

## The Evolution of Achene Morphology in *Ceratophyllum* (Ceratophyllaceae), IV. Summary of Proposed Relationships and Evolutionary Trends

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**ABSTRACT.** Multivariate analyses of species and subspecies of *Ceratophyllum* confirm the phenetic integrity of all groups recognized in preceding parts of this series. Relative morphological similarity decreases hierarchically with the greatest degree existing among conspecific subspecies and less characterizing separate species and certain species pairs. The pattern of relative morphological similarity provides for a hypothesis of interspecific phylogenetic relationships in *Ceratophyllum*, which is expressed by the recognition of three new sections within the genus: sect. **Ceratophyllum**, sect. **Muricatum**, and sect. **Submersum**. Relationships within two of the sections correlate with phytogeographic factors related to tectonic events. An evolutionary reduction series is apparent in the achene morphology of two sections of the genus, whereas increasing specialization characterizes a third section.

In preceding studies of this series, relationships within three species complexes in the genus *Ceratophyllum* were studied by statistical analyses of morphological data (Les 1986a, 1988a, 1988b). From those studies, six species and three subspecies were proposed for taxonomic recognition. Species of *Ceratophyllum* (*C. demersum* L., *C. echinatum* A. Gray, *C. muricatum* Cham., *C. platyacanthum* Cham., *C. submersum* L., and *C. tanaiticum* Sapj.) are morphologically distinct and are readily separable by multivariate statistical analyses. Each species is sympatric with at least one other species; however, no cases of natural interspecific hybridization have been reported. Thus the species appear to be fairly well isolated reproductively. Separation of the morphologically similar subspecies within a species is more difficult but can also be accomplished using multivariate statistical analysis. In all cases, subspecies within a species are allopatric and represent geographical subdivisions of a species as described by Radford et al. (1974) and Grant (1981). No natural hybrids have been documented among conspecific subspecies, presumably because their spatial separation results in effective reproductive isolation.

In parts I–III of this series, discussions of interspecific relationships in *Ceratophyllum* were confined to species complexes rather than to the entire genus. A logical extension of those studies is an analysis of all species and subspecies simultaneously, making it possible to test the taxonomic integrity of the proposed groups (i.e.,

the same clustering relationships should be upheld when all taxa are analyzed at once). Furthermore, the relative degree of morphological similarities among taxa is useful in a classical sense as an indication of interspecific evolutionary relationships and as a justification for hierarchical classification.

To conclude this series on achene evolution in *Ceratophyllum*, an analysis of morphological variation among all species and subspecies of the genus is carried out to test previous taxonomic dispositions and to provide a workable hypothesis of evolutionary relationships. Finally, trends in the evolution of achene morphology in *Ceratophyllum* that have been disclosed by numerical studies are summarized here.

### METHODS

A combined data set was compiled by scoring 19 vegetative and reproductive characters (table 1) for 767 OTU's representing nine taxa (*C. demersum*, *C. echinatum*, *C. muricatum* subsp. *australe* (Grisebach) Les, *C. muricatum* subsp. *kossinskyi* (Kuseneva-Prochorova) Les, *C. muricatum* subsp. *muricatum*, *C. platyacanthum* subsp. *oryztorum* (V. Komarov) Les, *C. platyacanthum* subsp. *platyacanthum*, *C. submersum*, and *C. tanaiticum*). The complete data matrix of 20 characters (see part I, Les 1986a) could be incorporated in these analyses because no characters were invariant as in some prior analyses of smaller species

groups. To provide a strictly morphological data set, one character (phenology) was removed from the final runs, although its inclusion or exclusion did not noticeably alter the results of the analyses. Where applicable, previously reported data were used (Les 1986a, 1988a, 1988b). A list of specimens and copy of the data matrix are available from the author upon request.

Clustering relationships of OTU's were examined by analyzing the first two axes of variation from a principal components analysis (PCA) performed using the NT-SYS numerical taxonomy program (Rohlf et al. 1974). A step-wise discriminate analysis including only the nine quantitative characters was performed using the BMDP statistical software package (Dixon 1981). An *F*-matrix was assembled for the nine taxa compared by discriminate analysis and levels of significance were computed for the values. A scatter diagram was constructed that depicted the mean of each cluster of OTU's plotted along the two canonical variables of the discriminate analysis. As an additional depiction of overall dissimilarity, the *F* values were entered into an average linkage cluster analysis using the UPGMA algorithm to construct a dendrogram (Kovach 1986). Phylogeographical maps were constructed from data in Les (1986c). Taxonomic sectional divisions were made for species groups by incorporating results from the numerical analyses with the phylogeographical data. The resulting orientation of species provided a framework for discussing trends in the evolution of achene morphology both within and between the putatively natural sections of *Ceratophyllum*.

## RESULTS

By the PCA analysis, OTU's of *Ceratophyllum* aggregate into distinct clusters that correspond with species designated in the previous analyses (fig. 1A). Three species clusters are also discernable in the PCA; one including OTU's of *Ceratophyllum muricatum* and *C. tanaiticum*, a second with OTU's of *C. demersum* and *C. platyacanthum*, and a third including OTU's of *C. submersum* and *C. echinatum* (fig. 1A). Factors one (23.34%) and two (14.69%) of the PCA accounted for an accumulated 38.03% of the total variation. The characters with the highest loading values for the PCA are fruit body width and maximum leaf order, respectively. Because of their high

TABLE 1. List of characters and character states used in numerical analyses of *Ceratophyllum*.

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1. Maximum leaf order.	2. Leaf, segment morphology (inflated/not inflated).
3. Leaf, denticle morphology (broad-based/narrow-based).	4. Plumule, first leaf morphology (simple/compound).
5. Leaf, maximum whorl diameter (mm).	6. Petiolar region (present/absent).
7. Fruit shape (elliptical/hemispherical).	8. Fruit, body length (mm).
9. Fruit, body width (mm).	10. Fruit, body thickness (mm).
11. Maximum length of basal fruit spines (mm).	12. Maximum length of facial fruit spines (mm).
13. Styler spine length (mm).	14. Number of lateral fruit appendages.
15. Maximum length of lateral fruit appendages.	16. Fruit, surface (smooth/warty/tuberculate/ridged).
17. Fruit, wing (present/absent).	18. Styler position (centered/eccentric).
19. Peduncle length (mm).	

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taxonomic value, these characters are useful for establishing major groupings in a key to species within the genus (Les 1986c).

An identical pattern emerges by discriminate analysis, although the clusters are somewhat less distinct (fig. 1B). This result is undoubtedly due to the removal of qualitative characters from the data set. Nevertheless, the groups corresponding with both the species and subspecies in the discriminate analysis differ significantly (table 2). Similar to the PCA, the character of fruit width had the highest correlation with the canonical variables of the discriminate analysis. A plot of the group means in the discriminate analysis (fig. 1C) indicates the overall pattern of clustering for species and subspecies within three larger groups.

The UPGMA dendrogram derived from *F* values depicts hierarchical relationships among species and subspecies that are consistent with the proposed taxonomic ranks; the highest similarity exists for subspecies within the species *C. muricatum* and *C. platyacanthum*, whereas a higher dissimilarity exists among individual species (fig. 2). Species also cluster hierarchically within larger groups similar to those depicted in the PCA. *Ceratophyllum tanaiticum* and *C. muricatum* cluster apart from other species; *C. echinatum* and *C. submersum* cluster together. In this analysis, *C. demersum* (fig. 2) occupies a central position between the latter cluster and *C. platyacanthum* (see discussion).

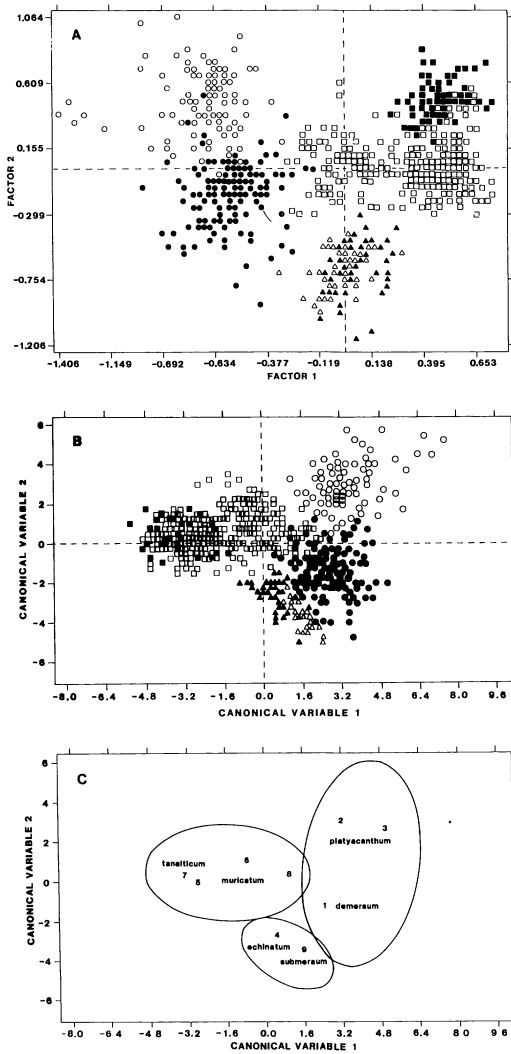


FIG. 1. Numerical analyses of *Ceratophyllum*. A. Principal components scatter-diagram depicting OTU's of *C. demersum* (closed circles), *C. echinatum* (open triangles), *C. muricatum* (open squares), *C. platyacanthum* (open circles), *C. submersum* (closed triangles), and *C. tanaiticum* (closed squares) generated by plotting the first two factors of variation. B. Scatter-diagram depicting OTU's of *C. demersum* (closed circles), *C. echinatum* (open triangles), *C. muricatum* (open squares), *C. platyacanthum* (open circles), *C. submersum* (closed triangles), and *C. tanaiticum* (closed squares) generated by plotting the two canonical variables of a stepwise discriminant analysis of the species. C. Representation of means from discriminant analysis of *Ceratophyllum* species in figure 1B: 1 = *C. demersum*, 2 = *C. platyacanthum* subsp. *platyacanthum*, 3 = *C. platyacanthum* subsp. *oryzetorum*, 4 = *C. echinatum*, 5 = *C.*

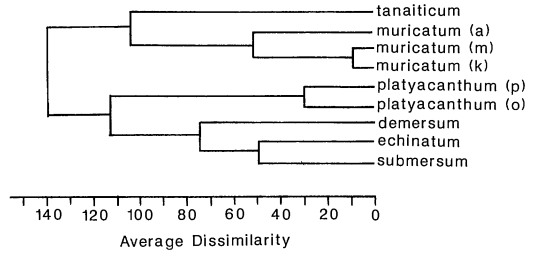


FIG. 2. UPGMA dissimilarity dendrogram of *F* values showing clustering relationships of six *Ceratophyllum* species. a = *C. muricatum* subsp. *australe*, m = *C. muricatum* subsp. *muricatum*, k = *C. muricatum* subsp. *kossinskyi*, p = *C. platyacanthum* subsp. *platyacanthum*, o = *C. platyacanthum* subsp. *oryzetorum*.

## DISCUSSION

A simultaneous numerical analysis of *Ceratophyllum* species and subspecies supports the integrity of taxonomic dispositions proposed earlier for species groups (Les 1986a, 1988a, 1988b). Subspecies of *C. muricatum* (Les 1988a) and those of *C. platyacanthum* (Les 1988b) cluster closely, and the six species (*C. demersum*, *C. echinatum*, *C. muricatum*, *C. platyacanthum*, *C. submersum*, and *C. tanaiticum*) remain distinct in all analyses.

The association of *C. echinatum* and *C. submersum* in numerical analyses of all *Ceratophyllum* species supports their close relationship as suggested previously (Les 1988a). These two species also are characterized by north temperate geographical distributions that are "mirror images" of each other with respect to the Atlantic Ocean (fig. 3A). *Ceratophyllum echinatum* is predominantly an eastern North American species (Les 1986b) and *C. submersum* a predominantly western European species (Les 1986c). Phytogeographically, this pattern is referred to as "Laurasian" and characterizes many angiosperm groups (Raven and Axelrod 1974; Schuster 1976). The morphological and phytogeographical affinities of *C. echinatum* and *C. submersum* indicate that these species possibly

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*muricatum* subsp. *kossinskyi*, 6 = *C. muricatum* subsp. *muricatum*, 7 = *C. tanaiticum*, 8 = *C. muricatum* subsp. *australe*, 9 = *C. submersum*. Solid lines indicate approximate limits of group OTU's.

TABLE 2. *F*-matrix for a stepwise discriminate analysis of nine *Ceratophyllum* species and subspecies. AUS = *C. muricatum* subsp. *australe*, DEM = *C. demersum*, ECH = *C. echinatum*, KOS = *C. muricatum* subsp. *kossinskyi*, MUR = *C. muricatum* subsp. *muricatum*, ORY = *C. platyacanthum* subsp. *oryzetorum*, PLT = *C. platyacanthum* subsp. *platyacanthum*, SUB = *C. submersum*, TAN = *C. C. tanaiticum*. All values are significant at  $P < 0.001$ ; degrees of freedom = 9, 750.

	DEM	PLT	ORY	ECH	AUS	MUR	TAN	KOS
PLT	141.49	—						
ORY	51.34	31.09	—					
ECH	94.08	153.81	92.81	—				
AUS	315.75	308.81	117.00	113.26	—			
MUR	158.25	136.62	76.12	109.07	64.36	—		
TAN	252.96	280.48	111.08	180.85	119.30	138.50	—	
KOS	19.68	31.84	40.04	47.34	43.57	10.84	65.46	—
SUB	60.75	173.48	75.34	52.22	166.56	124.61	169.01	36.00

diverged from a common ancestor having a North Temperate distribution prior to the separation of Europe and North America during the Tertiary period (Les 1986c). Following this hypothesis, it is appropriate to indicate the alliance of *C. echinatum* and *C. submersum* taxonomically by including them together in a newly recognized sect. *Submersum*.

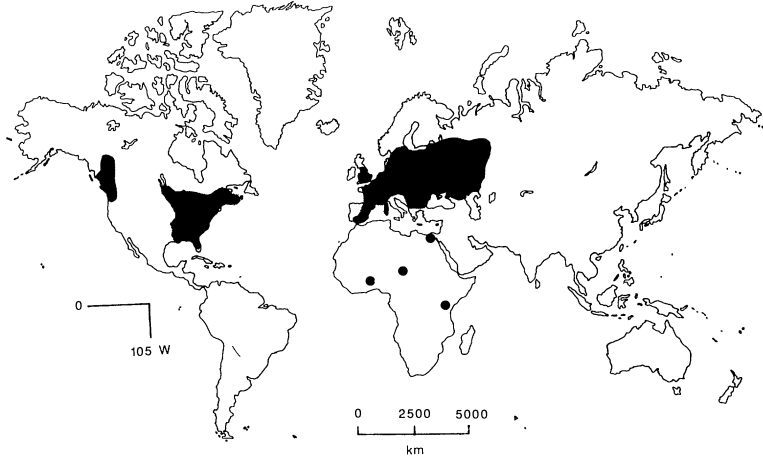
Numerical analyses also indicate a close relationship between *Ceratophyllum tanaiticum* and *C. muricatum*. The present distributions of the three subspecies of *C. muricatum* (fig. 3B) are clearly related to tectonic events that occurred during the breakup of Gondwanaland. *Ceratophyllum muricatum* subsp. *muricatum* occurs throughout the Paleotropics with concentrations in Africa and India (Les 1986c). In the Indo-Malaysian region, the distribution of this subspecies is relatively diffuse and probably reflects the geographical discontinuities between populations that must have existed during the breakup of Gondwanaland during the Cretaceous period (Les 1986c). The divergence of the New World *C. muricatum* subsp. *australe* from the Old World subsp. *muricatum* is attributed, at least in part, to isolating effects resulting from the opening of the Atlantic Ocean, which accompanied the breakup of Africa and South America (Les 1986c). *Ceratophyllum muricatum* subsp. *kossinskyi* is more temperate in its distribution and has probably diverged fairly recently from subsp. *muricatum* (Les 1986c). This hypothesis is supported by the numerical analyses, which indicate a high degree of similarity between these subspecies (figs. 1A, B, 2). The present distribution of *C. tanaiticum* (fig. 3B) is

also more temperate but its relationship to *C. muricatum* can be traced through the fossil record. The extinct Oligocene species *C. zaisanicum* Avakov, which once thrived in the Zaysan basin of the USSR (Avakov 1962), is intermediate morphologically between *C. muricatum* and *C. tanaiticum* (Les 1986c). The Zaysan region is situated geographically between the present northern limit of *C. muricatum* and the present distribution of *C. tanaiticum*, thereby implicating *C. zaisanicum* as a likely intermediate evolutionary stage in the divergence of *C. muricatum* and *C. tanaiticum*. With these factors in mind, these species are allied in a second newly designated sect. *Muricatum*.

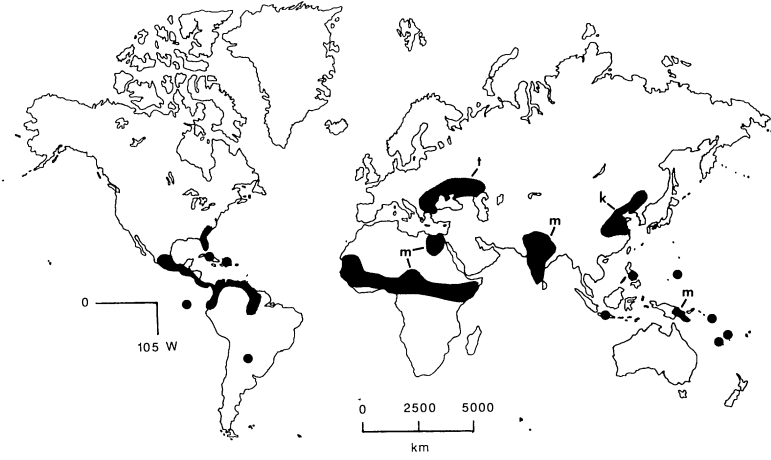
Phytogeographical affinities of the remaining species *C. demersum* and *C. platyacanthum* are obscure (fig. 3C) because of the present cosmopolitan distribution of the former, although *C. platyacanthum* is exclusively temperate and Old World (Les 1986c). The putative close relationship of these species (Les 1988b) is substantiated by their grouping in the PCA, and by their similar flavonoid chemistry (Les 1986c).

The grouping of *C. demersum* and *C. platyacanthum* with *C. echinatum* and *C. submersum* in the UPGMA analysis (fig. 2) should not be interpreted as evidence to combine these species within a single section. The UPGMA dendrogram has been included to provide an alternate depiction of relative dissimilarity among taxa, but this analysis must be interpreted carefully. The UPGMA clustering is based exclusively on *F* values derived from the discriminate analysis, which incorporates only the nine quantitative variables. Understandably, the PCA and actual

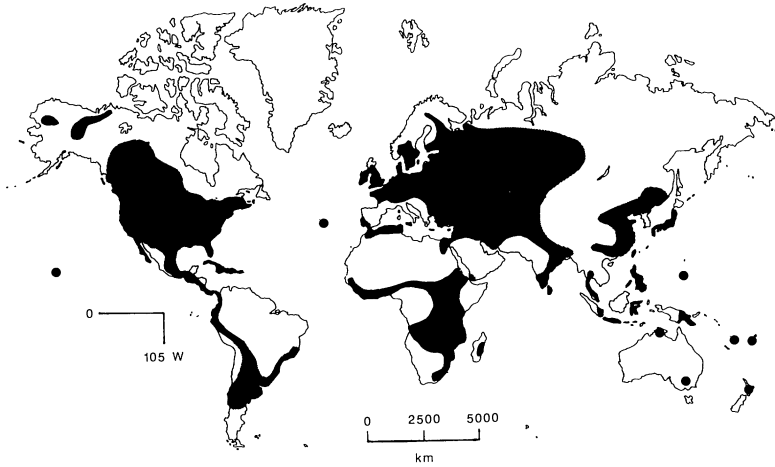
A



B



C



discriminate analyses provide a much clearer representation of group relationships. The somewhat closer clustering of *C. demersum* to *C. echinatum* and *C. submersum* than to *C. platyacanthum* in the dendrogram is undoubtedly a function of the character set analyzed. The unique presence of facial spines (quantitative characters) in *C. platyacanthum* would certainly isolate this species from all others in the UPGMA comparison, although its similarity to *C. demersum* by vegetative features (which are mostly qualitative characters and excluded from the analysis) is not a factor in determining the UPGMA clusters. The PCA analysis (which includes all characters) provides a better overall depiction of phenetic groups in the genus. In the PCA, the phenetic distance between *C. demersum* and *C. echinatum* is certainly much greater than that between *C. demersum* and *C. platyacanthum*. Accordingly, *C. demersum* and *C. platyacanthum* are allied in a third sect. *Ceratophyllum*.

#### NEW TAXONOMIC SECTIONS

**Ceratophyllum** L. sect. **Ceratophyllum**.—TYPE SPECIES: *Ceratophyllum demersum* L.

**Ceratophyllum** L. sect. **Submersum** Les, sect. nov.—TYPE SPECIES: *Ceratophyllum submersum* L.

Folia surculo apicis fasciculata diffusa; folia caulina smaragdina, laevia, edentata vel denticulata cum spinae parvulae persistentes in 2 series dispositae; spinae exsertae inconspicuo, cum vel sine basis telae latae; folia divisa dichotome ad 4 ordines. Achenia magna, 4.5–6.0 mm longae, 3.0–4.0 mm latae; cum vel sine spinae marginales; spinae faciales absentes.

**Ceratophyllum** L. sect. **Muricatum** Les, sect. nov.—TYPE SPECIES: *Ceratophyllum muricatum* Chamisso.

Folia surculo apicis fasciculata diffusa; folia caulina flavovirentia, laevia, edentata vel denticulata cum spinae parvulae persistentes in 2 series dispositae; spinae exsertae inconspicuo, sine basis telae latae; folia divisa dichotome ad 4 ordines. Achenia non magna, tantum 3.0–4.5 mm longae, 1.5–3.0 mm latae; cum spinae marginales; spinae faciales absentes.

#### TRENDS IN THE EVOLUTION OF ACHENE MORPHOLOGY IN *CERATOPHYLLUM*

The variational pattern of species and subspecies recognized here, their appropriate hierarchical morphological similarity, and the phytogeographical correlation of sectional divisions, are evidence that the taxa reflect cohesive, natural phylogenetic assemblages. Following this assumption, it is plausible to undertake a discussion of trends in the evolution of achene morphology within and between sections of *Ceratophyllum*.

An important aspect of fruit-spine variation in *Ceratophyllum* is the nearly universal correlation of spine lengths in species (Les 1986a, 1988a, 1988b). In particular, stylar and basal spine lengths correlate significantly in all taxa. Fruit spines that do not display independent length variation such as basal and stylar spines are probably regulated by common gene systems. As quantitative traits, fruit-spine lengths are probably determined polygenically (Les 1986a). Owing to the numerous combinations of phenotypic effects that could result from mutations at any genes that regulate spine lengths, a wide spectrum of length variation is possible and is observed commonly throughout the genus (Les 1986a, 1988a, 1988b). In instances where basal, stylar, and lateral spine lengths are highly correlated (such as in *C. echinatum*), a mutation at any gene that alters spine length would affect all three spine lengths simultaneously. If

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FIG. 3. Global distributions of *Ceratophyllum* sections. A. Geographical distribution of *Ceratophyllum* sect. *Submersum* representing *C. echinatum* (New World) and *C. submersum* (Old World). Dots represent isolated records of *C. submersum* (from data in Les 1986c). B. Geographical distribution of *Ceratophyllum* sect. *Muricatum* representing *C. muricatum* subsp. *australe* (New World), *C. muricatum* subsp. *muricatum* (m), *C. muricatum* subsp. *kossinskyi* (k), and *C. tanaiticum* (t). Dots (New World) represent isolated records of *C. muricatum* subsp. *australe* and (Old World) *C. muricatum* subsp. *muricatum* (from data in Les 1986c). C. Geographical distribution of *Ceratophyllum* sect. *Ceratophyllum* representing *C. demersum* and *C. platyacanthum* (not distinguished). Dots represent isolated records of *C. demersum* (from data in Les 1986c).

the phenotypic effect of such a mutation resulted in a shortening of spines, then a mutant fruit could appear quite spineless with respect to the spiny wild condition. This effect is precisely what has been observed in *C. echinatum* (Les 1988a) and this understanding makes it possible to rationalize better the proposed relationship between the spiny-fruited *C. echinatum* and spineless-fruited *C. submersum*.

Spine reduction occurs in all three sections of *Ceratophyllum* (fig. 4), with basally and laterally spineless-fruited variants observed in *C. demersum* (fig. 4A), *C. echinatum* (fig. 4O), and *C. muricatum* (fig. 4H, K, M). The normally spineless species *C. submersum* (fig. 4P) has been affiliated with nearly all of these variants, which are actually convergent with the species rather than related phylogenetically. In *C. submersum*, however, fruits never develop elongate spines and produce only a short awliform style (Les 1986b), thus the silencing of genes that promote spine length growth appears to be fixed in this species. The derivation of the spineless *C. submersum* from a spiny-fruited progenitor by reduction is further indicated by the withering away of a more elongate stylar appendage as the fruit of this species matures (Les 1986c).

The general fruit morphologies of subspecies of *C. muricatum* can also be related to reduction processes. Both subsp. *australe* (fig. 4J, K) and *kossinskyi* (fig. 4L, M) have fruits with reduced spinature compared with subsp. *muricatum* (fig. 4I). The fruit of *C. tanaiticum* (fig. 4G) with its narrow, flattened body, minute stylar spine, and short lateral and basal spines represents a highly reduced version of the fruit of *C. muricatum*. The extinct species *C. zaisanicum*, which probably represents a transitional evolutionary stage between *C. muricatum* and *C. tanaiticum*, is intermediate in its fruit spinature, particularly by the medium length of its stylar spines (Les 1986c). Because of these factors, spine-length reduction is regarded as an important evolutionary trend in sects. *Submersum* and *Muricatum*.

In sect. *Ceratophyllum*, achene innovations are more characteristic than reduction patterns. The development of a web-like marginal wing occurs commonly in this group (Les 1988b) and is a fixed character of *C. platyacanthum* subsp. *platyacanthum* (fig. 4F). Novel facial achene spines that characterize both subspecies of *C. platyacanthum* are found nowhere else in extant

species of the genus (Les 1988b). Phenotypes of *C. demersum* with reduced-spined fruits do occur (fig. 4A), but despite various attempts to recognize such variants taxonomically, they are sporadic and represent the wide range of fruit variation found in this species (Les 1986a).

The various achene phenotypes, which have evolved in *Ceratophyllum*, represent the outcome of both spine reduction and specialization. Spininess is assumed to represent the unspecialized condition in the group. This hypothesis is substantiated somewhat by the fruit morphology of the genus *Ceratostratiotes*, an extinct group apparently related to the extant *Ceratophyllum* (Les 1988c). Fossilized fruits of *Ceratostratiotes* are highly ornamented with various types of elongate spines (Les 1988c; Buzek 1982). Obviously, such a generalization must be considered carefully in specific instances such as the origin of facial spines in *C. platyacanthum* (fig. 4E, F), which appear to have arisen *de novo* in the genus (Les 1988b).

#### CONCLUSIONS

Historically, taxonomic difficulties in *Ceratophyllum* have been exacerbated by reliance on highly variable features as taxonomic characters without sufficient knowledge of intrapopulational, interpopulational, intraspecific, and interspecific variational limits. Extensive morphological variability in the genus presents a formidable obstacle for attempts to delimit truly "natural" groups. The use of multivariate statistical analysis surmounts these problems by making it possible to analyze numerous characters simultaneously, and by interpreting the overall variational patterns statistically, thereby providing a more objective means of assessing systematic relationships. Following the classical assumption that phenetic similarity represents evolutionary relationship, the numerical studies also provide a preliminary hypothesis of phylogenetic relationships. An appealing aspect of the hypothetical evolutionary relationships proposed here for *Ceratophyllum* species, is that they are consistent for the first time with phytogeographical data.

The clarification of natural groups in *Ceratophyllum* has also allowed for an analysis of evolutionary trends within and between groups of species arranged in more inclusive sectional aggregates. Variational studies including cor-

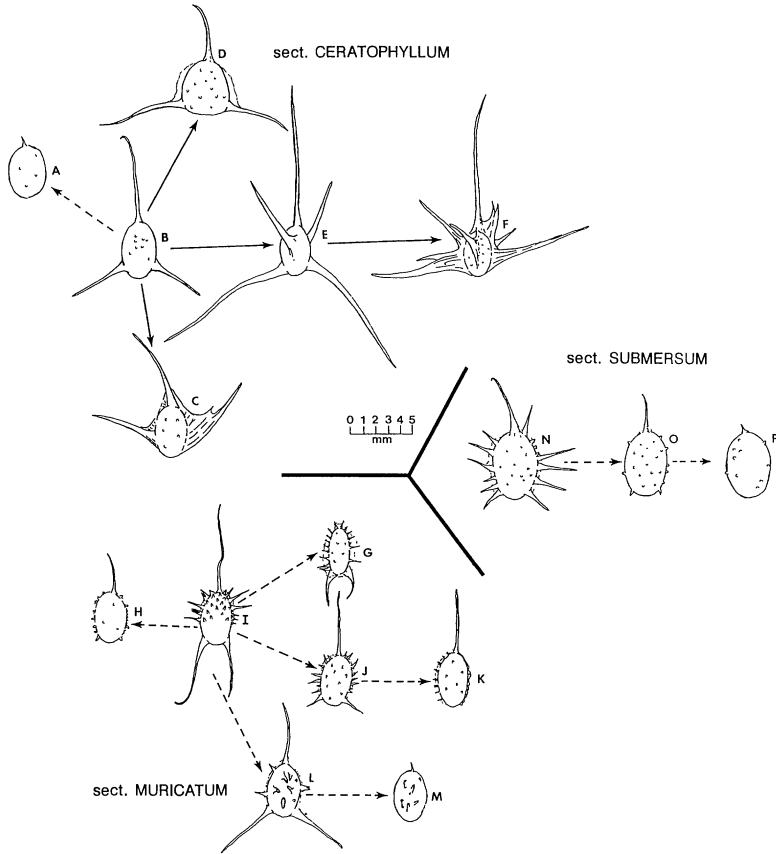


FIG. 4. Trends in the evolution of achene morphology in *Ceratophyllum* sections. Solid arrows = morphological specialization of achenes; broken arrows = morphological reduction of achenes. A-D. Achenes of *C. demersum*. A. "Spineless" phenotype, Tiehm & Mozingo 3187 (NY). B. "Typical" phenotype, Durer s.n. (B). C. "Winged" phenotype, Roberts 3010 (OS). D. "Winged" phenotype, Brass 24349 (A). E, F. Achenes of *C. platyacanthum*. E. Subsp. *oryzetorum*, Maire 6739 (NY). F. Subsp. *platyacanthum*, Durer s.n. (Z). G. Achene of *C. tanaiticum*, Tsvyelyev & Kolesnikova 278 (LE). H-M. Achenes of *C. muricatum*. H. "Spineless" phenotype of subsp. *muricatum*, Sarup s.n. (DAO). I. "Typical" phenotype of subsp. *muricatum*, Kapoor 1 (K). J. "Typical" phenotype of subsp. *australe*, Sperry 585 (US). K. "Spineless" phenotype of subsp. *australe*, Lorentz & Hieronymus 547 (GOET). L. "Typical" phenotype of subsp. *kossinskyi*, Jordanoff s.n. (K). M. "Spineless" phenotype of subsp. *kossinskyi*, Cowdry 923 (K). N, O. Achenes of *C. echinatum*. N. "Typical" phenotype, Fernald & Long 12346 (PH). O. "Spineless" phenotype, Skelton & Skelton 1483 (TRT). P. Achene of *C. submersum*, Sandwith s.n. (GH). All figures drawn to scale.

relation analysis have provided insights into trends in the evolution of achene morphology among *Ceratophyllum* species that include patterns of both reduction and specialization of fruit features. Generally, achene spininess may represent the unspecialized condition of immediate ancestors to *Ceratophyllum*.

The modified taxonomy resulting from this series of papers provides a much-needed framework for carrying out further testing of hypo-

thetical evolutionary relationships in *Ceratophyllum*.

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QK, RB, SASK, SGO, SIUC, SLU, SMU, SP, SSMF, TAI, TENN, TRT, TRTE, UARK, UBC, UC, UNA, US, USCH, USF, UVIC, UWM, UWO, V, VPI, WAG, WIB, WIN, WIS, WTU, and Z. Special thanks are given to C. M. Wilmot-Dear for allowing my examination of specimens at Kew, which were on loan to her from several of the above institutions at the time of my visit. I thank D. J. Crawford, K. L. Gross, and T. N. Taylor for their comments on earlier versions of this manuscript. I also thank the staff of the Cartographic Services laboratory at the University of Wisconsin-Milwaukee who assisted with the preparation of figures. Portions of this research were supported by NSF Grant BSR 8401147.

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