

## The Evolution of Achene Morphology in *Ceratophyllum* (Ceratophyllaceae), III. Relationships of the “Facially-spined” Group

DONALD H. LES

Department of Biological Sciences, The University of Wisconsin–Milwaukee,  
Milwaukee, Wisconsin 53201

**ABSTRACT.** Variational studies of *Ceratophyllum demersum*, *C. oryzetorum*, and *C. platyacanthum* indicate that these species are probably closely related but that each is separable by multivariate statistical analyses of morphological features. Basal, stylar, and facial fruit-spine lengths are correlated in *C. oryzetorum*. In *C. platyacanthum*, however, correlations between spine lengths are less pronounced than in other species studied previously. The spiny, marginal achene wing of *C. platyacanthum* accounts for a major phenotypic difference between fruits of this species and those of *C. demersum*. Observations of phenotypically similar fruit mutations occurring sporadically in isolated populations of *C. demersum* indicate that the feature probably has a simple genetic basis. Regardless, the presence of facial spines and unusually long stylar and basal spines are characters which effectively separate both *C. platyacanthum* and *C. oryzetorum* from *C. demersum*. From interpreting the results of variational analyses in context with phylogeographical and chromosomal data, a revised taxonomic scheme is proposed which maintains *C. demersum* and *C. platyacanthum* as distinct species, and recognizes *C. oryzetorum* as *C. platyacanthum* subsp. *oryzetorum* (V. Komarov) Les.

In this third part of variational studies in *Ceratophyllum*, relationships are investigated between *C. demersum* L., *C. oryzetorum* V. Komarov, and *C. platyacanthum* Cham. The latter two species are the only members of the genus possessing facial appendages on both fruit surfaces; hence the name “facially-spined” group is appropriate. Further separating these species from one another is the presence of a flattened, spiny wing in *C. platyacanthum* (Chamisso 1829), which is lacking on the achene margins of *C. oryzetorum* (Komarov 1937) and *C. demersum* (fig. 1). Wilmot-Deary (1985) merged these species, reducing *C. platyacanthum* to a variety of *C. demersum*. She did not recognize *C. oryzetorum* as distinct because of her interpretation that a continuous morphological gradation in fruit characters occurred from *C. demersum* to *C. platyacanthum*.

There are several factors which warrant a re-examination of relationships between *C. demersum* and members of the facially-spined *Ceratophyllum* using a quantifiable statistical approach. Patterns of apparently continuous variation often displayed by quantitative characters may actually reflect discrete groupings that are statistically rather than visually ascertainable. This has certainly been the case with several quantitative fruit features in other species of *Ceratophyllum* studied (Les 1986a, 1988a). In-

deed, the typical polygenic regulation of quantitative traits accounts for complex patterns of interpopulational variability observed in other *Ceratophyllum* species (Les 1986a). Accordingly, the observation of “intermediate forms” may be misleading and does not in itself justify the merger of species with characters which may be quite distinct at a statistical level (if not visually), or with regard to their patterns of overall morphological variability. Furthermore, although *C. demersum* is essentially cosmopolitan, the distributions of *C. platyacanthum* and *C. oryzetorum* are allopatric; hence there is a geographical component correlated with the differences noted in their fruit morphology. *Ceratophyllum platyacanthum* is distributed in western Europe whereas *C. oryzetorum* is reported from eastern Asia (Komarov 1937).

In this study, the relationships among *C. demersum*, *C. platyacanthum*, and *C. oryzetorum* are investigated using multivariate statistical analyses. Following the previous analyses of *Ceratophyllum* species (Les 1986a, 1988a), correlation of fruit-spine characters is examined using bivariate methods. The primary objective of this study is to determine whether the pattern of morphological variation in *C. demersum*, *C. oryzetorum*, and *C. platyacanthum* is indeed one of continuous gradation, or if these species cluster discretely when analyzed by a multivariate ap-

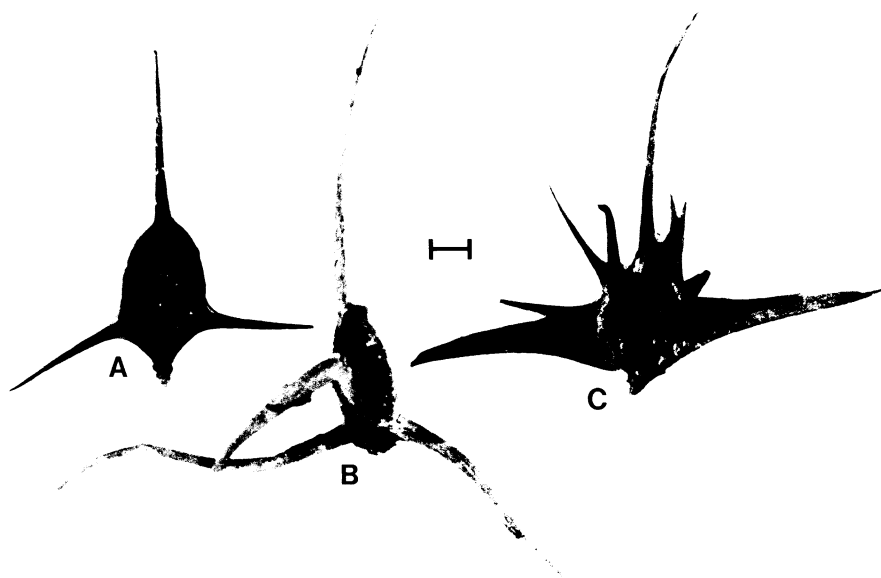


FIG. 1. Achenes of three *Ceratophyllum* species. A. *C. demersum* (Les 320, OS); B. *C. oryzetorum* (Maire 6739, NY); C. *C. platyacanthum* (Durer s.n., Z). Bar = 1 mm.

proach which evaluates overall variational patterns. These analyses are assessed for their potential to identify characters which may be useful taxonomically. Secondly, the correlation of fruit-spine lengths is investigated to determine whether the pattern observed in the species of *Ceratophyllum* studied previously is maintained. By answering such questions, it may be possible to ascertain further the probable evolutionary relationships among *Ceratophyllum* species.

#### METHODS

Specimens of *Ceratophyllum* were borrowed from 77 herbaria (see acknowledgments) and identified following Les (1986b). Fruiting specimens of *C. demersum*, *C. oryzetorum*, and *C. platyacanthum* were selected for the analyses. Each fruit with the associated vegetative specimen was treated as an individual operational taxonomic unit (OTU). The number of OTU's representing each species was limited by availability of material. A total of 150 OTU's from 150 populations of *C. demersum*, 13 OTU's from six populations of *C. oryzetorum*, and 89 OTU's from eight populations of *C. platyacanthum* was included in the analyses. Twenty characters (ta-

ble 1) were scored for each OTU; ten quantitative characters were used for the discriminate analysis. A list of specimens and copy of the data matrix are available from the author on request.

Clustering relationships of *C. demersum*, *C. oryzetorum*, and *C. platyacanthum* were investigated using the NT-SYS numerical taxonomy program (Rohlf et al. 1974). A UPGMA-HIGH dendrogram was generated, and a principal components analysis (PCA), analyzing the first two axes of variation, was performed following Les (1986a). To assess the significance of overlap observed in the cluster analyses, a stepwise discriminate analysis was conducted using the BMDP statistical software package (Dixon 1981). A matrix of *F*-statistic values was generated from the discriminate analysis.

Means, ranges, and standard deviations were computed and tabulated for basal spine, stylar spine, facial spine, and fruit-body lengths of each species. The correlation of the various fruit-spine lengths was evaluated by computing the value of the correlation coefficient (*r*) among stylar, basal, and facial spine lengths in *C. platyacanthum* and *C. oryzetorum*, as well as lateral spine lengths in *C. platyacanthum*. For *C. demersum*, previously reported values were used

TABLE 1. Characters and character states coded for OTU's used in numerical analyses of *Ceratophyllum demersum*, *C. oryzetorum*, and *C. platyacanthum*.

---



---

LEAVES: 1. maximum leaf-order (1-5). 2. segment morphology (inflated/non-inflated). 3. denticle morphology (broad-based/narrow-based). 4. first plumule-leaf morphology (simple/compound). 5. maximum leaf-whorl diameter (mm). 6. petiolar region (present/absent). FRUIT: 7. shape (elliptical/hemispherical). 8. fruit-body length (mm). 9. fruit-body width (mm). 10. fruit-body thickness (mm). 11. maximum basal spine length (mm). 12. maximum facial spine length (mm). 13. stylar spine length (mm). 14. number of lateral appendages. 15. maximum length of lateral appendages (mm). 16. surface (smooth/warty/tuberculate/ridged). 17. wing (present/absent). 18. phenology (1-12). 19. stylar position (centered/eccentric). 20. peduncle length (mm).

---

(Les 1986a). Means and correlation coefficients were computed using the SAS statistical software program (SAS 1982).

#### RESULTS

The OTU's of *C. demersum*, *C. oryzetorum*, and *C. platyacanthum* clustered into relatively discrete regions of the dendrogram generated by the UPGMA-HIGH algorithm. Two major clusters are evident; a cluster of *C. demersum* OTU's and a cluster including OTU's of both *C. platyacanthum* and *C. oryzetorum* (fig. 2). OTU's of *C. oryzetorum* comprise a minor cluster within that of *C. platyacanthum* (fig. 2). The cophenetic correlation coefficient of this dendrogram is 0.790 and only 3.5% of the OTU's fall outside of these clusters. By a PCA analysis of the first two factors of variation, two clusters of OTU's (*C. demersum* and *C. platyacanthum*) are again discernible. The OTU's of *C. oryzetorum* are intermediate, but are dispersed within a region of overlap between the two clusters (fig. 3A). Factors one and two accounted for 38.6% of the total variation resolved by the PCA. Adding a third axis of variation to the PCA accounted for 47.4% of the total variation, but did not further separate OTU's of *C. oryzetorum* from either of the two clusters. A stepwise discriminate analysis using 10 quantitative characters effectively separated all three species at a statistically significant level (fig. 3B; table 2). Lateral spine number, basal and facial spine length, and fruit

TABLE 2. F-matrix for a stepwise discriminate analysis of *Ceratophyllum demersum*, *C. oryzetorum*, and *C. platyacanthum* OTU's. All values are significant at *P* less than 0.001; degrees of freedom = 5, 245.

	<i>C. demersum</i>	<i>C. platyacanthum</i>
<i>C. platyacanthum</i>	187.71	—
<i>C. oryzetorum</i>	36.43	39.77

body length had the highest correlation with the canonical variables of the discriminate analysis. The matrix of *F* values (table 2) indicates a high degree of morphological dissimilarity between *C. demersum* and *C. platyacanthum* with respect to quantitative features. Although significant, the difference between *C. oryzetorum* and either of these species is much less (table 2).

The mean length of basal and stylar spines in *C. platyacanthum* and *C. oryzetorum* is greater than in *C. demersum*, and the mean fruit-body length of *C. platyacanthum* is less than that of either *C. demersum* or *C. oryzetorum* (table 3). Facial spines are lacking in *C. demersum*. The length of basal spines correlates significantly with stylar spine length in all three species (table 4). The facial spine length also correlates significantly with basal and stylar spine lengths in *C. oryzetorum* (table 4). In *C. platyacanthum*, lengths of facial spines do not correlate significantly with lengths of either basal or stylar spines to any great degree (table 4). In this species, however, the length of the lateral spines correlates significantly with that of both facial and stylar spines (table 4).

#### DISCUSSION

Variational analyses of *C. demersum*, *C. oryzetorum*, and *C. platyacanthum* illustrate that all three of these species are distinct morphologically. The groups of *C. demersum* and *C. platyacanthum* OTU's are discrete with only slight overlap in all dendrogram and cluster analyses performed (figs. 2, 3). The position of *C. oryzetorum* is essentially central to those of the other species. In the UPGMA dendrogram, OTU's of *C. oryzetorum* cluster within the group of *C. platyacanthum* OTU's, but retain the integrity of a distinct group (fig. 2). By PCA, OTU's of *C. oryzetorum* fall visually between those of the other species; by discriminate analysis, the OTU's of *C. oryzetorum* are distinct at a statis-

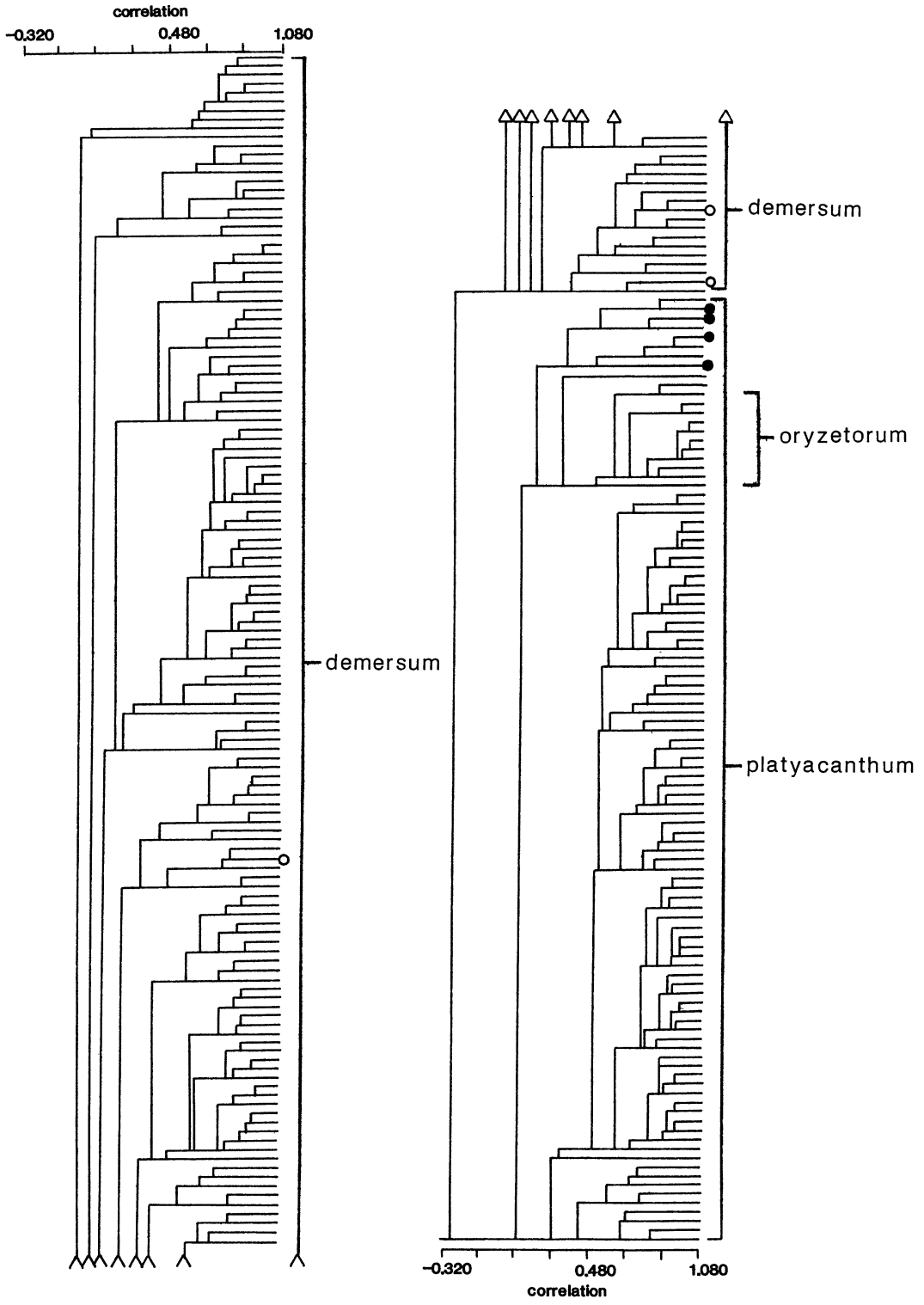


TABLE 3. Ranges and means ( $\pm 1$  s.d.) for various fruit characters compared among *Ceratophyllum demersum*, *C. oryzetorum*, and *C. platyacanthum*.

	Fruit length (mm)	Basal spine length (mm)	Facial spine length (mm)	Style length (mm)
<i>C. demersum</i>	3.5-6.0	0-13.0	—	0.5-15.0
( <i>N</i> = 150)	(4.4 $\pm$ 0.5)	(4.0 $\pm$ 2.6)	—	(6.1 $\pm$ 2.3)
<i>C. platyacanthum</i>	3.0-4.0	3.0-14.5	0-9.0	5.0-14.0
( <i>N</i> = 89)	(3.7 $\pm$ 0.3)	(8.9 $\pm$ 2.0)	(1.9 $\pm$ 2.1)	(9.4 $\pm$ 1.8)
<i>C. oryzetorum</i>	4.0-5.0	1.5-12.5	0.5-9.5	2.0-12.5
( <i>N</i> = 13)	(4.5 $\pm$ 0.4)	(8.4 $\pm$ 3.4)	(4.3 $\pm$ 3.0)	(9.1 $\pm$ 3.0)

tically significant level (fig. 3; table 2). Visually, the species are similar morphologically, particularly with respect to vegetative features, and their fruit characters appear to intergrade in a continuous series of variation as Wilmot-Dear (1985) observed. Actually, the species are distinct statistically with respect to overall variational patterns, and their recognition at some taxonomic level is justified. Variational analyses have identified "new" characters which correlate with those used historically to differentiate between these species taxonomically. In addition to the obvious presence of facial spines (a historical character), these analyses disclose that highly elongate stylar and basal spines also effectively separate both *C. oryzetorum* and *C. platyacanthum* from *C. demersum* (table 3). Similarly, the historical taxonomic feature of a spiny, flattened, marginal fruit-wing correlates well with a relatively small fruit body in *C. platyacanthum* (table 3). The recognition of several characters which correlate with each species is interpreted as justification for their continued recognition taxonomically.

The variational data provide one basis for assessing the placement of these species into appropriate taxonomic ranks; however, other information must also be considered. The numerous morphological differences which separate *C. demersum* and *C. platyacanthum* justify their maintenance at the species level; the similarity and shared features of *C. platyacanthum* and *C. oryzetorum*, however, may be more reasonably depicted taxonomically by recog-

nition at a sub-specific level. These conclusions are appropriate only if the noted morphological differences are genetically based, some mechanism of isolation between the species can be deduced, and the ultimate taxonomic disposition is concordant with phytogeographical data.

A pertinent taxonomic feature, the presence of facial achene spines, is undoubtedly a genetically based trait because populations show no variability in expression of the character (although intrapopulation length variation does occur), the trait is restricted to a small geographical range, and facial spines are absent in all other known species of *Ceratophyllum*. Therefore, the shared occurrence of facial spines in *C. oryzetorum* and *C. platyacanthum* is convincing evidence of their common ancestry. Also associated with the presence of facial spines is the occurrence of unusually long basal and stylar spines in these species. These fruit-spine lengths in other *Ceratophyllum* species have been shown to be under genetic control (Les 1986a).

Facially-spined *Ceratophyllum* occur only in western Europe and eastern Asia (Les 1986b). If *C. platyacanthum* and *C. oryzetorum* are closely related to *C. demersum* (whose range includes both regions), then their distinctness is presumably maintained by reproductive isolation. The nature of this isolation may be chromosomal. *Ceratophyllum demersum* is diploid with  $2n = 24$  (Les 1986b), whereas *C. oryzetorum* is hexaploid with  $2n = 72$  (Okada and Tamura 1981). The chromosome number of *C. platyacanthum* has not yet been determined. Shamrov (1981) re-

←

FIG. 2. UPGMA-HIGH dendrogram showing clustering relationships of *Ceratophyllum demersum*, *C. oryzetorum*, and *C. platyacanthum* OTU's. Open circles = OTU's of *C. platyacanthum* clustering with *C. demersum*; closed circles = OTU's of *C. demersum* clustering with *C. platyacanthum*. Leaf half of figure is an upper continuation of right half.

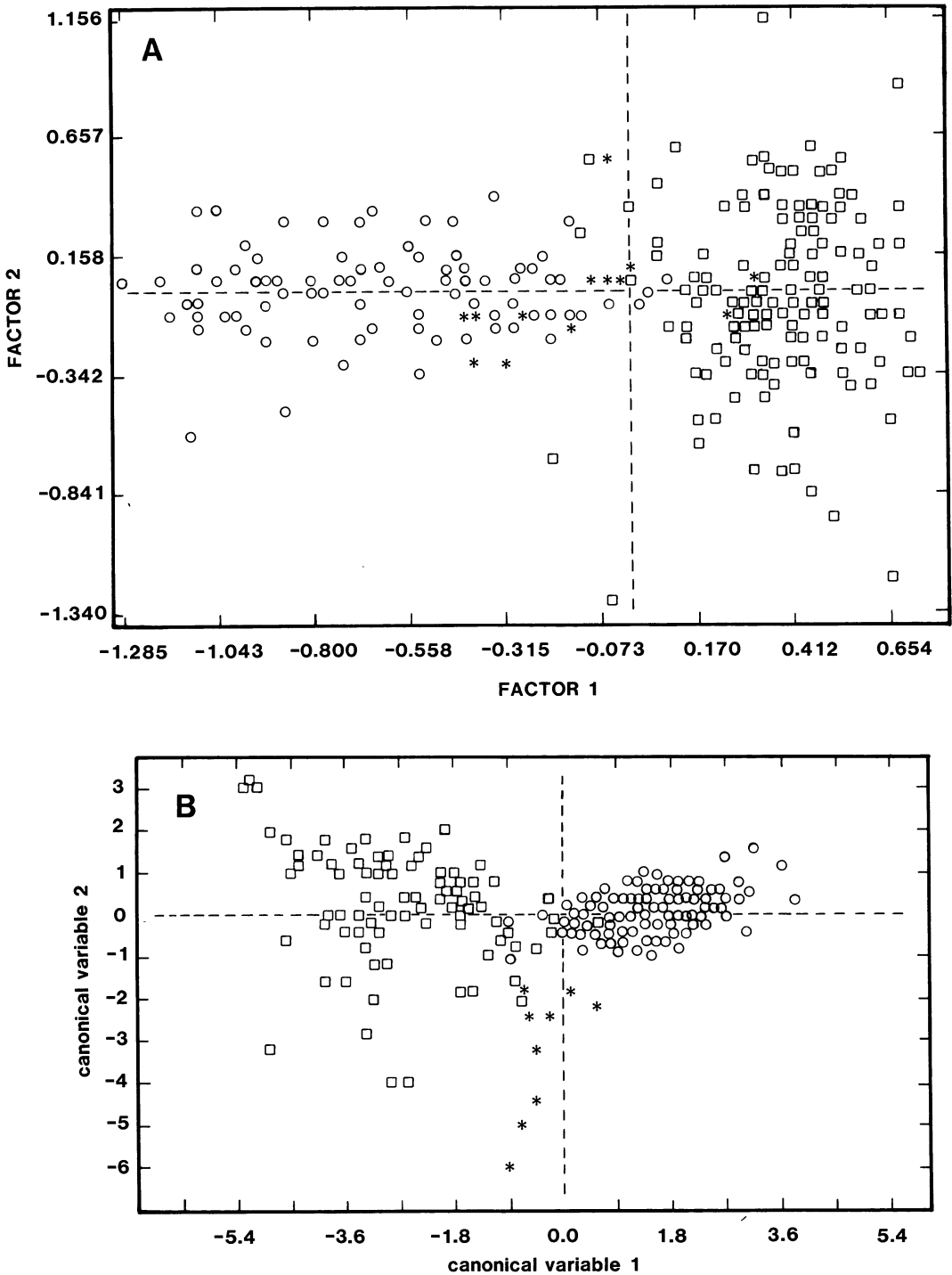


FIG. 3. Clustering relationships of *Ceratophyllum demersum* (circles), *C. oryzetorum* (asterisks), and *C. platyacanthum* (squares) OTU's. A. Principal components scatter-diagram generated by plotting factors 1 and 2. B. Scatter-diagram generated by plotting the two canonical variables of a stepwise discriminant analysis of OTU's.

TABLE 4. Values of the correlation coefficient ( $r$ ) for fruit-spine lengths in *Ceratophyllum demersum*, *C. oryzetorum*, and *C. platyacanthum* (levels of significance: \* =  $P$  less than 0.05; \*\* =  $P$  less than 0.01; \*\*\* =  $P$  less than 0.001).

		Basal spines	Facial spines	Stylar spines	Lateral spines
<i>C. demersum</i>	basal spines	1.00	—	0.77***	—
	stylar spines	0.77***	—	1.00	—
<i>C. oryzetorum</i>	basal spines	1.00	0.78**	0.80**	—
	facial spines	0.78**	1.00	0.78**	—
	stylar spines	0.80***	0.78**	1.00	—
<i>C. platyacanthum</i>	basal spines	1.00	-0.05	0.48***	0.19
	facial spines	-0.05	1.00	0.29*	0.41***
	stylar spines	0.48***	0.29*	1.00	0.48***
	lateral spines	0.19	0.41***	0.48***	1.00

ported a difference in the method of microsporogenesis in *C. demersum* and *C. platyacanthum*; i.e., successive in the former and simultaneous in the latter species, but it is not known whether this difference could affect fertility in hybrid offspring. Reproductive isolation may also be promoted by clonal growth and high inbreeding in *Ceratophyllum demersum* (Les 1986a, 1988b).

The spiny, winged achene margin of *C. platyacanthum*, which readily separates this species from both *C. demersum* and *C. oryzetorum*, probably has a relatively simple genetic basis. This conclusion is reached from observations of several anomalous populations of North American *C. demersum* in which fruit wings are produced. Winged fruits of *C. demersum* from one such population resemble typical fruits of *C. platyacanthum* (fig. 4A, C); however, fruits from this N. American population lack the facial spines characteristic of *C. platyacanthum*. Upon revisiting the "winged-fruited" population of *C. demersum* after ten years, no fruits with conspicuous wings were located. Instead, most fruits possessed peculiar lateral spines (fig. 4B). Because winged fruits arise sporadically in *C. demersum* (similarly winged phenotypes of the species were observed in collections from Montana and southern Ohio), the trait is probably determined by a single gene mutation. If this is the case, then sexual reproduction between "winged-fruited" individuals and "wingless" individuals may produce numbers of individuals heterozygous for the trait. It is possible that the spiny-margined but wingless fruit phenotypes found at the site ten years later, represent such intermediate phenotypes. With respect to this hypothesis, it is noteworthy that Haynald (1881) reported the occurrence of similar spiny-

margined fruits among winged-fruited individuals in populations of *C. platyacanthum* (as *C. pentacanthum* Haynald) in Europe. Accordingly, the essential difference between *C. oryzetorum* and *C. platyacanthum*, i.e., the absence or presence of a marginal fruit wing respectively, may involve only a very simple genetic change.

In *C. oryzetorum*, various fruit-spine lengths are correlated as in other species of the genus examined previously (table 4). In *C. platyacanthum*, however, the presence of a spiny lateral wing on the fruit is apparently associated with a disruption of the correlative relationship among fruit-spine lengths. In this species, basal spine lengths do not correlate with either facial or lateral spine lengths although the basal/stylar spine length correlation is maintained (table 4). Possibly, these anomalies and the smaller fruit body of *C. platyacanthum* (table 3) may be the result of pleiotropic effects.

*Ceratophyllum demersum* and *C. platyacanthum* are distinct morphologically, possess different modes of microsporogenesis, and should be recognized at the rank of species. The disposition of *C. oryzetorum*, however, is more difficult to resolve. If hexaploid, the species is presumably isolated from *C. demersum* chromosomally, and although it is vegetatively similar to that species, the presence of facial spines and elongate basal spines indicates a more definite relationship with *C. platyacanthum*. Individuals in some populations of *C. platyacanthum*, produce fruits with a reduced marginal wing (Wilmot-Dear 1985) resulting in phenotypes which resemble those of *C. oryzetorum*. These variants were the basis of the species name *C. komarovii* proposed by Kuzeneva (1935). At this site (Pavlovo Park, Leningrad, USSR), however, the genetic ability

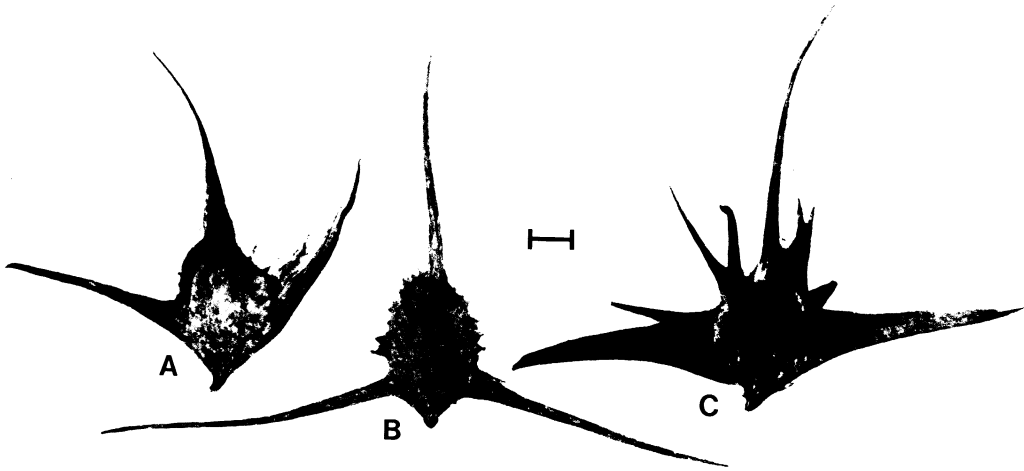


FIG. 4. Fruit variation in *Ceratophyllum demersum* and *C. platyacanthum*. A. "winged" achene of *C. demersum* (Roberts 3010, OS). B. "Spiny-margined" achene of *C. demersum* from same locality collected 10 years later (Les 349, OS). C. Achene of *C. platyacanthum* (Durer s.n., Z). Bar = 1 mm.

for producing well-developed fruit wings persists as evidenced by the phenotypes of achenes gathered at a later collection date, *Gussev* 2230 (LE!). These observations support the hypothesis that the marginal fruit wing of *C. platyacanthum* has a relatively simple genetic basis. What is less certain is the question whether the ability for producing winged achenes was lost in *C. oryzetorum*, or whether winged achenes arose de novo in *C. platyacanthum*. Regardless of this uncertainty, the distinction between winged and wingless fruits in facially-spined *Ceratophyllum* is not only clear-cut, but maintained geographically. Winged-fruited facially-spined *Ceratophyllum* occur exclusively in western Europe whereas wingless-fruited facially-spined *Ceratophyllum* occur exclusively in eastern Asia (Les 1986b). These observations are used to justify the recognition of *C. oryzetorum* as a subspecies of *C. platyacanthum*.

In summary, although *C. demersum*, *C. oryzetorum*, and *C. platyacanthum* appear to be relatively closely related on the basis of their vegetative similarity, the species are separable by reliable taxonomic characters and should not be merged. Facial spines and elongate stylar and basal spines on the achene are evidence for a common origin of *C. platyacanthum* and *C. oryzetorum*. In particular, the facially-spined achenes in these taxa are unique within *Ceratophyllum*. *Ceratophyllum platyacanthum* and *C.*

*oryzetorum* differ mainly by the presence of a spiny marginal wing on achenes of the former. This feature probably has a simple genetic basis, although it is restricted geographically to the western European segregate. More subtle differences such as the disruption of fruit-spine correlation and reduced fruit-body size in *C. platyacanthum* may be due to pleiotropic effects. The maintenance of facially-spined fruits in this group may be due in part to chromosomal isolation from *C. demersum*. Because anomalous chromosomal races of *Ceratophyllum* species persist as a result of vegetative propagation (Les 1986b), this aspect deserves further study. On the basis of these results, *Ceratophyllum demersum* and *C. platyacanthum* are maintained here as distinct species, whereas *C. oryzetorum* is recognized as a vicariant subspecies of *C. platyacanthum*.

#### NEW COMBINATIONS

1. *CERATOPHYLLUM PLATYACANTHUM* Chamisso, *Linnaea* 4:504. 1829.—*C. vulgare* var. *platyacanthum* (Cham.) Schleiden, *Linnaea* 11:540. 1837.—*C. demersum* var. *platyacanthum* (Cham.) Wimmer, *Fl. Schles.* 3:169. 1857.—*C. demersum* var. *platyacanthum* (Cham.) Jessen, *Deut. excurs.-fl.* 313. 1879, superfluous name.—*C. demersum* subsp. *platyacanthum* (Cham.) Nyman, *Consp. fl. eur.* 251. 1879.—



*C. demersum*  $\gamma$  *filifolium* Kuntze var. *platyacanthum* (Cham.) Jessen ex Kuntze, Revis. gen. pl. 2:644. 1891.—TYPE: Germany, In regione Berolinensis, 1821, *Schlechtendal s.n.* (holotype: B!; isotypes: HAL [2 sheets!]).

- 1a. CERATOPHYLLUM PLATYACANTHUM subsp. PLATYACANTHUM—*C. oxyacanthum* Schur, Enum. pl. Transsylv. 218. 1866, pro syn.—*C. polycanthum* Schur, Enum. pl. Transsylv. 218. 1866, pro syn.—*C. triacanthum* Schur, Enum. pl. Transsylv. 218. 1866, pro syn.—*C. gibbum* Laforet ex Nyman, Cons. fl. eur. 251. 1879, pro syn.—*C. pentacanthum* Haynald, Magyar Növényt. Lapok 57:111. 1881.—*C. demersum* var. *pentacanthum* (Haynald) Schumann in Martius, Fl. bras. 3(3): 750. 1894.—TYPE: Hungary, Kalocsa, lacum archiepiscopalis horti mei Colocensis, 17 Jun 1881, *Haynald s.n.* (holotype: BP—not found; isotypes: F [2 sheets!], GH!, MO!; topotypes: B!, BP!, CU!, DAO!, F!, G!, GH!, K!, US!).
- C. demersum* var. *notacanthum* Fouc., Fl. Ouest France, ed. 4:26. 1887.—TYPE: unknown; type locality: France, Charante-Inferieure, fosses des marais des environs de Rochefort, no date, *Foucaud s.n.* (topotypes: G!, Z!).
- C. komarovii* Kusen.-Proch. in Komarov, Fl. URSS 7:721. 1937.—TYPE: U.S.S.R., Leningrad prov., in stagnis prope opp. Slutzk (Pavlosk olim), Aug 1912, *Komarov s.n.* (holotype: LE!).
- 1b. *Ceratophyllum platyacanthum* subsp. *oryzotorum* (V. Komarov) Les, comb. et stat. nov.—*Ceratophyllum oryzetorum* V. Komarov, Izv. Bot. Sada Akad. Nauk SSSR. 30: 200. 1932.—TYPE: U.S.S.R., Nikolisk-Ussuriiskii, in valle fl. Suifun ad confluvium ejus Suputinka in canali irrigatorio oryzetorum prope p. Denisovka, 21 Aug 1930. *Komarov s.n.* (syntype: LE); in valle ipsa fl. Suifun non procul a pago Pokrovka in stagnis, 1 Sep 1930. *Komarov s.n.* (lectotype here designated: LE!).
- C. demersum* var. *quadrispinum* Makino, J. Jap. Bot. 1:21. 1917.—TYPE: Japan Higo Province, Heta-mura in Hotaku-gori, 22 Sep 1907, *Kodzuma s.n.* (holotype: TI—not found).
- C. pentacanthum* Hayata non Haynald, Icon. pl. Formosan. 8:130. 1919.—TYPE: Taiwan, Tai-

hoku pref., Nov 1896, *Makino s.n.* (holotype: TI!; isotype: TAI, photograph A!), later homonym.

- C. demersum* var. *pentacorne* Kitagawa, Rep. First Sci. Exped. Manchuria sect. 4(4):80. 1936.—TYPE: Taiwan, Taihoku pref., Nov 1896, *Makino s.n.* (holotype: TI!).

ACKNOWLEDGMENTS. I extend my thanks to the curators of the following herbaria for lending or allowing the examination of specimens used in this study: A, AAU, ALA, ALTA, B, BA, BH, BP, CAL, CAN, CU, CTES, DAO, DUKE, EMC, F, FI, FSU, G, GH, GOET, HAL, HIB, JEPS, K, KNK, KY, LE, LIL, LKHD, LSU, MICH, MO, MSC, MT, MTMG, MUHW, NCSC, NCU, NO, NY, OS, OSC, P, PENN, PH, QFA, QK, RB, SASK, SGO, SIUC, SLU, SMU, SP, SSMF, TAI, TENN, TI, TRT, TRTE, UARK, UBC, UC, UNA, US, USF, UVIC, UWO, V, VPI, WAG, WIB, WIN, WIS, WTU, and Z. I am grateful to D. J. Crawford, K. L. Gross, and T. N. Taylor for providing comments on earlier drafts of this paper. I also thank the staffs of Photographic Services and the Cartographic Services Laboratory of the University of Wisconsin-Milwaukee who assisted with the preparation of figures. Portions of this study were supported by an NSF Dissertation Improvement Grant BSR 8401147.

#### LITERATURE CITED

- CHAMISSO, L. A. 1829. De plantis in expeditione speculatoria Romanzoffiana observatis. *Linnaea* 4: 503-505.
- DIXON, W. J., ed. 1981. *BMDP statistical software*. Berkeley: Univ. of California Press.
- HAYNALD, L. 1881. *Ceratophyllum pentacanthum*. Magyar Növényt. Lapok. 57:109-115.
- KOMAROV, V. L. 1937. Family LXII. Ceratophyllaceae A. [sic] Gray. Pp. 15-20 in *Flora of the USSR*, ed. V. L. Komarov. Moskva-Leningrad: Izdatel'stvo Akademii Nauk SSSR.
- KUZENEVA, O. I. 1937. Diagnoses Plantarum Novarum in Tomo VII Florae URSS Commemoratatum. *Ceratophyllum* L. P. 721 in *Flora of the USSR*, ed. V. L. Komarov. Moskva-Leningrad: Izdatel'stvo Akademii Nauk SSSR.
- LES, D. H. 1986a. The evolution of achene morphology in *Ceratophyllum* L. (Ceratophyllaceae). I. Fruit-spine variation and relationships of *C. demersum*, *C. submersum*, and *C. apiculatum*. *Syst. Bot.* 11:549-558.
- . 1986b. Systematics and evolution of *Ceratophyllum* L. (Ceratophyllaceae): A monograph. Ph.D. dissertation, The Ohio State University, Columbus.
- . 1988a. The evolution of achene morphology in *Ceratophyllum* L. (Ceratophyllaceae). II. Fruit

- variation and systematics of the "spiny-margined" group. *Syst. Bot.* 13:73-86.
- . 1988b. Breeding systems, population structure, and evolution in hydrophilous angiosperms. *Ann. Missouri Bot. Gard.* 75:819-835.
- OKADA, H. AND M. TAMURA. 1981. Karyomorphological study on the Nymphaeales. *J. Jap. Bot.* 56: 367-375.
- ROHLF, F. J., J. KISHPAUGH, AND D. KIRK. 1974. *Numerical taxonomy system of multivariate statistical programs*. Stony Brook: State Univ. of New York.
- SAS. 1982. *Statistical software*. Cary, North Carolina: SAS Institute Inc. (release 82.3).
- SHAMROV, I. I. 1981. Some peculiar features of the development of the anther in *Ceratophyllum demersum* and *C. pentacanthum* (Ceratophyllaceae) [in Russian]. *Bot. Žurn. (Moscow and Leningrad)* 66:1464-1473.
- WILMOT-DEAR, C. M. 1985. *Ceratophyllum* revised.— A study in fruit and leaf variation. *Kew Bull.* 40: 243-271.