

## Phylogenetic Systematics of Pontederiaceae

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**ABSTRACT.** Six different methods of cladogram construction were applied to a data set embracing 34 species and subspecies of Pontederiaceae. Nineteen Wagner trees were constructed using different combinations of character subsets and outgroups. Although 12 trees were constructed using the largest character cliques uncovered by character compatibility analysis, these were highly unresolved. Four additional trees were constructed using phenetic methods. Trees resulting from the various procedures were compared using several optimality criteria. Wagner trees based on all 42 characters or on the subset of 27 reproductive characters were most successful according to these criteria. Branch-swapping trials, based upon common features found in the Wagner and other trees produced another 10 trees that were as successful as the Wagner trees. The number of about equally successful trees is partly a function of homoplasy. Two-thirds of the character state changes on the trees are homoplasious. The primitive breeding system of the Pontederiaceae is not clearly resolved, but heterostyly is probably a synapomorphy of only one lineage of the family. A vicariance explanation of the biogeography of the family, based on a Gondwanan distribution, seems less parsimonious than an origin in South America, followed by several eastward dispersals. While *Monochoria* and *Pontederia* are apparently monophyletic under different analyses, *Eichhornia* and *Heteranthera*, as presently circumscribed, are probably paraphyletic.

We had two main goals in undertaking this study. The first was to examine the evolutionary history of tristylly and several other systematic features in the small, aquatic, monocotyledonous family Pontederiaceae. The other was to assess the performance of several different numerical cladistic procedures using character distributions in this family as test data. Growing discussion of the theoretical bases of biological classification has spawned a bewildering array of individual methods. No comparative studies have evaluated all proposed methods, but several of the most popular, including single linkage clustering, UPGMA (average linkage) clustering, character compatibility analysis, and Wagner tree construction (Sneath and Sokal 1973), have been contrasted repeatedly (Farris 1979; Duncan et al. 1981; Sokal and Rohlf 1981). Many of these comparisons have used artificial data sets of uncertain relevance to biological classification. Others have used small sets of molecular biological data, which provide special problems of interpretation (Mickevich and Johnson 1976; Farris et al. 1983). We compared several common and unusual cladistic procedures using a set of morphological data from a monophyletic group and uniform optimality criteria.

The Pontederiaceae is a small, exclusively palustrial and aquatic family of herbaceous

monocotyledons. It is comprised of 6-9 genera and about 30-35 species, the majority of which are native to the New World tropics (table 1). A few species extend to cool temperate regions such as southern Canada and Japan. *Pontederia* (6 spp.) and *Hydrothrix* (1 sp.) are exclusively New World in their natural distribution whereas *Monochoria* (5 spp.) and *Scholleropsis* (1 sp.) are restricted to the Old World. *Eichhornia* (7 spp.) and *Heteranthera* (11 spp.) are predominantly Neotropical, but *E. natans* and *H. callifolia* are native to Africa. Several taxa have spread, as weeds or ornamentals, outside the limits of their native range. *Eichhornia azurea*, *E. crassipes*, *Pontederia cordata*, and *Heteranthera reniformis* have been introduced to the Old World tropics (Täckholm and Drar 1950; Backer 1951; Sculthorpe 1967) and *Monochoria vaginalis* has been introduced into Californian rice fields (Barrett and Seaman 1980).

Flowers among taxa of Pontederiaceae vary considerably in the morphological specializations associated with their breeding systems. Although most species have showy, entomophilous flowers, many also produce cleistogamous flowers (Solms-Laubach 1882). In *Heteranthera* and *Monochoria*, chasmogamous flowers are weakly enantiostylous, with stigmas bending to the left or right on different flowers of the same individual. These genera have dimorphic

TABLE 1. Taxa of Pontederiaceae, including some pertinent synonyms, codes, tristylous taxa, chromosome numbers, and generalized geographical distributions. Taxa and distributions adapted primarily from Solms-Laubach (1883), Schwartz (1927, 1930), Alexander (1937), Castellanos (1959), Verdcourt (1961, 1968), and Lowden (1973). Chromosome numbers from Fedorov (1969), Moore (1973, 1977), Goldblatt (1981), C. N. Horn (1985), and appendix 2 (\*). Chromosome numbers in parentheses are uncertain or erroneous counts. Abbreviations for geographical areas: AF—Africa, AS—Asia, AU—Australia, CA—Central America, NA—North America, SA—South America, WI—West Indies.

Taxa and synonyms	Code	Observed in field	Observed in glass-house	Tristylous	Haploid chromosome number	Native distribution
1. <i>Eichhornia azurea</i> (Swartz) Kunth	EAZU	+	+	+	16	CA, SA, WI
2. <i>E. crassipes</i> (Mart.) Solms-Laub.	ECRA	+	+	+	16 (15, 29)	SA, CA, WI
3. <i>E. diversifolia</i> (Vahl) Urb.	EDIV	+	+	—	15*	SA, WI
4. <i>E. heterosperma</i> Alex. (= <i>E. venezuelensis</i> Velasq.)	EHET	+	+	—	15*	CA, SA
5. <i>E. natans</i> (Beauv.) Solms-Laub.	ENAT			—		AF, SA, WI
6. <i>E. paniculata</i> (Spreng.) Solms-Laub. (= <i>E. meyeri</i> Schulz)	EPAN	+	+	+	8	CA, SA, WI
7. <i>E. paradoxa</i> (Mart.) Solms-Laub.	EPAR	+	+	—	8*	SA
8. <i>Heteranthera callifolia</i> Kunth (= <i>H. kotschyana</i> Solms-Laub., <i>H. potamogeton</i> Solms-Laub.)	HCAL			—		AF
9. <i>H. limosa</i> (Swartz) Willd. (= <i>H. rotundifolia</i> Griseb.)	HLIM	+	+	—	7	CA, NA, SA, WI
10. <i>H. oblongifolia</i> Mart.	HOBL	+	+	—	7*	CA, SA, WI
11. <i>H. peduncularis</i> Benth.	HPED	+		—		CA, NA
12. <i>H. reniformis</i> Ruiz & Pav. (= <i>H. multiflora</i> (Griseb.) Horn)	HREN	+	+	—	16, 24*	CA, NA, SA, WI
13. <i>H. seubertiana</i> Solms-Laub.	HSEU	+	+	—	24	CA, SA
14. <i>H. spicata</i> Presl	HSPI			—	8	CA, SA, WI
15. <i>H. zosterifolia</i> Mart.	HZOS			—		SA
16. <i>H. (Eurystemon) mexicanum</i> S. Wats.	EURY			—		NA
17. <i>H. (Zosterella) dubia</i> (Jacq.) MacMill. (= <i>H. graminea</i> Vahl)	ZDUB	+		—	15	NA
18. <i>H. (Z.) liebmanii</i> (Buch.) Shinn. (= <i>Z. longituba</i> Alex.)	ZLIE			—		CA, NA, WI
19. <i>Hydrothrix gardneri</i> J. Hook.	HYDR			—	9?	SA
20. <i>Monochoria africana</i> (Solms-Laub.) N. E. Brown	MAFR			—		AF
21. <i>M. brevipetiolata</i> Verdc.	MBRE			—		AF
22. <i>M. cyanea</i> (F. Muell.) F. Muell.	MCYA		+	—	15*	AU
23. <i>M. hastata</i> (L.) Solms-Laub. (= <i>M. elata</i> Ridl.)	MHAS		+	—	14 (17, 40, 42)	AS
24. <i>M. korsakovii</i> Reg. & Maack	MKOR			—	26	AS
25. <i>M. vaginalis</i> (Burm. f.) Presl (= <i>M. plantaginea</i> (Roxb.) Kunth, <i>M. ovata</i> Kunth)	MVAG	+	+	—	26 (13, 14, 30, 36, 37, 40)	AS
26. <i>Pontederia cordata</i> L. var. <i>cordata</i>	PCOR	+	+	+	8	NA, SA
27. <i>P. c.</i> var. <i>lancifolia</i> (Muhl.) Torr.	PLAN	+	+	+	8	CA, NA, SA, WI
28. <i>P. c.</i> var. <i>ovalis</i> (Mart.) Solms-Laub.	POVA	+	+	+	8*	SA
29. <i>P. parviflora</i> Alex.	PPAR	+	+	—	8	CA, SA
30. <i>P. sagittata</i> Presl	PSAG	+	+	+	8	CA
31. <i>P. (Reussia) rotundifolia</i> L.	RROT	+	+	+	16	CA, SA
32. <i>P. (R.) subovata</i> (Seub.) Lowd. (= <i>P. lagoensis</i> Warm.)	RSUB			+		SA
33. <i>P. (R.) triflora</i> (Seub.) Agrost., Velazq. & Velazq.	RTRI SCHO			+		SA AF
34. <i>Scholleropsis lutea</i> H. Perr.				—		

stamens: a single large, blue-anthered, "pollinating" stamen bends in a contrary direction to the style, and the remaining "feeding" stamens are smaller, straight, and usually yellow-anthered (Müller 1873; Iyengar 1932). *Eichhornia* and *Pontederia* both contain tristylous species. Unlike the enantiostyly of *Heteranthera* and *Monochoria*, tristily is a true genetic polymorphism in which all flowers of each individual possess one of three distinct, complementary, style- and stamen-length phenotypes (Ornduff 1966). Distyly, the other type of heterostyly recognized by Darwin (1877), with two floral phenotypes, has been attributed to the family incorrectly (Müller 1871, 1883). Heterostyly is rare among monocotyledons and Pontederiaceae is the only tristylous monocotyledonous family. Elsewhere, tristily is found only in the Lythraceae and Oxalidaceae, each of which also contains distylous taxa. Among heterostylous plants, Pontederiaceae are also atypical in possessing zygomorphic flowers. Several species of *Eichhornia* and *Pontederia* are non-tristylous, with monomorphic, self-pollinating populations. Are these independently derived from various tristylous ancestors by the evolutionary breakdown of tristily, or are they primitively monomorphic? Cladistic analysis might shed some light on the evolution of breeding systems in the family.

#### MATERIALS AND METHODS

*Taxa.* A standard circumscription of the Pontederiaceae is widely accepted (Cronquist 1981), but relatively minor variations in generic limits and species delimitations persist, in part because of inadequate monographic attention. Only one genus, *Pontederia*, has been the subject of a complete modern monograph (Lowden 1973), even though numerous regional revisions and floristic treatments have covered most members of the family. Our experience with the plants and assessment of references led us to accept 34 species and varieties as basic taxa for analysis (table 1). These are distributed among nine genera and subgenera. The supraspecific decisions of table 1, such as treating *Reussia*, *Eurystemon*, and *Zosterella* as subgenera of *Pontederia* and *Heteranthera* (cf. Alexander 1937), have no analytical consequences, since species level taxa and not genera are the units of analysis. Following most contemporary students of the family, we have been

conservative at the species level and have not recognized many proposed segregates, some of which are cited as synonyms in table 1.

*Outgroups.* Pontederiaceae are generally thought to derive from a liliaceous ancestor (Hutchinson 1959; Takhtajan 1980; Cronquist 1981), although some authors (Thorne 1983; Dahlgren et al. 1985) prefer a relationship with Commelinaceae. Within Liliaceae (LILI) we have used the unspecialized tribe Asphodeleae, to which members of Pontederiaceae key as Liliaceae in Hutchinson (1959), as the primary outgroup. This group is used to polarize characters for all analyses except those Wagner trees using other outgroups. Six Wagner trees were polarized using Commelinaceae (COMM) and the small, aquatic Australasian family Philodraceae (PHIL), a purported sister group (Dahlgren et al. 1985). Eight more Wagner trees were polarized using *Eichhornia paniculata* (EPAN) and *Monochoria cyanea* (MCYA), ingroups shown to be cladistically primitive using the three outgroups.

*Characters and advancement index.* We used 42 characters that distinguish among Pontederiaceae and that delimit Pontederiaceae from outgroups (table 2). Twenty-six of the characters are coded with two states, while the remainder have up to five ordered states. Assignment of plesiomorphic code 0 is based on states present in LILI (appendix 1), but coding was adjusted for different outgroups. Multistate characters were then ordered simply by quantitative value. Characters were chosen and scored after examination of standard floras and monographs, as well as through our experience with 21 species in the field and glasshouse (table 1). Charles Horn (pers. comm.) advised us on scoring of *Heteranthera* species. The subsets of 15 vegetative characters and 27 reproductive characters were used separately in some analyses. Furthermore, for the character compatibility analysis described below, multistate characters were recoded to consistent two-state characters (Meacham 1981), bringing the total to 66 for this analysis. No characters known to be part of the tristylous syndrome were included in the reproductive set for tree construction, but the distribution of tristily (table 1) was used in tree assessment. An Advancement Index assigned to each taxon (appendix 1) was the sum of character state changes from the plesiomorphic state without reference to any cladogram.

TABLE 2. Character state polarity. Numbers increase with deviation from plesiomorphic state; 1'—an apomorphic state independent of 1.

1. Duration	0 perennial	1 short-lived perennial; 2 annual
2. Habitat	0 terrestrial	1 aquatic
3. Submergence	0 emergent	1 mostly submerged
4. Habit	0 erect	1 procumbent
5. Rooting	0 attached	1 free floating
6. Submersed phase	0 short-lived	1 protracted
7. Axillary dwarf shoots	0 absent	1 present
8. Stipules	0 present	1 absent
9. Petiole	0 normal	1 inflated
10. Pulvinus	0 absent	1 present
11. Leaf width/length	0 0.3–0.5	1 0.1–0.3; 2 <0.1; 1' >0.5
12. Maximum leaf size	0 4–10 cm	1 >10 cm; 1' <4 cm
13. Leaf base shape	0 cuneate	1 cordate; 2 sagittate
14. Broadest point of blade	0 below middle	1 at middle; 2 above middle
15. Leaf apex shape	0 acute	1 obtuse
16. Inflorescence type	0 paniculate	1 derived paniculate; 2 spicate
17. Inflorescence exertion	0 exerted	1 enclosed in spathe
18. Infructescence attitude	0 erect	1 geniculate
19. Spathe	0 bracteate	1 leaflike
20. Peduncle pubescence	0 glabrous	1 hairy
21. Flower attachment	0 pedicellate	1 sessile
22. Flower number	0 50–100	1 10–50; 2 2–10; 3 1; 1' >100
23. Flower symmetry	0 actinomorphic	1 zygomorphic
24. Flower size	0 2–4.4 cm	1 >4.5 cm; 1' <2 cm
25. Cleistogamy	0 absent	1 present
26. % perianth fusion	0 0	1 10–25; 2 25–40; 3 40–60; 4 60–70; 5 70–80
27. Perianth persistence	0 caducous	1 persistent
28. Perianth color	0 blue/violet	1 yellow; 1' white
29. Tepal number	0 6	1 4
30. Tepal arrangement	0 3 + 3	1 3 + 1; 1' 5 + 1
31. Tepal fringing	0 entire	1 fimbriate
32. Stamen number	0 6	1 3; 2 1
33. Stamen diversity	0 monomorphic	1 dimorphic
34. Filament inflation	0 none	1 some inflated
35. Filament appendage	0 absent	1 present
36. Anther attachment	0 dorsifixed	1 basifixed
37. Anther torsion	0 straight	1 twisted
38. Ovary locule number	0 3	1 2; 2 1
39. Ovule number	0 >50	1 2–50; 2 1
40. Fruit type	0 dehiscent	1 indehiscent
41. Fruit wall	0 smooth	1 smooth-ribbed; 2 toothed-ribbed; 3 spiny
42. Seed length	0 <1 mm	1 1–1.5 mm; 2 >1.5 mm

*Tree construction.* Trees were constructed using six different procedures described in the literature as methods for deriving phylogenetic trees. The Wagner procedure of Farris (1970) is based on a search for a most parsimonious tree, which may not always be found by this algorithm (Felsenstein 1978b). Using the Wag-

ner 78 computer program written by Farris, we constructed 19 different Wagner trees by combining the full data set (WA) or the vegetative (WV) or reproductive (WR) sets, with the five outgroups listed above. Four extra WA trees resulted from shuffling the data decks before processing. We also used a computer algorithm for

the tree construction procedure (CS) proposed by Camin and Sokal (1965). This algorithm, outlawing reversals, uses character compatibility to seek a single most parsimonious tree. Using the 66 transformed two-state characters, the paper and pencil character compatibility procedure (CC) suggested by Meacham (1981) generated numerous equivalent cliques of compatible characters, each of which specified a slightly different, partially unresolved tree. The 26 characters of the largest cliques corresponded to 19–22 of the original characters.

Three tree-generating procedures are derived from phenetic analyses that were performed with the NTSYS computer package (Rohlf et al. 1974). UPGMA phenograms have often been treated as evolutionary trees when redrawn as cladograms (Sneath and Sokal 1973). The initial phenogram for our UP cladogram was based on a matrix of taxonomic distances. Fitch (1975) described a procedure for expanding a minimum spanning tree into a cladogram, and our MS tree was rooted between the two most distant taxa, as recommended by Fitch. Piazza and Cavalli-Sforza (1975) proposed a "spectral analysis" for constructing a cladogram from sign changes of a complete principal components analysis (PC). Each successive component produces a dichotomy in a fully resolved tree.

Finally, 22 fully resolved trees (CN) were constructed using branch swapping on groups common to the most parsimonious trees derived from the above procedures.

Each tree generated by these methods was submitted to the optimization procedure of Farris (1970) to determine character state changes along its branches. All characters were used in this optimization (including tristily), even if they were not used in constructing a particular tree initially. If there were no character state changes between a reconstructed ancestral node and a subtended contemporary taxon or higher internal node, the latter was collapsed into the ancestral node (i.e., branch lengths of zero were eliminated). These collapses provide hypotheses of ancestor/descendent relationships that may be tested by additional characters.

*Tree evaluation.* Trees were evaluated using eight different measures. First is the total number of character state changes along the branches of each tree, its length or parsimony.

This length can be decomposed into three portions, expressed as decimal fractions of 1. The consistency is the portion of the tree due to non-homoplasious character state changes (Kluge and Farris 1969). It is equal to the minimum possible length (63 character state changes for this data set, the number of apomorphic character states in table 2), divided by the total length for any tree. Although consistency is completely correlated with length within any given study, use of this index allows comparison of results between studies based on different characters or taxa. The homoplasious part of the tree may be apportioned to the fraction of parallelisms between branches and the fraction of reversals of character states along each branch. Because they might have different evolutionary responses, these two types of homoplasy are tallied separately here. They are treated together in the deviation ratio (Rodman et al. 1984), which measures the proportion of homoplasy in the sum of all intertaxon distances on the tree. Advancement correlations were calculated as product moment correlation coefficients of advancement indices with the branch length of each taxon from the root of the tree, thus independently measuring the reversals along those branches. Linkage values for each topology were calculated using an arithmetic unweighted pair group method and the implied cophenetic matrix was then compared to the matrix of Manhattan distances among the taxa using the cophenetic correlation coefficient (Sneath and Sokal 1973). This measures the distortion of intertaxon distances imposed by the topology, another independent measure of the efficiency with which each cladogram presents character distributions.

For all 24 trees with a length within 5% of that of the shortest tree (162–170 character state changes), each of the five independent optimality criteria, consistency, reversals (as 1–R), deviation ratio (as 1–D), advancement correlation, and cophenetic correlation were averaged to produce an overall measure of success, the effectiveness. This measure, like the individual measures adopted here, can be compared between studies as a general guide to the success of a tree in summarizing both character state distributions and the relationships among taxa.

*Biological and biogeographical analyses.* The distribution of tristily in the family (table 1)

TABLE 3. Cladistic summary of trees of Pontederiaceae. Minimum length = 6.3.

Tree	Outgroup	Characters	Length	Consistency	Parallels	Reversals	Deviation ratio	Advancement correlation	Cophenetic correlation	Effectiveness
WA1	LILI	all	162	0.389	0.352	0.259	0.53	0.669	0.787	0.611
WA2	LILI	all	164	0.384	0.342	0.274	0.71	0.661	0.800	0.572
WA3	LILI	all	164	0.384	0.348	0.268	0.59	0.657	0.806	0.598
WR4	LILI	rep	169	0.373	0.361	0.266	0.73	0.415	0.811	0.521
WV5	LILI	veg	202	0.312	0.282	0.406	0.87	0.446	0.563	—
WA6	COMM	all	167	0.377	0.348	0.275	0.70	0.774	0.681	0.571
WR7	COMM	rep	168	0.375	0.310	0.315	0.72	0.828	0.708	0.575
WV8	COMM	veg	204	0.309	0.387	0.304	0.87	0.285	0.470	—
WA9	PHIL	all	165	0.382	0.345	0.273	0.67	0.712	0.818	0.594
WR10	PHIL	rep	164	0.384	0.421	0.195	0.43	0.890	0.735	0.677
WV11	PHIL	veg	206	0.306	0.335	0.359	0.87	0.637	0.639	—
WA12	EPAN	all	164	0.384	0.342	0.274	0.75	0.799	0.808	0.593
WA13	EPAN	all	162	0.389	0.370	0.241	0.52	0.692	0.787	0.621
WR14	EPAN	rep	165	0.382	0.460	0.158	0.45	0.536	0.835	0.629
WV15	EPAN	veg	202	0.312	0.346	0.342	0.80	0.735	0.549	—
WA16	MCYA	all	162	0.389	0.352	0.259	0.52	0.744	0.780	0.627
WA17	MCYA	all	167	0.377	0.312	0.311	0.82	0.880	0.753	0.576
WR18	MCYA	rep	168	0.375	0.375	0.250	0.56	0.833	0.771	0.634
WV19	MCYA	veg	202	0.312	0.376	0.312	0.81	0.729	0.554	—
CC1	LILI	21	187	0.348	0.395	0.257	0.58	0.741	0.778	—
CC2	LILI	20	191	0.340	0.397	0.263	0.63	0.755	0.776	—
CC3	LILI	21	186	0.349	0.430	0.221	0.56	0.905	0.780	—
CC4	LILI	20	190	0.342	0.431	0.227	0.61	0.869	0.777	—
CC5	LILI	21	187	0.348	0.451	0.201	0.55	0.783	0.778	—
CC6	LILI	20	191	0.340	0.453	0.207	0.60	0.793	0.775	—
CC7	LILI	20	188	0.346	0.418	0.236	0.61	0.964	0.778	—
CC8	LILI	19	192	0.339	0.420	0.241	0.66	0.970	0.776	—
CC9	LILI	20	203	0.320	0.460	0.220	0.66	0.431	0.786	—
CC10	LILI	19	207	0.314	0.460	0.226	0.71	0.474	0.784	—
CC11	LILI	22	207	0.314	0.441	0.245	0.76	0.150	0.789	—
CC12	LILI	21	211	0.308	0.442	0.250	0.81	0.226	0.786	—
CS	LILI	all	236	0.275	0.280	0.445	1.17	0.560	0.705	—
UP	LILI	all	191	0.340	0.434	0.226	0.60	0.040	0.835	—
MS	LILI	all	180	0.361	0.372	0.267	0.64	0.350	0.800	—
PC	LILI	all	210	0.310	0.407	0.283	0.90	0.030	0.793	—
CN1	LILI	all	169	0.373	0.414	0.213	0.55	0.685	0.684	0.596
CN2	LILI	all	166	0.380	0.397	0.223	0.57	0.739	0.663	0.598
CN3	LILI	all	164	0.384	0.384	0.232	0.59	0.719	0.650	0.586
CN4	LILI	all	167	0.377	0.395	0.228	0.68	0.758	0.646	0.575
CN5	LILI	all	165	0.382	0.424	0.194	0.53	0.746	0.669	0.615
CN6	LILI	all	166	0.380	0.403	0.217	0.55	0.728	0.669	0.602
CN7	LILI	all	165	0.382	0.382	0.236	0.60	0.761	0.660	0.591
CN8	LILI	all	165	0.382	0.382	0.236	0.60	0.753	0.648	0.589
CN9	LILI	all	164	0.384	0.390	0.226	0.58	0.820	0.637	0.609
CN10	LILI	all	166	0.380	0.403	0.217	0.56	0.823	0.610	0.607
CN11	LILI	all	178	0.354	0.467	0.179	0.42	0.780	0.691	—
CN12	LILI	all	177	0.356	0.434	0.198	0.47	0.810	0.684	—
CN13	LILI	all	176	0.358	0.450	0.192	0.46	0.835	0.682	—
CN14	LILI	all	174	0.362	0.455	0.184	0.49	0.856	0.688	—
CN15	LILI	all	174	0.362	0.461	0.177	0.50	0.864	0.712	—
CN16	LILI	all	175	0.360	0.423	0.217	0.48	0.828	0.686	—
CN17	LILI	all	176	0.358	0.427	0.215	0.46	0.732	0.766	—
CN18	LILI	all	180	0.350	0.489	0.161	0.41	0.827	0.665	—

TABLE 3. Continued.

Tree	Outgroup	Characters	Length	Consistency	Parallelisms	Reversals	Deviation ratio	Advancement correlation	Cophenetic correlation	Effectiveness
CN19	LILI	all	181	0.348	0.459	0.193	0.50	0.851	0.634	—
CN20	LILI	all	176	0.358	0.461	0.181	0.48	0.837	0.634	—
CN21	LILI	all	179	0.352	0.419	0.229	0.58	0.820	0.615	—
CN22	LILI	all	180	0.350	0.444	0.206	0.54	0.832	0.632	—

was examined on the trees. The geographical distributions of taxa (table 1) were examined using a continental reduced area cladogram (Nelson and Platnick 1981). Chromosome numbers (table 1) were examined using a comparable reduced cytological cladogram. The reduced cladograms collapse monophyletic groups on the tree showing the features of interest into single branches.

#### RESULTS

*Evaluation of trees.* Sixty-three cladograms of Pontederiaceae were generated using the outlined procedures. These represent a minute fraction of the  $7.3 \times 10^{45}$  trees of different topology possible for 34 taxa (Felsenstein 1978a). Optimality criteria for 57 of the trees are presented in table 3. Excluded from this table are six additional unresolved trees based on 25 characters derived by character compatibility analysis. These presented similar topologies to the 12 character compatibility trees based on 26 characters, but resolved fewer groups. Some of the unresolved groups consisted of mixtures of two or three genera that were well distinguished by other methods. It did not seem worth the laborious calculations necessary to include them in the table.

Based on parsimony (shortest length) and consistency, the trees fall into five groups (table 3). The most parsimonious trees have lengths of 162 to 169 character state changes. The 24 trees in this group include the WA and WR trees and the first 10 CN trees. The second group of 13 trees has lengths of 174 to 181 and includes the remaining CN trees and the MS tree. The third group of trees, having lengths of 186 to 192, includes the first eight CC trees and the UP tree. The five WV trees, the four remaining CC trees, and the PC tree form the fourth group with lengths varying from 202 to 211. The fifth group consists only of the CS tree

with length 236. The five groups are separated by gaps of at least five character state changes and have internal gaps of three (in the fourth group, with external gaps of 10 and 25) or less. All members of the first group fall within 5% of the shortest length in the study and are well separated from the second and subsequent groups, which exceed this limit. Therefore, the first group was the major focus for evaluation.

Members of the first group have consistencies ranging from 0.373 to 0.389, that is, only about 38% of their length is due to minimal character state changes, and almost two-thirds of their character state changes are homoplasious. The other trees have up to three-fourths of their length homoplasious. The several different measures of homoplasy used here (table 3) show that different methods of tree construction favor different properties of the trees, but that these properties are not always consistent. The ratio of parallelisms to reversals, as expected, is high in the CC trees and low in WV trees, but it is also high in CN11–CN22. Deviation ratio is less consistent with respect to tree-forming algorithms, but is particularly high (much homoplasy) in the WV trees and consistently low in CN11–CN22. Advancement correlation is notably high in the WR trees and in some CC and CN trees and is very low in the phenetic-based trees. Finally, the cophenetic correlation is predictably high in the phenetic-based trees, but is equally high in some WA and WR trees and notably low in some WV trees.

On the basis of both parsimony and effectiveness, there are clear distinctions in the performance of the different tree-forming methods (table 4). WA and WR trees and CN1–CN10 are all good on both criteria, while WV trees, CS, UP, MS, and PC are all poor by both criteria. The CC trees are poor in parsimony and moderately good in effectiveness and CN11–CN22 are intermediate in parsimony and very

TABLE 4. Average length and effectiveness for trees constructed by different methods.

Method	Number of trees	Average length	Average effectiveness
Wagner (all-character)	9	164.0	0.596
Wagner (reproductive)	5	166.8	0.607
Wagner (vegetative)	5	203.2	0.449
Wagner (LILI ancestral)	5	178.1	0.508
Wagner (COMM ancestral)	3	179.7	0.508
Wagner (PHIL ancestral)	3	178.3	0.581
Wagner (EPAN ancestral)	4	176.7	0.576
Wagner (MCYA ancestral)	4	178.2	0.577
Branch swapping (CN1-CN10)	10	165.7	0.597
Branch swapping (CN11-CN22)	12	177.2	0.635
Character compatibility	12	195.0	0.582
Camín-Sokal	1	236	0.385
Phenetic	3	193.7	0.463

good in effectiveness. Looking at the Wagner trees with respect to polarizing taxa shows that the average parsimony is the same for all five taxa, but the average effectiveness divides them into two groups. The trees polarized by distant outgroups (LILI and COMM) are less successful on the other criteria than those polarized by the putative sister group (PHIL) or the two cladistically primitive ingroups (EPAN, MCYA). Since all of the 24 most parsimonious trees have moderate to high effectiveness (table 3), there is relatively little separation among them on this criterion either. However, WR4 is unusually low, WR10 is unusually high, and WA2, WA6, WR7, WA17, and CN4 are all below the main group of these trees in effectiveness, with a clear gap separating the remaining 17 trees.

*Tree topology.* The best trees by the above criteria have much in common, and we present just one complete cladogram (fig. 1). This is CN5, the tree with the sixth highest effectiveness in the most parsimonious group, but the tree with highest effectiveness not to split homostylous from tristylous *Eichhornia*. We find such a split unacceptable because of the clear relationships among these species. In this tree, as in almost all others, Pontederiaceae is a monophyletic group whose sister group is Philydraceae. The family is divided into two monophyletic groups, the tristylous *Eichhornia* + *Pontederia* branch with four synapomorphies, and the enantiostylous *Monochoria* + *Heteranthera* branch with two synapomorphies (table

5). Three of the four major genera are also preserved as monophyletic groups. *Monochoria* is simplest and most compact, with an average internal branch length of 1.6 character state changes and two defining synapomorphies. *Pontederia* is strictly monophyletic, as are its two subgenera, *Pontederia* and *Reussia*. These taxa have average internal branch lengths of 2.2, 1.8, and 2.7 character state changes, and four, four, and two synapomorphies, respectively. The monophyletic branch embracing species of *Heteranthera* is defined by three synapomorphies (table 5) and also contains the described monotypic genera *Hydrothrix* and *Scholleropsis*, and the proposed generic segregates *Eurystemon* and *Zosterella*. The average internal branch length for the monophyletic group is 3.1 character state changes. Of the two sub-branches of *Heteranthera*, the HREN-ZLIE sub-branch is defined by two synapomorphies, but the HPED-EURY branch has no singular synapomorphies. The fourth major genus of Pontederiaceae, *Eichhornia*, is paraphyletic on this cladogram. Most of the group is monophyletic, but *E. paniculata* is the sister group to the remainder of *Eichhornia* + *Pontederia*. The average internal branch length of *Eichhornia* is 7.7 character state changes, but even the monophyletic portion of the genus has no unique synapomorphies.

The similarities of the 24 trees with length less than 170 allow ready description of variation in topology without figuring all of them. Most of the less parsimonious trees, except the CS and WV trees, also have similar topologies. Arrangements of the genera with respect to each other fall into nine generalized topologies (fig. 2). Except for the relatively unparsimonious linear arrangement of the WV trees (topology IX), these topologies vary primarily in the positions of *Eichhornia* and *Monochoria*. The tristylous species of *Eichhornia* group with *Pontederia* in all branched topologies except V, so the differences are largely in the position of the homostylous species of *Eichhornia*. These are widely separated from the tristylous species in topologies III and VII and united with them in topologies I and V, while in the remaining topologies the two groups span the basal dichotomy of the tree. While *Eichhornia* species are always near the base of the tree, *Monochoria* varies from sister group of the remainder of the Pontederiaceae (VI and VII) to sister group of *Heteranthera* (I and III) or coordinate descendent of *Eichhornia* with *Heteranthera* (II and V)



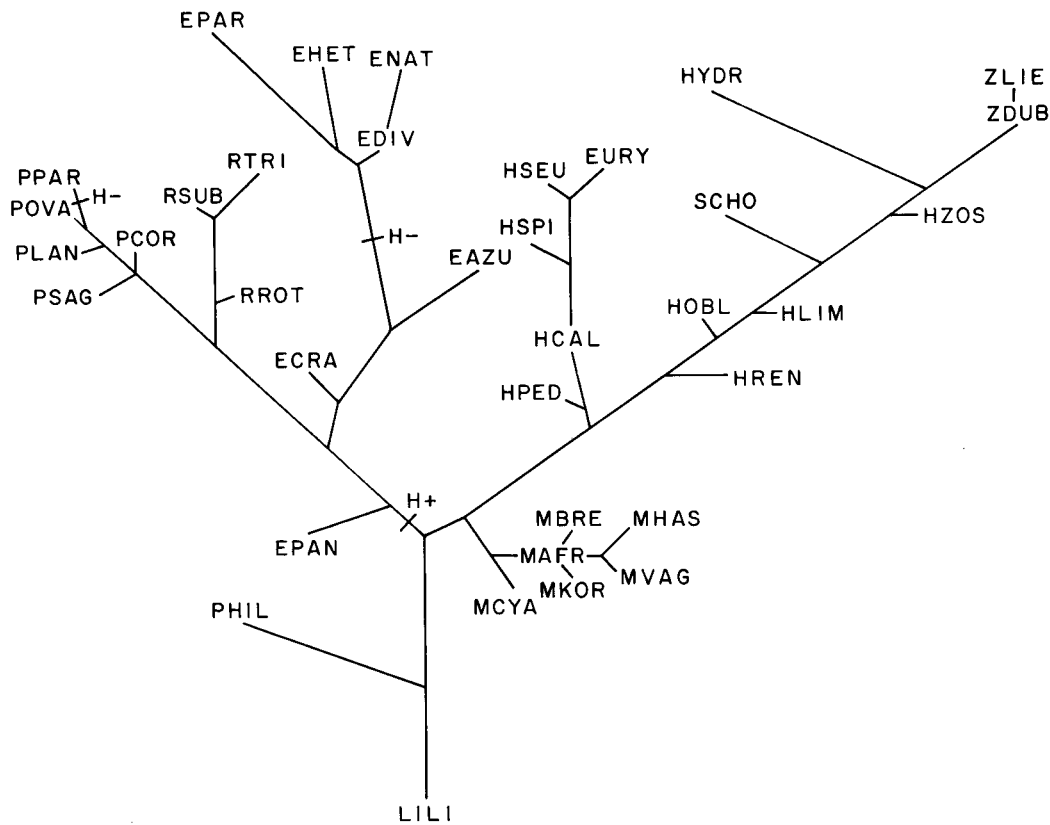


FIG. 1. Cladogram CN5. Abbreviations of taxa from table 1. Branch lengths are proportional to the number of character state changes. H+ and H- represent gain and loss of heterostyly, respectively. See table 5 for synapomorphies of selected clades.

to ancestor (IV) or descendent (VIII) of *Heteranthera*. Among these variant topologies, IV, VIII, and IX do not appear among the most parsimonious trees, but the rest are nearly equally parsimonious.

The arrangements of species within *Monochoria* and *Pontederia* are very similar in the different trees. The only variation in *Monochoria* is whether *M. cyanea* is part of a monophyletic *Monochoria* branch or causes the genus to be paraphyletic by attaching to the trunk of the tree adjacent to the remainder of the genus. The former is the more common condition, but the two variations may be equally parsimonious. Similarly, the only variation in *Pontederia* is whether subgenera *Pontederia* and *Reussia* are sister groups or subg. *Pontederia* becomes paraphyletic because *P. sagittata* is the sister group of both subg. *Reussia* and the remaining species of subg. *Pontederia*. Both arrangements are common but trees with two monophyletic subgen-

era are about four steps shorter than corresponding trees with a paraphyletic subg. *Pontederia*. This shows in the first eight CC trees (table 3), in which placement of *P. sagittata* is

TABLE 5. Synapomorphies of monophyletic major groups of Pontederiaceae. Character and character state numbers from table 2.

Taxon	Synapomorphies			
Pontederiaceae	26:2	27:1		
<i>Monochoria</i> +				
<i>Heteranthera</i>	33:1	36:1		
<i>Monochoria</i>	18:1	26:1		
<i>Heteranthera</i> s.l.	25:1	26:3	32:1	
HREN-ZLIE	17:1	22:3/4		
<i>Eichhornia</i> +				
<i>Pontederia</i>	1:0	18:1	23:1	tristyly
<i>Pontederia</i>	39:2	40:1	41:1	42:2
subg. <i>Pontederia</i>	10:1	16:1	22:1'	41:2
subg. <i>Reussia</i>	4:1	41:3		

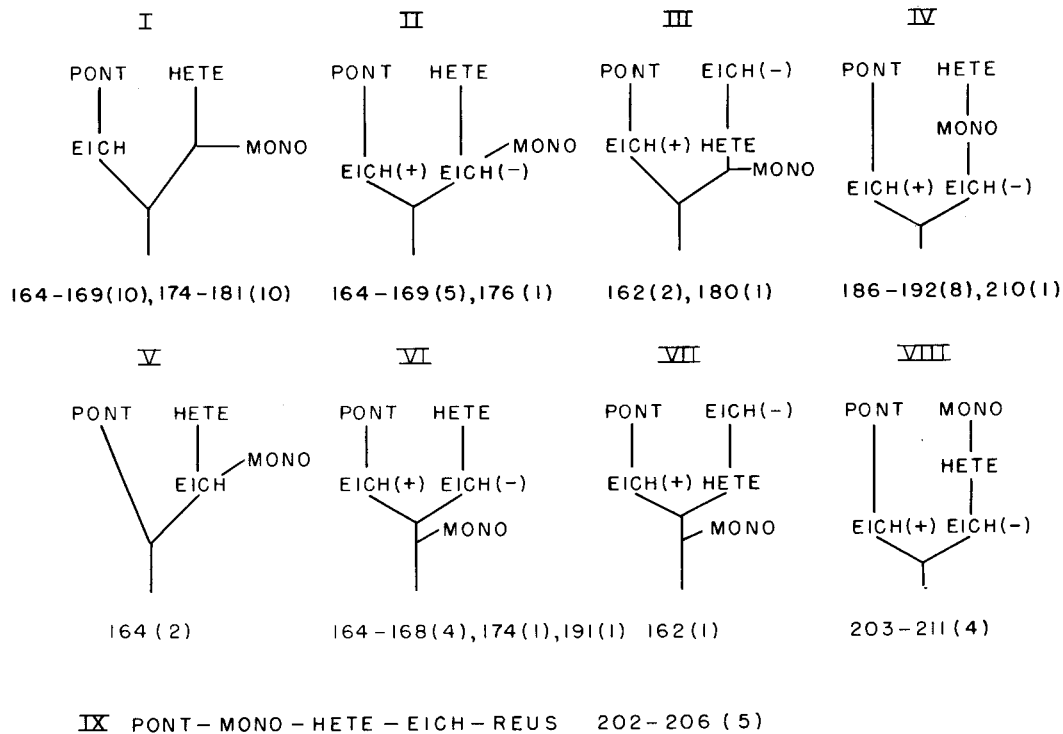


FIG. 2. Reduced cladograms of generic relationships in Pontederiaceae based on all trees except CS. Numbers below each cladogram indicate the range of lengths and the number of trees (in parentheses) sharing that general topology. Abbreviations: EICH—*Eichhornia*, HETE—*Heteranthera*, MONO—*Monochoria*, PONT—*Pontederia* and subg. *Pontederia*, REUS—subg. *Reussia*, (+)—tristylous species, (—)—homostylous species.

the only difference between CC1 and CC2, CC3 and CC4, CC5 and CC6, and CC7 and CC8.

Much of the topological variation among the trees lies in the varying arrangements of species of *Heteranthera*. In all trees, *Hydrothrix* and *Scholleropsis* are cladistically part of *Heteranthera*, as are the proposed generic segregates, *Eurystemon* and *Zosterella*. The cladistic affinities of these segregates to *H. seubertiana* and *H. zosterifolia* (fig. 1) are found in many of the trees. An arrangement with two major branches in *Heteranthera*, HPED-EURY and HREN-ZLIE, varying in their rooting positions, is also common, but other arrangements were nearly as parsimonious. No topology is clearly best for this clade.

*Eichhornia*, too, presents various equally parsimonious topologies, all of them paraphyletic. Using branch-swapping techniques, it was not possible to force a monophyletic topology on species of the genus. The least paraphyletic topology (fig. 1) includes *E. paniculata* as the sister

group of the rest of *Eichhornia* + *Pontederia*, but arrangements including as many as three or four separate groups contributing to the paraphyly of the genus are equally parsimonious. Most trees treat the homostylous species of *Eichhornia* as a clade that is often not closely associated with the tristylous species (fig. 2). Attempts to link individual homostylous species with phenetically similar tristylous species using branch swapping (CN18) produced a tree 15 steps longer than CN5, but with a very high effectiveness of 0.654 (table 3). In all trees, *Eichhornia diversifolia* was indistinguishable from the internal node ancestral to *E. natans*. All other relationships varied among trees.

The five WV trees and the CS tree, all with lengths greater than 200, have numerous branches containing mixtures of species from two or three genera. The vegetative characters (1/3 of the total) thus provide a poor measure of evolution in the character suite as a whole. This result was expected in Pontederiaceae, since

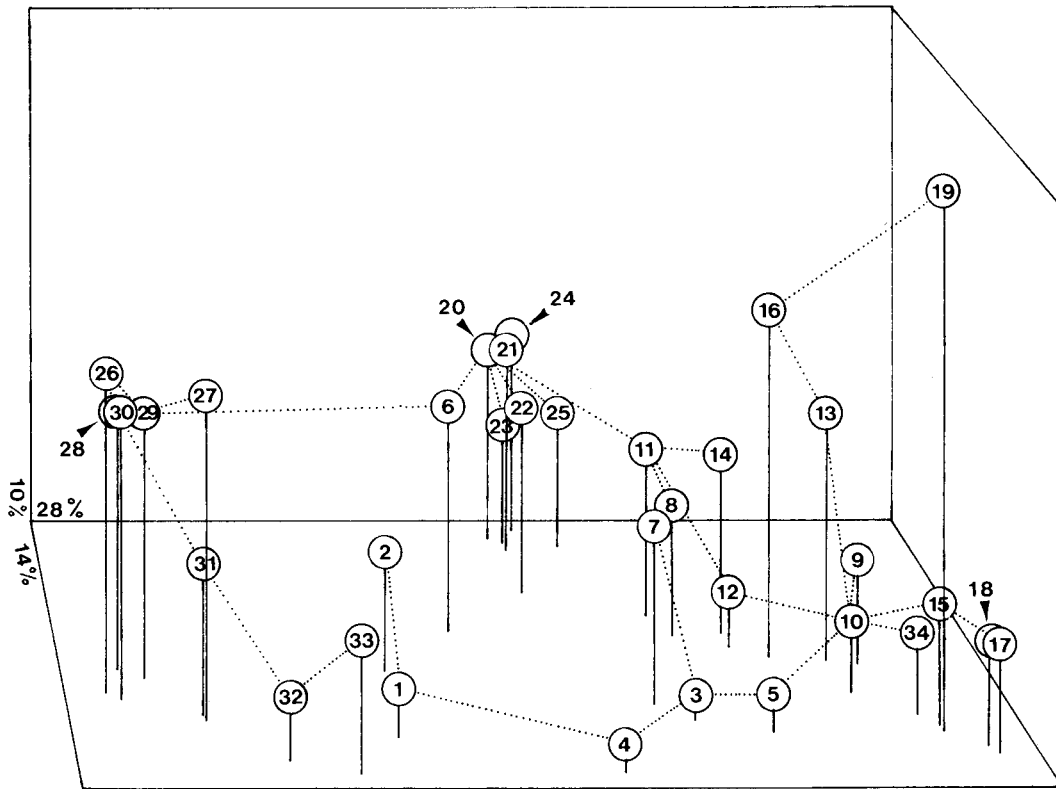


FIG. 3. Projection of Pontederiaceae into the space defined by the first three axes of a principal components analysis on correlations among the 42 characters. Numbers along axes refer to the percentage of variance accounted for by them. Taxa are numbered according to the sequence of table 1. Dotted lines form a minimum spanning tree.

vegetative characters in aquatic plants are often evolutionarily labile and highly homoplasious.

*Phenetic relationships.* The principal components analysis that formed the basis of the PC cladogram accounts for 52% of the character variance with the first three axes (fig. 3). The first component distinguishes the tristylous taxa from the non-tristylous members of the family (except *Pontederia parviflora*), with *Pontederia* and *Hydrothrix* as extremes and *Eichhornia* and *Monochoria* species in the middle region. The second component isolates *Monochoria* from the remainder of the family, with *Eichhornia paniculata* and the more primitive *Heteranthera* species as intermediates. The third component is not readily interpretable, but reinforces the groupings established by the other axes, with homostylous *Eichhornia* species joining *Heteranthera* and its segregates in a loose group separate from *Pontederia* and the tristylous *Eich-*

*hornia* species. The minimum spanning tree superimposed on the principal components projection (fig. 3) provides a similar view of phenetic relationships, except that *E. azurea* and *E. crassipes* are linked to the homostylous *Eichhornia* species rather than to the apparently spatially closer species of *Pontederia* subg. *Reussia*. Otherwise, *Monochoria* is the sole link between the tristylous and non-tristylous *Pontederiaceae*, and the homostylous *Eichhornia* species are linked to *Heteranthera*.

*Biology and biogeography.* According to the general cladogram (fig. 1), tristylous is a synapomorphy of the *Eichhornia-Pontederia* branch and was lost once in *Eichhornia* and once in *Pontederia*. A reduced cytological cladogram of Pontederiaceae based on the topology of CN5 is presented in figure 4. Counts based on  $x = 8$  predominate in the *Eichhornia-Pontederia* clade while no single base number dominates the

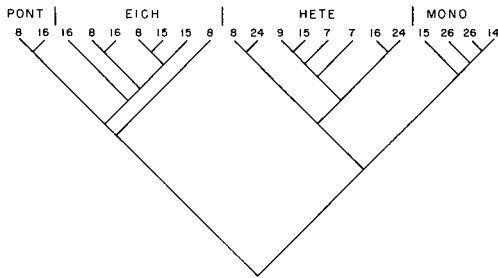


FIG. 4. Reduced cytological cladogram of Pontederiaceae based on topology of figure 1 and chromosome numbers given in table 1. Taxa without known chromosome numbers have been deleted and monophyletic groups sharing the same chromosome number are collapsed to single branches. Abbreviations: EICH—*Eichhornia*, HETE—*Heteranthera*, MONO—*Monochoria*, PONT—*Pontederia*.

*Heteranthera-Monochoria* clade. If  $n = 8$  is the primitive chromosome number in the family, then  $n = 7$  and  $n = 15$  appear to have arisen repeatedly. Two-thirds of the species in the family have been counted (table 1), but the chromosome numbers of the remaining species might well alter the preliminary diagram of cytological evolution we present in figure 5. A reduced area cladogram based on the topology of CN5 (fig. 6) shows the dominance of New World distribution for all clades except the exclusively Old World *Monochoria*. All other Old World species have New World sister groups.

#### DISCUSSION

*Evaluation of methods.* The Wagner tree method was the most successful of the cladistic procedures applied. Wagner trees and the derived CN trees were the most parsimonious trees and also performed well on the other optimality criteria, with the highest average effectiveness among the tree-forming algorithms. However, the Wagner tree method succeeded better with the full and reproductive data sets than with the smaller vegetative data set. Choice of outgroups had less effect on cladogram topology and similar topologies recurred in Wagner trees based on both the three putative outgroups and the two plesiomorphous ingroups. Deliberate branch shifting in the CN trees showed that there were many trees of nearly equivalent parsimony, but with im-

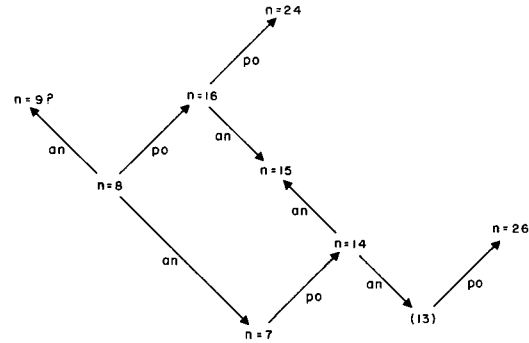


FIG. 5. Postulated chromosome number shifts in Pontederiaceae.  $n = 13$  is known only as a doubtful count from *Monochoria vaginalis* (table 1). Abbreviations: an—aneuploidy, po—polyploidy.

portant variations in branch topology. We do not know whether any of the trees we found is the most parsimonious for this data set, or even if there is a single most parsimonious tree. We considered trees falling within 5% of the length of the shortest tree to be nearly equivalent in parsimony. The additional optimality criteria we used helped to distinguish among trees, but the shortest trees also tended to perform well according to the additional tests. Our data set, with 61% or more homoplasious character state changes measured on each tree, is typical for much botanical data (although present hybridization is not a major factor in Pontederiaceae so far as we know). With such data sets we cannot recommend the phenetic-based methods for cladogram construction, but the character-compatibility method, effectively using only half of the available characters, still produced topologies similar to those of the Wagner trees, although less parsimonious. Wagner trees should be tested by additional appropriate branch swappings. In such branch swapping trials, character polarization by choice of a particular outgroup lacks the analytical importance it has in constructing Wagner trees.

*Taxonomy.* The generally accepted classifications of *Pontederia* (with two subgenera) and *Monochoria* are supported by our studies, but *Eichhornia* and *Heteranthera* present conflicts between cladistic relationships and current taxonomic treatments. *Eichhornia* is apparently paraphyletic but the variety of cladistic topologies for its species precludes confidence in any

particular set of relationships, and should encourage an intensive search for synapomorphies in the complex.

The cladistic relationships of the *Heteranthera* branch are also at variance with present taxonomic treatments. Cladistically, there is no justification for recognition of the proposed segregate genera accepted in the literature unless many more segregates are accepted. An enlarged circumscription of *Heteranthera* seems more appropriate. Some proposed segregates, such as *Zosterella* and *Eurystemon*, despite a few autapomorphies, have had only mixed acceptance in the past (Solms-Laubach 1883; Alexander 1937), and the cladistic relationship of the former to *H. zosterifolia* and of the latter to *H. seubertiana* argue for their continued inclusion in *Heteranthera*. *Scholleropsis* is usually recognized as a distinct genus, although its affinities with *Heteranthera* are generally recognized (Solms-Laubach 1883). Although it has more autapomorphies than either *Eurystemon* or *Zosterella*, its cladistic relationship to *H. limosa* and *H. zosterifolia* argues for inclusion in the larger genus. Because of its very distinctive autapomorphies, *Hydrothrix* was hesitantly attributed to Pontederiaceae in its original description (Hooker 1887), and its affinities have remained dubious (Hutchinson 1959). Our analyses link it with *Heteranthera* (*Zosterella*) *dubia* and *H. zosterifolia*, an alliance supported by a recent developmental study of *Hydrothrix* (Rutishauser 1983). Exclusion of these segregates from *Heteranthera* would leave an undiagnosable, paraphyletic genus. There is so little congruence between the cladistic relationship of the species and a previous infrageneric classification of *Heteranthera* (Solms-Laubach 1883) that this classification should be abandoned. A revised classification of *Heteranthera* must await further study of the genus, such as that in progress by Dr. C. N. Horn (1985).

**Breeding systems.** Our cladistic results show that tristyly arose only once within Pontederiaceae and that it is not the primitive breeding system of the family. The peculiar dimorphic stamens of the *Heteranthera*-*Monochoria* line are a pollination mechanism that may not have derived from a tristyly condition. Tristyly is a synapomorphy of the *Eichhornia*-*Pontederia* clade, but uncertainties surrounding cladistic relationships among *Eichhornia* species compli-

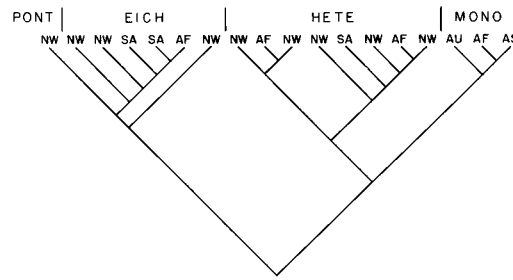


FIG. 6. Reduced area cladogram of Pontederiaceae based on topology of figure 1 and geographical ranges given in table 1. Monophyletic groups sharing endemic areas are collapsed to single branches. Abbreviations: AF—Africa, AS—Asia, AU—Australia, EICH—*Eichhornia*, HETE—*Heteranthera*, MONO—*Monochoria*, NW—New World, PONT—*Pontederia*, SA—South America.

cate the question of whether homostylous species of *Eichhornia* had tristylyous ancestors. The topology adopted in figure 1 derives the homostyles from tristylyous taxa, but other highly parsimonious trees separate the homostylous species from tristylyous *Eichhornia* + *Pontederia*. Several lines of evidence based on microevolutionary studies of breeding systems of *Eichhornia* support the hypothesis that homostylous species of the genus are derived from tristylyous ancestors (Barrett 1978, 1979, 1985a, unpubl.). Populations of *E. diversifolia*, *E. heterosperma*, and *E. paradoxa* exhibit residual tristylyous characters, such as varying pollen heteromorphism, stylar coloration, style length, and stamen insertion patterns that are associated with distinct self-pollinating floral phenotypes. These are best interpreted as semi-homostylous forms derived from the different morphs in a tristylyous system (S. C. H. Barrett unpubl. data). Each of the tristylyous *Eichhornia* species also contains self-pollinating homostylous populations (Barrett 1978, 1979, 1985a, 1985b). The morphology of *Eichhornia* species suggests alignments of each homostyle with a different tristylyous species: *E. paradoxa* with *E. paniculata*, *E. heterosperma* with *E. azurea*, and *E. diversifolia* and *E. natans* with *E. crassipes*, but these relationships did not emerge with any of the methods of tree construction. We suspect that the selfing syndrome of the homostyles provides enough characters (i.e., fewer and smaller flowers and more numerous, smaller seeds) to unite

these species during tree construction. In contrast, some of the features by which we recognize their relationships to the tristylous species are associated with the tristylous syndrome and were therefore excluded from analysis. Tristylous is a rare polymorphism and its breakdown to monomorphism has been recorded in all three families in which it occurs (Ornduff 1972; Charlesworth 1979; Ganders 1979; Barrett 1985b).

**Cytology.** Apparently, both polyploidy and aneuploidy have operated on an original base number of  $n = 8$  to produce the diversity of chromosome numbers seen in the Pontederiaceae (fig. 5). This number is also found, with many others, in the proposed outgroups for the family (Fedorov 1969). The paraphyly of  $n = 7$  in *Heteranthera*,  $n = 15$  in *Eichhornia*, and  $n = 26$  in *Monochoria* (fig. 4) are all conflicts of cytological evidence with the topology of CN5 (fig. 1). The associations of individual homostylous *Eichhornia* species with different tristylous species, as suggested in the section on breeding systems, would remove the conflict in this portion of the tree, but clarification of problems in *Heteranthera* and *Monochoria* await further cytological work.

**Biogeography.** Pontederiaceae is primarily a New World family and three of the four genera have their greatest number of species and individuals in South America, principally in Northern Brazil. North American taxa are generally more apomorphic than their South American congeners and may have entered North America some time following intercontinental contact in the Miocene (Smith and Briden 1977). Excluding *Monochoria*, there are only three Old World species in the family, *Eichhornia natans*, *Heteranthera callifolia*, and *Scholleropsis lutea*, all in Africa. The first and last of these are highly derived species with close cladistic relationships to more plesiomorphic South American species. *Heteranthera callifolia* is a plesiomorphic species, but has a still more plesiomorphic and cladistically more primitive congener in *H. peduncularis*. Given the structure of our cladogram (fig. 6), it is far more parsimonious to propose three separate dispersals from South America to Africa than to propose the numerous extinctions that would be required by a single, common vicariance event. Because of the wide cladistic separation of these three African species, their migrations were

presumably independent and separated in time, with the ancestor of *E. natans* perhaps the most recent arrival, since it is least changed from its nearest relative among the three species. The potential for long-distance dispersal embodied in the small-seeded habit of most members of the family and their occurrence in habitats frequented by migratory birds is common among aquatic plant groups (Sculthorpe 1967). None of our postulated long distance dispersers is among the larger-seeded species of *Eichhornia* or *Pontederia*.

*Monochoria* is the only genus of Pontederiaceae restricted to the Old World, with species in Africa, Australia, and south and east Asia. Since *Monochoria* is the sister group of *Heteranthera* in our analysis (fig. 6), its cladistic position is comparable to that of the three African species of *Eichhornia* and *Heteranthera*, and this position favors an early dispersal from South America to Africa, followed by diversification of *Monochoria* species in the Old World. The distribution of *Monochoria* species is in keeping with this hypothesis. These species become more apomorphic eastward from West Africa, and the cladistic relationships of the species (fig. 1) also reflect this west to east trend. *Monochoria cyanea* is the only truly anomalous species in this dispersalist interpretation of the biogeography of the Pontederiaceae. The apparently primitive features of this species in relation to those of its congeners take it out of the west to east pattern common to the other species of the genus. This species merits further study. Our conclusions about the biogeography of *Monochoria* and other Pontederiaceae contrast with those of Camp (1952), who postulated, on scant evidence, an Asian origin for the group with dispersal across the Pacific to South America.

A fossil find in the Eocene Deccan Intertrappean beds of India is of great interest for the biogeography of the family (Patil and Singh 1978). Structurally preserved root and stem fragments were originally identified as a new species of *Eichhornia* resembling the cladistically advanced *E. crassipes*, a common aquatic weed in India today. Since an advanced, larger-seeded *Eichhornia* species would not be expected in India under our interpretation of the biogeography of the family, the identity of these fossils should be checked. If they are correctly attributed to Pontederiaceae (and this is by no means

certain), they may represent *Monochoria*. Further study of this material could provide a test of our biogeographical interpretation.

*Conclusion.* Cladistic analysis of the Pontederiaceae has revealed much about the structure of variation and evolution in the family. It has shown areas of the traditional taxonomy that are in need of revision or re-evaluation. It has identified taxa that, on the basis of the characters examined, are indistinguishable from the ancestors of other taxa. It has helped to elucidate the evolution of breeding systems in the family, although some features are in conflict with genetic studies, which should encourage investigation of further characters. It points to the need for more cytological work, although existing information is largely concordant with the cladistic hypothesis presented in figure 1. It has favored the suggestion that Old World Pontederiaceae were derived from four separate dispersals from South America to Africa at various times in the past. These problems were

all clarified by trees generated through the Wagner method. The topology of cladograms generated by phenetic methods were not particularly successful in these applications, primarily because highly apomorphic taxa, like *Pontederia* or *Hydrothrix*, are treated as very distinct entities, rather than as derivatives of more plesiomorphic taxa. Faced with the extensive homoplasy of real botanical data, however, even the Wagner method, the best investigated here, failed to produce unambiguous topologies.

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*Note added in proof*

Three synonyms of Table 1 may well prove to be distinct taxa. *Heteranthera rotundifolia* and *H. multiflora* are treated as species distinct from *H. limosa* and *H. reniformis* by Horn (1985), in a treatment that was not available when our study was performed. We have also received seed of *Eichhornia meyeri* from Paraguay (Billiet & Jadin 3211 (BR)). Preliminary results of glasshouse culture suggest that it is distinct from *E. paniculata*. Each of these species is closely related to the taxon with which we synonymized it and their inclusion or exclusion would only minimally affect our conclusions.

APPENDIX 1. Character state distributions and advancement indices (AI) in Pontederiaceae and outgroups. Abbreviations from table 1 and text. Character sequence and coding from table 2. Data compiled from standard floras and monographs listed in table 1 from observations of C. N. Horn (pers. comm.) and from our own observations.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
LILI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COMM	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0
PHIL	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
EAZU	0	1	0	1	0	1	0	0	0	0	1'	1	0	2	1	2	0	1	1	0	1
ECRA	0	1	0	0	1	0	0	0	1	0	1'	1	1	1	1	2	0	1	1	0	1
EDIV	1	1	0	1	0	1	0	0	0	0	1'	1'	1	1	1	2	1	1	1	0	1
EHET	1	1	0	1	0	1	0	0	0	0	0	0	0	2	1	2	1	1	1	0	1
ENAT	1	1	1	1	0	1	0	0	0	0	1'	1'	1	1	1	2	1	1	1	0	1
EPAN	1	1	0	0	0	0	0	0	0	0	1'	0	1	0	0	0	0	0	1	1	1
EPAR	2	1	0	0	0	0	0	0	0	0	1	1'	0	1	0	2	1	0	1	0	1
HCAL	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	2	0	0	1	0	1
HLIM	2	1	0	0	0	0	0	0	0	0	0	0	1	1	1	2	1	0	1	0	1
HOBL	2	1	0	1	0	0	0	0	0	0	0	1'	1	1	0	2	1	0	1	0	1
HPED	1	1	0	1	0	0	0	0	0	0	1	0	1	0	0	2	0	0	1	0	1
HREN	1	1	0	1	0	0	0	0	0	0	1'	1'	1	1	1	2	1	0	1	0	1
HSEU	2	1	0	0	0	1	0	1	0	0	1	1'	0	1	0	2	0	0	1	1	1
HSPI	2	1	0	0	0	0	0	0	0	0	1	1'	1	0	0	2	0	0	1	1	1
HZOS	1	1	1	1	0	1	0	0	0	0	1	1'	0	1	0	2	1	0	1	0	1
EURY	2	1	0	0	0	1	0	1	0	0	1	1'	0	1	0	2	0	0	1	1	1
ZDUB	0	1	1	1	0	1	0	1	0	0	1	1'	0	1	0	2	1	0	1	0	1
ZLIE	0	1	1	1	0	1	0	1	0	0	1	1'	0	1	0	2	1	0	1	0	1
HYDR	2	1	1	0	0	1	1	1	0	0	2	1'	0	1	0	2	1	0	0	0	1
MAFR	1	1	0	0	0	0	0	0	0	0	1'	0	1	0	0	2	0	1	1	0	0
MBRE	1	1	0	0	0	0	0	0	0	0	1'	0	0	0	0	2	0	1	1	0	0
MCYA	1	1	0	0	0	0	0	0	0	0	1'	0	1	0	0	2	0	1	1	0	1
MHAS	1	1	0	1	0	0	0	0	0	0	1'	0	2	0	0	2	1	1	1	0	0
MKOR	2	1	0	0	0	0	0	0	0	0	1'	0	1	0	0	2	0	1	1	0	0
MVAG	1	1	0	0	0	0	0	0	0	0	1'	0	1	0	0	2	1	1	1	0	0
PCOR	0	1	0	0	0	0	0	0	0	1	1'	1	1	0	0	1	0	1	1	0	1
PLAN	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	1	0	1
POVA	0	1	0	0	0	0	0	0	0	1	1'	0	0	0	0	1	0	1	1	1	1
PPAR	0	1	0	0	0	0	0	0	0	1	1'	0	1	0	0	1	0	1	1	0	1
PSAG	0	1	0	0	0	0	0	0	0	1	1'	1	2	0	0	1	0	1	1	0	1
RROT	0	1	0	1	0	0	0	0	0	0	1'	1	2	1	0	2	0	1	1	0	1
RSUB	0	1	0	1	0	0	0	0	1	0	1'	0	1	1	1	2	1	1	1	0	1
RTRI	0	1	0	1	0	0	0	0	1	0	0	1'	0	1	0	2	1	1	1	0	1
SCHO	2	1	0	1	0	1	0	0	0	0	0	1'	0	1	1	2	1	0	1	0	1





APPENDIX 2. New meiotic chromosome counts in Pontederiaceae by S. C. H. Barrett and P. Sarkar. Voucher specimens in TRT.

- Eichhornia diversifolia*. *n* = 15. BRAZIL. **Pará**: Boca de Jari. Jul 1977. *Barrett 1122*.  
*E. heterosperma*. *n* = 15. VENEZUELA. **Guárico**: Calabozo. Jul 1977. *Barrett 1123*.  
*E. paradoxa*. *n* = 8. BRAZIL. **Sergipe**: Propriá. May 1982. *Barrett and Shore 1399*.  
*Heteranthera oblongifolia*. *n* = 7. BRAZIL. **Alagoas**: Pto. Real do Colegio. May 1982. *Barrett and Shore 1402*.  
*H. reniformis*. *n* = 24. COSTA RICA. **Guanacaste**: Canas. Nov 1976. *Barrett 1055*.  
*Monochoria cyanea*. *n* = 15. AUSTRALIA. **Northern Territory**: Tortilla Flats. Jun 1984. *Barrett 1430*.  
*Pontederia cordata* var. *ovalis*. *n* = 8. BRAZIL. **Mato Grosso**: Rondonópolis. Sep 1977. *Barrett 1124*.

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