

Morphology and vascular anatomy of the flower of *Lagerstroemia indica* L. (Lythraceae) with some phylogenetic implications

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Summary: The main patterns of the floral vascular system and the structure of the syncarpous gynoecium of one of the most primitive members of Lythraceae, *Lagerstroemia indica*, have been studied. The vascular system of the flower consists of a vascular cylinder, in which consequently closed gaps with diverged traces to floral organs or composed vascular stands appear. The histological differentiation and vascular anatomy confirm the prevalence of appendicular features in the floral tube of *Lagerstroemia indica*. The syncarpous gynoecium of *Lagerstroemia indica* is composed of fertile synascidiate and symplicate structural zones without an apocarpous zone. The most characteristic features of the gynoecium are a secretory epidermis on a massive placenta and on incomplete septa, prominent dorsal ridges inside the locules, and continuation of septal bundles into the style.

Keywords: *Lagerstroemia indica*, Lythraceae, Myrtales, flower morphology, vascular anatomy, hypanthium, gynoecium

Lythraceae, with 31 genera and 585 species, the third largest family of the Myrtales, are distributed worldwide and show a relatively great range of morphological variation (CONTI et al. 1997). It is the only non-monotypic family within Myrtales with a superior ovary (EICHLER 1878) and a multicellular archesporium in ovule (TOBE & RAVEN 1983) – both rather primitive characters for Myrtales. In contrast to most families of the Myrtales, in Lythraceae developmental studies of the flowers are rare (CHEUNG & SATTLER 1967; RONSE DECRAENE & SMETS 1991), and vascular-anatomical data are incomplete: they concern certain problems of comparative floral morphology, e.g. the nature of the calicules, i.e. members of the outer calyx (epicalyx) (CADET 1954), and infrageneric systematics (TOBE & RAVEN 1990).

Lagerstroemia L. comprises 53 woody species from southeastern Asia, eastern Africa and Australia (KOEHNE 1893; TOBE & RAVEN 1990). Its distinctive features of the flower are: epicalyx absent, petals long clawed, stamens are born at the base of floral tube, antesealous stamens solitary and prominent, antepetalous stamens multiple (4–10 in a fascicle) and smaller, and carpellary midrib intrusive into the locule (EICHLER 1878; TOBE & RAVEN 1990). Floral nectaries are absent, even on the inner surface of the hypanthium (TOBE & RAVEN 1990). FAEGRI & VAN DER PIJL (1979) wrote, that *Lagerstroemia indica* has pollen-flowers, which present pollen of short antepetalous stamens as a reward for pollinators. After KOEHNE (1893), the gynoecium of *Lagerstroemia* is isomerous to the corolla, and the carpels are antepetalous. RONSE DECRAENE & SMETS (1991) described centrifugal insertion of antepetalous stamens in *Lagerstroemia indica* and explained it by intercalary growth of the floral tube between the first stamens and petals.

It has been demonstrated that the vascular system of the flower is useful for infra-familial systematics of some myrtalean families (SCHMID 1972; EYDE 1982). Therefore, it is curious that it was almost fully ignored in other families. The present study tends to reveal the main patterns of

the vascular system of the flower and the structure of the syncarpous gynoecium of *Lagerstroemia indica*, one of the most primitive members of Lythraceae (GRAHAM et al. 1993).

Material and Methods

Flower buds and open flowers of *Lagerstroemia indica* were collected by the author in the Botanical Garden of the National Museum of Natural History NAS Lisbon, Portugal (21.08.1998). Material was fixed in 70% ethanol. Preanthetic floral buds were dehydrated with absolute ethanol and chloroform, and embedded in paraffin (melting point 54°C) according to the standard procedure after GERLACH (1984). Material was cut into 15 µm transverse sections with a rotary microtome 'MC-2' (USSR). Sections were deparaffined by xylol, stained successively with Mayer's haematoxylin and 0.5% safranin, dehydrated with xylol and mounted in Canada balsam. Figures were drawn by means of a camera lucida 'Lomo RA-1' (USSR) and a microscope 'Lomo Mikmed R-14' (USSR).

Results

General flower morphology and histology

The investigated material of *Lagerstroemia indica* has hexamerous, sometimes pentamerous or tetramerous flowers. The hypanthium is cup-like, 5 mm long, 8 mm in diameter, hexagonal in section, with antepetalous ridges. Sepals are valvate, triangulate, green, petals are clawed, with crumpled lamina, rose. Sepals disjoint from each other in centripetal direction, separating a petal base between them (Fig. 1 G).

Antesepalous stamens are solitary, large, and placed lower than fascicles of smaller antepetalous stamens at the base of the hypanthium. Each antepetalous fascicle unites 4–5 paired stamens (Fig. 1 E). Anthers are latrorse, dorsiflex, with a wide connective. The exothecium of the connective is composed of elongated cells, an endothecium is developed in the distal part of the theca (Fig. 4).

The cortex of the receptacle at the flower base is very wide: the diameter of the receptacle is sextuple the diameter of the vascular cylinder. The cortex has a 2–4-layered solid exoderm and a wide mesoderm with chloroplasts and large intercellular spaces. Druses and solitary prismatic crystals of calcium oxalate can be found. The inner surface of sepals and hypanthium above stamens bases are covered with a thick cuticular epidermis with large rectangular cells, situated on a layer of small cells (Figs. 1 D–G, 3 A). The inner and the outer epidermis of the hypanthium as well as the inner sepal epidermis have stomata (Fig. 3 A, E). Such a structure of the inner epidermis of the floral tube and calyx lobes may be an evidence of a rudimentary nectariferous function.

Vascular system of receptacle and floral cup

From the pedicel into the floral base of *Lagerstroemia indica* a hexagonal (in cross section), amphiphloic vascular cylinder enters (Fig. 1 A). In the receptacle this cylinder becomes a bit wider and, in its upper part, narrower again. In this cylinder closed gaps with diverged traces of the floral organs or composed vascular stands appear consequently (Fig. 5). All diverged vascular bundles are amphicrybal. At first diverge sepal median bundles, and then diverge antepetalous

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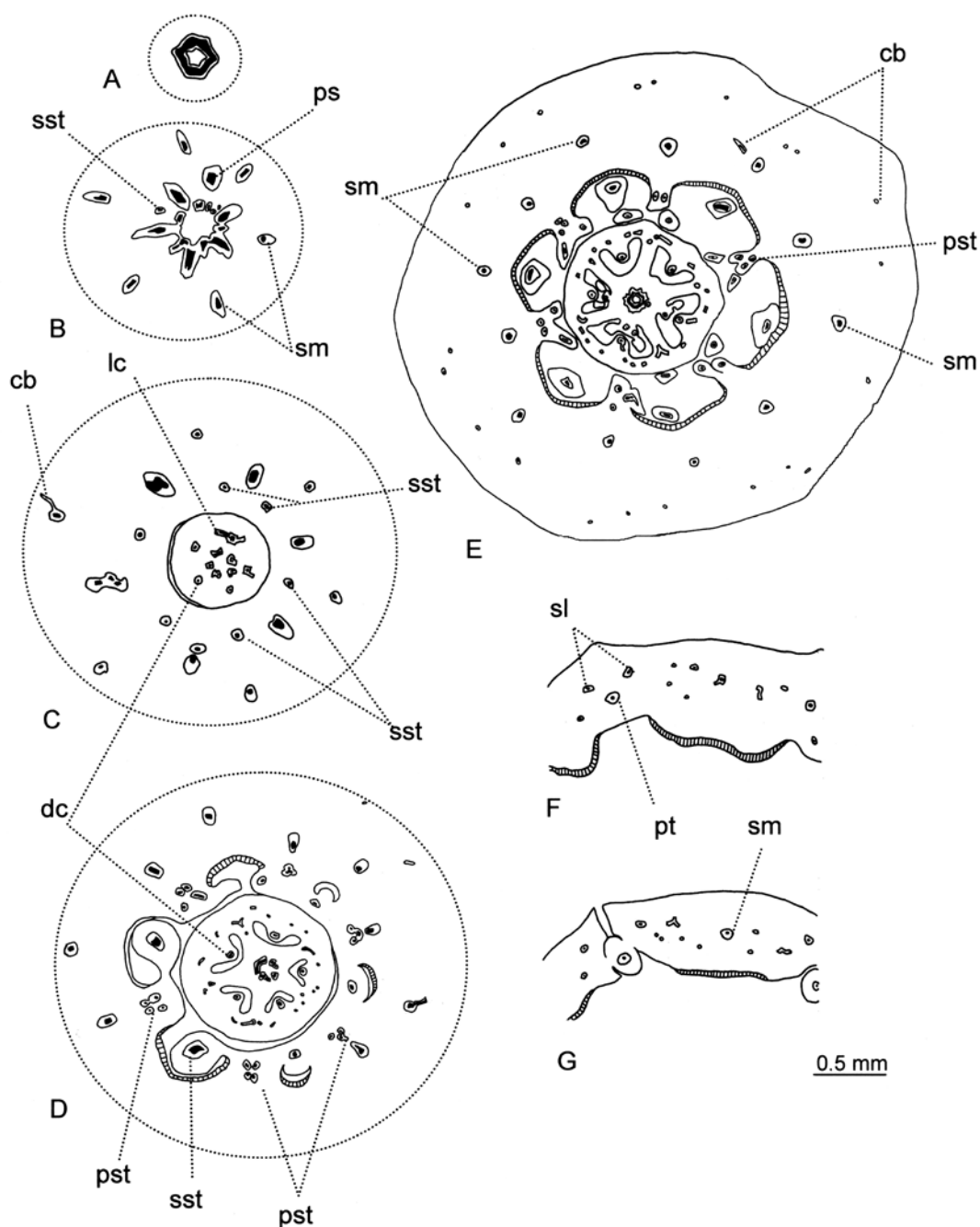


Figure 1: *Lagerstroemia indica*; ascending series of transverse sections of the floral base and floral cup (A–G): cb – cortical bundles; dc – dorsal carpellary bundle; lc – lateral carpellary bundle; ps – antepetalous strand; pst – antepetalous stamen bundles; pt – petal trace; sl – lateral sepal bundle; sm – median sepal bundle; sst – antesealous stamen trace. Large-celled epidermis of floral cup is hatched. In A–D cortex is not shown.

strands, which divide radially into an outer branch (petal-sepalous strand) and an inner branch (strand of antepetalous stamens) (Fig. 1 A–D).

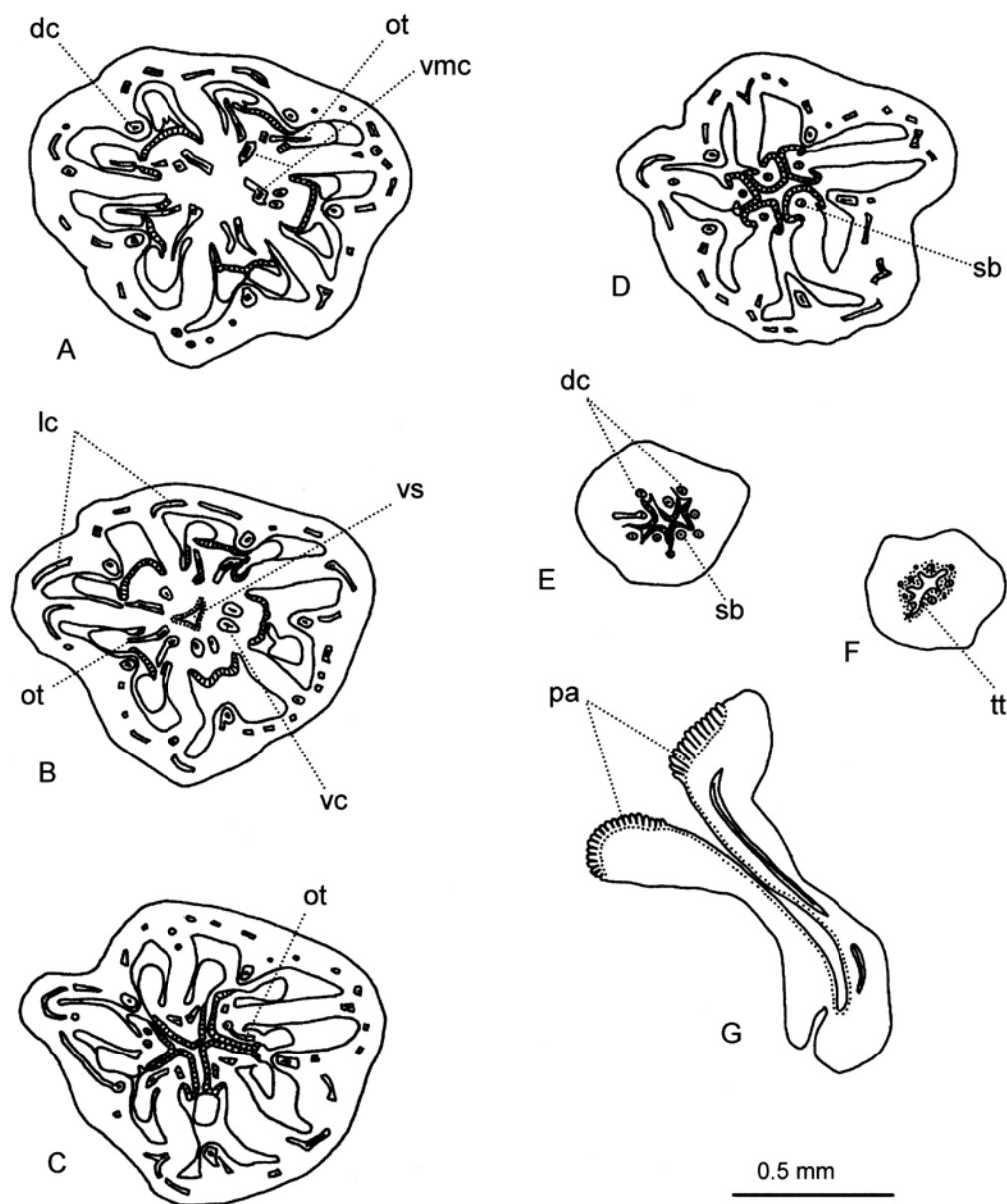


Figure 2: *Lagerstroemia indica*; series of transverse sections of the pistil (A–G) from the levels above section from Fig. 1 E: ot – ovule trace; pa – stigmatic papillae; sb – septal bundle; tt – transmitting tissue; vc – ventral carpellary bundle; vmc – ventral-median carpellary bundle; vs – ventral split. Secretory epidermis of placenta and septa is hatched.

The inner branch of an antepetalous strand divides into individual traces of antepetalous stamens: the two lowest traces diverge first, then the next two traces, and the fifth trace supplies the upper stamen (Fig. 1 D, E). This division corresponds to a centrifugal insertion of antepetalous stamens. Outer branches of the antepetalous strand at the upper part of the hypanthium split into two sepal lateral bundles and a petal trace (Fig. 1 E).

The traces of antesepalous stamens arise at the level of the appearance of antepetalous strands or slightly above. They either diverge independently or are coupled with sepal median bundles,

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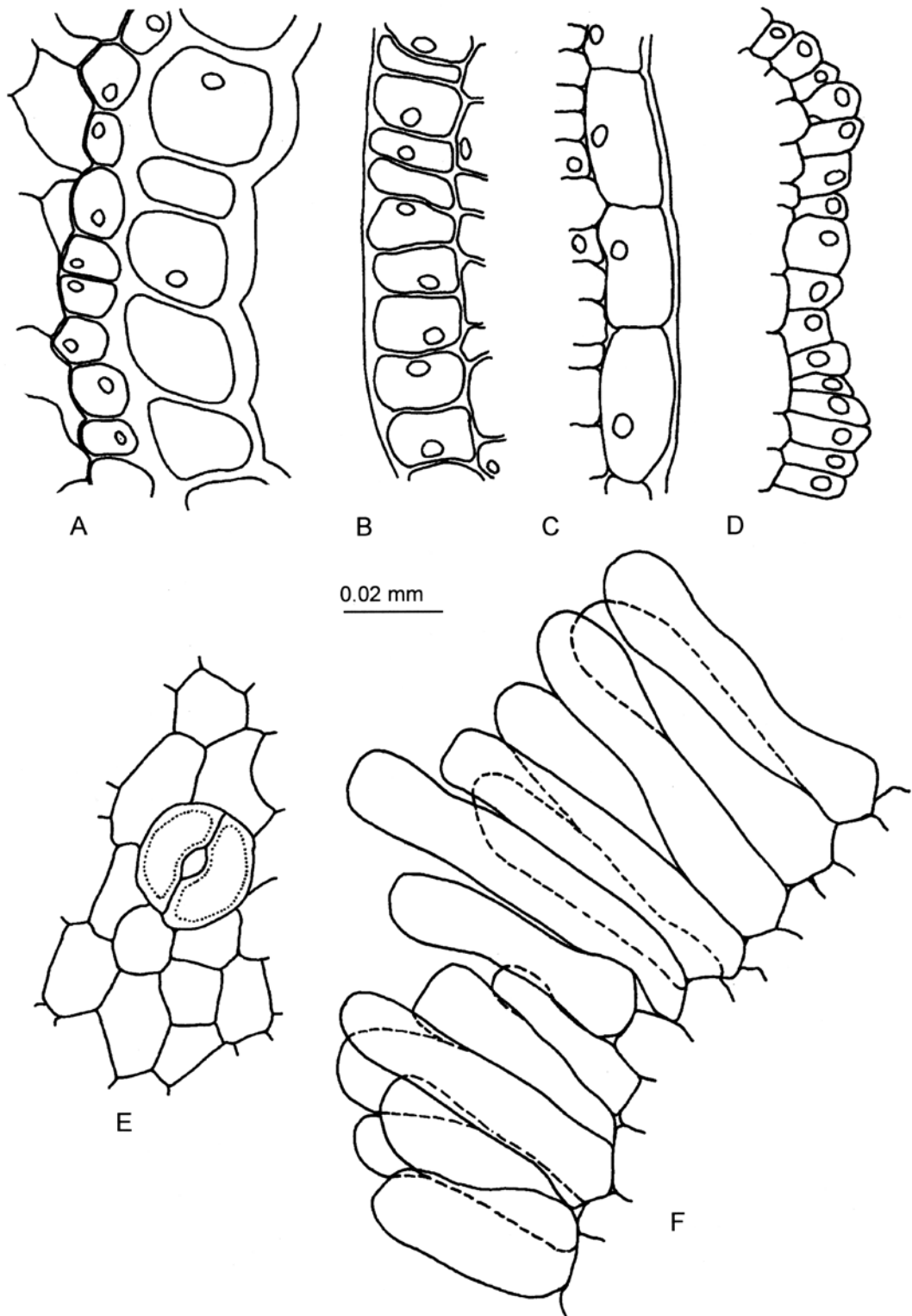


Figure 3: *Lagerstroemia indica*; epidermises of the floral cup (A, E) and pistil (B–D, F). A, inner epidermis of the floral cup; B, outer epidermis of the ovary; C, inner epidermis of the locule; D, secretory epidermis of placenta; E, frontal view of the stomium on the inner surface of the floral cup; F, stigmatic papillae, from Fig. 2G, enlarged.

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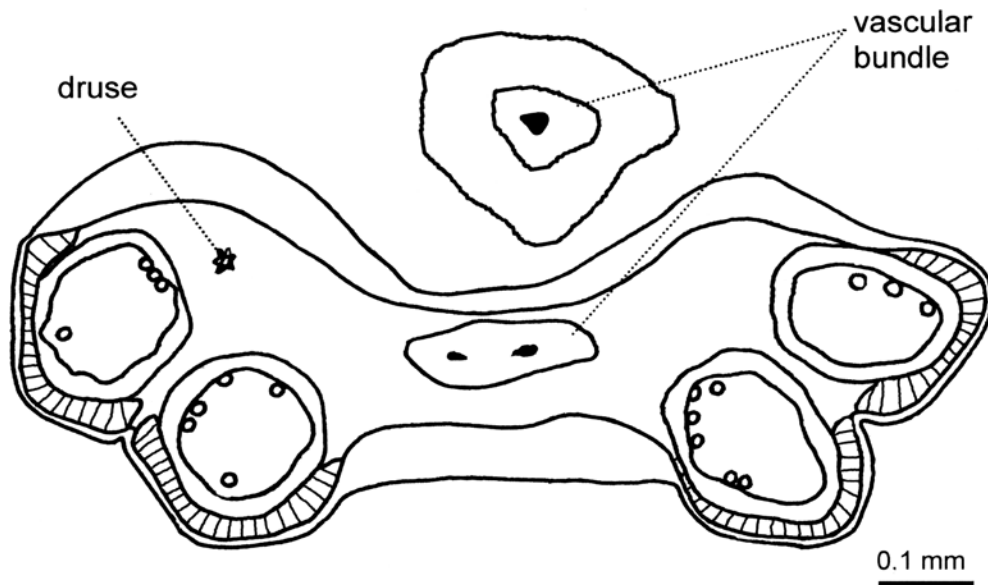


Figure 4: *Lagerstroemia indica*; transverse section of the anther of antesealous stamen. Endothecium is hatched.

or they diverge from the antepetalous strand (Fig. 1 B, C), or they are 'hanged', i.e. blind from the beginning. Sometimes vascular bundles of antesealous stamens bifurcate within the connective.

From the floral base at the boundary between exoderm and mesoderm, minute blind cortical bundles arise which make anastomoses with each other and with sepal median bundles (Fig. 1 C, E). Each sepal has a median bundle, two lateral bundles and some minute bundles from the cortex, petals have only one petal trace (Fig. 1 F, G).

Morphology, histology and vascularization of the gynoecium

The gynoecium of *Lagerstroemia indica* is pentamerous even in hexamerous flowers. The ovary is about 2–2.5 mm in all dimensions, possesses a short stalk (Fig. 1 C). In the lower $\frac{2}{3}$ part the ovary has five locules (Fig. 2 A), in the upper part it is unilocular (Fig. 2 C, D). The outer epidermis of the ovary consists of radially elongated cells with a thick cuticle (Fig. 3 B).

The inner epidermis of locules consists of flat cells with a thick cuticle (Fig. 3 C). Ovules are arranged in two separated rows on the prominent axial placentas, which are covered by a glandular epidermis (Fig. 3 D). Between rows of ovules the placenta approximates closely to the dorsal ridge of the carpel (Fig. 2 A), so that a transmitting duct between both epidermises is formed. Sometimes one locule is larger than the other, and the vascular system corresponds to the hexamerous gynoecium without septa.

At the height of $\frac{2}{3}$ of the ovary a triangular slit arises in its center, covered by a glandular epidermis. At a higher level this split connects three locules (Fig. 2 B), and another two locules above, so that the ovary becomes unilocular with incomplete septa and parietal placentas each having two uppermost ovules (Fig. 2 C). The glandular epidermis of placentas continues as glandular epidermis of the split. Two non neighboring septa get into contact in their proximal parts. Apical septa are absent. Septa become shorter above the uppermost ovules. At the proximal

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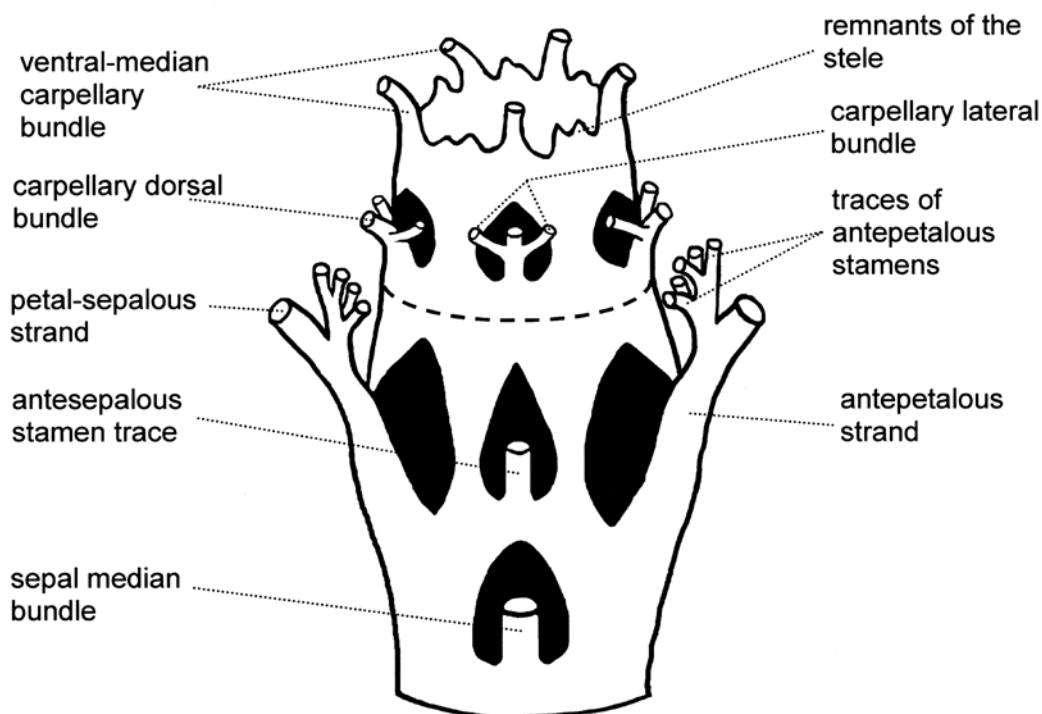


Figure 5: *Lagerstroemia indica*; reconstruction of the vascular system of the receptacle. Base of the gynoecium and floral cup is marked by dotted line.

top rounded expansions emerge, covered by a glandular epidermis. These expansions enter the style as folders of the inner carpel surface (Fig. 2 E, F).

The style is 16–20 mm long and bended downwards outside. It has a hollow folded canal covered by transmitting tissue. Stigma is slightly lobed, covered by one-celled papillae (Figs. 2 G, 3 F).

Above the perianth and the androecium traces arise, the vascular cylinder becomes pentangular. It is interrupted by five gaps of carpel traces, mostly in the radii of sepals. From each gap one bundle arises, and divides tangentially two carpellary lateral bundles whereas the median branch continues as carpellary dorsal bundle (Fig. 1 C). Above the closure of the gaps, five ventral-median carpellary bundles arise at the same radii (Fig. 1 E). Their gaps do not close, and remnants of the vascular cylinder end blindly soon (Fig. 5).

Dorsal carpellary bundles shift into the median ridges of the carpels, they make transversal bridges to lateral carpellary bundles and blind bundles in the ovary wall (Fig. 2 B, C). In our material there were no trans-septal bundles between dorsal or lateral bundles and ventral carpellary bundles, as it was referred by TOBE & RAVEN (1990). Lateral carpellary bundles end blindly in the upper part of the ovary. They do not enter the style.

Ventral-median carpellary bundles beneath placenta are divided into paired ventral bundles that give rise to ovule traces (Fig. 2 A–C). Above the placenta ventral bundles fuse in pairs between carpels and produce six septal bundles that enter the style (Fig. 2 D, E) as dorsal carpel bundles also do. In the style there are 10 bundles, 5 dorsal carpel bundles and 5 septal bundles, the last are more prominent and longer (Fig. 2 F).

Discussion

Morphological identification of the floral cup

Venation of floral organs of *Lagerstroemia indica* is typical for dicot flowers (GUÉDÈS 1979): three bundles in a sepal trace, one bundle in petal and stamen traces, five bundles in a carpel trace (dorsal, two lateral, and two ventral). Sequence of trace divergence from the stele (Fig. 5) corresponds to the acropetal organ initiation. The centrifugal branch of antepetalous stamen traces corresponds to the centrifugal development of these stamens (RONSE DECRAENE & SMETS 1991).

EICHLER (1878) called the floral cup in Lythraceae “Kelchtubus” (calyx tube), in contrary to the “Receptakulartubus” (receptacular tube) in Onagraceae. EICHLER (1878: 456) wrote: “Bei den Myrtifloren waltet der unterständige Fruchtknoten vor, in manchen Familien ... variiert er jedoch auch halbunterständig oder gänzlich vom Receptakulum (“Kelchtubus”) frei ...” (In Myrtales there is an inferior ovary, but in many families ... it is semi-inferior or quite free from the receptacle (“calyx-tube”)).

Flower development and vascular anatomy of Lythraceae give base for different interpretations of the floral cup, depending not on the method of study but on the author’s viewpoint. Thus, in contrast to the common view, that vascular anatomy often supports the appendicular concept and flower development supports the receptacular concept. CADET (1954) interpreted the hypanthium in *Lythrum salicaria* and *Peplis portula* – based on vascular anatomy – as receptacular. According to CADET (1954), perianth traces of calicules, sepals and petals arise at the top of the hypanthium like traces of vegetative leaves do in the stem. Vascular anatomy was an argument for the receptacular interpretation of the inferior ovary and hypanthium in Punicaceae (SINHA & JOSHI 1959), Onagraceae (DE VOS 1981), and Myrtaceae (STEPANOVA 2004; VOLGIN & STEPANOVA 2006), and for the appendicular interpretation in Combretaceae (TIAGI 1969; RODRIGUEZ 1993).

On the other hand, CHEUNG & SATTLER (1967) accepted the appendicular concept of the hypanthium in their study of the floral development of *Lythrum salicaria*, based on the presumption, that a floral organ can arise on another (here, a petal arises on the calyx tube).

The problem of morphological identification of the floral cup and the inferior ovary has upheld exhausting discussions for a long time. They were rejected by studies of the flower development and the postulation of a demythologization of this “pseudoproblem” (LEINS & ERBAR 1985) on the concept of intercalary growth and the principle of variable proportions (LEINS 1972), or the concept of continuity of plant organs (SATTLER 1978) and meristem fusion. Another skeptical view came from plant anatomists, who found that the vascular-anatomical method is too controversial for such a problem (PURI 1951; CARLQUIST 1969). Some adepts of this method considered that the evolution of the vascular system of epigynous or perigynous flowers goes into the direction of a reduction of axial bundles, transformation into the system of sympodial bundles without gaps, and increase of the reliability of the vascular system (VOLGIN 1988).

The amphiphloic vascular cylinder of the receptacle of *Lagerstroemia indica* is more characteristic for the vegetative stem of dicot angiosperms than for its flower (SCHMID & BECK 1971; GUÉDÈS 1979). Perhaps, such structure of the vascular system is formed by the cambial activity of the stele in the receptacle. In the vascular system of the receptacle all nodes of floral organs are clearly

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visible through their closed gaps (Fig. 5). The cylinder of vascular tissue enters the ovary, so the ovarian stalk and central column of the ovary must be interpreted as elongated floral apex, united with fused carpels (Fig. 1 C–E). As the vascular cylinder enters the ovary, the floral cup must be supplied only by traces and strands of fused traces of floral organs (stamens, petals and sepals). This fact supports the idea, that the floral cup in *Lagerstroemia indica* is fully appendicular. The histological differentiation of the floral tube reveals its similarity with calyx lobes (differentiation of exoderm and mesoderm, large-celled inner epidermis with stomata, and cortical bundles). In this respect, we suppose the prevalence of appendicular features in histology and vascular anatomy of the floral tube of *Lagerstroemia indica*.

Structural type of the gynoecium

Comparative-morphological analysis of the gynoecium has been provided on the concept of the vertical zonality of free and fused carpels by LEINFELLNER (1950). After LEINFELLNER, a coenocarpous (here: syncarpous) gynoecium has four structural zones: synascidiate, symplicate, hemisymplicate and asymplicate (here: apocarpous). These zones are defined by the presence of congenital fusions between carpels and between carpel margins (closure of the ventral slit). The following development of this concept is the model of structural types of the monocyclic syncarpous gynoecium by VOLGIN & TIKHOMIROV (1980). According to this model, there are at least six structural types of a syncarpous gynoecium, defined by combinations of LEINFELLNER's structural zones – except the hemisymplicate zone, which is regarded as an intermediate one (Tab. 1).

The syncarpous gynoecium of *Lagerstroemia indica* contains synascidiate and symplicate zones. Both are fertile. Placentas are axile in the first zone, and parietal in the second zone. Ovule traces are supplied with lateral carpellary bundles, without trans-septal anastomoses. The symplicate zone continues into the style. A capitate stigma is the result of a complete fusion between carpels up to their tops. This means, that the apocarpous zone is absent or almost fully suppressed. The syncarpous gynoecium of *Lagerstroemia indica* is referred to the fourth type after VOLGIN &

Table 1: Structural types of the monocyclic syncarpous gynoecium after VOLGIN & TIKHOMIROV (1980).

Type	Structural zones	Examples
1	synascidiate and apocarpous	<i>Tetragonia echinata</i> (Aizoaceae), <i>Nigella</i> (Ranunculaceae), <i>Pereskia pititache</i> (Cactaceae)
2	synascidiate, symplicate and apocarpous	The most widespread type: Aizoaceae, Apiaceae, Liliaceae, Onagraceae, Phytolaccaceae etc.
3	symplicate and apocarpous	Hypericaceae
4	synascidiate and symplicate	Examples are not known
5	synascidiate	Examples are not known
6	symplicate	Violaceae

TIKHOMIROV's model (1980): syncarpous gynoecium with synascidiate and symplicate structural zones. STEPANOVA (2004) and VOLGIN & STEPANOVA (2006) have showed the other examples of this type in Myrtaceae earlier.

The most characteristic features of the gynoecium of *Lagerstroemia indica* are: secretory epidermis of the placenta and incomplete septa, prominent dorsal ridges in locules, and continuation of septal bundles, derived from ventral carpellary bundles, into the style.

Systematical implications

A gynoecium with synascidiate and symplicate zones is exclusively common for Myrtales. It was found in Melastomataceae, Onagraceae (VAN TIEGHEM 1871), Punicaceae (SINHA & JOSHI 1959), Myrtaceae (VOLGIN & STEPANOVA 2006), and others. Sometimes there are comissural stigma lobes which imitate free carpel tops (EYDE 1982). The sister families to Lythraceae can be Trapaceae, Onagraceae, and Combretaceae (CONTI et al. 1996, 1997), which have some derived features: mostly parietal placentation, trans-septal ovule vascular supply, and no vascular tissue between locules of the ovary (RAM 1956; TIAGI 1969; DE VOS 1981).

The fundamental work of VAN TIEGHEM (1871) contains accurate figures with series of transverse sections of the flower of a Melastomataceae '*Oxymeris Zinnii*' (according to VAN TIEGHEM), where a complete vascular cylinder in the center of the ovary can be seen (Planche VIII, Fig. 242–243). Vascular bundles which retain above axile placentas enter the style (Planche VIII, Fig. 244–247). These bundles are born by the vascular cylinder and alternate with locules. The situation seems to be identical to the one revealed in *Lagerstroemia indica*.

After WILSON (1982), 'supracarpellary' vascular tissue is an evidence of residual apical activity of the receptacle. It is probable that activity of the floral apex in some members of Myrtales is quite intensive and prolonged. This presumption is supported by abundant vascular tissue of the receptacle in *Lagerstroemia indica* and '*Oxymeris Zinnii*' and by the presence of two or three whorles of carpels in *Punica granatum* (SINHA & JOSHI 1959). The same was found in Myrtaceae as 'infralocular plexus' of bundles in *Angophora intermedia* and other genera (STEPANOVA 2004; VOLGIN & STEPANOVA 2006). The other families studied have no vascular bundles in the base of the central column of the ovary (Onagraceae) (VAN TIEGHEM 1871; DE VOS 1981), or even no central column (Combretaceae). From the morphological viewpoint Lythraceae belongs to the basal myrtalean families, with predominantly axial placentation, axial ovule vascular supply, and abundant vascular tissue in the floral apex.

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