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Evolution of apocarpy in Alismatidae using phylogenetic evidence from chloroplast *rbc*L gene sequence data

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Abstract. The apocarpous groups in the monocotyledons are mainly concentrated in the subclass Alismatidae. The molecular phylogeny of Alismatidae based on analysis of chloroplast *rbc*L gene sequence data serves as a framework with which to evaluate character evolution with respect to the derivation of apocarpy in the group. 20 of the 27 genera in the subclass that display apocarpy have been included in our study. Our analysis indicates that apocarpy is polyphyletic within the subclass Alismatidae. Two independent origins of apocarpy in Alismatidae are explored in this study. Three separate origins of a single carpel and two separate origins of syncarpy in the subclass are also proposed. Basally connate carpel condition was the ancestral character in Alismatidae and evolved in two directions. It is possible for the unicarpellate condition to have been directly derived by reduction from syncarpy, and it could also be that the unicarpellate state has been derived from apocarpy by reduction in carpel number. The present results indicate that a progression has occurred in the evolution of carpels in Alismatidae from basally connate carpels through syncarpy or apocarpy to a single carpel.

Keywords: Alismatidae; Apocarpy; Basally connate carpels; *Rbc*L gene; Single carpel; Syncarpy; Unicarpellate.

Introduction

Apocarpy has been regarded as an ancestral character in the angiosperms (Bessey, 1915; Hutchinson, 1959). Doyle and Endress (2000) concluded that apocarpy is a primitive feature in angiosperms, but that in monocotyledons it represents a reversal from syncarpy. The apocarpous groups in the monocotyledons include almost all clades of the subclass Alismatidae (Cronquist, 1981) or Alismatiflorae (Stebbins, 1974; Thorne, 1976; Dahlgren and Clifford, 1982). Previous researchers hypothesized that the apocarpous groups in the Alismatidae were the most primitive monocotyledons (Hutchinson, 1959; Takhtajan, 1980; Cronquist, 1988). The origin of the monocotyledons from the Ranunculaceae was strongly advocated by Hutchinson (1973), who relied on the feature of apocarpy as evidence of their relationship. Although apocarpy is generally believed to represent the ancestral condition in Alismatidae (Cronquist, 1981), it has also been interpreted as derived by this subclass (Dahlgren and Rasmussen, 1983; Dahlgren et al., 1985).

The evolution of apocarpy is one of the most interesting evolutionary events in the history of monocotyledons. A better understanding of this evolution may provide valuable insight into the adaptive evolution in flowering plants and also assist in resolving the relationships among the apocarpous groups within the angiosperms. Several investigations into the origin and evolution of carpel form and structure have been reported (Taylor and Hickey, 1996; Igersheim et al., 2001). Owing to the sampling limitations in most studies, the evolutionary relationships of apocarpy and other gynoecium conditions, such as syncarpous, basally connate, and unicarpellate conditions in monocotyledons, are still obscure. Here, we present a phylogenetic analysis of chloroplast *rbc*L gene sequences for 46 species from 46 genera representing all currently recognized families and 81% of the genera in the subclass Alismatidae. Delimitation of families and genera are according to Cook (1990), Cronquist (1981), and Tomlinson (1982). Les et al. (1997) constructed a phylogeny of the subclass Alismatidae, and the origins and evolution of marine angiosperms (seagrasses) and hydrophily in the subclass were also estimated; however, for our purpose only one species from each genus was selected because the condition of carpel fusion was constant in each genus. In the present analysis, 20 of the 27 genera that display apocarpy in the subclass are included. The molecular phylogeny of Alismatidae is used as a framework on which to evaluate character evolution with respect to the evolution of apocarpy in the group.

Materials and Methods

Taxa Sampling

*Rbc*L sequences for 46 species of Alismatidae that were reported previously in Genbank were obtained. One *rbc*L sequence of *Lemna* (Lemnaceae) and five sequences of

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Araceae (*Symplocarpus foetidus*; *Lasia spinosa*; *Xanthosoma sagittifolium*; *Orontium aquaticum* and *Gymnostachys anceps*) reported in Genbank were used as outgroup (Table 1). In Alismatidae not all the species are apocarpous as suggested by Dahlgren et al. (1985). Several sources were used to identify syncarpous, basally

Table 1. Families and Genera of Alismatidae and outgroups with indications of : I. Carpel conditions (A=Apocarpous; B=Basally connate; U=Unicarpellate; S=Syncarpous); II. Genbank Accession No.

Family	Species	I	II
Alismataceae	*Alisma plantago-aquatica*	A	L08759
	Wiesneria filifolia	A	U80682
	Ranalisma humile	A	U80681
	Sagittaria latifolia	A	L08767
	Luronium natans	A	U80680
	Baldellia ranunculoides	A	U80677
	Damasonium alisma	B	U80678
	Echinodorus grandiflorus	A	U80679
Aponogetonaceae	*Aponogeton distachyos*	B	U80684
Butomaceae	*Butomus umbellatus*	B	U80685
Limnocharitaceae	*Limnocharis flava*	A	U80717
	Hydrocleys nymphoides	A	U80716
Cymodoceaceae	*Syringodium filiformis*	A	U03727
	Halodule beaudettei	A	U80689
	Amphibolis antarctica	A	U80686
	Cymodocea serrulata	A	U80687
Potamogetonaceae	*Potamogeton crispus*	A	U80722
	Groenlandia densa	A	U80720
	Coleogeton pectinatus	A	U80727
Ruppiaceae	*Ruppia megacarpa*	A	U80728
Zannichelliaceae	*Zannichellia palustris*	A	U03729
	Lepilaena australis	A	U80729
Scheuchzeriaceae	*Scheuchzeria palustris*	B	U03728
Posidoniaceae	*Posidonia australis*	U	U80718
Juncaginaceae	*Cycnogeton procerum*	A	U80713
	Triglochin maritimum	S	U80714
Lilaeaceae	*Lilaea scilloides*	S	U80715
Zosteraceae	*Zostera noltii*	U	U80733
	Heterozostera tasmanica	U	U80730
	Phyllospadix torreyi	U	U80731
Najadaceae	*Najas flexilis*	U	U03731
Hydrocharitaceae	*Halophila engelmannii*	S	U80699
	Hydrocharis morsus-ranae	S	U80701
	Enhalus acoroides	S	U80697
	Thalassia testudinum	S	U80711
	Nechamandra alternifolia	S	U80706
	Hydrilla verticillata	S	U80700
	Stratioles aloides	S	U80709
	Lagarosiphon major	S	U80703
	Ottelia alismoides	S	U80707
	Apalanthe granatensis	S	U80693
	Elodea nuttallii	S	U80696
	Egeria densa	S	U80695
	Limnobium spongia	S	U80704
	Blyxa aubertii	S	U80694
	Vallisneria americana	S	U03726
Araceae	*Symplocarpus foetidus*	S	L10247
	Lasia spinosa	S	L10250
	Xanthosoma sagittifolium	S	L10246
	Gymnostachys anceps	U	M91629
	Orontium aquaticum	U	AJ005632
Lemnaceae	*Lemna minuta*	U	AY034224

connate, apocarpous, and unicarpellate species within the lineages depicted by the *rbc*L cladogram (Esau, 1977; Cronquist, 1981; Dahlgren and Clifford, 1982; Tomlinson, 1982; Dahlgren and Rasmussen, 1983; Dahlgren et al., 1985; Les and Haynes, 1995; Les and Schneider, 1995; Igersheim et al., 2001).

Tree Reconstruction

Due to difficulties in obtaining the complete sequences for the entire coding region of *rbc*L for all taxa, we restricted our analysis to 1178 nucleotides of sequence data (position 28-1205 of the coding region) that were complete for all taxa. Sequences were aligned using CLUSTALW (Thompson et al., 1994). Phylogenetic analysis of the complete data set of 52 sequences was conducted using the test version of PAUP 4.0b4a (Swofford, 2000), and heuristic searches were done with COLLAPSE, MULPARS and TBR branch-swapping options to save all of the equally most parsimonious trees. All characters were of the type "unordered" and had equal weight. Gaps were treated as "missing." Bootstrap analysis of 1000 replications was performed to show relative support for individual clades. The Alismatidae cladogram was rooted using taxa from Araceae and Lemnaceae, which two families had been shown previously as the appropriate outgroup (Les and Schneider, 1995; Les et al., 1997). Carpel conditions were added to the data matrix of molecular characters, and two optimization options of ACCTRAN (which favors reversals over parallelisms) and DELTRAN (which favors parallelisms over reversals) of MacClade, Version 3.06 (Maddison and Maddison, 1996) were used to study the evolution of carpel fusion.

Results

Phylogenetic Structure of Alismatidae

Of 1178 total characters in the data matrix, 789 (67%) are constant characters; 94 (8%) are variable characters that are parsimony-uninformative; and 295 (25%) are parsimony-informative variable characters. Parsimony analysis of the data yielded 144 most parsimonious trees of 1285 steps with a consistency index (CI) of 0.426, retention index (RI) of 0.692, homoplasy index (HI) of 0.5743, and rescaled consistency index (RC) of 0.2945. The strict consensus tree of the 144 most parsimonious trees is presented in Figure 1.

The strict consensus of these trees indicates two major lineages in Alismatidae: One contains five families arranged in two subclades consisting of (1) Alismataceae and Limnocharitaceae and (2) Butomaceae, Hydrocharitaceae, and Najadaceae. The bootstrap value of this lineage is 73%. The other lineage includes ten families, in which: (1) Aponogetonaceae and Scheuchzeriaceae are basal; (2) one clade constitutes the families Lilaeaceae and Juncaginaceae; (3) one clade includes Cymodoceaceae, Posidoniaceae, and Ruppiaceae, and (4) another clade is comprised of Zosteraceae, Potamogetonaceae, and Zannichelliaceae. The bootstrap value of this lineage is 74%. The monophyly of Alismatidae is strongly supported with a bootstrap value of 99%. The strict consensus tree also indicates some unresolved polychotomies: (1) Alismataceae and Limnocharitaceae, (2) Lilaeaceae and Juncaginaceae, (3) Potamogetonaceae and Zannichelliaceae, and (4) Cymodoceaceae, Posidoniaceae, and Ruppiaceae (Figure 1).

Evolution of Carpel Fusion

Both ACCTRAN and DELTRAN gave similar results for all trees with respect to the evolution of apocarpy in the ingroup. Mapping the species with carpel fusion conditions onto the *rbc*L phylogeny indicates that in the first lineage of Alismatidae apocarpy has one independent origin in the clade Alismataceae and Limnocharitaceae with one reversal to basally connate in *Damasonium* (Alismataceae). In the second lineage the apocarpy has evolved independently at least once in the clade Potamogetonaceae, Zannichelliaceae, Zosteraceae, Ruppiaceae, Cymodoceaceae, and in Posidoniaceae. The syncarpy in *Lilaea* (Lilaceaceae) and *Triglochin* (Juncaginaceae) has possibly evolved once from apocarpy (*Cycnogeton*) while the syncarpy in Hydrocharitaceae also has an independent origin (Figure 2).

The *rbc*L phylogeny also indicates that the unicarpellate condition in Alismatidae has evolved independently in each of the three families Najadaceae, Zosteraceae, and Posidoniaceae. The basally connate condition is ancestral in Alismatidae. In addition, the unicarpellate condition in the outgroup may have had an independent origin, and the syncarpous condition has probably evolved twice: once in *Xanthosoma* and *Lasia*, and once in *Symplocarpus* (Figure 2).

Discussion

Molecular Phylogeny of Alismatidae

Preliminary summaries of interfamilial phylogenetic relationships in Alismatidae have been discussed by Les et al. (1993), Les and Haynes (1995), Les et al. (1997), and the references therein. The analysis given here presents another estimation of relationships based on the majority of the genera in the subclass. The molecular phylogeny of Alismatidae served as a framework on which to evaluate the evolution of characters. Compared to the *rbc*L gene analysis presented earlier by Les et al. (1997), the results are overall similar in showing the presence of the same two major clades. However they differ in details such as the topology of the families in the unresolved clade (Cymodoceaceae, Posidoniaceae, and Ruppiaceae). The low bootstrap value of this clade in the earlier study and the unresolved polychotomies in the present study indicated that the *rbc*L gene is not capable of resolving the position of Cymodoceaceae, Posidoniaceae and Ruppiaceae and that additional gene sequences should be included in further studies. However, the analysis of the evolution of carpel fusion based on the phylogeny of Alismatidae was little affected by this problem.

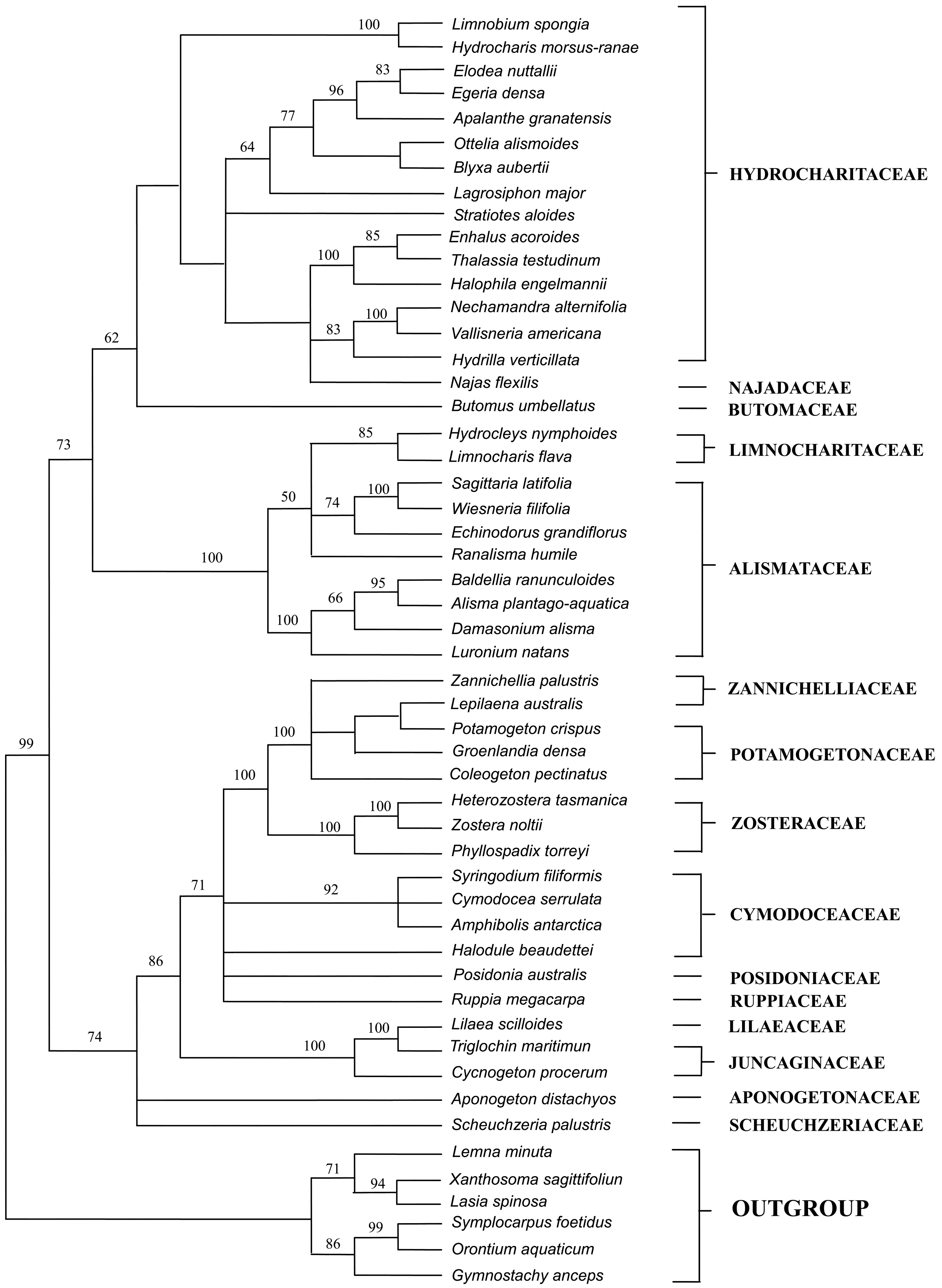

Figure 1. Maximum parsimony *rbc*L cladogram (strict consensus tree shown) of species from the 15 families typically recognized in the monocotyledon subclass Alismatidae with representatives from two outgroup families. The degree of internal support is indicated by bootstrap values. Values for nodes with <50% bootstrap support are excluded.

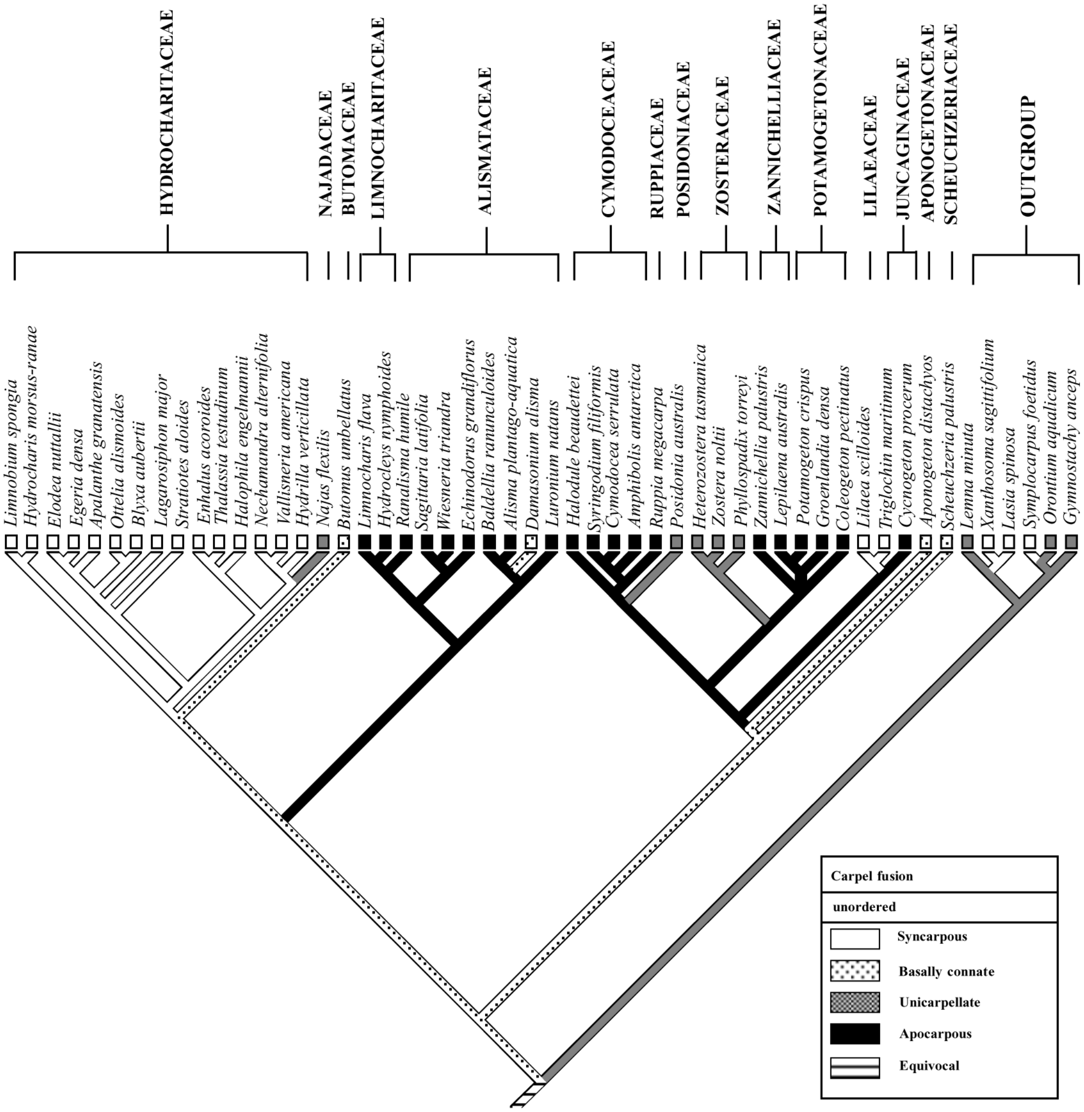

Figure 2. Example reconstruction of carpel fusion evolution for selected most-parsimonious phylogenetic trees based on the *rbc*L gene sequences analysis. The *rbc*L phylogeny indicates that apocarpy has evolved in two separate clades as indicated by the black branches. However, there is a reversal back to the basally connate carpels in *Damasonium* (Alismataceae).

Origins of Apocarpy in Alismatidae

Apocarpy as an ancestral character in angiosperms has never been seriously disputed (e.g., Hutchinson, 1973; Igersheim et al., 2001), but a question of degree still remains. Dahlgren and Rasmussen (1983) and Dahlgren et al. (1985) hypothesized that it must be a derived feature in monocotyledons, and Doyle and Endress (2000) also suggested that apocarpy in monocots represented a reversal. Mapping apocarpy on the *rbc*L cladogram indicates that apocarpy in Alismatidae has two independent origins (Figure 2). Apocarpy is likely to have evolved once in the apocarpous clade of Alismataceae and Limnocharitaceae (bootstrap value of 100%), except for *Damasonium*, the carpels of which are basally connate and probably represent a reversal. Another origin of apocarpy occurs in the clade of Potamogetonaceae, Zannichelliaceae, Zosteraceae, Cymodoceaceae, Posidoniaceae, Ruppiaceae, Lilaeaceae, and Juncaginaceae with the high bootstrap value of 86%. However, apocarpy evolved in three clades: (1) in the clade of Lilaeaceae and Juncaginaceae; (1) in the clade of Potamogetonaceae, Zannichelliaceae and Zosteraceae; and (1) in the clade of Cymodoceaceae, Ruppiaceae, and Posidoniaceae. Basal carpel connation was the ancestral character in Alismatidae, as indicated by the *rbc*L cladogram, and basally connate carpels evolved in two clades: (1) in Butomaceae and (2) in the clade of Aponogetonaceae and Scheuchzeriaceae. Apocarpy might have evolved from basally connate carpels. The present study not only supports the results of Dahlgren and Rasmussen (1983), Dahlgren et al. (1985), Doyle and

Endress (2000) and Igersheim et al. (2001), it also elaborates on the origins of apocarpy in monocotyledons, especially in Alismatidae.

Origins of a Single Carpel in Alismatidae

The relationship of Najadaceae (unicarpellate) and Hydrocharitaceae (syncarpous) has now been well established by cladistic analysis using anatomical, morphological, and molecular data (Miki, 1937; Shaffer-Fehre, 1991a, 1991b; Les et al., 1993; Les and Haynes, 1995; Tanaka et al., 1997). We support the merger of the families as suggested by Shaffer-Fehre (1991a, 1991b). It is possible for a single carpel to have been derived directly by reduction from syncarpy. It is also possible that a single carpel has been derived by reduction from apocarpy (e.g., in Zosteraceae and Posidoniaceae). Three origins of a single carpel in Najadaceae, Zosteraceae, and Posidoniaceae are indicated in the cladogram of Alismatidae. The unicarpellate condition in the outgroup has a separate origin.

Origins of Syncarpy in Alismatidae

Butomaceae (carpels are basally connate) are basal to the clade of Najadaceae and Hydrocharitaceae in the *rbc*L cladogram. The presence of syncarpy in Hydrocharitaceae is likely derived from basally connate carpels (Butomaceae). However, syncarpy in *Lilaea* and *Triglochin* may have an independent origin from apocarpy (*Cycnogeton*) in the clade of Lilaeaceae and Juncaginaceae (Figure 2). Syncarpy in the outgroup might have evolved independently twice from a single carpel in *Symplocarpus* and the clade of *Xanthosoma* and *Lasia*.

In conclusion, molecular phylogenetic studies of the subclass Alismatidae have provided insights into the evolution of carpel fusion. Several previous molecular phylogenetic analyses suggested that syncarpy was a derived feature in basal angiosperms and that it was probably polyphyletic (Doyle and Endress, 2000). Combining our results with those of earlier studies we conclude that apocarpy is an ancestral feature in angiosperms but that in monocotyledons it is a reversal (as Doyle and Endress, 2000), with possibly two independent origins of the apocarpy in Alismatidae. The present study does not support the hypothesis that apocarpy is ancestral in monocots, or that apocarpous Alismatidae are the most primitive monocots (Hutchinson, 1959; Takhtajan, 1980; Cronquist, 1988). Instead, the *rbc*L cladogram indicates that basally connate carpels are ancestral in Alismatidae. There has been a progression from basally connate carpels through syncarpy or apocarpy to a single carpel in the evolution of carpels in Alismatidae.

Several possible evolutionary advantages of syncarpy have been presented; (1) fused carpels mean that a single pollen delivery event can serve all carpels of a flower; (2) syncarpy permits an even distribution of pollen tubes among carpels; (3) the fusion of carpels means that pollen selection can occur in a single structure (Endress, 1982). However, the functional significance of the multiple origins of apocarpy in the subclass Alismatidae is still unknown, further detailed investigation may furnish us with more exact data to explore its functional significance.

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基於葉綠體 *rbc*L 基因序列對澤瀉亞綱 (Alismatidae) 離生心皮的起源與演化的研究

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單子葉植物離生心皮類主要集中在澤瀉亞綱。本文基於 *rbc*L 基因序列資料構建了澤瀉亞綱的系統發育關係，依據此系統發育關係為框架，討論了澤瀉亞綱不同心皮的起源與演化，尤其是離生心皮的起源與演化。本研究包括了澤瀉亞綱約 27 屬離生心皮植物中的 20 屬。研究結果表明離生心皮在澤瀉亞綱中是多次獨立起源的，據初步估計在澤瀉亞綱中離生心皮可能有 2 次獨立的起源。本文同時估計在澤瀉亞綱中單心皮至少有 3 次獨立的起源而基部合生心皮則是澤瀉亞綱最原始的心皮性狀。本研究揭示了澤瀉亞綱中不同心皮之間可能的演化過程，即從基部合生心皮向合生心皮或離生心皮方向演化，而單心皮，則很有可能是通過具多數、合生的心皮直接簡化而來；同時它也有可能從具多數、離生的心皮簡化而來。

關鍵詞：澤瀉亞綱；離生心皮；基部合生心皮；*rbc*L基因；單心皮；合生心皮。