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Cladistic analysis of the Lythraceae *sensu lato* based on morphological characters

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GRAHAM, S. A., CRISCI, J. V. & HOCH, P. C., 1993. **Cladistic analysis of the Lythraceae *sensu lato* based on morphological characters.** The Lythraceae *s. l.* comprise 31 mostly highly distinctive genera distributed worldwide. Cladistic analyses of the family were undertaken using 26 characters from anatomy, floral morphology, pollen, and seed morphology. Of four outgroup hypotheses, the Onagraceae offered the best heuristic assessment, generating 3746 trees with a tree length of 83 and consistency index and (C.I.) of 0.41. A strict consensus tree from the 3746 trees produced a basal monophyletic group of five genera (*Sonneratia*, *Duabanga*, *Punica*, *Lagerstroemia*, *Lawsonia*) characterized by anthotelic (determinate) inflorescences and wet stigmas, and a second clade with blastotelic (indeterminate) inflorescences, dry stigmas, and reduced carpel number. Successive weighting with Onagraceae as outgroup generated five most parsimonious trees with a tree length of 164 and C.I. of 0.75. Internal branches are weakly supported by only seven non-homoplasious characters. Significant results of the analysis include: (1) recognition of the two major clades and a total of seven monophyletic groups within the family; (2) the paraphyly of subfamily Lythroideae (Lythraceae *s. s.*); and (3) indication that genera endemic to the New World have been derived from more than one ancient Old World evolutionary line. The current taxonomic classification of the family is not closely correlated with results of the cladistic analysis.

ADDITIONAL KEY WORDS:—Myrtales – phylogeny – Punicaceae – Sonneratiaceae – taxonomy.

CONTENTS

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INTRODUCTION

The Lythraceae *sensu lato* are a highly diverse, primarily woody family of 31 genera and approximately 600 species in the order Myrtales. The family is distributed worldwide, mostly in mesophytic to wet habitats of the sub-tropics and tropics. Approximately equal numbers of genera are endemic to the Eastern and Western Hemispheres (Table 1). Types of habitat include tall to small trees, shrubs, perennial and annual herbs. These are adapted to a wide variety of vegetation types including mangrove swamps, rainforests, seasonally dry savannahs, coastal dunes, and fresh-water marshes. Sixty one percent of the genera (19 genera) are monotypic or ditypic.

When defined in the broadest sense, the family comprises four subfamilies, Lythroideae, Sonneratioideae, Duabangoideae, and Punicoideae (Dahlgren & Thorne, 1984; Thorne, 1992a, 1992b). One or more of the three latter subfamilies traditionally have been regarded as satellite families of Lythraceae *sensu stricto*. All members display numerous specialized features of the order: intraxylary phloem; vestured pitting of vessel elements; minute, divided, axillary stipular processes; brochidodromous leaf venation; ellagic acid-rich tissues; and a site of embryological features (Dahlgren & Thorne, 1984; Johnson & Briggs, 1984; Tobe & Raven, 1983). Within Myrtales, there are no autapomorphies which diagnose Lythraceae *s. l.* or *s. s.* The very generalized morphology of the family, together with the very distinctive genera, suggest that the family is of great age. Major monophyletic groupings are not readily apparent. Although clusters of two to four closely related genera can be recognized, major evolutionary lines uniting generic clusters are obscure.

Subfamily Lythroideae (Lythraceae *s. s.*) are herbs, shrubs, or trees with entire, generally opposite leaves, free of sclereids, and stems frequently 4-angled. Flowers are bisexual, perigynous, 4–6 merous, with a diplostemonous androecium, stamens inserted well below the rim of the hypanthium, colporate pollen, a superior to semi-inferior ovary with an unsunken style and unlobed stigma, axile placentation, and a multicellular archesporium. The fruit is a dry capsule containing numerous seeds with a multiplicative outer integument and endosperm absent at maturity. Development of the floral tube varies from broadly campanulate to tubular, and tubular hypanthia vary from actinomorphic to weakly or strongly zygomorphic. Heterostyly, for which the family is noted, occurs in six genera.

The recognition of three satellite families as subfamilies of Lythraceae expands the familial definition to include: stamens inserted at or near the rim of the hypanthium and semi-inferior to inferior ovary (*Sonneratia*, *Duabanga*, and *Punica*); leaves with sclereids (*Sonneratia* and *Duabanga*); berry type fruits

TABLE 1. The genera of Lythraceae *s. l.*, number of species, and geographical distribution in Western (W) or Eastern (E) Hemisphere (not including naturalized ranges).

Genus	Acronym	Special number	Geographical Distribution
Adenaria	ADEN	1	W—Mexico to Argentina
Ammannia	AMMA	25	E —Africa, Asia, with W extensions
Capuronia	CAPU	1	E —Madagascar
Crenea	CREN	2	W—coastal N. South America
Cuphea	CUPH	ca. 275	W—E. United States to Argentina
Decodon	DECO	1	W—E. United States (circumboreal ? in Cenozoic)
Didiplis	DIDI	1	W—E. United States
Diplusodon	DIPL	72	W—Brazil
Duabanga	DUAB	2	E —SE. Asia, Malaysia
Galpinia	GALP	1	E —E. Africa
Ginoria	GINO	15	W—Mexico, Caribbean
Haitia	HAIT	2	W—Hispanola
Heimia	HEIM	3	W—Texas to Argentina
Hionanthera	HION	4	E —Mozambique, Zimbabwe
Koehneria	KOEH	1	E —Madagascar
Lafoensia	LAFO	6	W—Mexico to Brazil
Lagerstroemia	LAGE	56	E —India to Australia, Philippines
Lawsonia	LAWS	1	E —E. Africa? origins unclear
Lourtella	LOUR	1	W—Peru
Lythrum	LYTH	35	E —Eurasia, North & South America
Nesaea	NESA	50	E —Africa, Mexico
Pehria	PEHR	1	W—Honduras to Colombia
Pemphis	PEMP	1	E —coastal E. Africa to S. Pacific
Peplis	PEPL	2	E —Eurasia
Physocalymma	PHYS	1	W—Bolivia, Peru, Brazil
Pleurophora	PLEU	11	W—Chile & Argentina to Brazil
Punica	PUNI	2	E —Eurasia? origins unclear
Rotala	ROTA	44	E —Asia, Africa, with W extensions
Sonneratia	SONN	5	E —SE Asia, to E. Africa, Australia, Micronesia, Melanesia
Tetrataxis	TETR	1	E —Mauritius
Woodfordia	WOOD	2	E —Africa to Indonesia

(*Sonneratia* and *Punica*), seeds with non-multiplicative outer integument and porate pollen (*Duabanga*) and a unicellular archesporium (*Punica*).

The most widely accepted concept of the Lythraceae during this century has been the narrow one proposed in the only monograph of the family (Koehne, 1903), which excludes *Sonneratia*, *Duabanga*, and *Punica*. This work is based exclusively on gross morphological characters (Table 2). Since Koehne's study, extensive new information on pollen morphology, chromosome numbers, and wood and floral anatomy has been accumulated and six new lythraceous genera described.

Although Koehne's treatment remains the only comprehensive reference to the taxonomy and classification of the Lythraceae, various workers have altered the limits of the family to include one or more of the three satellite genera. Melchior (1964), Hutchinson (1973), and Cronquist (1981) maintained the narrow view of the family proposed by Koehne, recognizing *Sonneratia* and *Duabanga* as constituting the Sonneratiaceae and *Punica*, the monotypic Punicaceae (Table 3). Dahlgren (1975) first included *Sonneratia* and *Duabanga* in the Lythraceae while recognizing Punicaceae; later, he recognized both Sonneratiaceae and Punicaceae (Dahlgren, 1980). Dahlgren & Thorne (1984) and Thorne (1981, 1992a, 1992b) adopted a broader concept of the family to

Table 2. Classification of the Lythraceae. Subfamilies are from Dahlgren & Thorne (1984); classification of subfamily Lythroideae (= the traditional Lythraceae) from Koehne (1903). Genera described after 1903 are enclosed in brackets. Unnamed series of Koehne are not included

Subfamily Sonneratioideae: *Sonneratia*
Subfamily Duabangoideae: *Duabanga*
Subfamily Punicoideae: *Punica*
Subfamily Lythroideae
  Tribe Lythreae—Septum of the ovary interrupted or split above the placenta, the placenta thus not continuous with the style.
    Subtribe Lythrinae—Seed without a margin, or when margined, the flowers always zygomorphic.
      1. *Rotala*; 2. *Ammannia*, 3. (*Hionanthera*); 4. *Peplis*; 5. *Didiplis*; 6. *Lythrum*; 7. *Woodfordia*; 8. *Cuphea*; 9. *Pleurophora*.
    Subtribe Diplusodontinae—Seeds dorsally compressed and encircled by a wing. Placenta of the mature fruit strongly depressed, basal. Flowers always actinomorphic.
      10. *Galpinia*; 11. *Pemphis*; 12. [*Capuronia*]; 13. *Diplusodon*; 14. *Physocalymma*; 15. *Lafoensia*.
  Tribe Nesaeeae—Septum of the ovary complete, the placenta thus continuous with the style. Flowers always actinomorphic.
    Subtribe Nesaeinae—Seed coat neither thickened nor winged.
      16. *Crenea*; 17. *Nesaea*; 18. *Heimia*; 19. *Decodon*; 20. *Pehria*; 21. *Adenaria*; 22. [*Koehneria*]; 23. [*Lourtella*]; 24. *Tetrataxis*; 25. *Ginoria*; 26. [*Haitia*]
    Subtribe Lagerstroemiinae—Seed coat either extended as a wing or the apex truly spongy.
      27. *Lagerstroemia*; 28. *Lawsonia*.

include *Sonneratia*, *Duabanga*, and *Punica* as subfamilies of Lythraceae, while admitting the inclusion of these taxa left the family "rather vaguely defined". Takhtajan (1980) first recognized Sonneratiaceae and Punicaceae as families closely related to Lythraceae, then modified his classification by removing *Duabanga* from the Sonneratiaceae as the new family Duabangaceae (Takhtajan, 1986). At present, the infrafamilial classification of the Lythraceae based on traditional morphological comparisons remains unsettled, with three major arrangements of the taxa espoused in the most recent treatments (Table 3). The close relationship of Lythraceae *s. s.* *Sonneratia*, *Duabanga*, and *Punica* is undisputed and any phylogenetic study of the Lythraceae would be incomplete without considering all of them.

Subfamily Lythroideae (Lythraceae *s. s.*) is divided into two tribes, distinguished only by complete septation of the ovary (Nesaeeae) versus incomplete septation (Lythreae) (Koehne, 1903; Table 2). Tobe (work in progress) has found septa are incomplete in all genera, thus removing the sole basis for tribal recognition. Palynological data (A. Graham *et al.*, 1985, 1987, 1990; Lee, 1979) and studies in wood anatomy (Baas & Zweypfenning, 1979) also fail to support the tribal divisions.

Classification of Lythraceae *s. l.* and specifically subfamily Lythroideae, which contains the majority of the genera, clearly needs reassessment. We present the first cladistic analysis of the Lythraceae *s. l.* as an initial step in understanding the evolutionary history of this diverse group and laying a sound phylogenetic foundation for a more natural classification of the family. Explicit methods of

Table 3. Summary of the three most recent classifications of Lythraceae *sensu lato*

Cronquist (1981): Lythraceae *s. s.*, Punicaceae, Sonneratiaceae
Takhtajan (1986): Lythraceae *s. s.*, Punicaceae, Sonneraticiaceae, Duabangaceae
Thorne (1992a,b): Lythraceae *s. l.*, incl. Punicoideae, Sonneratioideae, Duabangoideae, and Lythroideae

phylogenetic reconstruction are ideally suited for application to the Lythraceae. New information on the family allows comparison of a wider array of characters than previously were available. Cladistic analysis already has been applied to the order Myrtales, to which the family belongs (Johnson & Briggs, 1984), and to the putative sister family of Lythraceae, the Onagraceae (Hoch *et al.*, 1993). Explicitly constructed cladograms based on morphological characters should stimulate new phylogenetic hypotheses that can best be tested by the molecular systematic studies recently initiated at the ordinal and family level (Bult *et al.*, work in progress; Graham *et al.*, work in progress). A number of phylogenetic studies using molecular data and including some Lythraceae in the outgroups are already available for comparison (e.g. Bult & Zimmer, 1993; Conti *et al.*, 1993; Crisci *et al.*, 1990; Martin & Dowd, 1986; Sytsma & Smith, 1988, 1992). Some questions we address in the study are:

(1) What are the phylogenetic relationships of *Sonneratia*, *Duabanga*, and *Punica* to each other and to the remainder of the family?

(2) What are the basal members of the family? *Lagerstroemia*, for example, has been viewed both as the most advanced genus of the Lythraceae and as one of the most primitive (Baas & Zweypfenning, 1979).

(3) What monophyletic groups of genera can be demonstrated?

(4) What inferences of chromosome evolution and biogeographic history can be derived from results of the analyses?

(5) To what extent does the infrafamilial classification of Lythraceae *s. s.* currently in use agree with phylogenetic hypotheses generated by the morphological data set?

METHODOLOGY

The principles of phylogenetic systematics as originated by Hennig (1966) are used in this study. Only shared derived character states are considered indicative of recent common ancestry or monophyly. Cladistic analysis requires that the group to be analysed be monophyletic, that all descendants of a common ancestor be included within the group, and that the group be defined by one or more synapomorphies. Justification of the monophyly of individual genera in this study is presented below. The methodology extracts the branching patterns of character state distribution and estimates phylogenies based on those patterns. The principle of parsimony is employed in choosing among the numerous hypotheses generated.

Monophylesis of the Lythraceae sensu lato

The monophylesis of Lythraceae *s. l.* is inferred based on results of cladistic analysis of the order Myrtales (Johnson & Briggs, 1984) in which several homoplasious synapomorphies are described on the branch leading from the common ancestor of Lythraceae-Onagraceae to the Lythraceae *s. l.* clade. These comprise outer integument of the seed multiplicative, stigmatic lobing lost, teeth of leaf margin vestigial, opposite phyllotaxy fixed. In the consensus tree of Johnson & Briggs (1984, Fig. 7), the monophylesis of Lythraceae *s. l.* was established by the autapomorphy of a multiplicative outer integument in the seed. Unfortunately, the seed coat of the Duabangoideae is not multiplicative, but consists of a two-layered testa and two-layered tegmen. Although this condition is most likely derived through simplification, absence of a multilayered testa in *Duabanga* eliminates the only autapomorphy defining Lythraceae among 77 characters used to describe the order.

Monophylesis of the genera

The genera of Lythraceae are well delimited with two, or possibly three, exceptions, *Peplis* vs. *Lythrum*, *Hionanthera* vs. *Ammannia*, and possibly *Nesaea* vs. *Ammannia*. Although the genus *Peplis* has been submerged in *Lythrum* (Webb, 1967), *Peplis* maintained as a separate genus of either two or three species finds some support. Absence of nectaries (a synapomorphy) unites *P. portula* L., *P. alternifolia* Bieb., and *P. erecta* Req. ex Moris, whereas nectaries are present in *Lythrum* (Tobe *et al.*, 1986). Specialized pollen morphology unites *P. portula* and *P. alternifolia* (grains small with transverse mesocolpial striations, oval pseudocolpi with rounded apices). Pollen of *Lythrum* and *P. erecta* (= *L. borysthenicum* Litv.) have larger, more prolate grains with longitudinal mesocolpial striations and more linear pseudocolpi with acute apices (A. Graham *et al.*, 1987). For purposes of this analysis, *Peplis* is treated as a monophyletic taxon with two species, *P. portula* and *P. alternifolia*, based on the complex of characters that constitute the *Peplis* pollen type.

Recognition of *Hionanthera*, a genus of four species from Mozambique, has been questioned by Cook (1974), who considered it synonymous with *Ammannia*. *Hionanthera* appears to be distinguished from *Ammannia* by indistinct vs. distinct pollen pseudocolpi (A. Graham *et al.*, 1987) and capsules with few large seeds vs. numerous minute seeds (Panigrahi, 1986). However, neither genus has been well studied and more complete material is needed of *Hionanthera* before generic limits can be resolved.

The close relationship of *Ammannia* and *Nesaea* based on nearly identical morphology, including a unique synapomorphic interlocking striate pollen exine, has been obscured by their placement in opposing tribes. In the absence of different septal conditions, the genera can be distinguished only by their modes of capsule dehiscence, which are very similar. In *Ammannia*, capsules are irregularly dehiscent or indehiscent. In *Nesaea*, dehiscence is first circumscissile, followed by irregular tearing of the lower portion of the capsule. Once the small apical circumscissile lid falls away, the capsules are difficult to distinguish from those of *Ammannia*. Further comparisons of dehiscence modes are needed in more species of both genera to determine if the genera are indeed distinct. The presence of spiral thickenings in vessels of *Nesaea* and their absence in *Ammannia* (Baas & Zweypfenning, 1979) also needs to be substantiated in additional taxa. For purposes of this analysis, *Nesaea* is recognized as monophyletic based on the presumed autapomorphic capsule dehiscence mode.

Twelve of the 31 genera that constitute the Lythraceae *s. l.* are monotypic and are accepted as monophyletic by definition. These are *Adenaria*, *Capuronia*, *Decodon*, *Didiplis*, *Galpinia*, *Koehneria*, *Lawsonia*, *Lourtella*, *Pehria*, *Pemphis*, *Physocalymma*, and *Tetrataxis*. An additional six genera are ditypic; *Crenea*, *Duabanga*, *Haitia*, *Peplis*, *Punica*, and *Woodfordia*. Species of the genus *Crenea* lack a unique synapomorphy; the genus is recognized by the combination of 4-merous, actinomorphic flowers (symplesiomorphies) and basifixed anthers (apomorphic in *Crenea* and *Pleurophora*). *Duabanga* is the only genus of the family with porate pollen and a non-multiplicative seed coat. *Haitia* is distinguished by an encircling epicalyx on the hypanthium, a unique feature in the family. In *Punica*, the 1-celled archesporium and seeds with a sarcotesta are definitive autapomorphies. The two very similar species of *Woodfordia* share a suite of advanced features, including highly modified inflorescences (brachyblasts) unique in the family (Weberling, 1988).

Among the genera with three or more species, autapomorphies distinguish *Cuphea* (emergent placentas), *Diplusodon* (bipartite placentas with lunate septae), *Lafoensia* (plicate, deciduous hypanthia), *Lagerstroemia* (unilateral, winged seeds and revolute cotyledons), *Rotala* (transversely striated capsule walls), and *Sonneratia* (fruits indehiscent pulpy berries). The remaining genera are recognized by combinations of plesiomorphic and apomorphic characters occurring individually elsewhere in the family. The combinations are unique, but none of the following genera has a uniting synapomorphy: *Ammannia*, *Ginoria*, *Heimia*, *Hionanthera*, *Lythrum*, and *Pleurophora*.

Outgroup selection

The phylogenetic hypotheses that have been proposed for the order Myrtales provide a basis for choosing appropriate outgroups for cladistic analysis of the Lythraceae (Dahlgren & Thorne, 1984; Johnson & Briggs, 1984; Martin & Dowd, 1986). Findings of the first two studies were based on a broad array of data generated as part of a coordinated effort at reassessment and delimitation of the Myrtales (Raven, 1984).

Johnson and Briggs in their cladistic analysis of the order recognized three major complexes of families in the Myrtales: (1) lythracean including Lythraceae *s. l.*, Onagraceae, and Trapaceae; (2) melastomatacean *et al.*, including Melastomataceae *s. l.*, Combretaceae, Crypteroniaceae, Oliniaceae, Peneaceae, Rhynchocalycaceae, Alzateaceae; and (3) myrtacean including Myrtaceae, Heteropyxidaceae, and Psiloxylaceae. Their analyses also recognized an alternative placement for Lythraceae (one step longer than the most parsimonious tree) in the melastomatacean line as a sister to the melastomatacean families minus the Combretaceae. Hypotheses of phylogenetic relationship from their study are presented in simplified form in Fig.1A–E. Although Johnson and Briggs regard the relationship of the lythraceans as an open question their analyses provide a possible scenario in which Onagraceae-Trapaceae and Lythraceae have evolved from a common ancestor at an early age in the history of the order, with divergence of the lythracean line marked by grouping of vessels in the wood, change from trilacunar to unilacunar (one trace and one gap) nodes, and acquisition of valvate calyx lobes, an apical style base, and fibrous exotegmen of the seed coat. Subsequently, Onagraceae and Trapaceae have diverged extensively from Lythraceae and from each other (Johnson & Briggs, 1984: 719). No unique synapomorphies define the Lythraceae-Onagraceae-Trapaceae clade.

Dahlgren and Thorne (1984) arrive at substantially the same conclusions as Johnson and Briggs, based on intuitively generated hypotheses of phylogeny for the order. They agree to a close relationship of Lythraceae and Onagraceae, citing a combination of four shared derived characters as evidence for common

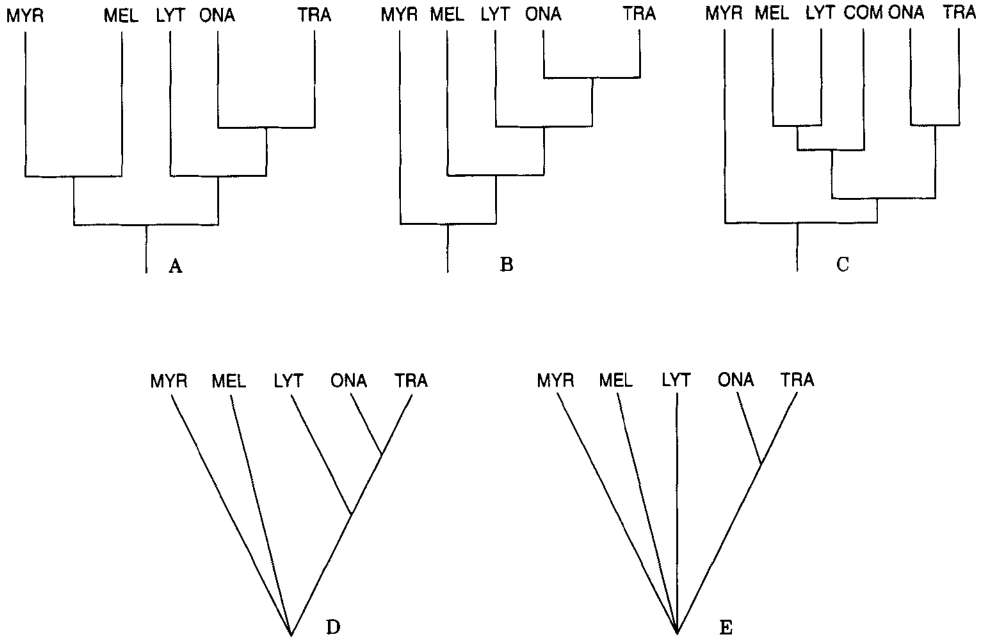

Figure 1A–E. Outgroup hypotheses for Lythraceae. A–C, Phylogenetic relationship of Lythraceae to remainder of Myrtales simplified from phylograms of Johnson and Briggs (1984; figs 3 & 4). D,E, Phylogenetic relationships of Myrtales from consensus trees of Johnson and Briggs (1984; figs 6 & 7). MYR = Myrtaceae, Heteropyxidaceae, and Psiloxylaceae; MEL = Melastomataceae *s. l.*, Combretaceae *s. l.*, Crypteroniaceae, Oliniaceae, Peneaceae, Rhynchocalycaceae, and Alzateaceae in A,B and Melastomataceae minus Combretaceae *s. l.* in C; LYT = Lythraceae; ONA = Onagraceae; TRA = Trapaceae.

ancestry. These are: absence of libriform septate fibres, leaf teeth with a single crater-like apex, pinnate-veined petals, and fibrous seed exotegmen. They suggest that the two families diverged from a common ancestor which, in turn, arose from basal myrtalean stock after divergence of the myrtacean complex. Subsequently, Trapaceae may have branched from the onagraceous line prior to the evolution of the numerous apomorphies defining Onagraceae. However, the Trapaceae are so specialized (e.g. unique leaf teeth with a double apex, a single pendulous ovule per locule, unique embryology, a starch-filled embryo) that it is difficult to relate them closely to any family with certainty. Dahlgren and Thorne concluded there were no obvious links between them and the Lythraceae.

An additional outgroup, the Melastomataceae *s.s.* is included here at the suggestion of a reviewer who regards the broader melastomatacean *et al.* outgroup defined above as possibly too heterogeneous and not monophyletic.

At present, phylogenetic hypotheses of lythracean relationships based on macromolecular information are very limited. Amino acid sequences for the N-terminal region of the small subunit of ribulose bisphosphate carboxylase (RuBisCo) have been determined for seven families of Myrtales including *Lythrum* and *Woodfordia* in Lythraceae (Martin & Dowd, 1986, 1991). The phylogenetic position of the Lythraceae varies widely in these studies, depending on the taxa included. The different hypotheses place Lythraceae as sister to all the Myrtales except Onagraceae, sister to Myrtaceae, or paraphyletic with relationships to Onagraceae and Combretaceae-Myrtaceae. These hypotheses find little support from other studies. The root of the tree inexplicably changes considerably with the addition of protein sequences from *Trapa* and *Punica* (Martin & Dowd, 1991). Nitrogenous base sequences from the chloroplast-encoded large subunit of ribulose bisphosphate carboxylase (*rbc*L) (Conti *et al.* 1993) suggest that a lythraceous-punicaceous ancestor may have given rise to Onagraceae but, as the authors indicate, more extensive sampling is needed before relationships can be drawn based on this gene. Nuclear ribosomal RNA studies of Onagraceae (Bult & Zimmer, 1993) have employed *Lythrum* as the outgroup taxon and nuclear ribosomal DNA sequencing is now in progress by Bult and co-workers for the genera of the Lythraceae.

The four outgroups selected for the initial analyses are Onagraceae, Onagraceae-Trapaceae, Melastomataceae *s. s.*, and Melastomataceae *et al.* (the several families constituting the middle melastomatacean branch of the Johnson and Briggs analysis). The use of the rest of Myrtales as an outgroup was rejected because the number of equivocal character states was too great to allow polarization of a sufficient number of characters.

Character selection

The Lythraceae character set consists of 26 characters: six are anatomical, four from vegetative morphology and habit, eleven from floral morphology, two from pollen, and three from seed morphology. There are 19 binary and 7 multistate characters. All multistate characters were treated as non-additive (unordered). Ideally, a larger character set is sought for construction of a phylogeny when the terminal taxa are as numerous as in this study. Attempts were made to define other characters for the analysis but had to be rejected for a number of reasons.

Characters were rejected if they were invariable within the family. Several of these are listed in the introduction and in the discussion of monophylesis of the family. Others, which were phylogenetically informative in the cladistic analysis of the outgroup Onagraceae, were uniform within the Lythraceae, e.g. deciduous stipules, sepal persistence after anthesis, pollen shed as monads, and equal development of inner and outer integuments (Hoch *et al.*, 1993). Characters autapomorphic for terminal taxa were also excluded (excepting autapomorphies in multistate taxa) because they are not informative with respect to internodes. Characters were rejected if morphological change graded so gradually as to depend on mathematical manipulations to define categories. Pollen shape was rejected for this reason as it varies continuously from prolate to oblate. A wide range of shape variation can sometimes exist even within individual pollen samples. Stomatal types were excluded because the majority of genera include more than one type and types can vary on individual specimens from anomocytic to anisocytic, anomo-actinocytic, or cyclocytic (Esser, 1987; pers. comm.).

Characters displaying complex variation patterns were excluded. Floral meristics is commonly employed in diagnosing lythraceous genera. However, the sepal, stamen, and carpel numbers are very flexible, and appear to vary independently, so that simply stating a meristic range for the flower inadequately describes the complexity present. Wood anatomical ray types are also rejected because of complex variation. Ray types in lythraceous wood are well-characterized (Baas & Zweypfenning, 1979) and the transformation series for ray types is relatively well established. However, transitions occur within lythraceous genera from one ray type to another and can also change with age of the specimens. Further, the specialized juvenilistic uniseriate rays that characterize a number of herbaceous perennial genera can be derived by reduction from more than one other ray type. Their appearance is most likely correlated with herbaceous habit and could confound phylogenetic interpretation. Many anatomical characters in Lythraceae show extensive variation that is useful diagnostically but difficult to incorporate in cladistic analyses.

Finally, characters incompletely known, unreliably described, or questionably homologous were omitted. Embryological studies within the family are scanty and many date from the last century. Embryological characters proved highly significant in cladistic reconstruction of Onagraceae and may be informative in Lythraceae, but sources are of varying reliability and information for the family is too fragmentary to be included (Tobe & Raven, 1983. The multicelled archesporium appears to be a synapomorphy for subfamilies Sonneratioideae, Duabangoideae and Lythroideae that does not occur elsewhere in the Myrtales (Tobe & Raven, 1983). *Punica*, together with Onagraceae and the remainder of the Myrtales, is characterized by a unicellular archesporium, but the number of archesporial cells is inadequately known in subfamily Lythroideae and the character was excluded from this study.

Apical leaf glands occur in the genera *Lafoensia* (Ross & Suessenguth, 1926), *Galpinia* and *Capuronia* (pers. observ.), *Punica* (Turner & Lersten, 1983), and in the mangrove genus *Sonneratia*(Rao & Chakraborti, 1982). In *Lafoensia* they are said to be water-secreting hydathodes, and as such may be an ecologically-induced construction for guttation. In *Punica*, sugars have been detected in the secretions and the glands are considered nectaries. Products of the glands of the other three genera have not been studied. Although the glands are structurally similar in all genera, it is not certain they are homologous. In hydathodes, the vascular bundles terminate exclusively in xylem, whereas in nectaries they terminate exclusively in phloem (Belin-Depoux, 1989). In another mangrove, *Avicennia* (Verbenaceae) abaxial leaf glands similar to those of *Sonneratia* secrete salt (Fitzgerald *et al.*, 1992). Uncertainty of homology of apical leaf glands in the Lythraceae led to their exclusion from the matrix.

A character only partially known but nevertheless utilized was stigma secretions. Wet vs dry stigma surface is included in the analysis, in spite of missing observations, because a significant pattern has emerged from present data that is expected to be further confirmed when data is complete (see further note under coding of char. 19).

Character coding

The character states observed for the Lythraceae are recorded in the data matrix (Table 4). In the Hennig86 analysis (see below p. 15), genera possessing more than one state or missing information are coded by the symbol '?'. For the PAUP analysis, which allows for polymorphisms, genera with mixed states are coded to indicate the states present and missing data are coded by the symbol '?'. The polarization of characters followed the method of Maddison *et al.*, (1984).

TABLE 4. Character coding for Lythraceae cladistic analyses

1. Habit: 0 = woody; 1 = herbaceous.
2. Vascular tracheids: 0 = absent; 1 = present.
3. Spiral thickenings in vessels: 0 = absent; 1 = present.
4. Septate wood fibres: 0 = present; 1 = absent.
5. Fibre dimorphism: 0 = absent; 1 = present.
6. Crystalliferous fibres: 0 = absent; 1 = present.
7. Leaf sclereids: 0 = absent; 1 = present.
8. Globose trichomes: 0 = absent; 1 = present.
9. Multicellular, glandular hairs: 0 = absent; 1 = present.
10. Inflorescence: 0 = anthotelic; 1 = blastotelic.
11. Floral symmetry: 0 = actinomorphic; 1 = zygomorphic.
12. Heterostyly: 0 = absent; 1 = present.
13. Stamen/sepal ratio: 0 = 2/1; 1 = 1/1; 2 = 3+/1.
14. Carpel/perianth ratio: 0 = 1/1; 1 = less than 1/1; 2 = greater than 1/1.
15. Stamen whorls: 0 = two whorls; 1 = one whorl, opposite sepals and petals or opposite only sepals; 2 = one whorl, opposite petals.
16. Pollen pseudocolpi: 0 = absent; 1 = 3 pseudocolpi, faint to distinct; 2 = 6 pseudocolpi, faint to distinct.
17. Pollen exine sculpture: 0 = psilate to coarsely scabrate; 1 = verrucate/rugulate; 2 = short fine striate; 3 = long coarse striate; 4 = 'onagraceous' (global to rod-like elements and viscin threads).
18. Anther attachment: 0 = versatile; 1 = basifixed.
19. Stigma surface: 0 = wet; 1 = dry.
20. Ovary position: 0 = inferior to semi-inferior; 1 = superior.
21. Ovary stipe: 0 = absent; 1 = present.
22. Nectary: 0 = present; 1 = absent.
23. Fruit: 0 = capsule; 1 = berry.
24. Seed compression: 0 = not compressed; 1 = slightly to strongly compressed.
25. Seed wing: 0 = absent; 1 = present, unilateral; 2 = present, encircling the seed body.
26. Seed internal epidurmal hairs: 0 = absent; 1 = present, straight; 2 = present, spirally twisted.

According to this method, when a character varies within a group, the state occurring in related groups (outgroups) is assumed to be plesiomorphic. When a character varies among related outgroups, one of two rules may apply. If the first two consecutive outgroups have the same character state as the group being analysed, that character state is the ancestral state. If characters alternate down the tree and the group being analysed has the same state as the most distant outgroup, that state is the ancestral state for the group (i.e. the outgroup node). If the first and last outgroup differ, the ancestral state decision is equivocal. Coding of outgroup characters is given in Table 4. The enormous diversity of characters in the large melastomatacean *et al.* branch results in ten characters being coded as equivocal.

Character states are based on published accounts and personal observations. Character states of the Melastomataceae *s. s.* were provided by S. Renner. Stem and leaf anatomical characters are taken from Baas (1986), Baas & Zweypfenning (1979), Bridgewater & Bass (1978), Keating (1984), Rao *et al.* (1987) and van Vliet & Baas (1984). Data sources for characters of floral and seed morphology include Duke & Jackes (1987), Furtado & Montien (1969), S. Graham (1977; pers. obs.), Graham & Lorence (1978), S. Graham *et al.* (1986, 1987), Jayaweera (1967), Koehne (1903), Leins (1988), Levin (1980), and Tobe (pers. comm.). Pollen characters of the outgroups are based on Patel *et al.* (1984) and pollen of the Lythraceae on A. Graham *et al.* (1985, 1987, 1990).

Char. 1–7. Stem and leaf anatomical characters. There are only four truly herbaceous genera in the family. The remaining genera produce secondary xylem, although in the herbaceous perennials *Nesaea*, *Ammannia*, *Lythrum*, *Pleurophora*, and *Cuphea*, this may be restricted to the lower parts of the stem. Habit ranges widely in the family from suffrutescent herbs to modest shrubs to rain-forest trees reaching 30 m. Anatomical characters are difficult to use because of the extensive quantitative overlap, the presence of obvious juvenilistic forms, extensive parallelism and/or reversibility, and the unknown influence of environment and age. Wood anatomical characters were selected that could be clearly polarized and unequivocally interpreted as presence-absence characters. Fibre dimorphism refers to the presence of bands of shorter, thinner-walled fibres with well-developed intercellular spaces that function like axial parenchyma in the secondary xylem (Baas & Zweypfenning, 1979). Leaf histology in Lythraceae is diverse, and leaves of *Sonneratia* and *Duabanga* are anatomically among the most complex in the family (Keating, 1984). Leaves of *Sonneratia* and *Duabanga* possess leaf sclereids but otherwise differ from each other and the rest of the Lythraceae in several ways. In spite of diversity of leaf structure, no phylogenetically informative characters could be identified except the sclereid character, others being autapomorphic for the terminal taxa, too variable, or impossible to assess because of the limited sample set.

Char. 8, 9. Globose glands and multicellular glandular trichomes are of restricted occurrence in Lythraceae. The association of globose glands and stipitate ovaries has argued for the close relationship of *Adenaria*, *Koehneria*, *Lourtella*, *Pehria*, and *Woodfordia* (S. Graham *et al.*, 1986, 1987). Multicellular glandular trichomes secreting resinous exudates are known only from *Pleurophora* and *Cuphea*, although a variety of other non-glandular multi- and unicellular trichome types occur in the family (Amarasinghe *et al.*, 1991; pers. obs.).

Char. 10. Inflorescences of the Myrtales have been studied by Briggs & Johnson (1979) and Weberling (1988). In Lythraceae, inflorescences either terminate in a flower (are anthotelic) or the shoot apex remains vegetative and flowers are produced laterally (blastotelic). At least three sets of terms are available to describe the two fundamental conditions. The terms proposed by Briggs & Johnson (1979) are followed because they offer precise definitions that are theory-free. Anthotelic of Briggs & Johnson is defined as ending in a flower bud and is approximately equivalent to 'determinate' and to the term monotelic of Weberling (1988). Blastotelic is defined as ending in a sprout, i.e. 'indeterminate' or polytelic *fide* Weberling. Weberling concluded that the anthotelic (monotelic) inflorescence is the primitive type for the order. Inflorescences in Onagraceae are blastotelic and thus advanced for this character. In Lythraceae, most genera are also blastotelic with the exceptions of *Sonneratia*, *Duabanga*, *Punica*, *Lagerstroemia*, *Lawsonia*, and *Galpinia*. Inflorescences of *Woodfordia* are highly modified and autapomorphic in Lythraceae. Although Weberling terms them 'brachyblastlike' and regards them as anthotelic derivatives, they are coded in this analysis as unknown because of their uncertain homology.

Char. 11. Floral symmetry. Several genera have flowers that are basically radial but display varying degrees of irregular symmetry in which stamens and style are more or less ventrally (abaxially) oriented (e.g. *Lagerstroemia* and *Lythrum*). In the rotate-flowered *Woodfordia* and *Pehria*, asymmetric positions of stamens and style are combined with unilateral, dorsal dehiscence of the capsule. Flowers with this type of weak asymmetry are coded actinomorphic. Zygomorphic flowers, as defined here, are restricted to genera in which bilateral symmetry extends to all floral parts including the carpels. Only *Cuphea* and *Pleurophora* qualify as zygomorphic by reason of having dorsal and ventral carpels unequal in size. In both genera, the dorsal carpel (locule) is much reduced.

Char. 12. Heterostyly. The Lythraceae are one of 24 families in which heterostyly occurs, and one of only three with tristylous forms (Ganders, 1979). Heterostyly is unquestionably polyphyletic in the angiosperms (Barrett & Richards, 1990). In Lythraceae, six genera contain heterostylic members. Three are heterostylous monotypic genera; *Decodon*, *Pemphis*, and *Adenaria* and three others have both heterostylic and homostylic taxa; these are *Nesaea* (Immelman, 1991), *Lythrum* (Koehne, 1903), and *Rotala* (Cook, 1974). *Decodon* and *Adenaria* are trimorphic. *Pemphis* is dimorphic, although Lewis (1975) has suggested that the genus evolved from a trimorphic form through loss of the mid-style morph. In *Lythrum*, where mono-, di-, and trimorphic species occur, trimorphy is considered primitive for the genus, with dimorphy derived through loss of the short-style form (Dulberger, 1970; Ornduff, 1979). There are no thorough studies of heterostyly in *Nesaea* (reputedly with mono-, di-, and trimorphic species), *Rotala* (mono- and dimorphic species), or *Adenaria* (weakly trimorphic and incipiently dioecious). Darwin (1888) concluded that *Lagerstroemia* was once heterostylous based on morphological differences in its two staminal whorls. Pronounced pollen dimorphism, which is characteristic of the genus, lends further support to this idea (Kim *et al.*, 1993).

Char. 13–15. Floral parts. Four-merous and 6-merous flowers occur in approximately equal numbers among both generalized and more specialized lythraceous genera; only one genus, *Decodon*, can be regarded as more or less consistently 5-merous. Merosity varies in many lythraceous genera. For the Myrtales, Dahlgren & Thorne (1984) concluded the 5-merous condition was probably ancestral, with 4-merous flowers arising early and becoming dominant. Four-merous flowers prevail in the outgroups Onagraceae and Trapaceae. In Lythraceae, reduction or multiplication of carpels, stamens, and sepals appears to have occurred more or less independently with stamen number showing the greatest variation. Number of petals is directly related to the number of sepals; it can be less than but is never more than sepal number because only one petal arises at each sinus of the fused sepals. Use of ratios of stamen to sepal number and carpel to perianth number is considered phylogenetically more informative than use of the single, but complex, floral-merosity figure.

Stamens arranged in two whorls in the floral tube (diplostemonous) are basic to the order (Dahlgren & Thorne, 1984). From the basic diplostemonous condition, one staminal whorl, (haplostemony) has arisen by simultaneous activation of antesepalous and antepetalous stamen initials in the developing bud. Fifteen genera are haplostemonous. A third condition (obhaplostemony) in which there is one whorl consisting only of antepetalous stamens is the exclusive condition in two genera and is found mixed in several other genera. Two monotypic genera, *Lawsonia* and *Capuronia*, are coded as haplostemonous, but the single whorl consists only of antesepalous stamens and possibly should have been coded separately from other haplostemonous genera.

Char. 16, 17. Pollen characters. Lythraceae display the greatest amount of variation in pollen morphology of any family in the order Myrtales (Patel *et al.*, 1984). Pollen of the Lythraceae is most diverse with respect to presence and number of pseudocolpi and exine sculpture pattern. Approximately half (15/31) of the lythraceous genera have faint to distinct pseudocolpi; 11 genera have six pseudocolpi; four have three pseudocolpi. Pseudocolpi are recorded as present if the exine is thinned in the mesocolpal area as seen in light microscope examination.

Exine sulpture states are restricted to four that are separated by clear gaps in sculpture type. Pollen exine of most genera is coded as psilate to coarsely scabrate, which encompasses a wide range of variation that is difficult to divide further without a large measure of subjectivity. Verrucate and rugulate exines are also combined because of the subtle gradation between these two states in lythraceous pollen.

Char. 18. Versatile anther attachment is the common condition throughout the Myrtales. In Lythraceae, basifixed anthers characterize just two genera, *Crenea* and *Pleurophora.*

Char. 19. In the order Myrtales, wet stigma surfaces are the typical state. In the Lythraceae and Onagraceae, both wet and dry stigma surfaces occur (Heslop-Harrison, 1990). In Onagraceae and in the order generally, wet surfaces are regarded as the primitive condition (Hoch *et al.*, 1993). Although the stigma surface condition is known in Lythraceae for only 15 genera, the character is included because it is perceived as one of the few phylogenetically informative morphological characters with no (or perhaps limited) homoplasy. Wet stigma surface is a symplesiomorphy for *Punica* and *Lagerstroemia*, genera with relatively large, fleshy stigmas. The condition in *Sonneratia* and *Duabanga* is unknown but the larger size of the stigma, especially in *Sonneratia*, suggests they are of the wet type. Dry stigmas have been observed in 13 lythraceous genera (Heslop-Harrison, 1990; pers. obs.). All have small capitate or punctiform stigmas, as do the genera in which the surface condition has not been recorded. It is likely that in the genera yet to be studied for this character, their small capitate to punctiform stigmas will be correlated with the dry stigma state.

Char. 20. The inferior ovary characterizes Onagraceae and is present in several families of the melastomatacean branch (as well as in most Myrtaceae). Within Lythraceae, *Punica* has a fully inferior ovary, *Sonneratia* and *Duabanga* have semi-inferior ovaries in which the floral tube is fused for about half the length of the ovary, and *Physocalymma* has an ovary fused to the tube for a quarter to a third of its length. In the remainder of the genera, hypanthia are loosely perigynous around a fully superior, sometimes stipitate, ovary.

Char. 21. Among the six genera sharing ovarian stipes, *Woodfordia* has the least developed stipe. The state is coded as mixed in this genus because it may be present or absent in individual specimens.

Char. 22. Nectaries are common throughout the Myrtales and are present in most onagraceous genera, including genera of the earliest evolutionary lines, *Ludwigia*, *Lopezia*, *Fuchsia*, and *Circaea* (Hoch *et al.*, 1993). The character is mixed in Lythraceae among and within genera. Nectaries in the Lythraceae also occupy a variety of positions with respect to the base of the floral tube. Evolutionary trends in nectary position in the family appear complex and have not been completely characterized. Eyde (1981) suggests that the ancestral site of the nectary for the Lythraceae is at the contact between the base of the gynoecium and its surrounding parts, with subsequent phyletic extension occurring either up the floral tube or up the gynoecium from the base. Because of the numerous autapomorphic nectary positions observed in lythraceous genera and the lack of full comparative information, the character is scored simply as present or absent.

Char. 23. Fruits of Lythraceae are, with two exceptions, thin- to thick-walled capsules displaying a variety of dehiscent and indehiscent modes. *Sonneratia* and *Punica* deviate by production of leathery-walled berries. Onagraceae mirror Lythraceae in having primarily capsular dehiscent fruits but also, in a few genera, indehiscent dry capsules or berries.

Char. 24–26. Seed morphology intuitively provides some of the most reliable phylogenetic characters in the family. They vary little within a genus. Seeds may be obpyramidal, or weakly to strongly bilaterally compressed. Compressed seed shapes are diverse, ranging from narrowly elongate, to obovoid or globose concave-convex with one side flattened, to discoid and strongly bilaterally compressed (Fig. 2). Evolutionary novelties appear as wings or, remarkably, as internal epidermal hairs that evert and become mucilaginous upon wetting. The hairs are of two distinct types; spiral (Fig. 2C,D) or straight (Fig. 2E). The chemical complexity of the spiral hair (Stubbs & Slabas, 1982) makes it highly unlikely that this feature evolved more than once in the family. *Punica* is autapomorphic for a fleshy sarcotesta. *Duabanga* is autapomorphic for a non-multiplicative, simple seed coat, the seed being little more than an enlarged ovule (Corner, 1976). The seeds of *Pemphis acidula* are here interpreted as not compressed and not winged. Koehne (1903) interpreted them as unilaterally compressed and encircled by 'thick' wings.

Data analysis

Cladistic analyses are primarily based on the maximum parsimony program Hennig86, Vers. 1.5 (Farris, 1988) run on an IBM-compatible PC. Separate analyses were run with each outgroup. Subsequently, PAUP vers. 3.0r (Swofford, 1990) was run on a Macintosh computer, using the Onagraceae to allow a comparison of branching patterns with and without polymorphic coding.

Hennig86 places no restrictions on character state changes, allows both additive and non-additive multistate characters, and estimates minimum length trees in which all branches are supported by at least one character-state change under at least one optimization along a branch. In determining minimum length trees, the program retains as many equally parsimonious cladograms as available memory allows. The commands mhennig* and bb* were used with each of the

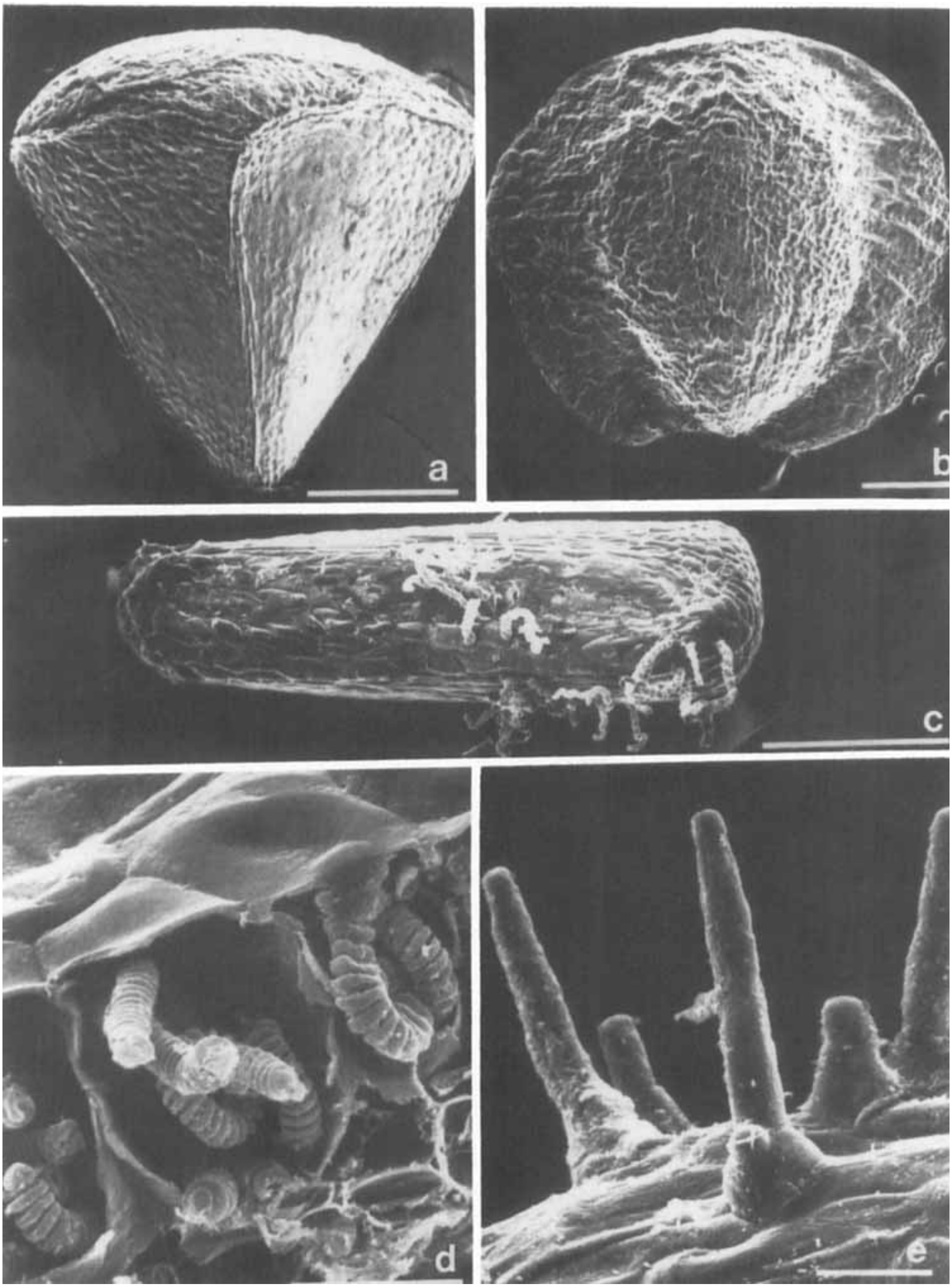

Figure 2A–E. Seed characters of Lythraceae. A, Obpyramidal, non-compressed seed of *Decodon verticillatus*; scale bar = 0.5 mm. B, Bilateral, compressed seed with encircling wing of *Galpinia transvaalica*; scale bar = 0.5 mm. C, Bilateral, compressed, elongated seeds with spiral everted hairs, *Woodfordia fruticosa*; scale bar = 0.25 mm. D, Epidermal cells in longitudinal section showing attached internal spiral epidermal hairs, *Cuphea micrantha*; scale bar = 0.25 mm. E, Straight internal epidermal hairs everted on seed surface, *Lythrum maritimum*; scale bar = 0.25 mm.

TABLE 5. Data matrix for four outgroups and the Lythraceae *sensu lato*. Outgroups are Melastomataceae *s. s.*, Melastomataceae and related families (see text), Onagraceae and Trapaceae, and Onagraceae. Polarized character states of Melastomataceae were provided by S. Renner. Character states of the other outgroups were polarized manually according to the method of Maddison *et al.* (1984). In the PAUP analysis, which allows for polymorphisms, the outgroup Onagraceae and the ingroup were coded as follows: (a = 0,1; b = 0,1,2; c = 0,2; d = 1,2; ? = missing data). In the Hennig86 analysis, both polymorphisms and missing data were coded by the symbol '?'

Outgroup Character States						
Melastom. *s.s.*	000??	00?00	00000	1?100	01010	0
Melastom. *et al.*	000?0	0?00?	00?0?	10??0	0?0??	0
Onagr-Trapa	000?0	0000?	00000	000?0	00000	0
Onagraceae	00000	00001	00000	04000	00000	0

Lythraceae Character States						
Duabanga	00010	01000	00d00	000?0	00000	0
Sonneratia	00000	01000	00220	100?0	00110	0
Punica	00001	10000	002d0	00000	00100	0
Lagerstroemia	00001	10000	00dac	20001	01001	0
Lawsonia	00001	10000	00001	200?1	00000	0
Lafoensia	00000	00001	00011	200?1	10012	2
Physocalymma	00001	10001	00211	010?0	01012	0
Diplusodon	00010	00001	00b1c	010?1	01012	1
Galpinia	00000	10000	00112	010?1	00012	0
Capuronia	00000	10001	00111	000?1	00010	0
Pemphis	00010	00001	01010	200?1	00000	0
Tetrataxis	00000	00001	00102	000?1	00010	?
Ginoria	00000	a0001	00c01	20011	01010	1
Heimia	01100	00001	00001	00011	01010	1
Haitia	00000	00001	00201	200?1	01010	1
Crenea	00000	00001	00201	211?1	01010	1

Lythraceae Character States *cont'd*						
Decodon	00000	00001	01010	00011	00000	0
Nesaea	00110	00001	0abab	22011	00010	1
Ammannia	00010	00001	00aa1	22011	00010	1
Rotala	10010	00001	0a1a1	20011	00010	1
Hionanthera	10010	00001	00111	22011	00010	1
Didiplis	10010	00001	00111	02011	00010	1
Lythrum	00000	00001	0aa10	12011	00010	1
Peplis	10010	00001	00110	12011	01010	1
Woodfordia	01000	0010?	00010	00011	a0010	2
Pleurophora	01000	00011	10111	00111	10010	2
Cuphea	00000	00011	10010	03011	00010	2
Lourtella	00000	10101	00010	000?1	00010	0
Pehria	00000	10101	00011	000?1	10010	2
Adenaria	00000	00101	01011	000?1	10010	0
Koehneria	00000	00101	00210	100?1	10010	0

three outgroups. Mhennig is a version of the WAGNER algorithm which provides a heuristic assessment of the data in cases where the data set is too large and complex to use the implicit enumeration ('ie' = branch and bound) commands for obtaining trees certain to be of minimal length. With mhennig, several trees are generated, each by a single pass through the data. Terminal branches are added in several different sequences. The shortest trees are retained and are available for branch-swapping by the bb* command. This command "will generate all the trees it can find" using all available tree space (Farris, 1988). Exact algorithms in cladistic analysis are said to be restricted in a practical sense to no more than 25 taxa no matter what program is employed (Sanderson, 1990). The large number of taxa and extensive incongruence in the Lythraceae data thus limited the analyses to heuristic assessments.

For each outgroup, a strict consensus tree, using the strict consensus option, was constructed based on the results generated by mhennig* and bb*. Results of mhennig* and bb* were also subjected to rounds of successive weighting (using 'xs w' command) which rapidly reduced the number of shortest trees. Successive weighting is accomplished by calculating the 'best fits' or weight of each character as the character's consistency index times its retention index times 10. The weights are rescaled so that weighting reaches 0 when the character fits the tree as poorly as possible, i.e. shows maximum homoplasy. When successive weighting no longer changed the number or length of trees, a strict consensus tree was constructed and the analysis terminated. Initial analyses based on three different outgroups were compared, after which the outgroup of choice, Onagraceae, was used for extended analysis.

PAUP offers the option of alternate coding in instances where a taxon includes more than one character state, an option not as directly available in Hennig86. Genera with mixed character states recorded by the symbol '?' in the matrix used for Hennig86 analyses were recoded for PAUP as indicated in Table 5. Results using PAUP are based on program choices of the heuristic search option and treatment of multistate taxa as polymorphisms.

RESULTS

Cladistic analysis

Table 6 summarizes results from Hennig86 and PAUP. With Hennig86 and Onagraceae as outgroup, the mhennig* and bb* commands generated 3746 trees with a tree length of 84 and C.I. of 0.41. With each of the other outgroups, over 4814 trees with a length of 86–83 and C.I. of 0.39–0.40 were produced; the exact number of possible trees is not known due to the limited memory of the computer. Strict consensus trees based on trees in computer memory for each outgroup are highly unresolved. However, all, except Melastomataceae *s. s.*, show the clades LAGE-LAWS, DECO-PEMP, GINO-HEIM-HAIT-CREN, LOUR-ADEN-KOEH-WOOD-PEHR-LAFO-PLEU-CUPH, and LAFO-PLEU-CUPH (Fig. 3A–D; the strict consensus tree for Melastomataceae *s.s.*, with 21 genera in an unresolved polychotomy, is omitted). The ONAG consensus tree (Fig. 3C), the only one based on total number of trees generated, is the best resolved. Two major clades occur: Clade I, a basal group consisting of SONN-DUAB-PUNI-LAGE-LAWS; and Clade II, comprising the remaining

TABLE 6. Summary of results for Hennig86 employing the commands mhennig* and bb*, followed by the results of the successive weighting procedure, and for PAUP employing the heuristic search option. C.I. = consistency index; R.I. = retention index. + indicates presence of an overflow of additional trees not retained in the computer memory. Melast. = Melastomataceae *s.s.*; Mela. *et al.* = Melastomataceae *s.l.*, Combretaceae, Crypteroniaceae, Oliniaceae, Peneaceae, Rhynchocalycaceae, and Alzateaceae; Onag-Trap = Onagraceae and Trapaceae

Outgroup	Number of Trees/weighted trees	Tree lengths	C.I.	R.I.	No. of characters with 0 weight
Melast.-Hennig86	4814+/1603	86/178	0.39/0.66	0.61/0.86	0/7
Mela. *et al.*-Hennig86	4814+/135	83/161	0.40/0.71	0.62/0.88	0/8
Onag.-Trap.-Hennig86	4814+/342	83/182	0.40/0.69	0.62/0.86	0/7
Onagraceae-Hennig86	3746/5	84/164	0.41/0.75	0.63/0.89	0/9
Onagraceae-PAUP	976/–	108/–	0.54/–	0.64/–	0/–

24 genera. In Clade II, *Decodon* and *Pemphis* are sister to the remainder of the family, which consists of two large monophylies, one with 16 genera, the second with 8 genera. Successive weighting after mhennig* and bb* yielded from 1603 to 5 most parsimonious trees, depending on the outgroup used (Table 6). The fewest most parsimonious trees (5 trees) were generated with Onagraceae as outgroup. Further analysis was restricted to the Onagraceae outgroup hypothesis because it offered the best heuristic phylogenetic assessment.

Employing the heuristic option of PAUP with Onagraceae as outgroup produced 976 trees with a tree length of 108 and C.I. of 0.54 (Table 6). The strict consensus tree (Fig. 3D) has a topology similar to that generated by Hennig86.

Two rounds of successive weighting were applied to the 3746 trees generated by mhennig* and bb* with the outgroup Onagraceae, after which the number of trees did not change. Five minimum-length trees with a length of 164 resulted. The strict consensus tree from the five trees and the alternative topologies are shown in Figures 4 and 5. After successive weighting the consistency index improved from 0.41 to 0.75 and the retention index increased from 0.63 to 0.89 (Table 6). In the final round of weighting, nine characters were weighted 0 (2, 3, 6, 13, 15, 16, 18, 22, 23); six characters were weighted 10 (1, 7, 9, 11, 19, 26); the remaining characters were weighted between 1 and 5.

The five most parsimonious trees are identical in showing the same seven monophyletic groups: (1) SONN-DUAB-PUNI-LAGE-LAWS (hereafter called Clade I); (2) The remainder of the family (Clade II); (3) PUNI-LAGE-LAWS; (4) LAGE-LAWS; (5) SONN-DUAB; (6) DECO-PEMP; and (7) PLEU-CUPH. Resolution is low in Clade II where 6 or 7 polychotomies appear, depending on the topology selected. In the deepest polychotomy, *Capuronia* and two branches which include 23 of the 31 genera form a trichotomy. The highly derived clade PLEU-CUPH is the most robust, supported by two non-homoplasious synapomorphies. Alternative topologies involve three clades (Fig. 5A–G). None of the five most parsimonious trees is identical to the strict consensus tree, which includes an additional polychotomy.

One of the five trees is selected as a specific hypothesis on which to base further discussion (Fig. 6). The selection does not imply preference for this hypothesis

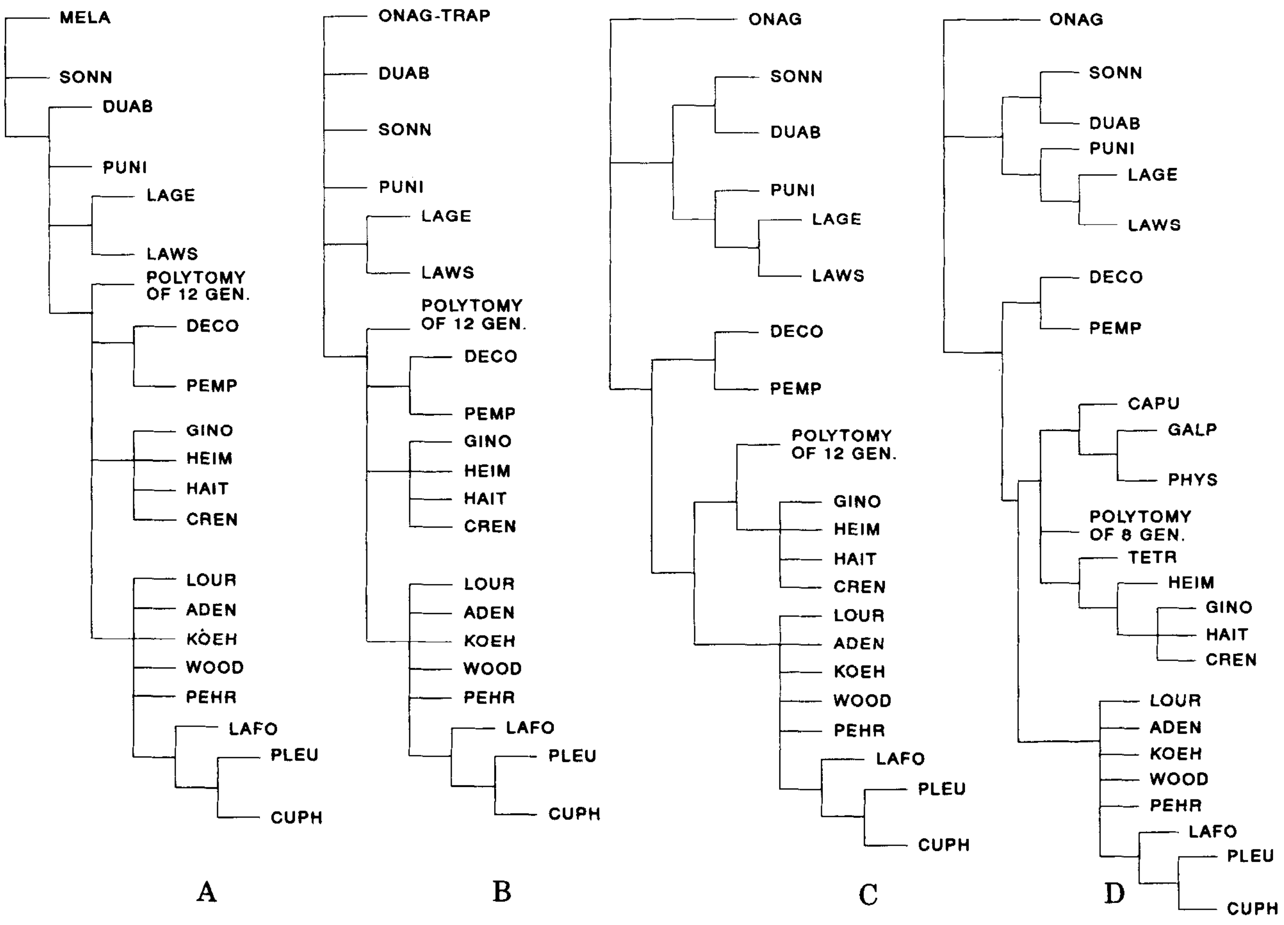

Figure 3A–D. Strict consensus trees generated employing three different outgroups. A–C, Using the options mhennig and bb* in Hennig86. A, Outgroup Melastomataceae *et al.*; strict consensus tree from first 4814 trees, length = 83, C.I. = 0.40. B, Outgroup Onagraceae-Trapaceae; strict consensus tree from first 4814 trees, length = 83, C.I. = 0.40. C, Outgroup Onagraceae; strict consensus tree from the total 3746 trees generated, length = 84, C.I. = 0.41. D, Using the heuristic option in PAUP with outgroup Onagraceae and polymorphisms coded (see text); strict consensus tree from 976 trees, length = 108, C.I. = 0.54.

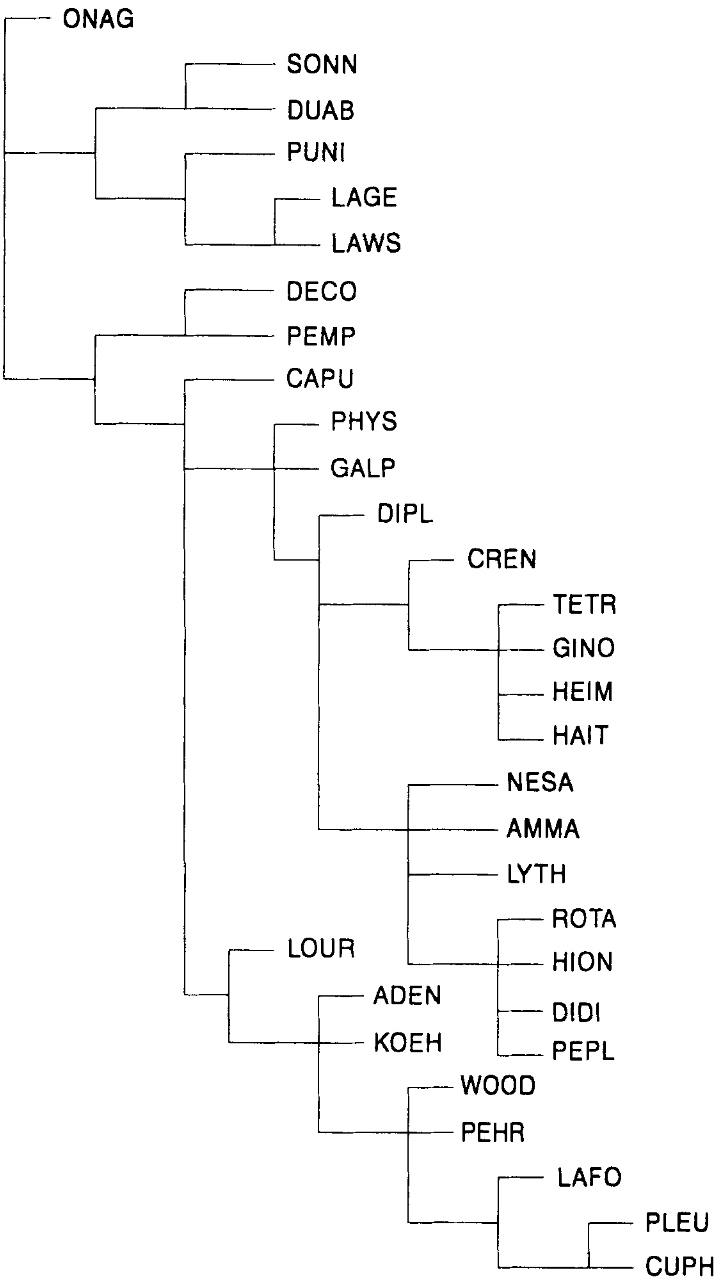

Figure 4. Using Hennig86 program with Onagraceae as outgroup, strict consensus tree from five most parsimonious trees after successive weighting procedure; tree length = 164, C.I. = 0.75.

over the other four. There is no compelling evidence from character changes to suggest any one of the five topologies is more probable than another.

Two major clades, Clade I and Clade II, compose the base of the cladogram (Fig. 6). Clade I is supported by the presence of determinate inflorescences which are otherwise seen only in *Galpinia* in Clade II. *Sonneratia* and *Duabanga* in

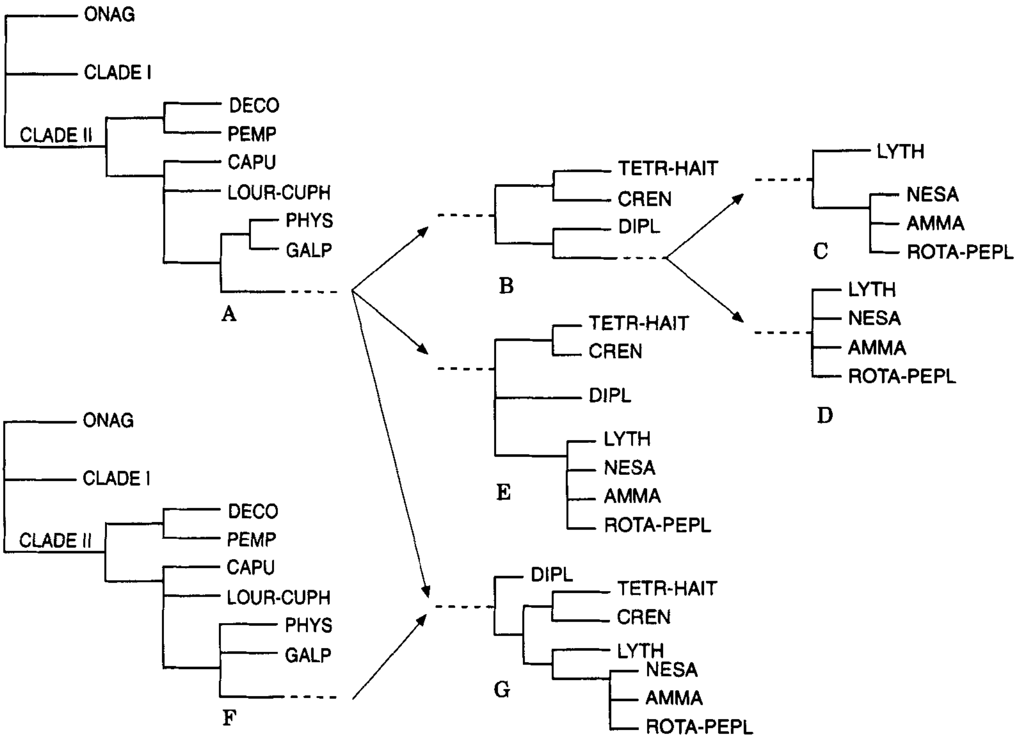

Figure 5A–G. Alternative topologies of the five most parsimonious cladograms with Onagraceae as outgroup. The following combinations produce the five most parsimonious cladograms: (1) A,B,C; (2) A,B,D; (3) A,E; (4) A,G; (5) F,G.

Clade I are a monophyly weakly supported by the single synapomorphy, presence of sclereids in the leaves. Base chromosome number, not included in this analysis, provides an additional synapomorphy (see Fig. 6). Clade II is supported by the synapomorphy of dry stigmas and by two homoplasious character states, carpel number less than perianth number and superior ovaries. The clade DECO-PEMP is sister group to the remainder of Clade II based on a single synapomorphy, heterostylous flowers. Clade II consists primarily of two large monophyletic groups in which six polychotomies appear. The group of eight genera LOUR → CUPH is supported by globose glands and a stamen/sepal ratio of 2/1. The large monophyletic group HAIT → PEPL is established by the synapomorphy of straight internal epidermal seed hairs. The ancestral branch to this group and its sister clade GALP-PHYS is only weakly supported by the verrucate/rugulate pollen exine. The most robust monophyletic groups in Clade II are in the grade LOUR → CUPH where WOOD-PEHR-LAFO-PLEU-CUPH is uniquely defined by spirally twisted internal seed hairs and PLEU-CUPH is further supported by the unique synapomorphies of multicellular glandular hairs and zygomorphic flowers. Overall, the phylogeny of Lythraceae is extremely weakly supported even after successive weighting, with branching patterns defined by a few, mostly homoplasious, characters.

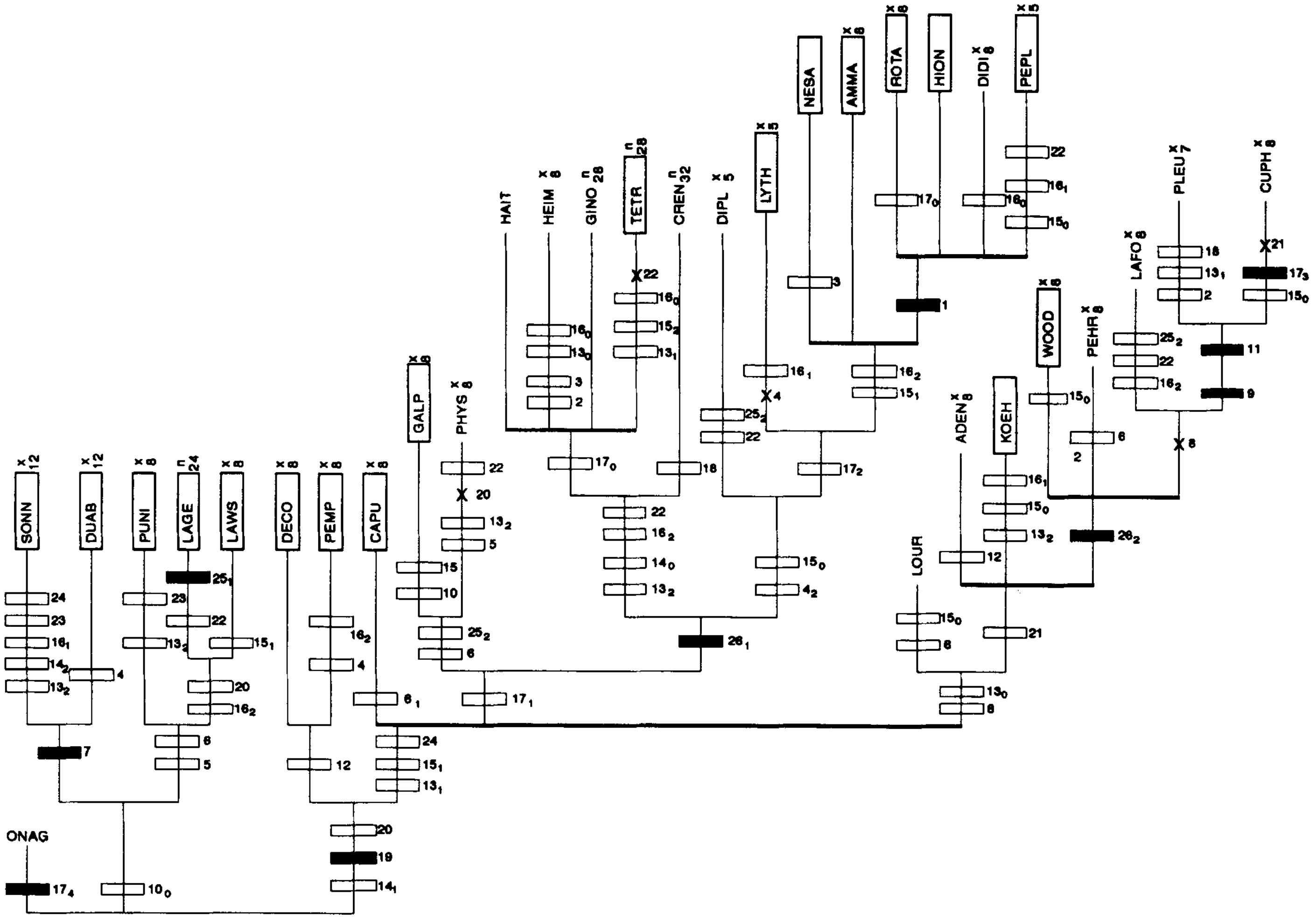

Figure 6. One of the five most parsimonious trees after successive weighting by Hennig86. Characters 2, 3, 6, 13, 15, 16, 18, 22, and 23 were weighted 0 on a scale of 0–10 where 10 is the maximum weighted value. Heavy bars are non-homoplasious characters. The symbol x indicates reversal of a binary character. Character state changes in multistate characters are recorded in subscript following the character number on the tree. Generic chromosome base numbers and geographic distribution are overlaid on the program results. Haploid numbers (n) are listed when the base number is uncertain. Old World genera are boxed and New World genera are not (see Table 1). Tree length = 164, C.I. = 0.75, R.I. = 0.89.

Character evaluation

The minimum number of changes possible is 35. In the most parsimonious tree selected for discussion there are 92 changes. Homoplasy is 38%. Only nine character states are non-homoplasious; two of these are autapomorphies on terminal branches. Five internal branches are supported by one non-homoplasious character state and a sixth branch by two non-homoplasious character states. Total number of changes (x) in character states on the most parsimonious tree chosen for analysis is given below.

1. *Habit* (1x). The family is primitively woody. The absence of secondary tissue development defines the clade ROTA-HION-DIDI-PEPL. These genera are small-statured annuals of marshy to aquatic habitats. Completely herbaceous species occur elsewhere in the family only in a few annual members of *Lythrum*, *Ammannia*, *Nesaea*, and *Cuphea*. The basal clade includes shrubs and trees of small stature (*Sonneratia*, *Punica*, *Lawsonia*, some *Lagerstroemia*) and tall forest trees (other *Lagerstroemia* and *Duabanga*). In Clade II, *Physocalymma* and some species of *Ginoria* and *Lafoensia* may be classified as tall trees, but the predominant form is the small tree-large shrub form and this form appears, based on cladistic analysis, to be plesiomorphic for Lythraceae. The reduction from small-tree habit to herbaceous perennial has occurred within both large monophyletic groups, in LYTH → PEPL and LOUR → CUPH. Further loss of secondary tissue formation correlated with an annual life cycle arose twice, once in the branch leading to ROTA-HION-DIDI-PEPL and again within the large genus *Cuphea*.

2. *Vascular tracheids* (3x). These are independently derived in *Heimia*, *Woodfordia*, and *Pleurophora*.

3. *Spiral thickenings* (2x). Vessels with spiral thickenings are independently derived in *Heimia* and *Nesaea*. Distribution of the derived states of characters 2 and 3 confirm the suggestion that they are 'incidental' wood anatomical specializations (Baas & Zweypfenning, 1979), without significant phylogenetic value.

4. *Septate wood fibres* (4x). The septae are lost independently in *Duabanga*, *Pemphis*, and in the ancestor of DIPL-PEPL, with one reversal in this group of eight genera.

5. *Fibre dimorphism* (2x). Fibre dimorphism characterizes the PUNI-LAGE-LAWS group, and also appears independently in *Physocalymma*. Baas & Zweypfenning, (1979) considered it unlikely that fibre dimorphism arose twice in the evolution of the family but two origins are postulated in the present hypothesis.

6. *Crystalliferous fibres* (5x). This character together with fibre dimorphism defines the branch ancestral to PUNI-LAGE-LAWS in Clade I. Crystalliferous fibres are gained independently four times in Clade II in genera that otherwise differ considerably morphologically and ecologically (Baas, 1986).

7. *Leaf sclereids* (1x). These are a unique synapomorphy of SONN-DUAB.

8. *Globose trichomes* (2x). The globose trichomes that characterize the clade LOUR-ADEN-KOEH-WOOD-PEHR are absent in the more highly derived clade LAFO-PLEU-CUPH.

9. *Multicellular glandular hairs* (1x). This character, together with zygomorphic floral symmetry establishes the most highly derived clade PLEU-CUPH.

10. *Inflorescence* (2x). The anthotelic inflorescence is the single character state supporting Clade I, whereas blastotelic inflorescences characterize Clade II, with the exception of *Galpinia*. Anthotelic inflorescences are considered more primitive than blastotelic ones in angiosperms generally (Takhtajan, 1991) and within the Myrtales specifically (Weberling, 1988).

11. *Floral symmetry* (1x). Zygomorphy is uniquely synapomorphic for PLEU-CUPH.

12. *Heterostyly* (2x). The condition appears first in the earliest members of Clade II in the branch ancestral to DECO-PEMP. Based on this analysis, tristyly subsequently evolved independently in *Adenaria*. Because heterostyly has also developed within *Nesaea*, *Lythrum* and *Rotala*, it appears to have arisen at least five times in the six lythraceous genera possessing this system.

13. *Stamen/sepal ratio* (10x). Within Clade I, only *Lawsonia* retains the outgroup condition of stamens double the sepal number. In *Sonneratia* and *Punica*, stamens have multiplied. Within *Duabanga* and *Lagerstroemia*, both multiplication (3+/1) and reduction (1/1) have occurred. The same flexibility in stamen number is apparent in the rest of the family. This character and character 15, which deals with stamen position, are among the most homoplasious in the study. Changes occur in all possible directions among the three states of character 13.

14. *Carpel/perianth ratio* (3x). Multiplication of carpel number of Clade I occurs in *Sonneratia* (also within *Punica* in one of the two species). The basal branch of Clade II is marked by decrease in carpel number so that the majority of genera in Clade II have fewer carpels (frequently 2–4) than perianth parts (4 or 6 sepals and petals). The monophyletic group CREN-TETR-GINO-HEIM-HAIT is marked by change to a 1/1 ratio. When floral-merosity (number of sepals and petals) is overlaid on the cladogram, each large monophyly comprises approximately equal numbers of 4-merous and 6-merous genera, suggesting that early Lythraceae were flexibly 4–6-merous, a condition persisting in several extant genera (e.g. *Decodon*, *Heimia*, *Ginoria*, *Ammannia*).

15. *Stamen whorls* (11x). Change in number of stamen whorls and stamen position has also been a repeated phenomenon of the analysis, with diplostemony to haplostemony occurring three times, haplostemony to obhaplostemony two times, and reversal from haplostemony to diplostemony (six times). The likelihood of such frequent fundamental ontogenetic changes in the lythraceous flower is hard to conceive. Results may be more due to the allowance for reversals on the path to maximum parsimony than a reflection of the probable course of evolution (Johnson & Briggs, pers. comm.).

16. *Pollen pseudocolpi* (12x). Transformations in states of pollen pseudocolpi have occurred in four directions; 0 → 3 pseudocolpi (3x), 0 → 6 pseudocolpi (5x), 6 → 3 pseudocolpi (1x), and 6 → 0 pseudocolpi (3x). Interestingly, pseudocolpi, once they are acquired, apparently do not increase in number. Lee (1979) suggested evolutionary relationships in the family based on phenetic analysis of pollen morphology in which groups of genera with no pseudocolpi, three, or six pseudocolpi were recognized. The present cladistically-based phylogenetic hypothesis conflicts with that history. Unfortunately, the number of pollen pseudocolpi, which is a convenient diagnostic generic character in Lythraceae, is one of the most homoplasious and least informative phylogenetic characters.

Muller (1981a) hypothesized that pseudocolpi serve a harmomegathic function, being adaptations to accommodate volume changes in pollen such as arise with changes in atmospheric humidity. A strong ecological basis for selection toward pseudocolpi might explain the extensive parallelism in this character. However, lythraceous genera sharing the same pseudocolpus state do not necessarily share the same habitat type, the same habit, or the same degree of pollen exine thickness, and it seems unlikely that their pollen experiences the same hormomegathic stresses.

17. *Pollen exine* (6x). Pollen exine of the outgroup Onagraceae, with its viscin threads and globular elements, bears little resemblance to the exine sculpture in Lythraceae. The pollen exine of Lythraceae, on the basis of this analysis, has developed in three directions and changed a total of six times. The coding of this character is conservative so that the diversity of exine sculpture is even greater than that implied by the four character states recognized.

18. *Anther attachment* (2x). Basifixed anthers have clearly arisen independently in the two genera in which they occur.

19. *Stigma surface* (possibly 1x). If the emerging pattern holds when the remaining genera are characterized for stigma type, dry stigmas will be one of the few unique synapomorphies of Clade II. Dry stigmas are linked to self-compatible breeding systems (Heslop-Harrison, 1990). This is the usual system in Lythraceae (to the extent that the systems are known) (Graham, pers. obs.). In Clade I, all genera, including those with wet stigmas, are self-compatible (East, 1940; pers. observ.), although in *Lagerstroemia*, *Lawsonia*, and *Punica* observations are from cultivated species in which self-compatibility could have been selected from earlier, primarily self-incompatible plants.

20. *Ovary position* (2x). By the outgroup comparison method, the proto-Lythraceae had ovaries partially fused to the hypanthium (hemi-epigynous to epigynous flowers), a state retained by *Sonneratia*, *Duabanga*, and *Punica*. Dahlgren and Thorne (1984) offer the opposing view that perigynous flowers with superior ovaries are ancestral in Lythraceae and in the order as a whole. Their rationale is that perigynous flowers in Lythraceae are combined with more probable plesiomorphic states than in any other family in the Myrtales and the family is in a 'central position' (basal position) in the order. They take the unparsimonious stand that flowers with an epigynous, inferior ovary evolved early in each myrtaceous family that has them. Eyde (1981), on the basis of floral morphology and anatomy, also postulates that proto-Onagraceae flowers were perigynous with superior ovaries, with epigyny evolving twice, in the main onagraceous line and the divergent *Ludwigia* line.

This analysis hypothesizes that perigynous flowers with superior ovaries arose twice within the Lythraceae, in the clade LAGE-LAWS and in the basal branch of Clade II. The exception in Clade II is *Physocalymma*, in which semi-inferior ovaries appear to have arisen secondarily. The fully superior ovary of *Lagerstroemia* and *Lawsonia* has been heavily weighted in the past in classifying the genera as members of Lythraceae *s. s.* In the Hennig86 analysis, the character was weighted just 3 in the final round of successive weighting. Polarization of ovary position is truly problematical and unlikely to be settled until the deepest branching events in the phylogeny of the order are better known, since Lythraceae is so close to those origins.

21. *Ovary stipe* (2x). The stipitate ovary would be uniquely synapomorphic for the advanced clade ADEN → CUPH except for its reversal in *Cuphea*.

22. *Nectary* (6x). Nectaries are present in the outgroup and in 23 of the 31 genera of Lythraceae. They are independently lost five times. A reversal to nectaries occurs in *Tetrataxis*. The distribution of this character on the cladogram suggests that loss of nectaries may be correlated with pollinator specialization in the predominantly outcrossing genera. Those that have lost nectaries primarily have large, more or less solitary, showy flowers with multiplicative, exserted stamens. Pollinator reward is the abundant pollen presented, rather than nectar. In the clade GALP-PHYS, nectar-bearing flowers of *Galpinia* are *c.* 3 mm long with six stamens per flower, whereas nectarless flowers of *Physocalymma* are *c.* 13 mm long with 24–28 long-exserted stamens. In the mostly nectarless clade CREN-TETR-GINO-HEIM-HAIT, flowers are generally showy and stamens numerous. The nectar-bearing exception is *Tetrataxis*, in which flowers are large but the floral tube is green, apetalous, and only 4-staminate. Nectaries have also been lost in the small-flowered *Peplis*, but here the loss is probably correlated with a change from outcrossing to selfing. Two nectary-bearing genera which are seeming exceptions to the rule of nectarless, large flowers with numerous stamens are *Sonneratia* and *Lafoensia*, both visited by bats (Backer & van Steenis, 1951; Sazima & Sazima, 1975, 1977).

23. *Fruit* (2x). Berry-type fruit is hypothesized as separately evolved in *Sonneratia* and *Punica*. Seeds within these leathery fruits have also evolved independently in different directions. The fleshy sarcotesta of *Punica* seeds is autapomorphic in Lythraceae, and very different from the dry, irregular, thick coat of *Sonneratia* seeds.

24. *Seed compression* (2x). Seeds offer some of the least homoplasious, most informative phylogenetic characters in the family. Compression from an obpyramidal form to a more or less bilateral form evolved once in Clade I in *Sonneratia* and once early in Clade II, where bilateral seeds are synapomorphic for the clade.

25. *Seed wing* (4x). Wings encircling bilaterally compressed seeds evolved independently three times in GALP-PHYS, *Diplusodon*, and *Lafoensia*. The tendency toward production of wings is also seen in some species of *Cuphea*, where seeds thin at the edge to form a narrow encircling margin or wing.

26. *Seed internal hairs* (1x for straight hairs, 1x for spiral hairs). Internal epidermal seed coat hairs appear first in the family in Clade II in the large monophyletic group HAIT → PEPL. Spiral hairs are uniquely synapomorphic for WOOD-PEHR-LAFO-PLEU-CUPH. In opposition to the cladistic findings, it is highly unlikely, given the complexity of this character and its presence only in Lythraceae among all angiosperms, that inverted seed coat hairs arose independently more than once.

DISCUSSION

The result of greatest significance is unequivocal recognition of two major clades in the Lythraceae *s. l.* The basal clade includes *Sonneratia* and *Duabanga*, *Punica*, *Lagerstroemia*, and *Lawsonia*, consequently establishing as primitive for the family the woody genera with anthotelic inflorescences, actinomorphic, homostylous, nectariferous flowers with two stamen whorls and wet stigma surfaces, psilate to coarsely scabrate pollen, and hairless seeds.

The two basal clades do not correspond to the historic taxonomic divisions of the family (Table 2), in which *Lagerstroemia* and *Lawsonia* are included in the subfamily Lythroideae (Lythraceae *s. s.*). *Punica,* long recognized as closely related to the Lythraceae and usually treated as a separate family, phylogenetically shares immediate common ancestry with *Lagerstroemia* and *Lawsonia.* Subfamily Lythroideae is thus paraphyletic because not all descendants of the immediate ancestor are included in the subfamily. The relationship of *Lagerstroemia* and *Lawsonia* as sister genera agrees with their taxonomic placement together as the subtribe Lagerstroemiinae Koehne. *Sonneratia* and *Duabanga* constitute a monophyly based on the unique shared possession of leaf sclereids; the phylogeny lends only weak support for combining *Sonneratia* and *Duabanga* taxonomically. The two genera, particularly *Sonneratia,* have accumulated numerous autapomorphies which accounts for their taxonomic recognition as separate families (Takhtajan, 1986) or subfamilies (Dahlgren & Thorne, 1984).

In the remainder of the family, the clades DECO-PEMP, CREN-HAIT-HEIM-GINO, LOUR-ADEN-KOEH-WOOD-PEHR-LAFO-PLEU-CUPH, and LAFO-PLEU-CUPH consistently appear in all analyses, no matter which of the three major outgroup hypotheses is employed; there is little further resolution of phylogenetic relationships.

Homoplasy in the family is pervasive. Its level is probably somewhat higher than average for a plant group based on morphological data. Although the large number of taxa in the study is influential in raising the amount of homoplasy in the analyses (Sanderson & Donoghue, 1989; Table 1 in Platnick, 1989), the plasticity of the morphological characters employed has contributed substantially to the complexity of the cladograms. Internal branches are weakly supported overall. Five polychotomies remain on the most highly resolved tree after successive weighting.

The analysis does not support the current classification of subfamily Lythroideae (Lythraceae *s. s.*) (Table 2). Koehne's tribal delimitations are based on erroneous observations (Tobe, unpubl.) and the subtribes, distinguished primarily by presence or absence of wings on the seeds, combine genera from different large monophyletic groups. Further subdivision of subtribes into series (not included in Table 2) relies heavily on differences in floral merosity, a problematic character in Lythraceae, as this study indicates.

Koehne was well acquainted with lythraceous material from all parts of the world and his classification clearly reflects his unstated ideas about the evolutionary history of the family. He strongly rejected inclusion of *Sonneratia, Duabanga,* and *Punica* in the Lythraceae based on their staminal insertion at or near the rim of the hypanthium (Hallier, 1981) and on their semi-inferior to inferior ovaries (Koehne, 1903: 12). His intuitive phylogeny of the family, published in a study of its geographic distribution (Koehne, 1886), is reproduced here as Figure 7. Koehne considered the small African genus *Nesaea* to be the oldest extant member of Lythraceae and central to diversification of the family (Koehne, 1903: 20). This view is in diametrical opposition to the phylogenetic hypotheses presented here in which the most basal members are woody shrubs and trees and the small, primarily herbaceous, marsh genera NESA-AMMA-ROTA-HION-DIDI-PEPL are highly derived taxa.

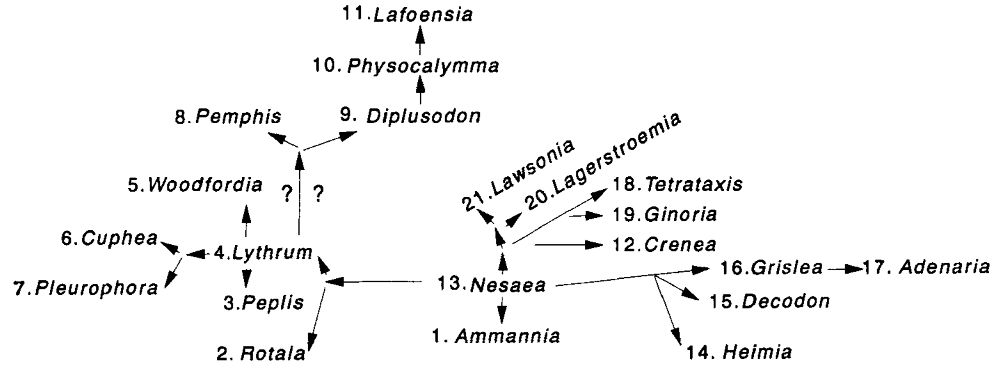

Figure 7. Intuitive phylogeny of Lythraceae, redrawn from Koehne (1886).

Chromosome numbers and biogeographic data provide additional evidence for phylogenetic relationships and are overlaid in Fig. 6. Generic base numbers are given where they are known with some certainty; otherwise, haploid numbers are cited. The basic number of the family is clearly $x = 8$. The clade SONN-DUAB differs from the remainder of the family in having $x = 12$, which is the probable basic number for the order Myrtales (Graham *et al.*, 1993). The difference in basic number is a symplesiomorphy for SONN-DUAB. Five of the eight earliest genera are apparently ancient polyploids (*Duabanga*, $n = 24$; *Punica*, $n = 14, 16$; *Lagerstroemia*, $n = 24, 25$; *Decodon* and *Pemphis*, $n = 16$). Four genera have $x = 5$. In three (with a range of $n = 5, 10, 15, 25, 30$), the base of 5 is probably derived through aneuploid reduction from an ancestral $x = 8$. These are *Lythrum*, *Peplis*, and *Nesaea*, whose basic number is less certain because it is known from only one unconfirmed count of $n = 30$. The fourth genus, *Diplusodon*, in which all species counted have $n = 15$, is most likely derived by aneuploid reduction from an ancient tetrapoloid with $x = 8$ (Graham, 1992). Chromosome numbers are as homoplasious as other features, and neither polyploidy nor aneuploidy are restricted to select monophyletic groups.

Cladistic analysis indicates that Old World and New World genera do not represent separate monophyletic lines. Rather, cladistic relationships suggest that there was early, extensive, multidirectional evolution from an Old World origin. Present distribution of the early members of the family is from tropical and subtropical east Africa to southeast Asia and Indo-Malaysia (Table 1; Fig. 6). *Decodon* is included among Old World genera in spite of its present day restriction to eastern North America because it is represented by an extensive record of fossil seeds dating from the middle Eocene of northern Europe and North America to the present (Cevallos-Ferriz & Stockey, 1988; Graham & Graham, 1971; Tiffney, 1982). Each of the monophyletic groups of Clade II includes endemic Old and New World genera, implying long isolation following early radiation. The branch LYTH → PEPL, comprising most of the recently derived herbaceous genera, has origins in the Old World. *Nesaea* and *Hionanthera* are African, and *Rotala* and *Ammannia* Afro-Asian, in origin: *Lythrum* perhaps evolved in southeastern Europe and *Peplis* in Euro-Asia; one line of *Lythrum* subsequently became established in North America, where it is presented today by ten species. Origin of the monotypic aquatic *Didiplis*, an endemic of the eastern United States, remains obscure, although close relationship to *Peplis* or *Lythrum* has been suggested (Koehne, 1903; Tobe *et al.*, 1986; Webb, 1967). All genera of the LYTH → PEPL clade except *Hionanthera* have dispersed secondarily to the Western Hemisphere. In Clade II, the monophyletic group LOUR → CUPH has two east African-Asian genera but has diversified primarily in South America, where six of the eight genera are endemic.

The oldest fossil remains assigned to the family are fruits and seeds from the lower Eocene London Clay flora (Reid & Chandler, 1933) and fruits, seeds and flowers from the (presumed) Eocene Deccan Intertrappean beds of India (Sahni, 1943). The oldest macrofossils attributed with some certainty to modern genera of the family are leaves of *Lagerstroemia* from the middle Eocene of India and fruits and seeds of *Decodon* and *Lawsonia*-like seeds from the middle Eocene of British Columbia (Cevallos-Ferriz & Stockey, 1988; Graham & Graham, 1971).

Earliest pollen records of likely Lythraceae are from the Upper Eocene of northern South America and are referred, inconclusively, to *Crenea* (Muller, 1981b). Other fossil pollen assigned to modern lythraceous genera appear only later in the Miocene (Germeraad *et al.*, 1968; Graham & Graham, 1971; Muller, 1981b; van Campo, 1976). Onagraceous pollen types are confirmed from much older deposits of late Cretaceous (Maestrichian) age in California and South America (73–65 ma) (Drugg, 1967; Pares Regali *et al.*, 1974a, 1974b; Romero, 1990). It is likely that both families were well differentiated by the end of the Cretaceous, and that one or more ancestral lythraceous lines had radiated into eastern South America by that time, although fossil evidence has not been discovered to substantiate this claim. The extensive separation of South America and Africa from late Cretaceous onward makes later dispersal westward from Africa much less probable, an observation supported by the presence of distinctive fossil pollen floras on the two continents after the Paleocene (Raven & Axelrod, 1974; Smith *et al.*, 1981). Subsequently, widespread extinction and isolation must have followed to account for the numerous, small, highly distinctive genera that now characterize the family. The phylogenies generated in this study reflect this substantial loss of connecting forms by their weakly supported internal structure.

It is unlikely that additional morphological, anatomical, palynological, or cytological characters will ever provide robust support for the lower branches of these trees. Macromolecular characters from nuclear and chloroplast DNA sequences (Bult *et al.*; Graham *et al.*, work in progress) offer the most promising new sources of information for elucidating relationships in the family, as they are beginning to do in the Onagraceae. Ultimately, comparison and synthesis of morphological and molecular data should produce the best estimate of evolution and diversification in the Lythraceae and provide the basis for a new classification consistent with relationships based on common ancestry.

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