grain. — 23. Light micrograph of *P. acidula*, polar view illustrating tetracolporate condition and faint pseudocolpi (indicated by arrows). — 24. Light micrograph of *K. madagascariensis*, polar view, illustrating tricolporate condition and faint pseudocolpi (indicated by arrow). Scale equals 5 μ m in Figures 18–20; 10 μ m in Figures 21 and 22; 10 μ m in Figures 23 and 24. Figures 18–20 from D'Arcy & Rakotozafy 15317 (MO); Figures 21 and 22 from Kibiwa 1204 (MO); Figure 23 from von Mueller 3 (K); Figure 24 from Lam & Meeuse 5430 (K).

TABLE 1. Comparison of *Koehneria* with *Pemphis*, *Lagerstroemia*, and putative allies. Data based on observations of the authors and on Koehne (1903).

Characters	<i>Koehneria</i>	<i>Pemphis</i>	<i>Adenaria</i>	<i>Pehria</i>	<i>Woodfordia</i> ^a	<i>Lagerstroemia</i>
Number of species	1	1	1	1	2	53
Geographic distribution	Madagascar	E. Africa & Madagascar to Pacific	SE Mexico to N. Argentina	Honduras to Colombia	E. & W. Africa (1 sp.) & Madagascar & E. Asia (1 sp.)	E. & W. Asia, W. Pacific
Inflorescence	solitary, axillary	solitary, axillary	compact, much-branched cyme, dense, umbelliform	compact, much-branched cyme, few-flowered, loose	compact, much-branched cyme, few-flowered, loose	racemose or panicle
Leaves	thick, ± coriaceous	thick, fleshy	herbaceous, dry	herbaceous, dry	thick, ± coriaceous	primarily herbaceous
Floral morphology						
Floral forms	monomorphic	dimorphic	trimorphic	monomorphic	monomorphic	monomorphic
Symmetry	actinomorphic	actinomorphic	actinomorphic	actinomorphic, weakly zygomorphic	weakly zygomorphic	actinomorphic
Merosity	6-merous	6-merous	4 (or 5)-merous	4 (or 5)-merous	(4-)6-merous	(4-)6(-8)-merous
Shape	campanulate	campanulate	campanulate	cyathiform	cyathiform to tubular	campanulate
Length	4.5-8.5 mm	4.0-7 mm	2.5-4.5 mm	5.0-9.0 mm	9.0-15(-20) mm	5-17 mm
Lobe position	strongly reflexed	erect	erect	weakly reflexed or erect	erect	erect to reflexed
Epicalyx length	0.0-2 mm	ca. 0.5 mm	0.0 mm	0.2-0.5 mm	0.2-0.3 mm	0.0-2 (?) mm
Petal number	6	6	4 (5)	4 (5)	(4) 6	6+
Petal shape	broadly obovate	elliptic	obovate-oblongate	narrowly lanceolate	narrowly lanceolate	ovate-obovate
Petal size	5.5-10 mm × 4.0-7 mm	7.5-8.0 mm × 5.5-6.0 mm	4.0-4.2 mm × 1.0-1.2 mm	4.2-4.5 mm × 1.3-1.6 mm	1.0-3.0 mm × 0.2-0.5 mm	5-25 mm × 3-20 mm
Petal color	rose-purple	white	white (or pale rose)	red	red	rose-purple, white
Stamen number	(16-)18(-20)	12	8 (10)	8 (10)	(8) 12	15-200
Stamen position	episepalous doubled, epipetalous single	episepalous & epipetalous single	episepalous & epipetalous single	episepalous & epipetalous single	episepalous & epipetalous single	episepalous single or numerous, epipetalous numerous

TABLE 1. Continued.

Characters	<i>Koehneria</i>	<i>Pemphis</i>	<i>Adenaria</i>	<i>Pehria</i>	<i>Woodfordia</i> ^a	<i>Lagerstroemia</i>
Stamen chorisis	present in epise- palous stamens	absent	absent	absent	absent	present in epise- palous & epipetalous, or epipetalous sta- mens only
Stamen lengths	episepalous longer	episepalous longer	all \pm equal	all \pm equal	episepalous longer	episepalous longer or all equal
Ovary shape	globose	turbinate	turbinate	globose	\pm fusiform	globose-oblong
Locule number	2 or 3	3	2	2	2	3-6
Ovary stipe	present	absent	present	present	present, very short, to absent	absent
Style length	7-15 mm	1-5 mm	1-4 mm	7-8 mm	13-14 mm	variable, exceeding stamens
Stigma shape	punctiform	capitate	distinctly bilobed	punctiform	punctiform-barely capitate	punctiform
Trichomes						
Non-glandular on leaf	unicellular, falcate	unicellular, elon- gate with thick base, stiff	unicellular & mul- ticellular, weak	unicellular & mul- ticellular, weak	unicellular, falcate	various
Glandular						
Shape	globose	absent	globose, globose with neck	globose	globose, globose with neck	absent
Location on flo- ral parts	outer floral tube & upper half of ovary	absent	outer floral tube, upper half of ovary, petals	outer floral tube, petals	outer floral tube	absent
Nectaries	present, base of floral tube	present, from base to stamens	present, from base halfway to sta- mens	present, from base to stamens	present, base of floral tube	absent
Ovary wall thick- ness	4-5 cells	7-20 cells	8-9 cells	6-7 cells	6-7 cells	?
Ovary wall spe- cialization	inner epidermal cells enlarged	cells of upper $\frac{1}{3}$ of ovary tannifer- ous & solidified	inner epidermal cells enlarged	inner epidermal cells enlarged	inner epidermal cells enlarged	?

TABLE 1. Continued.

Characters	<i>Koehneria</i>	<i>Pemphis</i>	<i>Adenaria</i>	<i>Pehria</i>	<i>Woodfordia</i> ^a	<i>Lagerstroemia</i>
Capsule dehiscence	septifragal-mar-ginical	circumscissile	indehiscent	loculicidal, splitting adaxially	indehiscent or splitting variously, incl. loculicidal	loculicidal
Seed size	1.2-1.3 mm × 0.9-1.0 mm	3.0-3.2 mm × 1.5-1.9 mm	0.9-1.1 mm × 0.5-0.6 mm	0.7-0.9 mm × 0.3-0.4 mm	0.7-0.8 mm × 0.4-0.5 mm	7-12 mm × 3-5 mm
Seed wing	absent	absent	absent	absent	absent	present
Seed hairs	absent	absent	absent	absent	present	absent
Cotyledon position	plane	plane	plane	plane	plane	revolute
Pollen morphology						
Colpi number	3	4	3	3	3	3
Pseudocolpi	3 faint, 1/mesocolpus	8, 2/mesocolpus	0	0	0	0 or 6 faint, 2/mesocolpus
Exine sculpture	faintly scabrate	psilate-faintly scabrate	scabrate	scabrate	scabrate	verrucate
Size (P × E)	19-26 μm P × 14-20 μm E	40-55 μm P × 35-54 μm E	18-22 μm P × 20 μm E	22-28 μm P × 18 μm E	16-22 μm P × 16 μm E	35-55 μm P × 25-46 μm E
Chromosome nos.	unknown	2n = 32	2n = 32	2n = 32	2n = 16	Various, 2n = 16-50

^a Data based primarily on *Woodfordia fruticosa* in this ditypic genus.

TABLE 2. Anatomical character summary of *Koehneria* and putative allies.

	<i>Koeh-</i> <i>neria</i>	<i>Pem-</i> <i>phis</i>	<i>Ade-</i> <i>naria</i>	<i>Pehria</i>	<i>Wood-</i> <i>fordia</i>	<i>Lager-</i> <i>stroemia</i> ^a
Leaf Anatomy						
Unicellular hairs broad-based	+	—	+	±	+	±, — ?
Globose glands present	+	—	+	+	+	—, ? ^b
Stomata on both leaf surfaces	—	+	+	—, +	—	—
Epidermal mucilage cells	++	++	++	—, +	—, +	+
Lamina isobilateral	—	+	—	—	—	+, —
Major veins vertically transcurrent	+	—	+	+	+	+
Wood Anatomy						
Fibers septate	+	—	+	+	±	+
Parenchyma scanty or absent	+	—	+	+	+	— ^c
Rays mainly of erect cells	+	—	±	+	+	—

^a Leaf anatomical data on *Lagerstroemia* are scanty considering the large number of species.
^b Metcalfe and Chalk (1950) recorded glands for *Lagerstroemia*, and Furtado and Srisuko (1969) described a number of *Lagerstroemia* species with (gland-) dotted leaves; these records could not be confirmed (see also text).
^c One group of *Lagerstroemia* species has scanty parenchyma but is characterized by conspicuous fiber dimorphism, a feature absent from *Koehneria*. The other species of *Lagerstroemia* have abundant parenchyma.
++ = character very pronounced or abundant; + = character present; ± = character weakly pronounced or infrequent.

Mexico [*R. Torres 1369, Breedlove 25581, 38133*, (KE-Graham)]. None have been seen on collections from Central or South America. Trichomes vary in the length of the neck produced. In *Woodfordia* they can be seen in all stages of development from the common globose form to short- or long-necked forms. The thick orange content, possibly resin, extends part way into the neck but is not extruded at the apex as in typical glandular trichomes. There is no evidence on which to determine whether the globose or necked form is the derived state. However, if the globose gland is derived from a typical multicellular gland through loss of the apical extension, the loss is nearly complete, being retained on limited parts of the flower only. Multicellular glandular hairs are uncommon in the family (common only in *Cuphea* and *Pleurophora*); have a broad multicellular base rather than a narrow, nearly stalked one; and produce a clear, sticky resin unlike the thick orange contents of the globose glands. This suggests globose glands are not homologous to other multicellular glandular trichomes in the Lythraceae but may be a new trichome type developed in the ancestor of this group of genera.

Anatomical attributes of *Koehneria* are closely comparable to those of *Pehria*, *Woodfordia*, and *Adenaria* (Table 2). *Pehria* differs by possessing specialized chambered crystalliferous fibers (Baas & Zweypfenning, 1979). This difference, how-

ever, does not preclude close phylogenetic affinity and, on the whole, anatomy supports the association of the genera circumscribed by the trichome and ovary characteristics.

The pollen of *Koehneria* differs from that of *Adenaria*, *Pehria*, and *Woodfordia* by the presence of faint pseudocolpi. *Koehneria* pollen, however, does not display any specialized features that point to a specific generic relationship. Several genera or portions of genera show the same general shape, triporate condition, and exine sculpturing seen in *Koehneria*. These include *Adenaria*, *Pehria*, and *Woodfordia*, but also the distantly related *Physocalymma*, *Heimia*, and some species of *Lagerstroemia*. The pollen data do not rule against a close alliance with *Adenaria*, *Pehria*, and *Woodfordia* but provide no direct evidence for any more specific relationship.

Although they share a number of specialized morphological and anatomical features, genera of this alliance differ to a substantial degree from each other (Table 3). *Adenaria* is a monotypic, small-shrub genus of New World seasonally evergreen and semievergreen forest zones. Its leaves are herbaceous with glands and uni- and multicellular weak hairs, which are most abundant along the veins on the abaxial side of the leaf (Fig. 29). The four-merous flowers with erect calyx lobes appear in dense umbelliform axillary clusters and are weakly tristylic. There are three

Table 3. Comparison of selected morphological features of *Koehneria*, *Adenaria*, *Pehria*, and *Woodfordia*. Derived characteristics shared between two or more genera boxed; characteristics unique to a genus bold-boxed.

Character	Koehneria	Adenaria	Pehria	Woodfordia
Inflorescence	solitary, axillary flower	compact, much branched cyme, umbelliform clusters	compact, much branched cyme, open clusters	compact, much branched cyme, open clusters
Leaf texture	±coriaceous	herbaceous	herbaceous	±coriaceous
Floral forms	monomorphic	trimorphic	monomorphic	monomorphic
Floral symmetry	actinomorphic	actinomorphic	actino- to weakly zygomorphic	weakly zygomorphic
Merosity	6-merous^a	4-merous	4-merous	6-merous
Shape	campanulate	campanulate	cyathiform	cyathiform to tubular
Calyx lobes	strongly reflexed	erect	weakly reflexed to erect	erect
Petal shape	broadly obovate	obovate - oblanceolate	narrowly lanceolate	narrowly lanceolate - linear
Petal color	rose-purple	white to rose	red	red
Stamen number	18	8	8	12
Stamen lengths	2 lengths	1 length	1 length	2 lengths
Paired episepalous stamens	present	absent	absent	absent
Stigma	punctiform	bilobed strongly	punctiform	punctiform
Ovary stipe	present, long	present, long	present, long	present, very short to absent
Globose glands	present	present	present	present
Nectary	basal, well-separated from stamens	basal one-half distance to stamens	basal to stamens	basal, well-separated from stamens
Ovary inner epidermal cells	enlarged	enlarged	enlarged	enlarged
Capsule dehiscence	septifragal-marginicidal	indehiscent	loculicidal	indehiscent or splitting variously
Seed hairs	absent	absent	absent	present, spiral
Pollen pseudocolpi	3, faint	0	0	0

a. Polarity of floral merosity at the family level in Lythraceae is not clear. Both the 4- and 6-merous condition may have been derived from an ancestral 5-merous one. Flowers of ca. one-half the genera vary from 3-5-merous, but are basically 4-merous, while the remaining genera vary from 5- to 6-merous, but are most commonly 6-merous. Another view regards 6-merism as primitive in the family (Tobe, unpubl. data).

stamen lengths, but within a single flower there is only one stamen whorl and the filaments are more or less equal in length (Nevling, 1958). The breeding system of the genus has not been fully explored but limited pollen viability data suggest

the genus might be evolving from heterostyly to dioecy in a way similar to that observed in certain heterostylous Rubiaceae (Bawa, 1980). In two collections of short-styled flowers, 44% viable grains were produced (based on counts of 500

grains stained in cotton blue-lactol phenol). In one intermediate-styled collection pollen was 60% viable. In contrast, flowers from four long-styled collections formed no pollen, the microsporangia in each instance containing amorphous, dark-stained contents (Graham, unpubl. data). Other characteristics of *Adenaria* not found in *Koehneria* are the unusual (for Lythraceae) deeply bilobed stigma, more extensively developed nectariferous tissue, and indurate, indehiscent capsule.

Pehria is similar to *Adenaria* in habit and distribution. It is also a monotypic shrub genus of Central and northern South America found at elevations from 90 to 1,300 m in a variety of habitats ranging from dry deciduous woods to pine-oak and tropical cloud forests. Its leaves, like those of *Adenaria*, are herbaceous, without tomentose indument, and, in addition to the globose glands, bear mostly multicellular, uniseriate, weak trichomes mixed with sparser short unicellular ones (Fig. 28). The flowers are 4-merous, as in *Adenaria*, but are monomorphic with a more elongate floral tube, deep red petals, a punctiform stigma, extensive nectary development extending from the base of the ovary to the stamen insertion, and thin-walled, loculicidally dehiscent capsules. *Adenaria* and *Pehria* are more similar morphologically than either is to *Koehneria*; anatomically *Koehneria* and *Adenaria* are most similar.

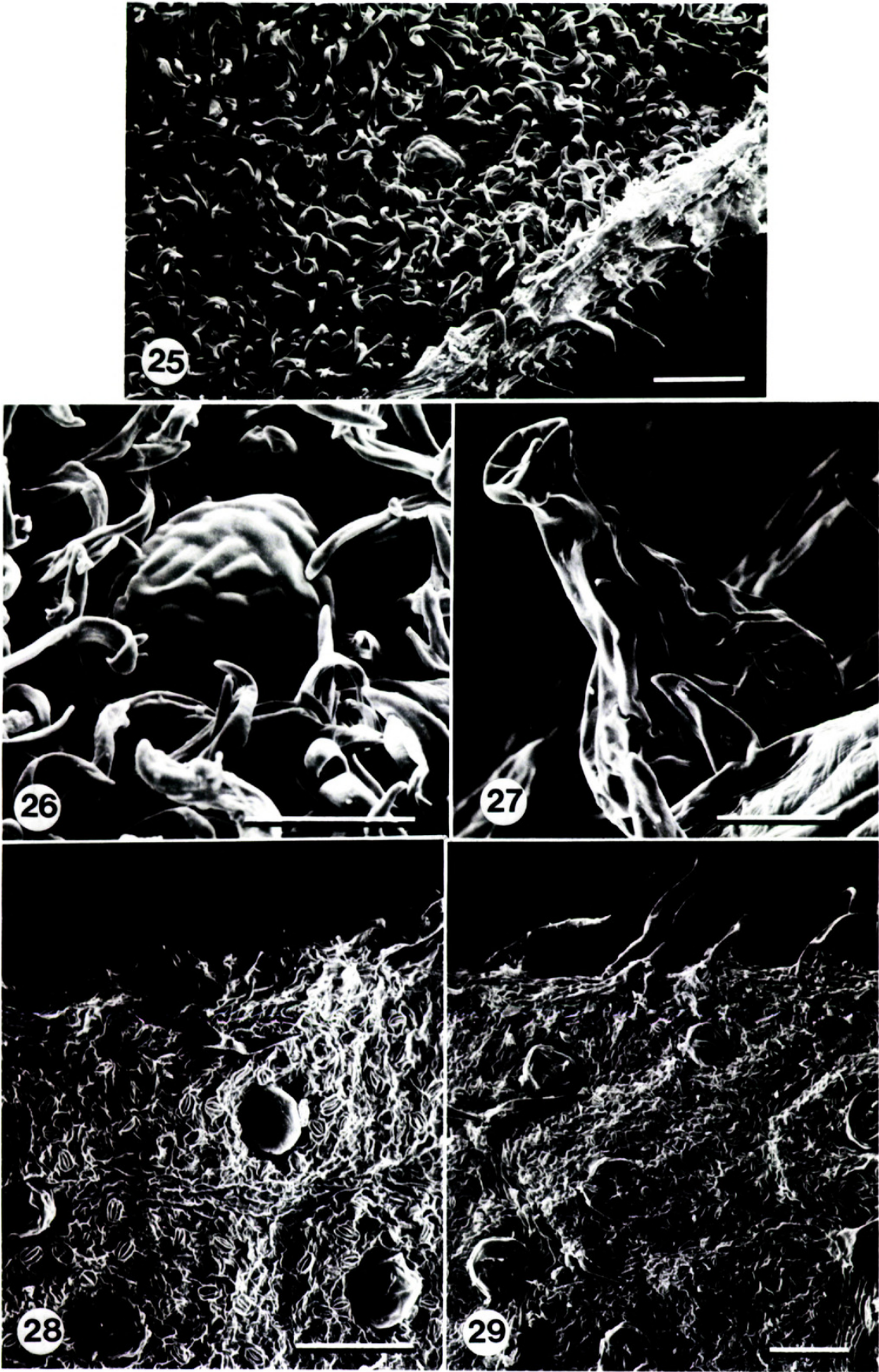
The genus *Woodfordia* comprises two species of shrubs of semixerix habitats. *Woodfordia uniflora* is found in Nigeria, Cameroon, eastern Sudan, Ethiopia, and Uganda (Keay, 1954). *Woodfordia fruticosa* grows with *Koehneria* in Madagascar (possibly as an early introduction because of its alleged aphrodisiacal properties?) and further ranges from Pakistan through northern India and southern China to Sumatra, Java, and Timor. In total leaf vestiture *W. fruticosa* and *Koehneria* are virtually identical in having slightly sunken glandular trichomes interspersed in a dense cover of unicellular falcate hairs (cf. Figs. 12, 13, 25, 26). The leaf texture is also similar, although slightly more coriaceous in *Koehneria*. Similarities in leaf vestiture may be attributed to a close phylogenetic relationship, although it is also possible this is the result of evolutionary convergence as a response to the similar environmental stress imposed by the seasonally dry habitats in which these two genera occur.

In most other derived characteristics, beyond the previously mentioned shared trichome and

ovary characters, *Koehneria* and *Woodfordia* are dissimilar. The flowers of *Woodfordia* are six-merous as in *Koehneria* but have elongate tubes that appear weakly zygomorphic due to the arrangement of stamens and style on the lower side of the flower and to the frequent splitting of the persistent floral tube and enclosed capsule along only the adaxial side of the flower at maturation. The same zygomorphic tendencies are also seen in *Pehria*. Its floral tube and petals are bright red and the ovary stipe is scarcely developed to absent, rather than conspicuous. A further apomorphy of *Woodfordia*, not present in the other genera of this group, is the spiral, inverted epidermal hairs of the seed coat. These unusual hairs occur in only three other genera of the family, in the zygomorphic genera *Cuphea* and *Pleurophora*, and in the actinomorphic *Lafoensia*. Most likely, they have been independently derived in *Lafoensia*. They are absent from the seed coat of *Koehneria*, *Adenaria*, and *Pehria*.

In summary, *Koehneria*'s nearest relatives are the genera *Adenaria*, *Pehria*, and *Woodfordia*, an interpretation based on a three-character synapomorphy unique to the group. Beyond sharing this character set, the genera have differentiated extensively and more specific relationships cannot be determined from present information. *Koehneria*, among the four, displays the most derived features (Table 3), but differentiation has occurred in different directions and at different rates for individual characters in each of the genera, making comparisons for purposes of establishing phylogeny difficult. For example, in *Koehneria* the inflorescence has been reduced to a solitary axillary flower, while at the same time the primitive campanulate flower shape and basal nectary have been retained. In *Woodfordia* a less advanced inflorescence type, i.e., numerous flowers in a basically cymose inflorescence, is combined with a more advanced elongate floral tube, in which the nectary has remained basal.

The present distribution of *Koehneria* and allied genera in two hemispheres apparently reflects an early and extensive dispersal from a common African center of origin. The earliest incontrovertible fossil records of the Lythraceae are from the lower Eocene London Clay flora and the Eocene Deccan Intertrappean beds of India and suggest an Old World, warm-temperate origin for the family (Graham & Graham, 1971). The diversity of taxa present in the Eocene indicates a history for the family extending at least back into the Paleocene. The fossil record in combination with distribution patterns of ex-



FIGURES 25–29. Scanning electron micrographs of trichomes of *Woodfordia fruticosa* [USDA-Miami PI 19882 (KE-Graham)], *Pehria compacta* [Ortiz 878 (KE-Graham)], and *Adenaria floribunda* [Torres 1369 (KE-

tant lythraceous genera suggests east Africa as a plausible place of origin for the family. The distribution of the *Koehneria* alliance is consistent with this model. Migrations during the early Tertiary, to place *Adenaria* and *Pehria* or their ancestors in the American flora, would have been possible geologically and climatically, either westward to South America or via a north Atlantic land route (Raven & Axelrod, 1974; Smith et al., 1981). A history of overland dispersal of plant forms related to *Koehneria* finds some support from fossil evidence. Fossil seeds from the Miocene of Denmark have been related to modern *Koehneria* seeds (Friis, 1985). Identical seeds are recorded from the older Oligocene floras of England (Chandler, 1957) and the northeastern United States (Tiffney, 1981; flora presumed to be Oligocene) with affinities tentatively attributed to Lythraceae by the authors. A separate, later migration from Africa is necessary to explain the present distribution of *Woodfordia fruticosa* in Pakistan, northern India, southern China and islands southward. *Koehneria* may have evolved from ancestral, less xerophytic, forms in Africa and spread to Madagascar where it survives today, or it may have evolved in situ. Understanding of differentiation in this alliance and in the family generally would be greatly enhanced by discovery of fossil remains from the critical Paleocene epoch in Africa. In the absence of a substantiating fossil history, the present morphological and distributional patterns of *Koehneria* and relatives are regarded as the result of heterobathymic divergence and extensive dispersal coupled with widespread extinctions. These processes have obscured or erased evidence of the intervening history of the genera to the extent that determination of phylogenetic affinities of *Koehneria* may be made to the level of the four-genera alliance, but not to a specific modern genus.

SYSTEMATIC TREATMENT

In view of the significant differences in morphological, anatomical, and palynological features, *Pemphis madagascariensis* is here assigned to the monotypic new genus *Koehneria*.

The generic name honors B. A. Emil Koehne (12 Feb 1848–12 Oct 1918), Berlin, whose finely detailed and self-illustrated monograph of the Lythraceae remains today the single complete study of the family.

Koehneria S. A. Graham, H. Tobe & P. Baas, gen. nov. TYPE: *Koehneria madagascariensis* (Baker) S. A. Graham et al. \equiv *Lagerstroemia madagascariensis* Baker. \equiv *Pemphis madagascariensis* (Baker) Koehne.

Fam. Lythraceae. Frutex, alt. 0.5–2(–4) m, undique cinereo-tomentellus. Folia petiolis subnullis, oblonga, 15–70 mm longa, 5–20 mm lata, utraque pagina nigropunctulata, necnon subtus tomentello-albicantia. Flores solitarii, nigro-punctulati, axillares, 6-meri, campanulati, lobis reflexis; petala 6, rosea; stamina 18, episepala gemina, epipetala singula altius inserta; ovarium globosum, breviter stipitatum, apice nigro-punctulatum; stylus longissime exsertus. Capsula 2–3 locularis, septifraga marginicidalis; semina numerosa, cuneato-compressa. Ab *Pemphis* s. str. differt pilis glanduliferis, staminibus 18, ovario stipitato.

Shrubs with ash-gray bark and short, terete branches bearing white indument; nodes slightly buttressed; buds ovoid to triangular, compressed. Leaves opposite, subcoriaceous, sessile or nearly so, oblanceolate to linear-oblong, both sides with black punctulate glandular trichomes, these denser on the abaxial side and interspersed in a tomentum of white, falcate, non-glandular hairs. Flowers solitary, or rarely 2, axillary, pedicellate, campanulate, glandular punctulate and pubescent, 6-merous, homomorphic; lobes strongly reflexed at anthesis, alternating with 6 short appendages (epicalyx). Petals 6, bright rose-purple, longer than the floral tube. Stamens (16)–18(–20), the episepalous ones paired, the epipetalous ones single and inserted higher in the tube. Pollen prolate-spheroidal, tricolporate with circular pore and 3 faint pseudocolpi, the exine faintly scabrate. Ovary globose, distinctly stipitate, 2–3-locular, glandular-punctate and lightly pubescent at the apex; style long exserted; stigma punctiform. Capsule dehiscence septifragal marginicidal; seeds deltoid- to cuneate-compressed; cotyledons flat.

A monotypic genus with the following species:

←
Graham)].—25. Tomentose lower leaf surface of *W. fruticosa*.—26. Multicellular, globose, glandular trichome surrounded by unicellular, non-glandular trichomes on lower leaf surface of *W. fruticosa*.—27. Multicellular, glandular trichome with neck on pedicel of *W. fruticosa*.—28. Lower leaf surface of *P. compacta* with globose glandular trichomes and stomata prominent.—29. Lower leaf surface of *A. floribunda* with globose glandular trichomes and elongate non-glandular trichomes prominent. Scale equals 100 μ m in Figures 25, 28, and 29; 50 μ m in Figure 26; 25 μ m in Figure 27.

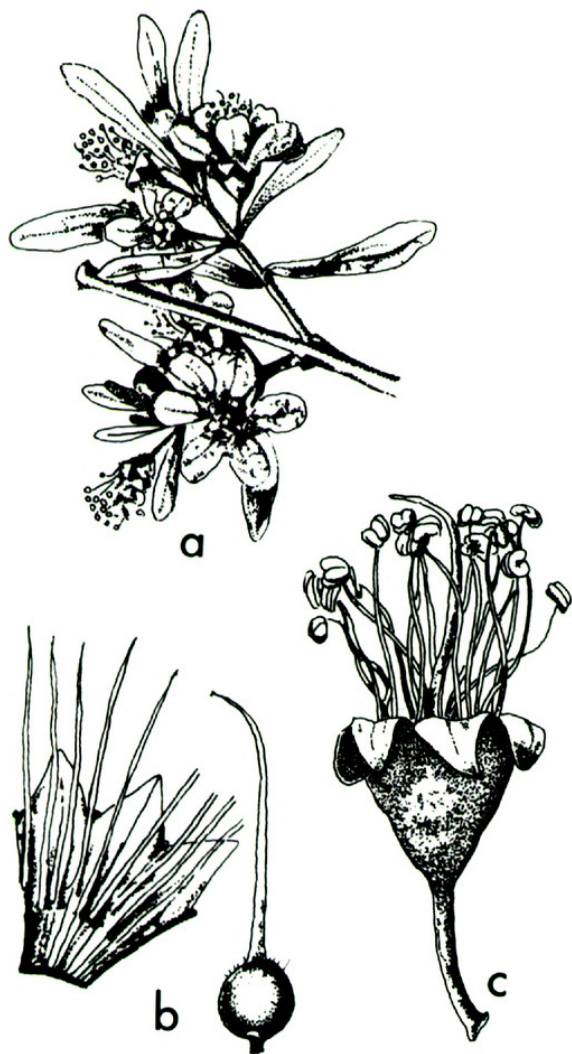


FIGURE 30. *Koehneria madagascariensis*. —a. Flowering branch, $\times 1$. —b. Stamen insertion on opened partial floral tube and gynoecium, $\times 3$. —c. Flower with reflexed lobes, $\times 3$. From Koehne, 1903.

Koehneria madagascariensis (Baker) S. A. Graham, H. Tobe & P. Baas, comb. nov. (Fig. 30). *Lagerstroemia madagascariensis* Baker, J. Linn. Soc. (Bot.) 18: 270. 1881; J. Bot. (n. s.) 11: 112. 1882. *Pemphis madagascariensis* (Baker) Koehne, in Engler, A., ed., Das Pflanzenreich. IV. 216. Heft 17. p. 187. 1903. TYPE: Madagascar: "Ibara" (Bara) country, communicated May 1880, Langley Kitching s.n. (holotype, K!).

Pemphis punctata Drake del Castillo, Bull. Soc. Linn. Paris 2: 1222. 1896. LECTOTYPE here designated: Horombe, 18 Jun 1890, *Catat* 4356 (P!). Two syntypes are cited in the protologue, *Catat* 4356 and 4358; both specimens present at P. The new species name is written on the label of *Catat* 4356 in the hand of Drake, while the other specimen bears the name in the hand of a French botanist,

P. Danguy (pers. comm., A. Lourteig, 1984). Since both syntypes are otherwise equally representative of the species, the specimen annotated by the author of the species is selected as lectotype.

Shrubs 0.5–2(–4) m tall, trunk diam. to 4 cm, with smooth ash-gray to gray-brown bark ex-corticating in very narrow to thread-like whitish strands, the inner bark red-brown; stems much branched, the branches terete, short, 4–10(–20) cm long, covered in fine, white or red-brown indument; nodes opposite, buttressed by the raised bases of the leaf scars, especially on the youngest branchlets; internodes telescoped toward the branch extremities with the season's leaves then tending to cluster at the ends of the branches; leaf scars semi-circular, projecting outward and tapering downward from the stem, bearing a row of red-purple, erect, thick, stipular processes adaxially between the scar and the stem, the processes falling away with age; buds ovoid to triangular in outline, compressed parallel to the stem surface. *Leaves* deciduous, opposite, entire, thick, rigid, subcoriaceous, sessile or nearly so, the petioles to 2 mm long; blades oblanceolate to oblong, rarely narrowly linear, 15–70 mm long, 5–20 mm wide, the bases attenuate, tapering to a brief petiole, the apices rounded to acute, occasionally thickened to a minute apiculate tip; upper blade surfaces deep green, conspicuously black glandular punctate when dry, the glandular hairs orange when fresh, interspersed with minute, fine, whitish soft hairs, the venation not prominent; lower blade surfaces white tomentose, thickly invested with minute, fine, soft pointed hairs interspersed with black glandular trichomes, generally denser than on the upper surface, the midvein raised, red-brown, visible against the white indument. *Flowers* solitary, rarely 2, axillary, mostly appearing at the distal-most nodes of the branchlets; pedicels 2–12 mm long, erect to spreading, stout when short, filiform when long, bearing 2 linear, caducous bracteoles 0.5–1.5 mm long at or near the base. Floral tubes (5–)6-merous, homomorphic, obovoid-turbinate in bud with 6 processes (appendages *sensu* Koehne) projecting outward from the bud at the sinuses of the calyx lobes; floral tubes campanulate at anthesis, 2.5–5 mm long excluding lobes, 2.5–5 mm wide at the mouth, coriaceous, whitish pubescent, with 6 strongly reflexed deltoid calyx lobes, the lobes 2–2.5 mm long, 1.5–3 mm wide at their base, slightly shorter to distinctly shorter than the subtending tube; appendages present between the lobes to varying

degrees as a result of greater or lesser fusion of the margins of adjacent lobes, mostly ca. 0.5–1 mm long; external surface of the flower and pedicel glandular-punctate and finely pubescent, sometimes suffused rose in color; internal surface glabrous, deep rose-purple. *Petals* 6, attached within the tube at the base of the calyx sinuses, bright rose-purple, obovate to broadly oblong, venation simple, the midvein thick, bearing 4 or 5 secondary veins, without anastomoses between the veinlets, 5.5–10 mm long, 4–7 mm wide, including a claw 0.25–1.5 mm long. *Stamens* (16–)18(–20), occasionally increased by splitting of a filament near its base to form a double stamen, or reduced by absence of 1 of an episepalous pair, 6 single stamens epipetalous, 12 paired stamens episepalous, the epipetalous ones higher in the tube than the episepalous ones at ca. three-fifths vs. two-fifths the length of the tube, often slightly shorter than the episepalous stamens; filaments slender, well exserted, deep rose-purple, ca. 10 mm long, frequently persistent in the fruiting floral tube; anthers bright yellow, bisporangiate, dorsifixed medianly with a slender connective, strongly revolute at dehiscence, caducous. *Pollen* prolate-spheroidal, tricolporate, with three faint pseudocolpi; colpi meridionally elongated, equatorially arranged, equidistant, straight, 10–16 μm long, extending to within 3 μm of the pole, tapering to an acute apex, the costae colpi narrow, ca. 1 μm wide; exine faintly scabrate, tectate, with an ectexine bridge frequently present over the pore; pseudocolpi shorter than the colpi, 7–9 μm long, represented by a thinner granulated exine; pore circular, at midpoint of the colpus, 2.5–3 μm in diam.; grain size 19–26 μm long (P) \times 14–20 μm wide at the equator (E). *Ovary* 2- or 3-locular, globose, thick-walled at anthesis, deep red-purple with mixed white pubescent and black glandular-punctate apex, stipitate, the stipe ca. 1 mm long, 0.5–0.7 mm wide at anthesis, surrounded at the base by a narrow ring of nectariferous tissue; placentation axile, the placenta swollen, fleshy, nearly globose; septa incomplete at the apex of the ovary; ovules numerous in each locule, attached over the entire placental surface, anatropous, erect; style red-purple, well exserted, 7–15 mm long, distinctly longer than the stamens, narrowing to the apex; stigma punctate, no wider than or only slightly wider than the narrowed apex of the style. *Capsule* exceeding the persistent floral tube by 2–3 mm at maturity, dry-walled, red-brown, septifragal marginicidally dehiscent from the apex for ca. one-half the

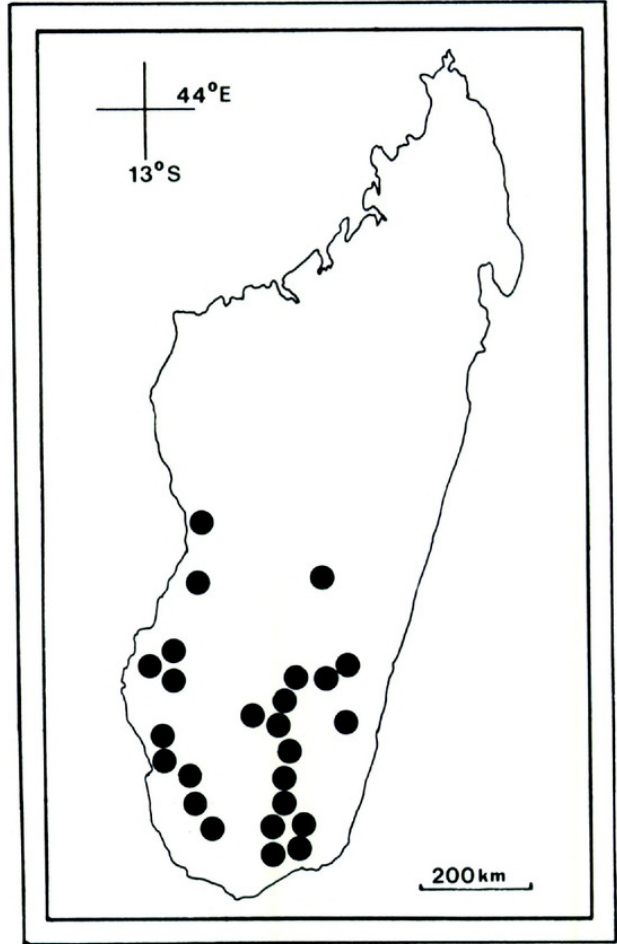


FIGURE 31. Distribution of *Koehneria madagascariensis* in Madagascar.

length. Seeds numerous, deltoid- to cuneate-compressed, the chalazal end broadest, 1.2–1.3 mm long, 0.9–1.0 wide, the cotyledons flat, not revolute.

Common names. Pisopiso and Kipsisopiso, meaning “cat-cat,” used by the Bara tribe, who find the flowers of the plants pretty, just as they find cats pretty (Rakotozafy, pers. comm. to Dorr); Hazobotsy, meaning “white wood,” also used by the Bara tribe (Dorr, pers. comm.).

Phenology. Flowering peaks approximately from late June to September, beginning prior to appearance of the new season’s leaves. However, some flowering occurs virtually all year, depending on local conditions, the flowers then borne with current season’s leaves. Capsule maturation beginning in August; seeds freely dispersed, with empty capsules persistent until the next flowering period.

Distribution. (Fig. 31.) Savannahs of semi-arid western and southern Tuléar Province and

bases of the central-south mountains in Fianarantsoa Province; in open grasslands and dry thickets on red calcareous soils, at altitudes of 100 to 800 m (Perrier de la Bâthie, 1954). These areas are characterized by a distinct dry season (six months or more) that is most prolonged in the southwest. Rainfall is irregular, between 500 and 1,000 mm per year, but less than 500 mm in the southwest. Mean temperature of the coldest month is 20°C (Koechlin et al., 1974). Specimens studied are cited below by phytogeographic province following Humbert (1955) and then alphabetically by collector.

Specimens examined. Est: Dist. Farafangana, Antahambohobe-Ivohibe, *Rakotovao s.n.* (*Réserves Naturelles 8102*) (TAN); Antahambohobe-Ivohibe, without collector (*Service des Eaux et Forêts 1945*) (TAN). Centre: Mahabo, *J. Bosser 9749* (TAN); 75 km sud de Betroka, *J. Bosser 13943* (TAN); Tsivory, *Catut 4358* (P); Common in the valleys to east of Ihosy, *W. Deans Cowan s.n.* (BM); 9 km N of Ihosy, *W. D'Arcy & A. Rakotozafy 15317* (MO); Domaine du centre moyen, au sud d'Ambalavao, *B. Descoings 977* (MO); Environs d'Ihosy, *B. Descoings 2775* (TAN); R. N. 7, P. K. 541, near La Brioché and 23 km S of the crossing of the Zamandao River, *L. J. Dorr 3923* (MO); R. N. 14, 36.1 km S of junction of R. N. 13 and R. N. 7, *L. J. Dorr 3933* (MO); 'Est d'Ihosy, *H. Humbert 4897* (BM); Haute Mananara, près poste forestier d'Imonty (Ambatohaly), *M. Keraudren 1519* (KE-Graham, P); Ihosy, montée vers l'Horombe, *J. & M. Peltier 2764* (TAN); Zazafotsy, Réserve 11, *Euphorbia* forest, *A. Richard 0114* (K). Ouest: Befandriana-Sud, 150 m, *O. Appert 40* (K, MO); Precise locality unknown, chiefly in Betsileo-land, *R. Baron 261* (K); Ambalavao, *J. Bosser 3578* (TAN); Nord de Belo Sur Tsiribihina, forêt tropophile, *J. Bosser 18134* (MO); Ranohira, *W. Rauh 10410* (TAN); between Beraketa and Antanimora, *W. D'Arcy & A. Rakotozafy 15320* (MO); Ambatofinandrahana, *P. Morat 126* (TAN); N. de Belo (Ouest), forêt sèche, *P. Morat 139* (TAN); Horombe, *P. Morat 2211* (MO); Ankilivalo (Ankazoabo) en savane, *P. Morat 2525* (TAN); Plateau de Bemaraha, without collector, *Herb. Jard. Bot. Tananarive 6154* (MO); Ampandrandava pas Betioky, without collector, *Herb. Jard. Bot. Tananarive 5111* (TAN). Sud: Ouest d'Ejeda, *J. Bosser 229* (MO); Imanombo, *Bosser 3877* (MO); Ifotaka, *J. Bosser 4029* (MO); Environs de Tuléar, *F. Chauvet 300* (KE-Graham, P); Androy, *R. Decary 2607* (US); Antanimora, *R. Decary 2935, 9198* (TAN); Behara, without collector (*Réserves Naturelles 2689*) (K, TAN); Tranomoro, *R. Decary 9013* (TAN); Environs Tuléar, *Dequaire 27541* (KE-Graham, P); Sud, without precise locality, *B. Descoings 542* (TAN); Bas Mangoky, *B. Descoings 778* (TAN); Vallée Moyenne du Mandrare près d'Anadabolava, *H. Humbert 12437* (KE-Graham, P, TAN, US); Rt. Nationale no. 7 at 63 km NE of Tuléar, *D. Lorence 1923* (MO); Tuléar, *A. Rakotozafy 767* (TAN); Behara, Amboasary, *Tsilizy s.n.* (*Réserves Naturelles 8338*) (TAN); Entre Antanimora et Betroka, *Ursch s.n.* (TAN); Ampanihy, route Ejeda, without collector, *Herb. Jard. Bot. Tananarive 4217*

(TAN). Without precise locality or collector, (*Herbier de la station agricole de l'Alaotra 4615, 24086*) (MO).

The genus is showy in bloom, with the large bright rose petals extending well beyond the shorter floral tube, and the flowers scarcely obscured by the elongate leaves, which are not fully developed at first flower appearance. The plant is widely distributed on the drier side of the island and is still quite common in the south-central area and the southwest. At the time of its original discovery, it was reportedly very common in the type area, where it grew with the equally abundant *Woodfordia fruticosa* (Baker, 1882).

The tribal position of *Koehneria* is not specified because tribal limits in the family were erected on an erroneous distinction between complete septal development (*Nesaeae*) and incomplete septal development (*Lythraeae*). Tobe (in prep.) has found that, in fact, all genera are characterized by incomplete septal development. Studies in wood anatomy and palynology support the interpretation that there is no major natural division in the family corresponding to the present tribes (Baas & Zweypfenning, 1979; Lee, 1979).

EXCLUDED NAMES

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