

The Taxonomic Significance of Plumule Morphology in *Ceratophyllum* (Ceratophyllaceae)

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ABSTRACT. The plumule morphology of the species of *Ceratophyllum* was studied for the purposes of: 1) determining the extent of variability in forking of the first epicotyl leaves, and 2) evaluating plumule features as taxonomic characters by assessing interspecific and intraspecific (inter- and intrapopulational) variation. Embryos from specimens collected throughout the ranges of eight of the species (*Ceratophyllum australe*, *C. demersum*, *C. llerenae*, *C. muricatum*, *C. oryzetorum*, *C. platyacanthum*, *C. submersum*, and *C. tanaiticum*) exhibited no variation in morphology of the first epicotyl leaves. In all instances the leaves were simple. In addition, no intrapopulational variation in the character was detected in *C. demersum*, *C. llerenae*, or *C. submersum* (rarity of material prohibited study of intrapopulational variation in the other five species). In contrast, embryos from specimens collected throughout the range of the ninth species, *C. echinatum*, possessed forked leaves at all nodes of the plumule. In *C. echinatum*, interpopulational variability was observed in the number of segments produced by the forked plumule leaves at the first node. The segment number is not correlated geographically, and most combinations of segment number can be observed within a single population. The unusual plumule morphology of *C. echinatum* is distinctive within the genus and has probably resulted from phylogenetic reduction of the lower plumule axis. These observations support recognition of *C. echinatum* as a distinct species.

The embryo morphology of *Ceratophyllum* has been interpreted variously since early studies of its structure in the 18th century. Gaertner (1788) provided a preliminary description of the embryo, but regarded the two cotyledons as a separate organ, the "vitellus" (Aboy 1936; Schleiden 1837). Richard (1808) described the embryo of *Ceratophyllum* with four cotyledons rather than two. Brongniart (1827) considered the possibility that in *Ceratophyllum*, the cotyledons represent outgrowths of the radicle, in which case the first foliage leaves constitute the "true" cotyledons. Schleiden (1837, 1838) was the first to identify correctly the two cotyledons of *Ceratophyllum* based upon his discovery of epicotyledonary internodes in some mature seeds.

Most botanists eventually recognized the embryo of *Ceratophyllum* with two cotyledons, above which a pair of simple, decussate plumule (epicotyl) leaves arise. Arber (1920) further remarked that forked leaves do not occur in the plumule until the fourth node above the cotyledons, but are preceded by juvenile (simple, linear) leaves.

In 1936, however, an important observation was made by Aboy (1936) who studied *Ceratophyllum demersum* and the poorly known eastern American species *C. echinatum*. She report-

ed a difference in the leaf morphology at the first plumule node between the two species (Aboy 1936, p. 25): "In the young plant of *C. demersum* var. *echinatum*" [= *C. echinatum*], "the first pair of leaves may fork once or twice In the young plant of *C. demersum*, . . . the first pair of leaves never fork[s]." Aboy based her conclusion upon examination of only one collection of fruits of *C. echinatum*, so a fundamental distinction between plumule-leaf forking characters of individuals of *C. demersum* and *C. echinatum* throughout their ranges could only be implied. Evidence supporting Aboy's work appeared soon afterwards in a paper by her mentor, W. C. Muenscher (1940), who concluded that not only did the seedlings of *C. demersum* and *C. echinatum* exhibit different plumule morphologies at the first node above the cotyledons (as Aboy described), but at the second node as well. At that level, *C. demersum* consistently produced simple leaves only, whereas seedlings of *C. echinatum* produced forked leaves at all plumule nodes. As Arber (1920) had already observed, he found that forked leaves did not occur in *C. demersum* until the third or fourth node above the cotyledons. Muenscher (1940, p. 232) regarded these seedling differences to be the "most constant character" with which to separate *C. demersum* and *C. echinatum*,

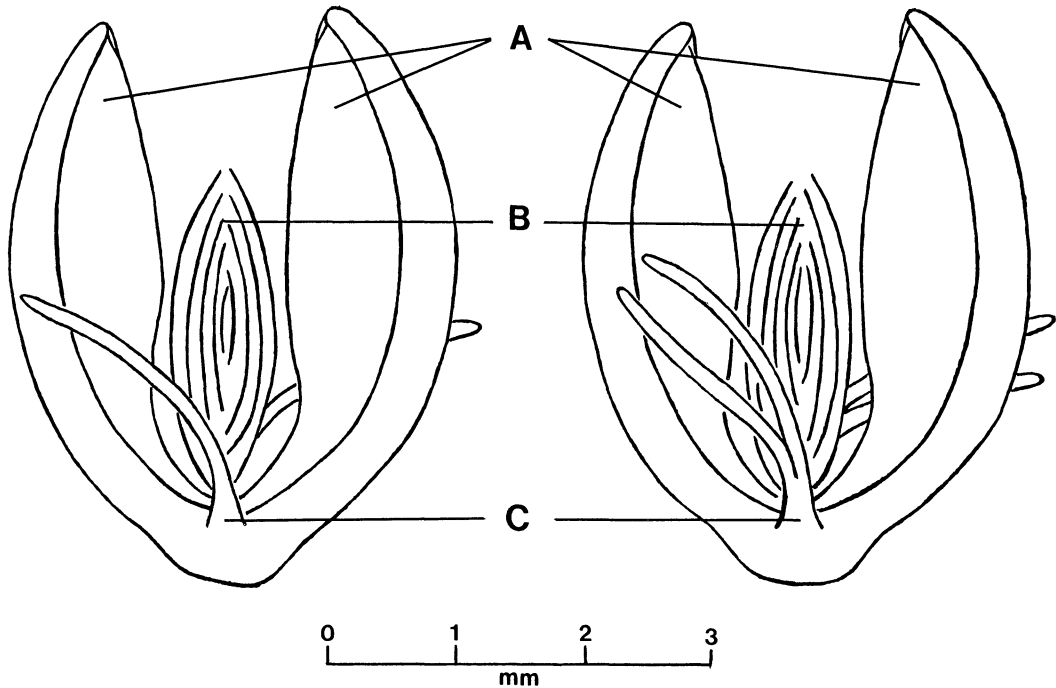


FIG. 1. Representative first plumule leaf morphologies in *Ceratophyllum*. a. Cotyledons. b. Plumule. c. First leaves of plumule (epicotyl); left: 1+1 arrangement of first plumule leaves in *Ceratophyllum demersum* (Les 345, OS); right: 2+2 arrangement of first plumule leaves in *Ceratophyllum echinatum* (Roberts 770, OS).

and subsequently used plumule features to assist in the distinction between *C. demersum* and *C. echinatum* in the United States (Muenscher 1944).

Lowden (1978, p. 135) challenged the taxonomic use of embryonic leaf characters stating, "... the number of lobes on the first node plumule leaves is hardly an acceptable character for distinction between species, since simple lobed first node plumule leaves were found in *C. muricatum* . . . , *C. demersum* . . . , and *C. submersum* . . ." Lowden also reported finding simple, two- and three-lobed first plumule leaves within a single collection of *C. echinatum* [= *C. muricatum* sensu Lowden].

Morphological reduction in *Ceratophyllum* has rendered several structures too highly modified to be of use taxonomically. Therefore, the possibility that embryo morphology may differ between certain species in the genus deserves further investigation.

The taxonomy presented here represents my current concept of the genus as consisting of nine species worldwide (*Ceratophyllum australe*,

C. demersum, *C. echinatum*, *C. llerenae*, *C. muricatum*, *C. oryzetorum*, *C. platyacanthum*, *C. submersum*, and *C. tanaiticum*). While based in part on Chamisso's (1829) preliminary monograph, Komarov's (1937) treatment of Soviet species, and Fassett's (1953) revision of North American taxa, the treatment incorporates modifications developed from my own studies (Les 1980, 1982, 1983, 1984a, b, and unpubl.). In this study, the variability associated with plumule morphology in these species is examined throughout their geographic ranges, and an assessment of the taxonomic applicability of embryo morphology is made.

MATERIALS AND METHODS

Specimens of *Ceratophyllum* were examined by the author in preparation of a monograph of the genus. Achenes were removed from herbarium specimens and soaked in a 50% solution of glycerin and distilled water for 24 hours prior to dissection (samples were taken only from specimens with several to many fruits, either in the packets or on the sheet). Pericarps were

TABLE 1. Comparison of leaf forking variation in plumules of *Ceratophyllum*. An asterisk denotes a mixed collection.

	First node	Second node	Third node	Fourth node
<i>C. australe</i>				
<i>Lowden 3414</i> (OS)	1+1	1+1+1+1+1+1	1+1+1+1+1+2	—
<i>Wiersema 2024</i> (USF)*	1+1	1+1+1+1+1+1	1+1+1+1+1+1	1+1+2+2+2+2
<i>C. demersum</i>				
<i>Les 345</i> (OS)	1+1	1+1+1+1+1	1+1+1+1+1+1	1+1+1+1+1+2
<i>Hicks s.n.</i> (OS)	1+1	1+1+1+1+1	1+1+2+2+2+2	—
<i>C. echinatum</i>				
<i>Patterson s.n.</i> (NY)	2+4	2+2+2+2	2+2+2+2+2+4	—
<i>Weatherby 3590</i> (NCSC)	2+2	2+2+2+2	2+2+2+2	2+2+2+2+2
<i>C. llerenae</i>				
<i>Fassett 28553</i> (SMU)	1+1	1+1+1+1+1+1	1+1+2+2+2+2	—
<i>Weirsema 2024</i> (OS)	1+1	1+1+1+1+1	1+1+1+1+1+2	—
<i>Wiersema 2024</i> (OS)	1+1	1+1+1+1+1	1+1+1+1+1+1	1+1+1+1+2+2
<i>C. muricatum</i>				
<i>Adam 30465</i> (MO)	1+1	1+1+1+1+1+1	1+1+2+2+2+2	—
<i>Wight 1038</i> (A)	1+1	1+1+1+1+1	1+1+1+1+1+1	1+1+2+2+2+2
<i>C. oryzetorum</i>				
<i>Maire 6739</i> (JEPS)	1+1	1+1+1+1+1+1	1+2+2+2+2+2+2	—
<i>Sputirki s.n.</i> (LE)	1+1	1+1+1+1+1	1+1+1+2+2+2+2	—
<i>C. platyacanthum</i>				
<i>Foucaud 1942</i> (F)	1+1	1+1+1+1	1+2+2+2+2+2	—
<i>Gussev 2282</i> (LE)	1+1	1+1+1+1+1	1+1+1+1+2+2	—
<i>C. submersum</i>				
<i>Leulin s.n.</i> (MO)	1+1	1+1+1+1	1+1+1+1+1+1	1+1+2+2+2+2
<i>Les 389</i> (OS)	1+1	1+1+1+1	1+1+1+1+1+1	1+1+2+2+2+2
<i>C. tanaiticum</i>				
<i>Poriukei 59-919</i> (LE)	1+1	1+1+1+1+1	1+1+1+1+2+2	—
<i>Tsvelev & Kolesnikova 278</i> (LE)	1+1	1+1+1+1+1+1	1+1+1+1+1+2	—

removed by slitting the lateral margins with a razor blade; the seeds were removed and soaked for an additional 24 hours. The integuments and residual endosperm were removed and embryo features were observed at 45–90× magnification. Plumule leaf morphology at the first node above the cotyledons was scored for the number of segments produced by one leaf plus (+) the number produced by the leaf opposite at the same node (fig. 1). This notation is used throughout the text. The dissected embryos were placed in glycerin-containing entomological “genitalia vials,” which were then returned to the specimen packets.

Sample size varied for each species depend-

ing on the availability of fruiting material. Plumule morphologies of all nine species were compared by examining the variation in leaf forking at the first through fourth epicotyl nodes (table 1). Two to three individuals of each species were included in this comparison (because embryo features are being examined, each is an individual, thus a single specimen with several fruits will contain several distinct individuals). Interpopulational data for each species were obtained by examining one individual from each available population. In all, 103 different populations were examined as follows: *C. australe* (four populations), *C. demersum* (39 populations), *C. echinatum* (26 pop-

ulations), *C. llerenae* (nine populations), *C. muricatum* (five populations), *C. oryzetorum* (two populations), *C. platyacanthum* (five populations), *C. submersum* (11 populations), and *C. tanaiticum* (two populations). Vouchers are cited in table 2. Intrapopulation variation in plumule leaf morphology was examined in only four species (*Ceratophyllum demersum*, *C. echinatum*, *C. llerenae*, and *C. submersum*) due to lack of sufficient fruiting material of the other taxa. It should be noted that no morphological variation was detected in first plumule leaves of the excluded species during the interpopulational survey. To conserve material, only one embryo was examined from each herbarium sheet cited unless noted otherwise (see table 2). A total of 129 individuals from 12 populations of the four species was examined as follows: *C. demersum* (50 individuals from four populations), *C. echinatum* (42 individuals from four populations), *C. llerenae* (seven individuals from two populations), and *C. submersum* (30 individuals from two populations). Vouchers are cited in table 2.

Because segment number of first plumule leaves varied both between and within populations of *Ceratophyllum echinatum*, the segment arrangements observed are summarized in table 3.

A dot distribution map was prepared for *Ceratophyllum echinatum* from specimens examined (a list of vouchers for the mapped specimens can be obtained from the author). Distributions cited for all species (table 2) are based upon material examined, and a list of these vouchers is also available from the author. Leaf morphologies at the first plumule node were mapped for *C. echinatum* at the sites from which the vouchers were collected. Maps of the other species were excluded because their first plumule leaf morphology did not vary.

RESULTS

Interspecific variation in plumule leaf forking is summarized in table 1. *Ceratophyllum echinatum* is the only species in the genus that possesses forked leaves at the first and second nodes of the plumule. In the other eight species, forked leaves do not appear until the third or fourth epicotyl nodes.

The character of simple leaves at the first plumule node did not vary between populations of *Ceratophyllum australe*, *C. demersum*, *C.*

lherenae, *C. muricatum*, *C. oryzetorum*, *C. platyacanthum*, *C. submersum*, and *C. tanaiticum* examined throughout their distributional range (table 2). In *C. echinatum*, the character of leaf forking at the first plumule node did not vary between populations examined. The segment number of the first plumule leaves did vary between populations of this species, and 1+2, 2+2, 2+3, 2+4, 3+3, 3+4, and 4+4 arrangements were observed (table 2).

The character of simple leaves at the first plumule node did not vary within populations examined of *Ceratophyllum demersum*, *C. llerenae*, and *C. submersum* (table 2). In *C. echinatum*, the character of leaf forking at the first plumule node did not vary within four populations examined. Segment number of the first plumule leaves did vary in three of the four populations examined (table 2). Inter- and intrapopulational variation in segment number of the first plumule leaves of *C. echinatum* is summarized in table 3.

Segment numbers of the first plumule leaves in *Ceratophyllum echinatum* are not correlated geographically (fig. 2). Most of the variations in segment number observed between populations were found within a single population from Maine (table 3). First plumule leaves most often exhibited the 2+2 arrangement both between and within populations of the species (table 3).

Fully developed fruits of *Ceratophyllum echinatum* were found that lacked seeds, establishing the first report of parthenocarpy in the genus.

DISCUSSION

The species *Ceratophyllum australe*, *C. demersum*, *C. llerenae*, *C. muricatum*, *C. oryzetorum*, *C. platyacanthum*, *C. submersum*, and *C. tanaiticum* possess simple leaves at the first and second plumule nodes and do not produce forked leaves until the third (fig. 3b) or fourth (fig. 3a) epicotyl node. In these species, the presence of simple decussate leaves at the first node above the cotyledons is a character that did not vary either between or within the populations examined. This similarity in plumule morphology precludes the use of epicotyl leaf forking characters for making taxonomic distinctions between these species. The consistent occurrence of forked leaves at the first and second epicotyl nodes in *C. echinatum* constitutes a use-

TABLE 2. Distributions of taxa and list of specimens examined for interpopulational and intrapopulational variation. Numbers in square brackets indicate segment numbers of first plumule leaves observed in specimens of *Ceratophyllum echinatum*. First plumule leaves were simple in all other cases. Numbers in normal brackets indicate the number of individuals examined from that collection if more than one.

Ceratophyllum australe Griseb.

Distribution: New World; U.S.A. (Florida), Dominican Republic, Ecuador, Argentina.

Vouchers: U.S.A.: Florida, *Blodgett*, *s.n.* (NY). ARGENTINA: *Lorentz & Hieronymus* 547 (GOET). DOMINICAN REPUBLIC: *Lowden* 3414 (OS). ECUADOR: *Wiersema* 2024 (USF); a mixed collection of *C. australe* and *C. llerenae*.

Ceratophyllum demersum L.

Distribution: Cosmopolitan.

Vouchers: U.S.A.: Arizona, *Taylor & Minckley* *s.n.* (NCU). California, *Ferris* 2042 (SMU). Illinois, *Eggert* *s.n.* (MO). Iowa, *Thorne* 30288 (FSU). Kansas, *McGregor & Sperry* 4676 (SMU). Louisiana, *McAtee* 2171 (US). Michigan, *Gleason* 819 (DUKE); *Les* *s.n.* (EMC) {15}. Minnesota, *Metcalfe* 1899 (US). Missouri, *Englemann* *s.n.* (PH). Montana, *Blanchard* *s.n.* (MICH). Nebraska, *Thomson* 70 (US). New York, *Phelps* 1577 (NY). Ohio, *Les* 329 (OS) {15}; *Les* 349 (OS) {10}; *Hicks* 731 (OS). Pennsylvania, *Wahl* 20541 (PENN); *Lippincott* *s.n.* (PH). Texas, *McCart* 5826 (DUKE). Vermont, *Les* 345 (OS) {10}. CANADA: British Columbia, *Warrington & Retzer* *s.n.* (WIB). Manitoba, *Cody* 25063 (DAO). Ontario, *Morton* 3055 (CAN). Saskatchewan, *Hudson* 2001 (DAO). ARGENTINA: *Pedersen* 4680 (MO). BULGARIA: *Vyhodcevsski* *s.n.* (UBC). CEYLON: *Nowicke & Jayasuriya* 414 (MO). CZECHOSLOVAKIA: *Petrok* *s.n.* (GH). DENMARK: *Jeppensen & Holm-Nielsen* *s.n.* (A). FRANCE: *Jeanpert* *s.n.* (F). INDIA: *Perrotet* *s.n.* (GH). INDONESIA: *BIO-TROP* *s.n.* (UNA). IRAN: *Bornmuller* *s.n.* (B). MEXICO: *Orozco & Glez* 1 (MO); *Wiggins & Demaree* 4905 (NY). PAPUA NEW GUINEA: *Leach, Osborne, & Balciunas* 7670 (OS); *Balciunas & Naoni* 7671 (OS). SWEDEN: *Wahlstedt* *s.n.* (F). TANZANIA: *Tanner* 2086 (JEPS). U.S.S.R.: *Kenig* *s.n.* (NO).

Ceratophyllum echinatum A. Gray

Distribution: New World; temperate North America (fig. 2).

Vouchers: U.S.A.: Alabama, *Wiersema* 1898 (UNA) [empty]; *Wiersema* 226 (UNA) [2+2]. Connecticut, *Weatherby* 3590 (NCSC) [2+2]. Florida, *Poppleton* 708 (USF) [3+4]; *Shuey* 2215 (USF) [empty]. Georgia, *Thorne* 1464 (NY) [2+2]; *Thorne* 4870 (F) [empty]; *Thorne* 4870 (F) [4+4]. Illinois, *Patterson*

TABLE 2. Continued.

s.n. (F) [2+2], (MO) [2+2], (NY) [4+2], (US) [4+4], (WIS) [2+2]. Kansas, *Stephens* 85950 (NY) [2+2]. Louisiana, *Sundell* 2128 (NO) [2+2]. Maine, *Steinmetz & Steinbauer* 1118 (CAN) [2+3], (DAO) [2+3], (DUKE) [2+2], (F) [4+4], (KY) [3+3], (MICH) [2+2], (MO) [2+2], (NCSC) [4+4], (NCU) [2+2], (NO) [2+2], (NY) [2+2, 2+4] {2}, (PENN) [2+2], (PH) [2+2], (US) [2+2], (WTU) [2+2]. Maryland, *Killip* 36965 (PENN) [2+2]. Massachusetts, *Ahles* 84411 (TENN) [2+2]. Michigan, *Belcher* *s.n.* (MSC) [2+2] {15}. New Jersey, *Long* 4457 (PH) [2+2]. Ohio, *Roberts* 711 (JEPS) [2+2; one leaf two-lobed], (MICH) [2+2], (MO) [2+2], (NY) [2+2], (OS) [2+2], (PH) [2+1]; *Roberts* 770 (OS) [2+2]; *Roberts* 4473 (OS) [2+3]. Pennsylvania, *Porter* *s.n.* (PH) [3+3]. Tennessee, *Patrick* 2050 (TENN) [2+2]. Texas, *Correll & Mitchell* 34443 (JEPS) [2+2; with "extra" node bearing simple leaf—see discussion]. Washington, *Buckingham* 3112 (WTU) [2+3]. CANADA: British Columbia, *Warrington & Harcombe* *s.n.* (WIB) [2+4]. Ontario, *Garton* 16626 (MICH) [2+2].

Ceratophyllum llerenae Fassett

Distribution: New World; tropical and subtropical Americas.

Vouchers: U.S.A.: Florida, *Killip* 40732 (US); *Klaphaak* *s.n.* (WIS); *Shuey* M1122 (USF). Georgia, *Sperry* 585 (FSU). MEXICO: *Orozco & Glez* 5 (MO). EL SALVADOR: *Fassett* 28553 (GH, SMU) {2}. NICARAGUA: *Haynes* 8292 (OS). VENEZUELA: *Gonzalez & Wiersema* 2200 (UNA). ECUADOR: *Wiersema* 2024 (OS, USF) {5}.

Ceratophyllum muricatum Cham. (inc. *C. kossinskyi* Kuzen.)

Distribution: Old World; Africa, India, China.

Vouchers: CHINA: *Chiao* *s.n.* (NY); *Ching* 3898 (JEPS). EGYPT: *Sieber* *s.n.* (MO). INDIA: *Wight* 1032 (A). SENEGAL: *Adam* 30465 (MO).

Ceratophyllum oryzetorum Kom.

Distribution: Old World; eastern Asia.

Vouchers: U.S.S.R.: *Ussuriysk. Suputirki* *s.n.* (LE). CHINA: *Maire* 6739 (JEPS).

Ceratophyllum platyacanthum Cham.

Distribution: Old World; Europe, western Asia.

Vouchers: FRANCE: *Foucaud* 1942 (F). GERMANY: *Heinrich* *s.n.* (B); *Durer* *s.n.* (B). HUNGARY: *Haynald* *s.n.* (B). U.S.S.R.: *Gussev* 2282 (LE).

Ceratophyllum submersum L.

Distribution: Old World; Europe, W. Asia, Africa, New Guinea.

Vouchers: DENMARK: *Arenklit, et al.* *s.n.* (MO). ENGLAND: *White* *s.n.* (B). FRANCE: *Jeanpert* *s.n.*

TABLE 2. Continued.

(F). GERMANY: <i>Braun s.n.</i> (GH); <i>Inlispy s.n.</i> (B). PAPUA NEW GUINEA: <i>Brass 6458</i> (A). SWEDEN: <i>Les 379</i> (OS) {15}; <i>Luelin s.n.</i> (MO). SWITZERLAND: <i>Les 389</i> (OS) {15}. TANZANIA: <i>Richards 24607</i> (NY). U.S.S.R.: <i>Diechenko s.n.</i> (A).
<i>Ceratophyllum tanaiticum</i> Sapjæg.
Distribution: Old World; endemic; lower Don R. region, U.S.S.R.
Vouchers: U.S.S.R.: Volga delta, <i>Tsvelev & Kolesnikova 278</i> (LE); Aleshnovsk, <i>Poriukei 59-919</i> (LE).

ful taxonomic character for separating this species from others in the genus.

Ceratophyllum echinatum displays a considerable range of both inter- and intrapopulational variation in plumule leaf morphology. Although the first pair of plumule leaves forks in most of the individuals examined, there were two instances where simple leaves were found at the first plumule node of this species. In one case [Correll & Mitchell 34443 (JEPS)], an embryo had a single simple leaf at the first node above the cotyledons, above which a normal pair of forked leaves was present (fig. 3c). Because this is the only report of alternate phyllotaxy in *Ceratophyllum*, the single leaf may represent the vestige of an "extra" node between the cotyledons and first pair of plumule leaves. At the first plumule node of another embryo [Roberts 711 (PH)], I observed one forked and one simple leaf (fig. 3d). Another individual from that gathering [Roberts 711 (JEPS)] had one forked and one "lobed" leaf at the first plumule node (fig. 3e), but four other individuals examined (see table 2) had decussate forked leaves at the first plumule node (fig. 3f). In the "aberrant" forms (possessing simple or lobed leaves at their first plumule node), forked leaves were always produced at both the second and third plumule nodes. Simple leaves were absent in the plumules of all other individuals of *C. echinatum* examined in this study.

Lowden (1978) ruled plumule morphology unacceptable for making taxonomic distinctions between *Ceratophyllum muricatum*, *C. demersum*, and *C. submersum*. His conclusion is valid only if these taxa are regarded sensu stricto, because all three species exhibit the same plumule morphology (table 1). Lowden (1978), however, included both *C. llerenae* and *C. echi-*

TABLE 3. Segment number variation in first plumule leaves of *Ceratophyllum echinatum*.

Populations examined (table 2)	# of individuals of each plumule form						
	1+2	2+2	2+3	2+4	3+3	3+4	4+4
U.S.A.: Illinois, <i>Patterson s.n.</i>	0	3	0	1	0	0	1
U.S.A.: Ohio, <i>Roberts 711</i>	1	5	0	0	0	0	0
U.S.A.: Michigan, <i>Belcher s.n.</i>	0	15	0	0	0	0	0
U.S.A.: Maine, <i>Steinmetz & Steinbauer 1118</i>	0	10	2	1	1	0	2
Summary from 26 populations	1	47	5	3	2	2	4

natum in *C. muricatum*. In this regard, his conclusions are not acceptable. Because he assumed a priori that *C. echinatum*, *C. llerenae*, and *C. muricatum* were conspecific, the differences in plumule morphology between specimens of *C. echinatum* and the last two taxa indicated to him a wide range in variability in a single species. The question of distinctness between *C. muricatum* and *C. llerenae* cannot be clarified on the basis of evidence from plumule morphology and will not be discussed further. The distinctness of *C. echinatum* is supported by plumule morphology and must be emphasized. The few simple plumule leaves observed in *C. echinatum* by Lowden (1978) and myself do not invalidate the use of forked first plumule leaves as a distinguishing character for this species for several reasons. Simple leaves are rarely found either within or among populations of the species throughout its range (table 3). Moreover, those encountered were associated with forked leaves either at the same or adjacent plumule node (fig. 3c-e). It was coincidental that Lowden (1978) examined only the population of *C. echinatum* from Ohio in which several single leaves occurred. In all specimens I examined, the second plumule node (even in individuals from the Ohio population) had only forked leaves, a characteristic distinct from any other species (table 1). Muenscher's (1940) observation that forking at both the first and second node plumule leaves is characteristic of *C. echinatum* is supported by this study.

Rare simple-leaved forms of *C. echinatum* may represent transitional stages during phylogenetic reduction of the lower axis. In figure 3,

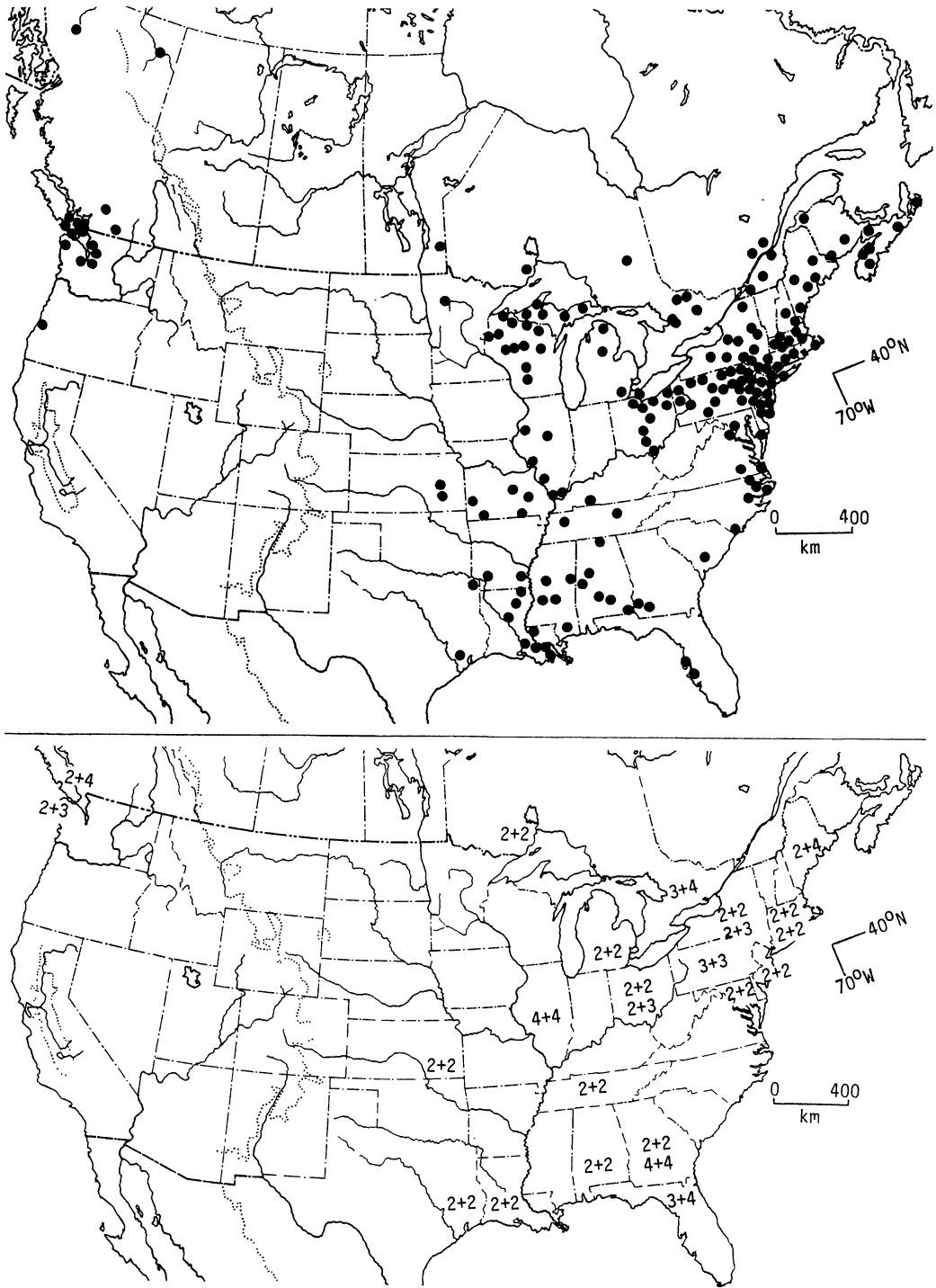


FIG. 2. Distribution of *Ceratophyllum echinatum* (above) and plumule morphologies of specimens of *C. echinatum* studied (below).

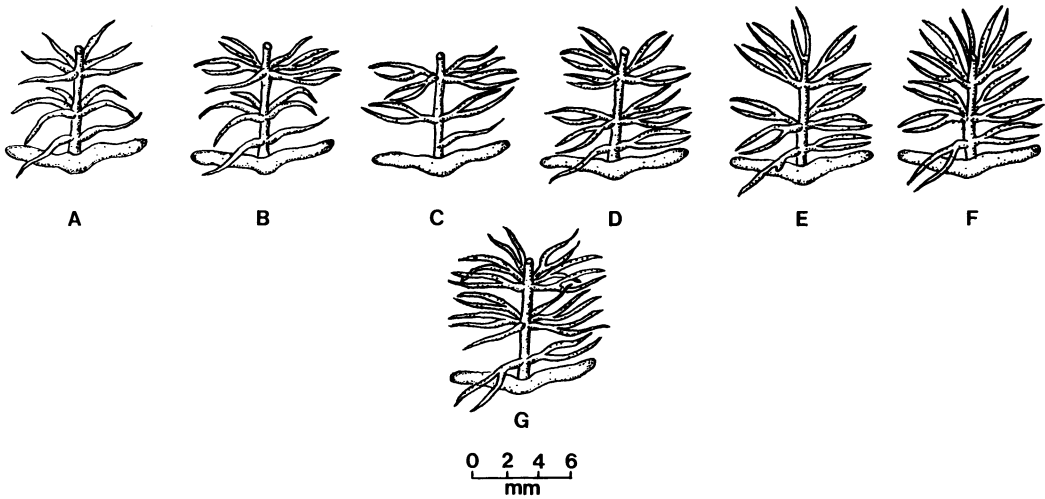


FIG. 3. Plumule variation in *Ceratophyllum demersum* and *C. echinatum* with internode lengths greatly exaggerated. a. *C. demersum* (Les 345, OS). b. *C. demersum* (Hicks s.n., OS). c. *C. echinatum* (Correll & Mitchell 34443, JEPS). d. *C. echinatum* (Roberts 711, PH). e. *C. echinatum* (Roberts 711, JEPS). f. *C. echinatum* (Weatherby 3590, NCSC). g. F₁ hybrid between *C. demersum* and *C. echinatum* (Les 397, OS).

the anomalous plumule types of *C. echinatum* (fig. 3c-e) have been arranged between usual plumule configurations of *C. demersum* (fig. 3a, b) and *C. echinatum* (fig. 3f). It is conceivable that reduction of the lower plumule axis could have progressed through morphological stages similar to those exemplified in figure 3b-f. This hypothesis of axial reduction is supported by Schleiden (1837), who observed the presence of a small internode between the cotyledons and first pair of plumule leaves in several embryos of *Ceratophyllum demersum*. The absence of this region in most embryos of *C. demersum* indicates that this species may have undergone at least a partial reduction of the lower plumule axis.

Hybridization also may account for the presence of simple leaves in the plumule of *Ceratophyllum echinatum*. Only one F₁ hybrid resulted from numerous crosses made between *C. demersum* and *C. echinatum* (Les unpubl.), but its plumule morphology was intermediate to both parental types (fig. 3g). In this case, the hybrid appeared to have "lost" most of the simple-leaved nodes characteristic of the *C. demersum* parent, but the same morphology could also result if forked leaves were inherited as a dominant trait from the *C. echinatum* parent. A more

detailed genetic analysis will be necessary to clarify the potential alteration of plumule morphology via hybridization.

Of the individuals of *Ceratophyllum echinatum* examined in this study, the 2+2 morphology of first plumule leaves was most common, with other arrangements occurring in less than 30% of the individuals (table 3). A similar distribution of plumule arrangements in *C. echinatum* was reported by Muenscher (1940). The distribution pattern of segment number variants based on interpopulational sampling (fig. 2) does not indicate that particular arrangements have geographical affinities. Also, most variations were found within a single population from Maine, U.S.A., and the proportions of each variant were similar in both the inter- and intrapopulational surveys (table 3). Therefore, the individuals examined from the interpopulational survey probably represent only a sample of the range in plumule variation possible in any given population.

Forked first plumule leaves occur throughout the range of *Ceratophyllum echinatum* (fig. 2), whereas all populations examined of *C. illerrenae* had simple first plumule leaves. This distinction held even in southern Georgia and Florida, the only zone of geographic overlap

between these species. Treatment of these taxa as conspecific because of superficial similarities (e.g., Lowden 1978) is not warranted on the basis of their distinctive plumule morphologies.

CONCLUSIONS

The plumule morphology characterized by simple leaves at the first two to three nodes has been strongly conserved in most species of *Ceratophyllum*. *Ceratophyllum echinatum* is the only species within the genus with a plumule in which forked leaves occur at all nodes. Occasionally, individuals of *C. echinatum* are found bearing simple plumule leaves, but these are aberrant forms and probably represent relic stages in reduction of the lower epicotyl axis in this species. Although aberrant simple-leaved forms of *C. echinatum* occur, the character of leaf forking at the first plumule node is useful to distinguish taxonomically this species from others in the genus. If simple leaves are found at the first plumule node, the second node also should be examined. The presence of forked leaves at either of these nodes is diagnostic for *C. echinatum*. Whenever possible, several individuals of a population should be examined to insure against chance sampling of aberrant forms. Forking varies at the first plumule node in *C. echinatum*, and segment number of each leaf may range from one to four. Fruits of *C. echinatum* also may be devoid of embryos due to parthenocarpy.

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