

HAGSTRÖM'S CONCEPT OF PHYLOGENETIC RELATIONSHIPS IN *POTAMOGETON* L. (POTAMOGETONACEAE)

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Summary

Hagström's concepts of relationships in *Potamogeton*, as reflected by the subgeneric, sectional, and subsectional divisions in his classification of the genus are investigated by reconstruction of an evolutionary "tree" deduced from phylogenetic inferences stated in his monograph. These relationships are explored in the context of results from phenetic and cladistic numerical analyses performed using characters taken from the Hagström monograph that are scored for 26 subsections. The Hagström classification represents an amalgam of phenetic and cladistic interpretations and the hierarchy does not depict accurately fundamental evolutionary relationships indicated by numerical analyses. Recommendations are provided for developing and testing evolutionary hypotheses that are independent of relationships inferred by this long-standing but problematic classification.

Introduction

The "pondweed" genus *Potamogeton* (Potamogetonaceae) represents a cosmopolitan group of herbaceous perennial hydrophytes widely distributed in fresh to brackish waters. Comprising approximately 80–100 species worldwide (Cook et al., 1974; Wiegleb, 1988), the genus is renowned for its extensive morphological diversity including heterophyllous species (with morphologically dissimilar floating and submersed foliage) and strictly submersed homophyllous species. Two morphological groups are often recognized in subgenus *Potamogeton*, the "broad-leaved" and the "linear-leaved" species (e.g., Fernald, 1932; Ogden, 1943), although it is uncertain whether either group represents a natural evolutionary lineage (Les, 1983).

A taxonomic history of *Potamogeton* is summarized elsewhere (e.g., Haynes, 1974; Wiegleb, 1988). The greatest influence on contemporary classification of *Potamogeton* was made by Hagström (1916) who produced a comprehensive monograph of the genus that incorporated earlier observations of Raunkiær (1903), Chrysler (1907), and others.

Hagström's scheme recognized approximately 138 species globally, and subdivided the genus into two subgenera, five sections, and 26 subsections. In North America, modifications of the Hagström scheme were made by Fernald (1932) who treated the "linear-leaved" species, and by Ogden (1943) who treated the "broad-leaved" species. These studies recommended only trivial alterations to the Hagström classification such as the removal of series *Nuttalliani* from subsection *Hybridi*, its elevation to subsectional status, and the establishment of a new subseries (*Panormitani* Fern.) within subsection *Pusilli*. Hagström's work essentially remains as the fundamental framework for classification of *Potamogeton* worldwide, and despite some criticism (e.g., St. John, 1925), it has been used as the foundation for various comparative systematic investigations (e.g., Les, 1983; Sorsa, 1988).

Contemporary taxonomists have typically focused on which taxa should or should not be recognized within subsections of *Potamogeton* (e.g., Haynes, 1974, 1985; Reznicek and Bobbette, 1976). Some, however, have expressed doubt whether the Hagström classification accurately represents related species groups. Haynes, for example (1985: 173), stated his approach ". . . to prepare treatments of one or a few subsections at a time, *without considering whether the subsection should be recognized . . .*" [emphasis ours]. If revisionary

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studies in *Potamogeton* are to continue focusing on subsections, then it should be demonstrated that the general framework of the Hagström classification does indeed depict natural related groups.

Certainly, a reasonable degree of confidence in the naturalness of the Hagström system can be justified because of the considerable amount of anatomical and morphological data that has been incorporated into the classification. On the contrary, recent studies have presented arguments that the subsections may be at least partially artificial. From an assessment of chromosomal data (Les, 1983) the distribution of chromosome numbers generally agrees with the subsections recognized by Hagström, although some anomalies exist. Two discrete chromosomal lineages may occur in the genus ($x=7$; $x=13$), and although most subsections are uniform chromosomally, others like *Pusilli*, *Amplifolii*, and *Oxyphyllii* possess species with chromosome numbers possibly representing different evolutionary lineages (Les, 1983). Similarly, a detailed study of pollen morphology in *Potamogeton* points to many discrepancies where pollen types do not correlate well with the subsections recognized by Hagström, but instead are scattered among several of the subsections (Sorsa, 1988).

A major criticism of the Hagström scheme is that overall systematic relationships among subsections of *Potamogeton* are undefined (Les, 1983; Sorsa, 1988). Hagström (1916) presented no phylogenetic scheme to accompany his classification, and his precise concept of phylogeny in the genus is lost among the myriad of comments that he made regarding interspecific and intersectional/subsectional affinities.

Presently, systematists emphasize that classifications should reflect explicit hypotheses of phylogenetic relationships. The lack of an explicit basis for the Hagström classification is justifiably a reason to reconsider its appropriateness for use in modern systematic studies and to call for an evaluation of the scheme. Indeed, more than 70 years since the publication of Hagström's classification, basic evolutionary questions in *Potamogeton* remain to be answered. For example, do heterophyllous or homophyllous species represent the ancestral condition in *Potamogeton*? There have been three different interpretations of this question (Fig. 1). Although Hagström's perspective (that the genus evolved from submersed linear-leaved plants) is a widely followed hypothesis, it is also the most unorthodox, and the matter is far from settled (Les, 1983; Wiegleb, 1988).

In developing his classification of *Potamogeton*, Hagström used what is termed a phyletic or "evolutionary" approach (sensu Mayr, 1981). His study predated the development and application of cladistic and phenetic methodologies by 35–45 years. Hagström presumably assessed all available attributes of the Pondweeds to develop his concept of evolutionary lineages within the group. Such evolutionary classifications did not present explicit justifications for group relationships and followed no "rules" against postulating some relationships on the basis of overall similarities (i.e., a phenetic approach) and others on the basis of shared unique features (i.e., a cladistic approach) within a single classification. Hagström (1916) apparently did use such an eclectic approach in his phyletic classification of the group. Typically his groups were based on their overall similarity, but lineages were often defined on the basis of what can be interpreted as "shared derived" characters. He often addressed the evolutionary polarities of characters, which allows for some idea of phylogenetic directionality to be deduced from his scheme. His consideration of character polarities, however, was inconsistent throughout the treatment, and conflicting data were occasionally dismissed as character state reversals (e.g., Hagström, 1916: 151–152). Eclectic classifications are generally regarded to be of little systematic value because "... the presumed phylogeny cannot be recovered from such a classification" (Dahlgren and Rasmussen, 1983: 271).

In this study, we first present an assessment of the major phylogenetic lineages in *Potamogeton* that are represented by the Hagström classification. To achieve this, we have reconstructed an evolutionary "tree" using specific statements of relationships expressed

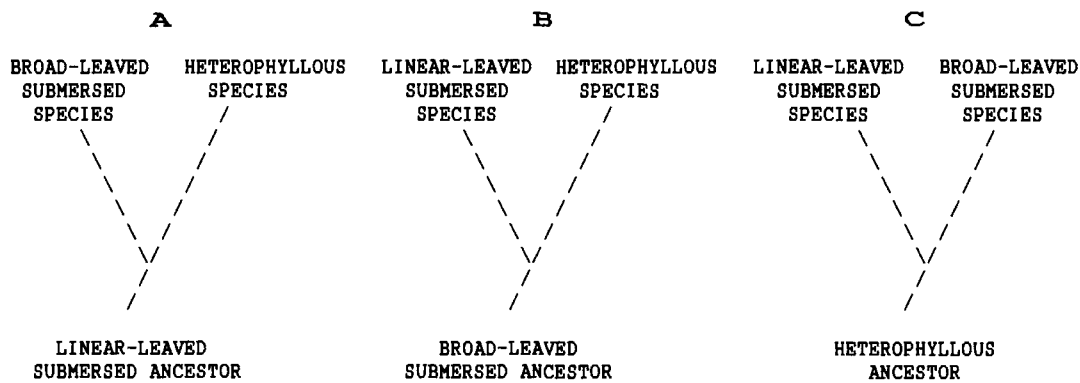


Fig. 1. Three phylogenetic hypotheses of relationships among morphological groups in *Potamogeton*. A: linear-leaved homophyllous ancestry (from Hagström, 1916). B: broad-leaved submersed ancestry (from Raunkiær, 1903). C: heterophyllous ancestry (from Schenck, 1886; Chrysler, 1907).

in Hagström's monograph. This tree approximates Hagström's eclectic concept of phylogeny in the genus *Potamogeton* and provides the first representation of an evolutionary basis for his classification scheme. We then compare this phyletically derived tree to dendrograms and cladograms generated by phenetic and cladistic analyses of character data taken directly from the monograph. This approach provides a means of assessing whether or not the Hagström classification depicts the same fundamental groups and evolutionary lineages as those generated by the more explicit and objective phenetic and cladistic analyses. The use of cladistics and outgroup rooting further provides an objective means of assessing the ancestral morphological condition within *Potamogeton*. The results of these comparisons serve as a means to evaluate the limitations associated with use of the Hagström classification in systematic studies.

Methods

We identified 45 statements in the "Critical Researches" that reflect Hagström's conception of phylogenetic relationships among the subgenera, sections, and subsections of *Potamogeton*. This "appendix" is too lengthy to include in the present report, but is available upon request to the authors. The statements were used to construct a "rooted" branching diagram (i.e., a phyletic "tree") that we view as maximally concordant with the essence of Hagström's phylogenetic statements (Fig. 2). We admit that such an approach has obvious limitations. We compared fewer characters than Hagström discussed because of our inability to score many characters unambiguously for all subsections. Occasionally, it was also necessary to make decisions of "typical" characters in subsections including species with contrasting states. On the other hand, Hagström's descriptions of character states that we used in our analyses were in close agreement with more recent treatments (e.g., by Ogden, 1943 and Fernald, 1932). Overall, the character set is representative of the morphological diversity existing within the genus.

This hypothetical "tree" was then compared to others derived from phenetic and cladistic analyses to see whether or not a similar topology could be generated using the same characters that Hagström emphasized in his treatment. From the "Critical Researches," we were able to score 29 characters reliably for the 26 subsections (OTU's) including reproductive, anatomical, and vegetative (morphological) features (Table 1). A basic data matrix of these characters and states (Table 2) was first converted into a dissimilarity matrix of normalized euclidean distances. The resulting values in the dissimilarity matrix were used to construct a dendrogram (Fig. 3) using the UPGMA algorithm (Kovach, 1986). The phenetic analysis was performed only with subsections of *Potamogeton* and therefore excluded subsection *Densi* (see discussion). The basic data matrix was then used to perform

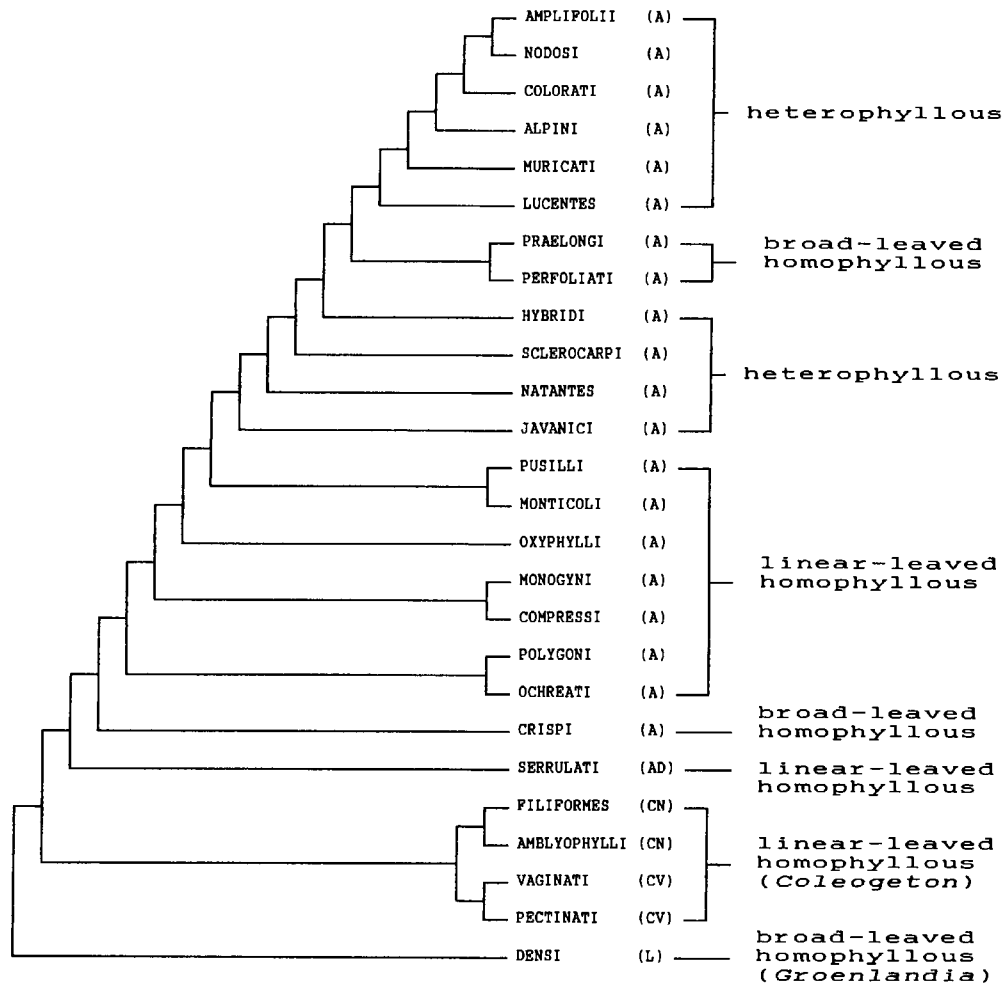


Fig. 2. Hagström's concept of phylogeny in *Potamogeton*. "Phyletic tree" depicting subsectional relationships interpreted from phylogenetic statements made in Hagström's "Critical Researches" (1916). Sections are abbreviated: A = *Axillares*, AD = *Adnati*, CN = *Connati*, CV = *Convoluti*, L = *Laterales*. Morphological groups are indicated.

cladistic analyses following a maximum parsimony approach carried out with the PAUP version 2.4 program (Swofford, 1985). Using Hagström's interpretations as a guideline, eight characters (14, 18–24) were treated as unordered, and the remaining 21 characters were treated as ordered. We used alternating branch swapping (SWAP=ALT) for rearranging tree topologies in search of shorter trees and multiple parsimony (MULPARS) to search for multiple equally parsimonious trees (Swofford, 1985). We employed outgroup rooting used subsection *Densi* as the outgroup. Occurrences of different chromosome number series were mapped onto the completed cladogram using data taken directly from Les (1983) and supplemented by several "anomalous" counts initially omitted from this work (from same references cited in Les, 1983). A second version of cladistic analysis was performed by recoding floating-leaf characters as missing data for all homophyllous subsections. The missing data are treated as "all possible states" and do not affect the tree locations to which unplaced taxa are added (Swofford, 1985).

Results

Hagström's concept of phylogenetic relationships in *Potamogeton* (Fig. 2) depicts the genus as primitively submersed and homophyllous (Hagström, 1916: 53–54). A major

Table 1. Characters and states used in numerical analyses of *Potamogeton* subsections (compiled from Hagström, 1916).

Reproductive characters:

1. fruit beak (0 = absent; 1 = low and wartlike; 2 = acute; 3 = drawn out; 4 = drawn out and curved back)
2. dorsal keel (1 = strong; 2 = weak; 3 = rounded)
3. lateral fruit keels (0 = absent; 1 = present)
4. style beak (0 = absent; 1 = present)
5. stigma papillae (0 = major; 1 = minor)
6. fruit type (0 = drupelet; 1 = achene)
7. pollination (0 = aquatic; 1 = upper water surface; 2 = wind)

Anatomical characters:

8. hypodermal vascular bundles (0 = absent; 1 = present)
9. hypodermal strands (0 = absent; 1 = present)
10. hypodermal bast cells (0 = absent; 1 = present)
11. pseudo-hypodermis (0 = absent; 1 = 1-layered; 2 = 2-layered; 3 = 3-layered)
12. endodermis (0 = thick; 1 = thin)
13. endodermis type (0 = "o" cells; 1 = "o-o" cells; 2 = "o-u" cells; 3 = common "u" cells; 4 = gramineus-u cells)
14. central cylinder type (0 = proto; 1 = trio; 2 = eight; 3 = four; 4 = oblong; 5 = circular)
15. peduncle hypodermis (0 = absent; 1 = strands; 2 = strands and bundles)
16. peduncle rigidity (0 = stiff; 1 = flexible)
17. peduncle endodermis (0 = absent; 1 = present)

Vegetative characters:

18. floating leaf shape (0 = broad or ovate; 1 = oblong-lanceolate; 2 = small ovate; 3 = linear-lanceolate; 4 = absent)
 19. floating leaf nerves (0 = 0; 1 = 1-10; 2 = 11-23; 3 = 24+)
 20. floating leaf base (0 = cordate; 1 = obtuse rounded; 2 = tapering; 3 = absent)
 21. floating leaf apex (0 = obtuse-acuminate; 1 = acute-cuspidate; 2 = acute; 3 = round-obtuse; 4 = absent)
 22. floating leaf petiole (0 = distinct; 1 = indistinct; 2 = sessile; 3 = absent)
 23. submersed leaf base (0 = cordate/amplexicaul; 1 = cordate/semiamplexicaul; 2 = tapered attenuate; 3 = rounded; 4 = straight)
 24. submersed leaf apex (0 = cucullate; 1 = slightly retuse; 2 = cuspidate; 3 = acute-cuspidate; 4 = acute-attenuate; 5 = round-obtuse; 6 = linear)
 25. submersed leaf petiole (0 = distinct; 1 = indistinct; 2 = sessile)
 26. leaf margin (1 = entire; 2 = serrate)
 27. submersed leaf nerves (0 = 1-5; 1 = 6-11; 2 = 12-21; 3 = 22+)
 28. submersed leaf shape (0 = narrowly linear; 1 = linear; 2 = broad; 3 = very broad)
 29. vernation (0 = adplicate; 1 = convolute; 2 = involute)
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dichotomy separates the linear-leaved homophyllous subgenus *Coleogeton* (section *Connati* with subsections *Filiformes*, *Amblyophylli*, and section *Convoluti* with subsections *Vaginati*, and *Pectinati*) from subsections of subgenus *Potamogeton* (Hagström, 1916: 53-54). Subsection *Serrulati* (section *Adnati*) is intermediate between the subgenera but included in subgenus *Potamogeton* (Hagström, 1916: 13). In the remainder of subgenus *Potamogeton* (section *Axillares*) the linear-leaved homophyllous subsections (*Ochreati*, *Polygoni*, *Oxyphylli*, *Compressi*, *Monogygni*, *Monticoli*, *Pusilli*) and broad-leaved subsection *Crispi* comprise a monophyletic group, as do the remainder of the broad-leaved homophyllous subsections (*Perfoliati* and *Praelongi*) with the heterophyllous subsections *Javanici*, *Natantes*, *Sclerocarpi*, *Hybridi*, *Lucentes*, *Muricati*, *Alpini*, *Colorati*, *Nodosi*, and *Amplifolii* (Hagström, 1916: 57). Subsection *Javanici* is ancestral to the heterophyllous subsections (Hagström, 1916: 123, 128). Subsection *Densi* (section *Laterales*) is basal in this diagram because

Table 2. Character states (of characters in Table 1) coded for 26 subsections of *Potamogeton* used in numerical analyses.

Subsection	Character number																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
<i>Alpini</i>	2	2	0	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	2	2	1	3	0	2	1	1	1	2	3	2
<i>Amblyophylli</i>	2	3	0	1	0	1	0	0	1	0	0	0	3	3	0	1	1	4	0	3	4	3	4	5	2	1	1	0	0	0
<i>Amplifolii</i>	2	1	0	0	1	1	2	0	0	0	1	0	0	0	0	0	0	0	3	1	2	0	2	1	0	1	2	3	2	
<i>Colorati</i>	1	2	0	0	1	1	2	1	1	1	2	0	2	0	0	0	0	1	2	1	2	1	2	0	1	1	2	3	2	
<i>Compressi</i>	0	3	0	1	1	1	2	0	0	1	1	0	0	1	2	0	0	4	0	3	4	3	3	3	2	1	0	1	0	
<i>Crispi</i>	4	1	0	0	1	1	2	0	0	1	1	0	0	4	0	0	4	4	0	3	4	3	4	1	2	2	0	2	0	
<i>Densi</i>	2	2	0	1	1	0	2	0	0	0	0	1	0	4	0	0	4	4	0	3	4	3	1	1	2	2	1	2	2	
<i>Filiformes</i>	1	3	0	1	0	1	0	0	1	0	0	0	3	3	0	1	1	4	0	3	4	3	4	5	2	1	0	0	0	
<i>Hybridi</i>	2	1	1	0	1	1	2	0	1	1	0	0	0	1	0	0	0	2	2	2	3	0	2	1	2	1	0	2	2	
<i>Javanici</i>	3	1	0	0	1	1	2	0	0	1	1	0	0	5	0	0	3	1	2	2	2	4	4	2	1	0	1	0	1	
<i>Lucentes</i>	2	1	0	0	1	1	2	1	1	0	1	0	4	4	0	0	0	1	2	2	0	1	2	2	1	1	1	3	2	
<i>Monogyni</i>	2	1	0	0	1	1	2	0	0	1	0	0	0	5	1	0	0	4	0	3	4	3	2	4	2	1	0	1	0	
<i>Monticoli</i>	0	1	0	0	1	1	2	0	0	1	0	0	4	0	0	0	4	4	0	3	4	3	4	4	2	1	0	1	0	
<i>Muricati</i>	2	1	1	0	1	1	2	0	1	1	0	0	0	2	0	0	2	3	1	3	0	2	1	1	1	1	2	3	2	
<i>Natantes</i>	2	1	0	0	1	1	2	1	1	0	1	0	3	1	0	0	0	0	3	0	1	0	4	5	0	1	0	0	2	
<i>Nodosi</i>	2	1	0	0	1	1	2	0	0	0	0	0	0	1	0	0	0	1	3	2	2	0	2	1	0	1	2	3	2	
<i>Ochreati</i>	0	1	1	0	1	1	2	0	0	0	3	0	0	4	1	0	0	4	0	3	4	3	3	1	2	1	0	1	0	
<i>Oxyphylli</i>	0	3	0	1	1	1	2	0	0	1	0	0	0	4	0	0	4	4	0	3	4	3	3	2	1	0	1	0	0	
<i>Pectinati</i>	4	3	0	1	0	1	1	1	1	1	2	0	3	4	1	1	1	4	0	3	4	3	4	5	2	1	0	0	0	
<i>Perfoliati</i>	0	3	0	0	1	1	2	0	0	0	2	0	0	1	0	0	0	4	0	3	4	3	0	1	2	1	3	3	1	
<i>Polygoni</i>	0	1	0	0	1	1	2	0	0	0	0	0	0	1	0	0	4	4	0	3	4	3	3	4	2	1	0	1	0	
<i>Praelongi</i>	2	1	0	0	1	1	2	1	1	1	2	0	3	0	0	0	4	4	0	3	4	3	1	0	2	1	3	3	1	
<i>Pusilli</i>	2	3	0	1	1	1	2	0	1	1	0	0	0	5	0	0	0	4	0	3	4	3	2	2	1	1	1	1	0	
<i>Sclerocarpi</i>	0	1	1	0	1	1	2	0	1	0	0	0	2	3	0	0	1	2	2	2	3	0	2	1	1	1	0	1	2	
<i>Serrulati</i>	0	1	0	1	1	1	2	0	0	0	1	0	1	1	0	0	0	4	0	3	4	3	3	4	2	2	0	1	0	
<i>Vaginati</i>	1	3	0	1	0	1	1	1	1	1	0	0	3	2	1	1	1	4	0	3	4	3	4	5	2	1	0	0	0	

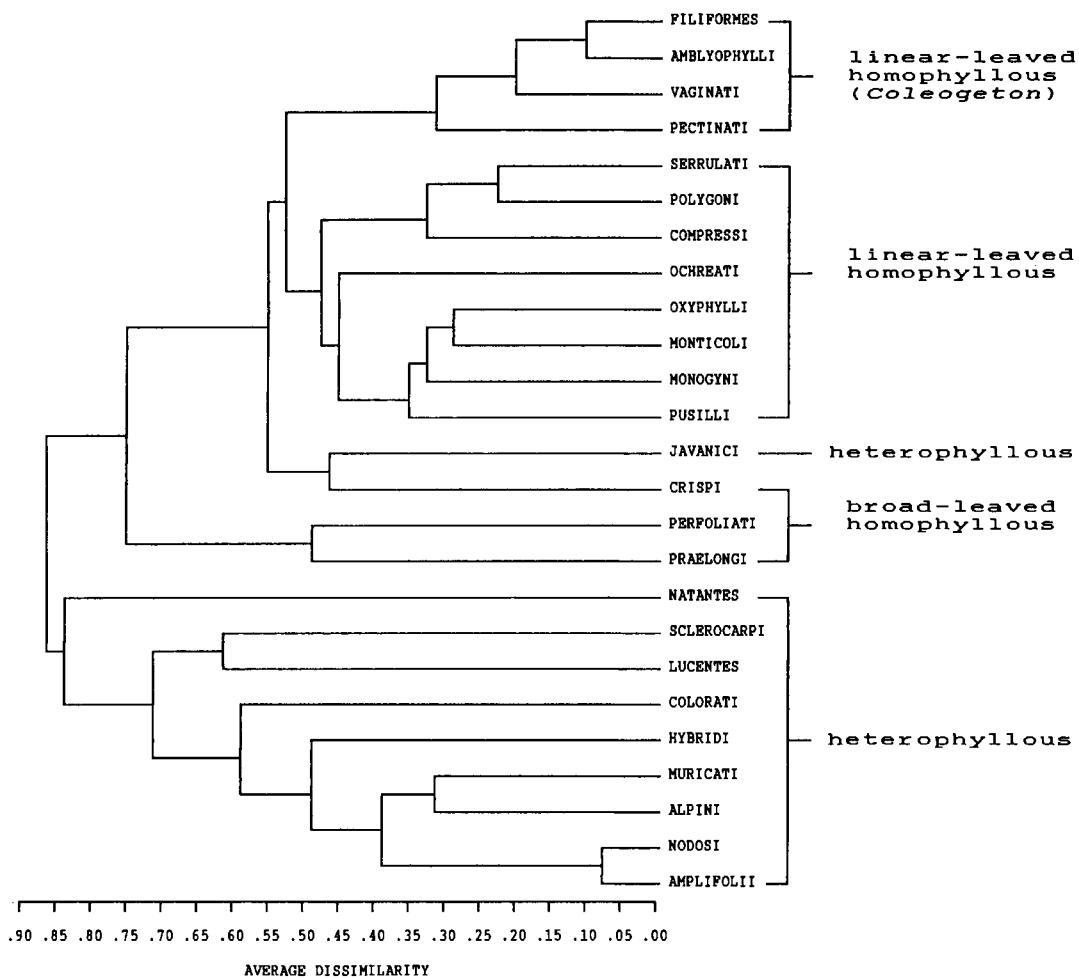


Fig. 3. UPGMA dendrogram depicting phenetic relationships among subsections of *Potamogeton* generated from a matrix of normalized euclidean distances of 29 characters scored from Hagström's "Critical Researches" (1916). Clusters corresponding to morphological groups are indicated.

Hagström believed it appropriate to treat the group as a separate but closely related genus, *Groenlandia* (Hagström, 1916: 259).

A UPGMA dendrogram (Fig. 3) reconstructs some but not all of "Hagström's" group relationships. Notably, subsection *Serrulati* (section *Adnati*) clusters among linear-leaved homophyllous subsections, but not discretely between subgenera *Coleogeton* and *Potamogeton* (Fig. 3).

Subsections within subgenus *Coleogeton* cluster together, and also within the sections designated by Hagström (*Amblyophylli* and *Filiformes* in section *Connati*; *Pectinati* and *Vaginati* in section *Convoluti*). Linear-leaved homophyllous subsections (*Compressi*, *Monogyne*, *Monticoli*, *Ochreati*, *Oxyphylli*, *Polygoni*, *Pusilli*, and *Serrulati*) cluster together, and as a secondary group with subgenus *Coleogeton*. Subsections *Javanici* (heterophyllous), *Crispi*, *Perfoliati*, and *Praelongi* (broad-leaved homophyllous) cluster in an intermediate position between the linear-leaved homophyllous subsections and the heterophyllous subsections (*Alpini*, *Amplifolii*, *Colorati*, *Hybridi*, *Lucentes*, *Muricati*, *Natantes*, *Nodosi*, *Sclerocarpi*) in the phenogram (Fig. 3). The heterophyllous subsections (excluding *Javanici*) form a discrete cluster (Fig. 3). Hagström's opinion of near relationships between subsections *Amplifolii* and *Nodosi* and between *Perfoliati* and *Praelongi* (Fig. 2) is supported by their close clustering in the phenetic analysis (Fig. 3). His proposed relationships between sub-

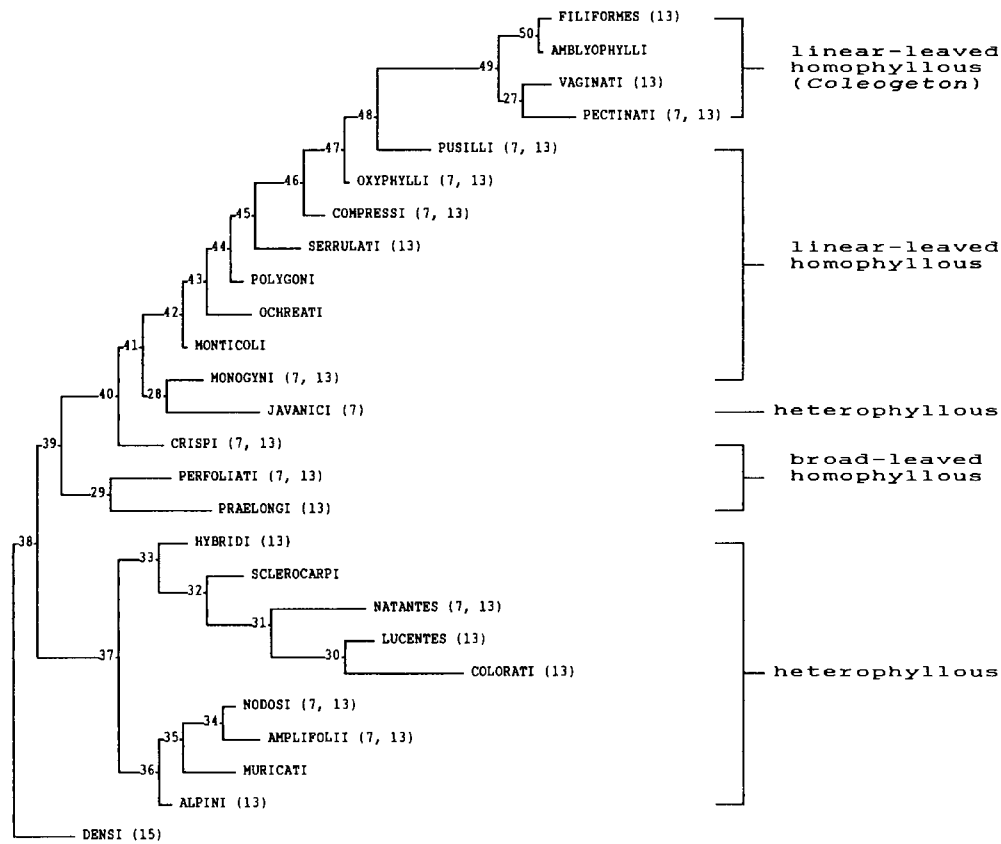


Fig. 4. PAUP maximum parsimony cladogram depicting cladistic relationships among *Potamogeton* subsections based on outgroup rooting using 29 characters scored from Hagström's "Critical Researches" (1916). Nodes are numbered following Tables 3-4. Chromosome number series (in parentheses) are mapped using data from Les (1983). Clades corresponding to morphological groups are indicated.

sections *Ochreatei* and *Polygoni*, *Monogyne* and *Compressi*, and *Pusilli* and *Monticoli* (Fig. 2) are not supported by a close grouping in the phenetic analysis.

Overall, the phenetic "network" of groups from the top (subgenus *Coleogeton*; linear-leaved homophyllous groups) to the bottom (broad-leaved homophyllous groups; heterophyllous groups) of the dendrogram (Fig. 3) represents an inverse of Hagström's general concepts of phylogenetic relationships in the genus (Fig. 2).

Maximum parsimony methods generated three trees of equal minimal length (164 steps) but with low consistency (0.421) using subsection *Densi* as the outgroup. A representative tree is presented in Fig. 4 (the topology of the other trees did not differ substantially from this one). Branch lengths ranged from 0-10.000 (Table 3) with the greatest length occurring between nodes 48 and 49, the point of attachment for subsections representing subgenus *Coleogeton* (Fig. 4). Apomorphies between nodes of the cladogram (numbered in Fig. 4) are listed in Table 4.

General groupings of subsections by cladistic analysis (Fig. 4) were similar to clusters observed in the dendrogram (Fig. 3). By cladistic analysis, relationships were substantiated among sections and subsections within subgenus *Coleogeton*. In this cladogram, both subgenus *Coleogeton* and the heterophyllous subsections (excluding *Javanici*) are monophyletic. The phenetic intermediacy of broad-leaved submersed subsections (*Perfoliati*, *Praelongi*, *Crispi*) between the heterophyllous subsections and the linear-leaved homophyllous

Table 3. Nodal linkages and branch lengths for PAUP parsimony cladogram (Fig. 4) of *Potamogeton* subsections.

Subsection	Connected		Node	Connected to node	
	to node	Branch length		to node	Branch length
<i>Amblyophylli</i>	50	0.000	27	49	2.000
<i>Vaginati</i>	27	2.000	28	41	1.000
<i>Pectinati</i>	27	4.000	29	39	4.000
<i>Serrulati</i>	45	3.000	30	31	6.000
<i>Crispi</i>	40	3.000	31	32	6.000
<i>Ochreatei</i>	43	4.000	32	33	4.000
<i>Polygoni</i>	44	1.000	33	37	3.000
<i>Monogyni</i>	28	3.000	34	35	3.000
<i>Compressi</i>	46	1.000	35	36	1.000
<i>Oxyphylli</i>	47	0.000	36	37	3.000
<i>Monticoli</i>	42	0.000	37	38	7.000
<i>Pusilli</i>	48	4.000	38	39	2.000
<i>Javanici</i>	28	8.000	39	40	5.000
<i>Hybridi</i>	33	2.000	40	41	2.000
<i>Sclerocarpi</i>	32	3.000	41	42	3.000
<i>Perfoliati</i>	29	5.000	42	43	2.000
<i>Praelongi</i>	29	8.000	43	44	1.000
<i>Natantes</i>	31	7.000	44	45	1.000
<i>Lucentes</i>	30	2.000	45	46	4.000
<i>Nodosi</i>	34	1.000	46	47	3.000
<i>Alpini</i>	36	1.000	47	48	3.000
<i>Muricati</i>	35	4.000	48	49	10.000
<i>Colorati</i>	30	9.000	49	50	3.000
<i>Amplifolii</i>	34	3.000	50	<i>Filiformes</i>	1.000
<i>Densi*</i>	38	6.000			

* Designated outgroup taxon.

subsections (including heterophyllous subsection *Javanici*) is consistent with the cladistic analysis which positions this broad-leaved group as ancestral to the linear-leaved subsections at the point where they diverge from the heterophyllous group (Fig. 4). In the cladogram, the heterophyllous subsection *Javanici* is distinct from other heterophyllous subsections and is shown as more closely related to submersed homophyllous species (it is a sister group of subsect. *Monogyni*). The cladistic analysis does not support Hagström's concept that subsection *Serrulati* is distinct or that it occupies a phylogenetic position connecting subgenera *Coleogeton* and *Potamogeton*. Subgenus *Coleogeton* does not stand as a separate and early diverging lineage in *Potamogeton*, but rather appears as more recently derived from subsection *Pusilli*. Cladistically, *Coleogeton* represents a highly specialized group of homophyllous linear-leaved species rather than an ancestral lineage in *Potamogeton*.

The topology of the cladogram using missing data entries for floating-leaf characters of homophyllous subsections is essentially the same as that discussed above with one major exception. This manipulation results in the breakup of the subsections *Perfoliati* and *Praelongi*, with the former joining to subsection *Alpini* and the latter to subsection *Colorati*.

Discussion

How accurately does the Hagström classification portray natural groups within *Potamogeton*? The reconstruction of Hagström's eclectic concept of phylogeny in the genus provides an elementary step towards answering this question. With this hypothetical evo-

Table 4. Apomorphy list for nodes of PAUP cladogram (Fig. 4) of *Potamogeton* subsections. Characters and states refer to Table 1.

Node	Ancestor	Character	Ancestral state	Derived state	Node	Ancestor	Character	Ancestral state	Derived state	
27	49	8	0	1	39	38	11	0	1	
		15	0	1			29	2	1	
28	41	14	4	5	40	39	10	0	1	
							14	1	4	
29	39	11	1	2			23	1	4	
		27	1	3			27	1	0	
		28	2	3			29	1	0	
30	31	14	1	4	41	40	24	1	4	
		22	0	1			28	2	1	
		24	5	2	42	41	1	2	0	
		27	0	1			10	1	0	
31	32	3	1	0	43	42	15	0	1	
		8	0	1			23	4	3	
		11	0	1	44	43	14	4	1	
		13	2	3						
		21	3	2						
		24	1	5			45	44	4	0
32	33	13	0	2	46	45	2	1	3	
		18	2	1			10	0	1	
		28	2	1			24	4	3	
33	37	3	0	1	47	46	11	1	0	
		9	0	1			14	1	4	
		27	1	0			15	1	0	
34	35	18	2	1	48	47	1	0	2	
		21	3	2			9	0	1	
		25	1	0			49	48	5	1
35	36	19	2	3	7	2			1	
					13	0			3	
					16	0	1			
36	37	20	2	1			17	0	1	
		27	1	2			23	3	4	
		28	2	3			24	3	5	
37	38	18	4	2			28	1	0	
		19	0	2	50	49	7	1	0	
		20	3	2			10	1	0	
		21	4	3			14	4	3	
		22	3	0						
		23	1	2						
		25	2	1						

lutionary basis for his classification, we are able to test the overall topology of a phylogenetically derived tree using comparisons with hierarchical groupings of subsections determined by phenetic and cladistic analyses. Because all analyses rely on the same set of data, we can gain insight into some of the methodological logic that Hagström used to formulate the concept of relationships inferred by his classification.

An integral part of Hagström's phylogenetic concept was that the genus arose from linear-leaved homophyllous ancestors (Fig. 1). More recent assessments argue that heterophyllous

species preceded the linear-leaved homophyllous group (e.g., Les, 1983; Wiegleb, 1988). This question is easily tested by cladistic analysis using the genus *Groenlandia* [= *Potamogeton* sect. *Laterales* subsect. *Densi*] as the outgroup. Although Hagström's work predates the outgroup concept, his comments advocating the recognition of subsection *Densi* as a separate ancestral genus (Hagström, 1916: 259–260) warrant its use as the outgroup of *Potamogeton* in a cladistic analysis. This interpretation is also supported by the chromosome number of $2n=30$ in *Groenlandia* (Palmgren, 1939), an "anomalous" number in the genus *Potamogeton* with numerical series based either upon $x=7$ or $x=13$ (Les, 1983) and the unique pollen morphology (Sorsa, 1988) of *Groenlandia*. The cladogram of *Potamogeton* rooted using subsection *Densi* (= *Groenlandia*) as the outgroup (Fig. 4) implicates either heterophylly or broad-leaved homophylly as the primitive morphological condition in *Potamogeton* depending on the specific interpretation. Because subsection *Densi* is broad-leaved homophyllous, a reasonable explanation is that heterophyllous subsections (excluding *Javanici*) represent one clade diverging from broad-leaved homophyllous ancestors, and the homophyllous linear-leaved groups (including *Javanici*) another. This interpretation supports the hypothesis of Raunkiær (1903) who rationalized that the terrestrial ancestors of *Potamogeton* would have presumably been homophyllous and broad-leaved (he cites *P. praelongus* as a likely ancestral species), and heterophylly in the genus would have evolved as a consequence of adaptation to an aquatic existence. This conclusion is consistent with a later opinion (Les, 1983: 319), that heterophyllous species represent "an intermediate stage between terrestrial ancestors" [i.e., broad-leaved homophyllous species] "and adoption of the hydric habit" [i.e., complete submergence characteristic of various linear-leaved homophyllous species].

By cladistic analysis, Hagström's perspective of a homophyllous linear-leaved ancestor for *Potamogeton* is incompatible with parsimonious character state transitions. Although Sorsa (1988) offers palynological support for Hagström's hypothesis of the ancestral nature of linear-leaved submersed species, he did not consider the association of pollen features in subgenus *Coleogeton* to pollination modes. The retention of the pollen aperture in *Coleogeton* was interpreted by Sorsa (1988) as evidence of the "lower evolutionary level" of those species. Dahlgren and Rasmussen (1983), however, indicate that the presence or absence of pollen apertures in the Potamogetonaceae and allied families probably reflects adaptations to wind or water pollination. This is an important point because both aerial and submersed flowers occur in *Coleogeton* and in other members of the genus (Philbrick and Anderson, 1987).

The distribution of chromosome numbers in *Potamogeton* has also been used in attempts to clarify the question of ancestral groups in *Potamogeton*. Les (1983) concluded that $x=7$ species preceded $x=13$ species and forwarded two hypotheses regarding the single or multiple origins of $x=13$ species by aneuploidy. A major problem in assessing chromosome numbers in *Potamogeton* involves the interpretation of a high degree of intraspecific chromosome number variation in the genus. Wiegleb (1988) questioned the conclusions of Les (1983), charging that the work failed to recognize a wider occurrence of $x=7$ chromosome numbers (especially $2n=42$) among many species in the genus. In actuality, however, Les was aware of discrepancies in chromosome numbers published for several species, but reported the number corroborated by the greatest number of counts (Table 1 in Les, 1983). For example, the single count of $2n=42$ for *P. natans* (Stern, 1961) was discounted in light of the eight separate counts of $2n=52$ for the species (Les, 1983). Similarly, Les (1983) recognized *P. fryeri* as an $x=7$ species because all four published chromosomal accounts for the species consistently reported that number. The work of Les (1983) preceded the first documentation of extensive intraspecific chromosome number variation in *Potamogeton* (*P. pectinatus*) reported by Kalkman and Van Wijk (1984). It is premature, however, to predict that such widespread chromosomal variability occurs in all other pondweed species as well. Wiegleb's (1988) opinion that $2n=26$ represents "the basic chromosome

number" of *Potamogeton* disregards important considerations such as the lower $x=7$ chromosome number ($2n=14$) reported for populations of *P. foliosus* (Wiegand, 1899) and *P. perfoliatus* (Moore, 1973). The question is complicated further by the $x=15$ chromosome number of the "outgroup" *Groenlandia* ($2n=30$), a number that could be derived from any number of aneuploidy scenarios. A lesson apparent from the examination of chromosome numbers in *Potamogeton* is that phylogeny must be used to clarify the chromosomal trends rather than using chromosomal trends to clarify the phylogeny of the group. Occurrences of chromosome number series mapped onto the cladogram (Fig. 4), indicate that extensive chromosome number modifications have probably occurred in the history of many modern species. A re-inspection of the original data set used by Les (1983) in his earlier study also reveals that many pondweed species with variable reported chromosome counts (e.g., *P. crispus*, *P. indicus* [= *P. nodosus*?], *P. monoginous* [= *P. trichoides*], *P. orientalis*, *P. pectinatus*, and *P. zosterifolius*) include at least one $x=7$ number. This distribution may indicate that the $x=7$ chromosomal series did originally permeate many lineages of *Potamogeton*, which subsequently acquired $x=13$ species independently. We continue to support the concept of the ancestral nature of the $x=7$ lineage in *Potamogeton* based upon the overall arguments presented in Les (1983). The numerical variation observed in the genus (e.g., Fig. 4) may simply support the "multiple origin" of $x=13$ species (Les, 1983) as a more reasonable explanation than a single origin of species in this chromosomal series.

A fundamental concept of Hagström's classification extending from his belief in the primitiveness of submersed linear-leaved species, is the unique nature of subgenus *Coleogeton* (Fig. 2). Subsections of *Coleogeton* cluster discretely in the dendrogram (Fig. 3) and the subgenus exhibits a phenetic relationship to other linear-leaved homophyllous groups. Similarly, subgenus *Coleogeton* is separated in the cladistic analysis by the highest branch length in the cladogram (Table 3) with eight apomorphies defining the group (Table 4). Hagström's diagnosis of subgenus *Coleogeton* (1916: 13) specifically mentions five of the eight apomorphic character states identified by the cladistic analysis. From these observations, we suggest that Hagström not only recognized the phenetic integrity of *Coleogeton*, but also its possession of specific shared-derived characters. These results support Hagström's characterization of species placed in subgenus *Coleogeton* as occupying an isolated position in the genus (cf. Wiegand, 1988). The cladistic relationships of subgenus *Coleogeton*, however, raise arguments for its continued taxonomic recognition as a separate subgenus. Although *Coleogeton* appears to be monophyletic, it shares many of the homophyllous linear-leaved subsections as sister groups (Fig. 4). A more fundamental division in the cladogram occurs between nodes 37 and 38 (Fig. 4) which is the clade separating the heterophyllous subsections. This branch is supported by seven apomorphies (Table 4). If it is desirable to recognize subgenera in *Potamogeton*, then it may be more appropriate to treat the heterophyllous subsections (excluding *Javanici*) as one subgenus and the remaining subsections (including "*Coleogeton*") as another. Before such a decision is made, however, it will be necessary to demonstrate convincingly the monophyly of both groups.

Hagström's concepts of relationships within subgenus *Coleogeton* are strongly supported both by the phenetic and cladistic analyses. The clustering of subsections *Amblyophylli* and *Filiformes* in the dendrogram (Fig. 3), and their occurrence as sister groups in the cladogram (Fig. 4) are consistent with their common placement into section *Connati* (Fig. 2b). Similarly, subsections *Vaginati* and *Pectinati* (section *Convoluti*) cluster closely (Fig. 3) and also as sister groups (Fig. 4).

Hagström's proposed relationship of section *Adnati* (subsection *Serrulati*) to the subgenera of *Potamogeton* (Fig. 2) is unambiguous from his statements (1916: 13, 53-54, 58). The unique nature of subsection *Serrulati* is not, however, supported by either the phenetic or cladistic analyses. In both cases, *Serrulati* exhibits a relationship to *Polygoni* and *Compressi* within the linear-leaved subsections (Figs. 3, 4). Palynologically, subsection *Serrulati*

associates with subsections *Compressi*, *Monogyni*, *Ochreatei*, and *Pusilli* rather than with any *Coleogeton* (Sorsa, 1988). This association of *Serrulati* with the linear-leaved subsections is consistent with clustering and cladistic relationships (Figs. 3, 4). There is no obvious substantiation for the placement of subsection *Serrulati* within a separate section (i.e., *Adnati*) to represent an isolated phylogenetic position between the subgenera as Hagström believed.

Hagström clearly emphasized a close relationship of *Monogyni* and *Compressi* (1916: 64–65, 68, 74), however, no support for this relationship is provided by either the phenetic or cladistic analyses (Figs. 3, 4). He also considered subsection *Ochreatei* as ancestral to all linear-leaved groups (Hagström, 1916: 78). Cladistically, this subsection is preceded by the linear-leaved subsections *Monogyni* and *Monticoli* (Fig. 4), although it is necessary to consider the instability of the cladogram with respect to some linear-leaved groups (see below).

Hagström's view of *Ochreatei* and *Polygoni* as closely related (1916: 78) is supported by the cladistic analysis in which they are sister groups (Fig. 4) but not by the phenetic analysis in which they do not cluster closely (Fig. 3). Hagström (1916: 78) pointed out the relationship of subsections *Ochreatei*, *Polygoni*, *Oxyphylli*, and *Compressi* on the basis of their common broad, rounded leaf base. This character is one of two apomorphies supporting the branch (basal to this group) between nodes 42 and 43 (Tables 3, 4) of the cladogram.

Hagström expressed a close relationship among linear-leaved subsections *Ochreatei*, *Polygoni*, *Oxyphylli*, *Compressi*, *Monogyni*, *Monticoli*, and *Pusilli* (1916: 64–65, 68, 74, 78, 80, 82, 85, 87, 120, 128). Phenetically, these subsections (with subsection *Serrulati*) represent a distinct cluster (Fig. 3). Similarly, the cladistic analysis shows the same groups to be fairly closely related (excluding subsection *Monogyni*), although the specific interrelationships within this group of subsections are depicted quite differently by the phyletic, phenetic, and cladistic diagrams (Figs. 2–4). In the cladistic analysis, few apomorphies support the nodes (41–48) in that section of the cladogram (Fig. 4). We also observed that trees of only a few steps greater length are quite unstable with respect to these subsections with some groups (e.g., *Pusilli*) changing positions in such analyses. Certainly, much of the homoplasy associated with this data set involves these particular subsections. This result may be the function of a very close relationship, or perhaps, an indication that at least some linear-leaved subsections as circumscribed by Hagström may be artificial.

To Hagström, floating-leaved heterophyllous species originated from the linear-leaved submersed species. On several occasions, he pointed out the possible relationship between *Pusilli* and *Javanici* (1916: 88–89, 123, 128, 129), the latter which he believed to represent the most primitive of the heterophyllous subsections (1916: 123) (Fig. 2a). The relationship of subsection *Javanici* to other Potamogetons is problematic. Using chromosomal evidence, Les (1983) viewed the subsection as a potentially ancestral lineage. Phenetically, *Javanici* clusters among the broad-leaved homophyllous subsections (Fig. 3), an appealing correlation to the possible primitiveness of these groups as indicated by the outgroup analysis discussed above. The cladogram (Fig. 4), depicts the clade with *Javanici* and *Monogyni* as immediately derived from the broad-leaved homophyllous subsections. Neither arrangement supports Hagström's concept that all heterophyllous groups are monophyletic and originated with *Javanici* (Fig. 2). The cladogram does not, however, support the hypothesized ancestral position for subsection *Javanici* (Les, 1983).

One cryptic statement in Hagström's treatise is particularly difficult to interpret. A possible polyphyletic origin for heterophyllous pondweeds is suggested by the statement (1916: 57): "These [floating-leaved] species derive their origin partly from the submerged narrow-leaved, partly from the submerged broad-leaved forms, between which the difference is not very prominent indeed." This comment, however, was not clarified during subsequent discussions of heterophyllous subsections which Hagström essentially viewed

as derived from the *Javanici*. Both the phenetic and the cladistic analyses support either a polyphyletic origin of heterophylly in subsection *Javanici*, or a parallel loss of floating leaves among homophyllous subsections.

Hagström's exact concept of relationships regarding *Perfoliati* and *Praelongi* is vague. His deferred discussion of these subsections (with *Densi*) to the end of his treatment (after considering relationships of all heterophyllous groups) indicates that he was uncertain of their exact relationship to other subsections. Only one ambiguous statement (1916: 198) offers some suggestion of a relationship of these broad-leaved groups to the heterophyllous *Lucentes*, the disposition represented in our reconstruction (Fig. 2). Phenetically, the position of these subsections is clearly intermediate between the linear-leaved subsections and the heterophyllous ones (Fig. 3). By cladistic analyses (Fig. 4), they represent a clade ancestral to the linear-leaved homophyllous species. Repeating the cladistic analysis using missing data statements for floating-leaf characters of homophyllous species results in a breakup of the clade with subsections *Perfoliati* and *Praelongi*. In this manipulation, *Perfoliati* joins to the cladogram (Fig. 4) between nodes 36 and 37, whereas *Praelongi* joins to *Colorati* as a sister group. This result emphasizes the similarity of broad-leaved homophyllous Pondweeds to heterophyllous representatives, an observation consistent with Hagström's belief in a close relationship between the two morphological groups (Hagström, 1916: 57). The wide separation of these two subsections, however, is inconsistent with most authors' (and Hagström's) view that they are closely related. Topology in the remainder of the cladogram is essentially unchanged with respect to the first variation of the analysis where floating-leaf characters were "weighted" by coding them as absent rather than as missing in all homophyllous groups (Table 1). Because the latter method of analysis does not result in a wide separation of subsections *Praelongi* and *Perfoliati*, we believe that the first cladogram (Fig. 4) is a more realistic representation of overall relationships.

Following *Javanici*, Hagström apparently regarded *Natantes* as the next group evolutionarily in the heterophyllous lineage (1916: 128, 134). This conclusion is supported phenetically by the basal position of subsection *Natantes* with respect to other heterophyllous subsections in the dendrogram (Fig. 3). Cladistically, however, *Natantes* is derived from a lineage preceded by the heterophyllous subsections *Hybridi* and *Sclerocarpi* (Fig. 4). Hagström's concept of a close relationship among subsections *Alpini*, *Muricati*, *Amplifolii*, and *Nodosi* (Fig. 2) is substantiated by their phenetic clustering (Fig. 3) and monophyly (Fig. 4).

The classification of *Potamogeton* presented in Hagström's "Critical Researches" is often consistent with relationships indicated by phenetic and cladistic analyses that incorporate morphological and anatomical data from the monograph. On the other hand, the classification fails to depict several major evolutionary trends reflected by cladistic analyses. Hagström's phyletic approach to classification of the genus is interpreted as a scheme in which relationships were based upon logic that today would be described as both phenetic and cladistic. These factors, exacerbated by Hagström's insistence of the primitiveness of the linear-leaved homophyllous condition, resulted in a classification where the arrangement of groups does not appear to follow a reasonable evolutionary scheme. Some portions of the classification (such as subsections within subgenus *Coleogeton*) appear to depict relationships quite accurately, whereas in other instances (e.g., the placement of *Natantes* or *Javanici*), they are uncertain. We advocate a complete re-assessment of phylogenetic relationships in *Potamogeton* and point to some basic problems associated with this task.

There are several difficulties in pinpointing an ancestral lineage in *Potamogeton*, even if broad-leaved homophyllous groups are accepted as primitive. A major problem of interpretation relates to the potential loss of floating leaves in the genus. Some heterophyllous species such as *P. illinoensis* (subsection *Lucentes*) and *P. vaseyi* (subsection *Javanici*) typically exist without floating leaves, and the occasional production of floating leaves on some broad-leaved homophyllous species such as *P. richardsonii* (Thieret, 1971; Les, 1983)

emphasizes the difficulty with determining whether some homophyllous species are primitively so, or were actually primitively heterophyllous. Similarly, the possibility could also be argued that *Groenlandia* (subsection *Densi*) was primitively heterophyllous. It is pertinent to mention that floating-leaved species occur in the Aponogetonaceae (Rataj and Horeman, 1977), a family that is ancestral to the Potamogetonaceae lineage in cladistic analysis of the entire "Ariflorae-Triuridiflorae-Alismatiflorae complex" (Dahlgren and Rasmussen, 1983). Thus the question of the ancestral morphological condition cannot be resolved by these studies. We can, however, clarify the issue. Our cladistic analysis indicates the unlikelihood that homophyllous linear-leaved species represent the primitive morphological condition in the genus. The interpretation most congruent with outgroup analysis using subsection *Densi*, is that broad-leaved homophyllous plants were ancestral to this group (Fig. 1b).

A further difficulty associated with floating-leaf loss concerns the monophyly of homophyllous linear-leaved Pondweeds as indicated by the cladistic analysis. An alternate possibility exists that some linear-leaved groups diverged from homophyllous broad-leaved groups, whereas the origin of others may have involved a convergent loss of floating leaves among one or even several of the heterophyllous groups. This prospect suggests that linear-leaved homophyllous groups may actually represent a highly polyphyletic assemblage. This factor could explain the low consistency index of the cladogram, and the instability of homophyllous linear-leaved subsections in cladograms of a few more steps in length. The clustering of these subsections in both the phenetic and cladistic analyses may actually represent groupings based upon similar (but convergent) shared reductionary features rather than indicating their close phylogenetic relationship. Palynological data also reflect the possible polyphyly of linear-leaved groups. "D-type" pollen is characteristic of all heterophyllous groups and the broad-leaved subsections *Perfoliati* and *Praelongi* (Sorsa, 1988). Some linear-leaved groups (subsections, *Oxyphylli* and *Monticoli*) possess "D-type" pollen as well, whereas most other linear-leaved groups possess "B-type" pollen (Sorsa, 1988).

Regardless of their method of analysis, it is an unsettling but undeniable fact that many of the morphological and anatomical features of *Potamogeton* relied upon by Hagström and others are inadequate characters for determining precise phylogenetic relationships in the genus due to intractable interpretations of homology, convergence and parallelism. Although cladistic analyses of data support the concept that the genus evolved from broad-leaved homophyllous ancestors and diverged into two major lineages representing the heterophyllous species and the linear-leaved homophyllous species, these conclusions can be challenged by the possibility of convergence and parallelism in many of the characters used in the analysis.

Because Hagström's classification represents an amalgam of essentially phenetic and cladistic concepts of relationships, it is difficult to test meaningfully. Our analysis of the Hagström scheme has clarified some general *hypotheses* of relationships in the group by using phenetic and cladistic analyses. Because precise relationships among subsections remain inadequately resolved, our work is intended as a hypothetical framework to guide further systematic studies rather than to serve as a replacement for the Hagström scheme in a taxonomic sense. A revised taxonomy will be meaningful only when phylogenetic relationships in the group are understood with certainty.

We recommend that subsequent systematic research in *Potamogeton* take into consideration the following factors. Hagström's widely followed scheme of taxonomy that has been used commonly to direct systematic studies in *Potamogeton* should not be taken *prima facie* as an accurate representation of evolutionary relationships in the genus. Fundamental concepts of evolutionary relationships that form the basic framework of the classification are inconsistent with subgeneric and intersubsectional relationships indicated by both phenetic and cladistic analyses. Various inconsistencies exist within finer levels of the classification hierarchy as well.

There are several alternatives. If the characters used by Hagström are regarded as adequate for supporting a hypothetical phylogeny, then our cladistic analysis of these characters provides one alternate hypothesis of relationships. With strong opposition to Hagström's heavy reliance on anatomical features (e.g., Sorsa, 1988; Wiegleb, 1988) it is doubtful whether this alternative will gain wide acceptance. We emphasize, however, that Hagström's use of anatomy for classification is often exaggerated. His monograph includes a wide variety of non-anatomical features (see Table 1) that he also considered taxonomically. In any case, the low consistency index of this cladogram is sufficient warning that many of the expressed relationships (especially among linear-leaved groups) are tentative and researchers wishing to use our cladogram as a hypothesis of evolutionary relationships in *Potamogeton* should be fully aware of the limitations discussed in this paper. We point out that relationships expressed by our cladistic analysis of Hagström's monographic data are fairly compatible with several alternative classifications. The subdivision of *Potamogeton* into four subgenera (e.g., Hermann, 1956) combines heterophyllous and broad-leaved homophyllous species (subg. *Potamogeton*), groups linear-leaved homophyllous species (subg. *Hydatogeton*), separates Hagström's subsect. *Crispi* (subg. *Batrachoseris*), and maintains recognition of subgenus *Coleogeton*. The classification followed by Von Weihe (1972) recognizes two subgenera (excluding *Groenlandia*): subgenus *Potamogeton* with section *Potamogeton* (broad-leaved homophyllous and heterophyllous species) and section *Graminifolii* (linear-leaved homophyllous species), and subgenus *Coleogeton*. The classification followed by Dandy (1975, 1980) is essentially the same as that used by Hermann (above), but is arranged using two subgenera (*Potamogeton* and *Coleogeton*), the former including three sections: section *Potamogeton* (heterophyllous and broad-leaved homophyllous species), section *Batrachoseris* (=Hagström's subsect. *Crispi*), and section *Graminifolii* (linear-leaved homophyllous species). The classification of Koch followed by Fryer, Bennett, and Morgan (1915) recognizes five groups: *Enantiophyllii* (*Groenlandia*), *Coleophylli* (=Hagström's subgenus *Coleogeton*), *Chloephylli* (linear-leaved homophyllous species), *Homophylli* (broad-leaved homophyllous species), and *Heterophylli* (heterophyllous species). These groups would associate quite closely with the major clades indicated by our cladistic analysis (Fig. 4).

A second option would be to completely re-evaluate and revise the morphological/anatomical data presently available for *Potamogeton* and to use the modified data set in a comprehensive cladistic analysis of the genus. There would certainly be an advantage to including more recent data such as chromosomal and palynological features, as well as clarification of a few inaccuracies (e.g., coding of character 7 in Table 1). Such a major endeavor is encouraged, but goes well beyond the scope of the present study. We can see only a minimal advantage to using this option, however, because of the homoplasy associated with many of the characters presently available for phylogenetic study.

In preference to either of these alternatives, phylogenetic relationships in *Potamogeton* should be established using methods that maximize the likelihood of homology and minimize possibilities of convergence and parallelism. Otherwise, phylogenetic conclusions drawn from highly homoplasious data sets will be no more convincing than those made in previous studies. Here, a suggested approach would be a cladistic analysis of genomic divergence at the molecular level. Because this approach overcomes many of the problems of convergence associated with morphological features (Sytsma and Schaal, 1985), its application to phylogenetic questions in *Potamogeton* is appropriate. A comparison of phylogenetic trees derived from molecular data and those obtained from morphological data may provide a feasible means of distinguishing among the variety of possible interpretations presented here.

We strongly advocate the continued use of experimental methods for the study of relationships (e.g., Reznicek and Bobbette, 1976; Roberts and Haynes, 1986) and hybridization (e.g., Haynes and Williams, 1975; Hellquist and Hilton, 1983) in *Potamogeton*.

There is little to be gained from compiling lists of proposed "good species" and "good hybrids" (e.g., Wiegleb, 1988) unless there is compelling evidence to accept such conclusions. Having learned an important lesson from our predecessors, it is time to abandon opinionated approaches toward taxonomy in *Potamogeton* and to pursue objective empirical solutions to systematic questions in the genus.

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