NORTH AMERICAN CERATOPHYLLUM

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This paper is a taxonomic study of the genus Ceratophyllum as it occurs in the Western Hemisphere north of the Equator. The field work in Central America was done from 20 September 1950 to 13 March 1951, while the writer was a guest at the Instituto Tropical de Investigaciones Científicas; this was made possible by the cooperation of the Wisconsin Alumni Research Foundation and the Chicago Natural History Museum. The facilities of the Gray Herbarium were graciously made available during the spring of 1951. For loans of herbarium material the writer is indebted to the curators of the Chicago Natural History Museum (F), the Missouri Botanical Gerden (MO), the New York Botanical Garden (NY), the University of California (UC), and the United Stass National Museum (US).

PATTERNS OF VARIATION IN CERATOPHYLLUM

The leaves of Ceratophyllum are borne in whorls of from 6-10 at each node, and are cut into many slender divisions. It is the mass of bushy overlapping leaves toward the tip of the stem that gives the plant its common name of 'Coontail'.

Each leaf is usually forked into 2 equal divisions, and each division may be forked again. The ultimate segments are nearly round in cross-section, and bear along the upper side two rows of minute teeth. At the tip of each segment there are 2 bristles. When the plant is pressed, the leaf-segments usually become flattened, and the teeth appear as if they were in a single row on one side (Figs. 5-8). The leaf-segments appear to be hollow, and have cross-partitions at rather close intervals.

The fruit is a nutlet; it is ellipsoidal and flattened, tipped by the spine-like style, and is often provided with spine-like or tooth-like outgrowths (Figs. 104-107).

On this basic pattern of leaves and fruits are imposed several different series of variation. In the leaves there may be variation in amount of forking, in width of the segments, in the degree of tapering at base, and in the coarseness and distribution of the teeth. The fruit may be unarmed, or it may bear long spines or short teeth from the base; the surface may be roughened or it may be smooth; the margin may be winged or not winged.

It is the problem for the taxonomist to determine, in this maze of variation patterns superimposed one on another, which patterns represent differences between species and which are variations within a species. This problem is most graphically shown in Figs. 1-3. contrary to appearances, Figs. 1&2 represent the same species, and Fig. 3 is another species.

In Ceratophyllum this problem is complicated by two circumstances. First, the fruit, whose variation patterns are commonly the most fundamental in any group of Flowering Plants, is rare in the genus: examination of some 681 collections of C. de-mersum from North America, as found in 6 leading herbaria, yielded only 38 with fruits. Second, the variations within a species may be far more conspicuous than the differences

between species, as is demonstrated by Figs. 1-3.

INTERSPECIFIC DIFFERENCES

In the Americas there appear to be two widespread species of Ceratophyllum. In C. echinatum the fruit has along each margin 3-7 spreading spines connected by a wing (Figs. 76-80) with thread-like terminal segments on which the teeth are so slender as to be nearly invisible (Figs. 95-100). In C. demersum the fruit has only a single pair of spines near the base, in addition to the terminal spine (Fig. 104), the leaves are once or twice forked (Figs. 37-75) or rarely even simple (Figs. 61,63), with larger and more conspicuous teeth terminating a mound of green tissue (Figs. 81-94).

INTRASPECIFIC VARIATION

C. demersum is a species of many different aspects (Figs. 1, 2, 4, 11, 12, 20, 21, 27, 30). If individual leaves are taken from plants, several more or less easily dis tinguishable types may be seen. (1) The commonest type of leaf is once or twice forked, 7-16 mm long, with basal segments 0.5-0.8 mm wide with sides essentially parallel except where widened below each forking (Figs. 37-43), and terminal segments 0.2-0.5 mm wide with 1-6 teeth (Figs. 5-10, 13-16). (2) A slender type of leaf is 15-22 mm long, the narrower basal segment 0.4-0.6 mm wide and the terminal segments 0.1-0.3 mm wide (Figs. 50-58); the teeth are smaller than in the common type (Figs. 24, 28, 84, 85). These plants superficially resemble C. echinatum (compare Figs. 1&3; 30 & 31), but they are classified under C. demersum because the leaves are only once or twice forked, the teeth have a definite green base, and the fruit has 3 spines. (3) Leaves tapered, the basal segment with very narrow base and flaring sides (Fig. 59-65); even the terminal segments are wider than the base of the leaf (Figs. 17-19).(4) Short stubby leaves only 3-5 mm long, with segments 0.5-1 mm wide (Figs, 66-69).(5) Leaf-segments inflated, nearly or quite toothless, and slightly constricted at the crosspartitions to give a jointed aspect. Only 3 individuals of this type have been seen, one from Washington (Thompson 7593 in UC), one from Holland (Fig. 90) and one from $C_{\underline{h}i}$ le (Fig. 91). The last-named collection has fruit, which is clearly that of C. demersum.

In the field, a careful observer will see great differences in aspect from plant to plant or from clone to clone, even in the same body of water. Thus, we find two collections from Selkirk, New York, by Fernald, Wiegand & Eames, with the comments on the labels, for no. 14283, 'Foliage stiff and rather hard', and for no. 14285, 'Fresh foliage soft'. In Laguna del Jocotal, in southeastern El Salvador, the writer found several clones differing among themselves about as much as herbarium sheets from far-separated regions might differ; one clone had slender branches with yellowish leaves white jointed at base, while a neighbor had dark green foliage with inconspicuous green leaf-bases.

C. echinatum, on the other hand, is almost as uniform as C. demersum is variable. The leaves are from 17-21 mm long, the basal segments have parallel sides, and the terminal segments are very slender, 0.1-0.2 mm wide (Figs. 77-80), with 3-8 minute and obscure teeth which have little or nothing of a base of green tissue (Figs. 95-100). A few scattered individuals have the leaves curiously inflated, the basal segment narrowed to only 0.2-0.5 mm at base but expanded above to as much as 1.5 mm (Fig. 76).

TAXONOMIC TREATMENT

- a. Leaves commonly once or twice forked (Figs. 37-75) or rarely simple; marginal teeth on leaf-segments on a broad base of green tissue (Figs. 81-94); fruit not winged, with a terminal spine and two basal spines that may be long (Fig. 104) or much reduced ... 1. C. demersum.
- a Leaves 2-4 times forked (Figs. 76-80); marginal teeth on leaf-segments with little or no base of green tissue (Figs. 95-103); fruit with a narrow wing and sometimes with marginal spines
 - b. Body of fruit 3 mm or more wide, with marginal spines

 - c. Margin of fruit with 16-18 teeth that are mostly less than 1 mm long (Fig. 106); spray of leaves 5-9 cm in diameter (Fig.35) terminal segments of leaves with 10-20 clearly marked teeth...3. C. Llerenae
 - b. Body of fruit less than 2 mm wide, without marginal spines (Fig. 107)4. C. floridanum
- 1. CERATOPHYLLUM DEMERSUM L., Sp., Pl. 2:992. 1753. The name is here used in its traditional sense for the plant of the Americas. Linnaeus originally applied the name to European plants but doubtless had something more than C. demersum in its strict sense. Certainly, the Hort. Cliff. referred to two plants, the one without spines margining the fruit and the other with two basal spines. In Europe, where variation in leaf type apparently equals that in America, there is even more variation in fruit. The several fruit types, which appear impressive in their differences, are not, to judge from the small amount of material I have seen from Europe, correlated with leaf types. Several species have been pased on fruits with different kinds of outgrowths: cf. Ascherson & Graebner V. 2: 538.543.1929.
- C. demersum ranges, in the Western Hemisphere, from southern Canada to Central America and the West Indies (Map 1), and in South America from Ecuador and Brasil to Argentina. Published reports and herbarium material so labelled give the species something approaching a world-wide distribution. With such a far-flung range, and such variation in leaf and fruit, we may well expect to find several species represented. Indeed, such may yet prove to be the case, when sufficient material has been accumulated, especially of the rarely occurring fruiting individuals. But in the Americas, at least, C. demersum seems to be but one wide-ranging species. Irrespective of leaf-type, all fruits are of the same basic type (their variation in North America will be discussed in the next paragraph). This fruit-type has a long straight terminal spine and two basal spines, i.e., it is the fruit of C. oxyacanthum Cham., Linnaea 4:504. 1829. It is conceivable that, should the name C. demersum L. prove to be applicable to a specific segregate present only in the Old World, Chamisso's name might be taken up for the American plant.
- In the Americas but one basic type of fruit is represented in what we call C. demersum: this has a wingless body, a long terminal spine, ans 2 basal spines. The

length of the basal spines varies from a maximum of 6 mm to a minimum of 0.1 mm. There appears to be no correlation of length of basal spines with leaf-type nor with geography, and when we find several fruiting individuals from one locality the whole range of variation appears. The following table presents the lengths of basal spines from 36 collections in 6 herbaria, arranged by states:

New York: St. Lawrence Co., Phelps 1677 (NY)	n m
St. Lawrence Co., Muenscher & Maguire 1121 (F)3.5 m	ı m
Lake George, Burnham 25 (US)5.5 m	ı m
Illinois: Cook Co., Chase (WIS)2.5 m	ı m
Menard Co., Hall (F)	n m
Mt. Carmel, Schenk (MO)5.0 m	n m
St. Clair Co., Eggert (UC)1.5 m	n m
St. Clair Co., E_{ggert} (MO)5.0 m	
Fish Lake, St. Clair Co., $E_{f ggert}$ (MO)0.5 m	
Fish Lake, St. Clair Co., E_{ggert} (MO)	ı m
American Bottoms, St. Clair Co., Eggert (MO)	
Missouri: St. Louis, Eggert (MO)	
St. Louis, Engelmann (NY)	
St. Francois River, Widman (MO)4.0 m	ım
•	n m
Jackson Co., Mackenzie (NY)1.0 m	
Iowa: Clay Co., Hayden 10127 (NY)4.0 m	n m
	n m
Arco, Metcalf 1799 (US)	
South Dakota: Aberdeen, Griffeths (MO)3.5 m	
Washebaugh Co., Over 2076 (US)	
Louisiana: St. Martinville, McAtee 2171 (US)	
Florida: Lee Co., Hitchcock 553 (NY)	
Cuba: Prov. Santa Clara, Britton & Wilson 5762 (NY)	
Washington: Skagit Co., Eyerdam 1310 (F)	m
California: San Joaquín Co. <i>Mason 11851</i> (NY)	ı m
Bear Valley, San Berbardino Co., Parish 1147 (NY)	
Bear Valley, San Bernardino Co., Parish 1147 (NI)	
Bear Valley, San Bernardino Co., Parish 1147 (MO)	
a n. a Ci i i i	n m
Ramona, San Diego Co., Brandegee (UC)	
Baja California: northern Lower California, Orcutt (NY)	
37 I) 7 G 110 I O 11 (1777)	n m
77 III 7 G 74 I O 77 (170)	n m
Sierra San Pedro Mártir, Wiggins & Demaree 4905 (UC)	
	1 111

Individuals with very short basal spines are probably what have given rise to reports of C. apiculatum Cham. from 'California near San Francisco' (Torr.& Gray, Fl. N. Am. 1: 55. 1838) C. submersum L. from San Francisco (Chamiso, Linnaea 4: 503. 1829) and from Puerto Rico (DeCandolle, Prod. 3: 74. 1828), and to C. demersum var. apiculatum Greke from Central America (Martius, Fl. Bras. 3, pt. 3: 748. 1894).

2. CERATOPHYLLUM ECHINATUM Gray, Ann. Lyc. N.Y. 4:49.1837, excluding plant from Surinam; Gray, Manual 40. 1848, in part; Fernald in Gray's Manual, ed. 8:637.1950. C. demersum var. echinatum Gray, Manual, ed. 2:383, 1856.

From southern Quebec to northern Michigan, south to Florida and eastern México (Map 2, dots). The leaves of this species are very similar to those of the European C. submersum; the latter species has a fruit that lacks marginal spines.

Gray cited two collections in his original description of C. echinatum: the first was from Princeton, New Jersey, collected by Torrey, and the second from Surinam communicated by Schweinitz. The latter is what is being described in this paper as C. Llerenae. The sheet from New Jersey has leaves 3 times forked into filiform segments, and the fruit is perfectly characteristic of what we now call C. echinatum. Of the two collections cited by Gray, the Torrey collection from New Jersey may therefore become LECTOTYPE, and the one from Surinam excluded as belonging to another species.

In the first edition of the Manual (1848), Gray treated all Ceratophyllum of North America under the name C. echinatum, with a description based on the idea that young achenes had but 2 basal spines and mature ones had several marginal spines.

3. CERATOPHYLLUM LLERENAE, n. sp., planta magna; frondibus 5-7 c m diametro; foliis fere 3- dichotomis; segmentis terminalibus cum 10-20 dentibus; fructus marginibus alatis, cum 16-18 dentibus brevibus. Guatemala to Trinidad and Brasil.

GUATEMALA: Depto. de Amatitlán, 1 July 1921, Tonduz 594 (GH); Charcos a orillas de la linea ferrea a Laguna, Depto. de Amatitlán, 1200 m, 1 July 1921, Coridux 549 (US). EL SALVADOR: Laguna Jagüey, 20 km SSW of San Miguel, 4 January 1591, Fassett 28553 (TYPE in Herbarium of Chicago Natural History Museum). CO-LOMBIA: Cienaga de Oro, Dep. Bolívar, 28 January 1918, Pennell 4129 (NY). VENEZUE LA: yerba submergida en las acequias de la ex-laguna de Caratipauo, inmediaciones de Maracay, Edo. Aragua, 26 May 1941, Salazar 12 (US). TRINIDAD: no locality, Crueger (GH). DUTCH GUIANA: Surinam, 'communicated by Schweinitz', (NY, cited by Gray under original description of C. echinatum).

- C. Llerenae was probably the basis of the report of C. demersum var. cristatum K. Sch. and C. cristatum Spruce from Brazil (Mart., Fl. Bras. 3, pt. 3:748. 1894), and the station cited there is included on Map 3. There is an earlier C. cristatum Guill. & Perr. from Africa (Fl. Seneg. Tent. 296. 1833).
- C. Llerenae is named for Dr. Carlos A. Llerena of San Salvador, whose in terest and efforts were of such importance in the establishment of the Instituto Tropical de Investigaciones Científicas. The specific name is pronounced, 'Yay-ray-nee'.
- 4. CERATOPHYLLUM FLORIDANUM, n. sp., foliis 2- vel 3- dichotomis; seg mentis terminalibus capillaribus cum 7-13 dentibus minutis; fructibus ovalibus, 3-4 m m longis, 1.7-2.2 mm latis, marginibus anguste alatis sine dentibus.—Florida Keys (Map 2, cross).

FLORIDA: grassland northwest of Watson Hammock, Big Pine Key, Monroe Co., 8 Nobember 1950, Killip 40723 (TYPE in U.S. National Herbarium); same locality, 29 January - 16 February 1940, Killip 32868 (US); 'South Florida', Blodgett (NY); 'Florida', A.W. C. [hapman] (NY).

This resembles the European C. submersum, but that species has the fruit 4.5-6 mm long and 3-4 mm wide, and the teeth on the leaves broad-based more like those of C. demersum. In absence of fruit it is difficult to distinguish C. floridanum from C. echinatum, but the former species has a few more teeth on the leaves.

ILLUSTRATIONS

Figs. 1-80 were made photographically, with paper negatives instead of film. The natural size figures were produced by printing directly from the pressed plant on chloride paper to make a negative. The enlargements were made by projecting the image of a pressed leaf onto bromide paper. These pictures have not been retouched, and such loss of detail as may be seen in Fig. 76 is because the leaf was not quite flat and so made imperfect contact with the paper. In the series Figs. 37-80, all the leaves grouped under a number came from the same plant.

Figs. 81-103 were made with a low-power compound microscope and camera lucida. Figs. 104-107 are free-hand drawings and are somewhat generalized.

Figures 1-3 Ceratophyllum, habit, x 1. 1. C. demersum. Oregon, Degener 18291 (MO).

2. C. demersum. Wisconsin, Steenis 612 (WIS). 3. C. echinatum. Missouri, Steyermark 12072 (MO).

Figures 4-11. C. demersum, common type. Fig. 4. Habit, x 1. Illinois, Chase 6875 (MO) Figs. 5,6. Leaves, x 4. Illinois, Chase 6875 (MO). Figs. 7, 8. Leaves, x 4. New York, Palmer 471 a (MO). Figs. 9, 10. Leaves, x 4. Michigan, Jones 13983 (GH). Fig. 11. Habit, x 1. Michigan, Jones 13983. (GH).

Figures 12-16. C. demersum, common type. Fig. 12. Habit, x 1. Texas, Trelease (MO). Figs. 13-16. Leaves, x 4. Texas, Trelease (MO).

Figures 17-20. C. demersum, tapered type. Figs. 17, 18. Leaves, x 4. Wisconsin, Seymour 10003 (WIS). Fig. 19. Leaf, x 4. Wisconsin, Steenis 612 (WIS). Fig. 20. Habit, x 1. Wisconsin, Steenis 612 (WIS).

Figures 21-22. C. demersum, slender type. Fig. 21. Leaf, x 4. Wisconsin, Wadmond & Fassett 19367 (WIS). Fig. 22. Habit, x 1. Wisconsin, Wadmond & Fassett 19367 (WIS).

Figures 23-27. C. demersum, slender type. Fig. 23. Leaf, x 4. Florida, Hitchcock 553 (MO). Figs. 24, 25, 26. Leaves, x 4. Pennsylvania, Adams & Tash 515 (MO). Fig. 27. Habit, x 1. Pennsylvania, Adams & Tash 515 (MO).

Figures 28-30. C. demersum, slender type. Figs. 28, 29. Leaf, x 4. Oregon, Degener 18291 (MO). Fig. 30, Habit, x 1. Oregon, Degener 18291. (MO).

Figures 31-34. C. echinatum. Fig. 31. Habit, x 1. Illinois, Patterson (MO). Fig. 32. Fruit, x 4. Illinois, Patterson (MO). Fig. 33. Leaf, x 4. Florida, Simpson (MO). Fig. 34. Habit, x 1. Missouri, Steyermark 12072 (MO).

Figure 35. C. Llerenae. Habit, x 1. El Salvador, Fassett 28553 (WIS).

Figure 36. C. Llerenae. Leaf, x 4. El Salvador, Fassett 28553 (WIS).

Figures 37-49. C. demersum, common type: leaves, x 1. Fig. 37. Santo Domingo, Fuertes 934 B (GH). Fig. 38. Cuba, Wright 3673 (GH). Fig. 39. New York, Phelps 450 (GH). Fig. 40. Baja California, Wiggins & Demaree 4905 (GH). Fig. 41. District of Columbia,

Ward (GH). Fig. 42. Quebec, Victorin & Rolland 46767 (GH). Fig. 43. Minnesota, Met calf 1935 (GH). Fig. 44. Vera Cruz, LeSueur 137 (GH). Fig. 45. Honduras, Edwards (GH). Fig. 46. Florida, Muenscher 14070 (GH). Fig. 47. Santo Domingo, Fuertes 875 (GH). Fig. 48. Cuba, Jack 6217 (GH). Fig. 49. Argentina, Venturi 7818 (GH).

Figures 50-58. C. demersum, slender type: leaves, x 1. Fig. 50. Argentina, Eyerdam & Beetle 22853 (GH). Fig. 51. Texas, Innes & Moore 1092 (GH). Fig. 52. Texas, Innes & Moore 1092 (GH). Fig. 54. Cuba, Marie-Victorin 58199 (GH). Fig. 55. Nebraska, Kiener 19529 (GH). Fig. 56. Puerto Rico, Sintenis 1023 (GH). Fig. 57. Baja California, Wiggins & Gillespie 3953 (GH). Fig. 58. California, Mason 11851 (GH).

Figures 59-65. C. demersum, tapered type: leaves, x 1. Fig. 59. New York, Burnham & Muenscher 16567 (GH). Fig. 60. Pennsylvania, Benner (GH). Fig. 61. Wisconsin, Smith 7564 (WIS). Fig. 62. Chihuahua, Hartman 610 (GH). Fig. 63. Wisconsin, Fassett 5240 (WIS). Fig. 64. Washington, St. John 2124 (GH). Fig. 65. Sonora, Rose, Standley & Rose 15135 (GH).

Figures 66-69. C. demersum, stubby type: leaves, x 1. Fig. 66. Delaware, Commons (GH). Fig. 67. Florida, Carter 30 (GH). Fig. 68. New Brunswick, Svenson & Fassett 2002 (GH). Fig. 69. Nebraska, Kiener 17776 (GH).

Figures 70-75. C. demersum from Europe: leaves, x 1. Fig. 70. Sweden, Nyman (GH). Fig. 71. France, Jeanport 730 (GH). Fig. 72. Ireland, Praeger (GH). Fig. 73. Germany, Braun (GH). Fig. 74. Russia, 3312 (GH). Fig. 75. Germany, Braun (GH).

Figures 76-80. C. echinatum: leaves, x 1. Fig. 76, Louisiana, Langlois 59 (GH). Fig. 77. Connecticut, Harger (GH). Fig. 78. Florida, Chapman (GH). Fig. 79. Pennsylvania, Adams (GH). Fig. 80. New York, Chamberlain & Moore (GH).

Figures 81-83. C. demersum, common type: parts of leaves, x 20. Fig. 81. Nevada. Wat son (GH). Fig. 82. Honduras, Edwards AQ-3 (GH). Fig. 83. Florida, Muenscher 14070 (GH).

Figures 84-85. C. demersum, slender type: parts of leaves, x 20. Fig. 84. Puerto Rico, Sintenis 1023 (GH). Fig. 85. Baja California, Wiggins & Cillespie 3993 (GH).

Figures 86-87. C. demersum, tapered type: parts of leaves, x 20. Fig. 86. Washington, St. John 2124 (GH). Fig. 87. Sonora, Rose, Standley & Rose 15135 (GH).

Figures 88-89. C. demersum, stubby type: parts of leaves. x 20. Fig. 88. Florida, Carter 30 (GH). Fig. 89. New Brunswick, Svenson & Fassett 2002 (GH).

Figures 90-91. C. demersum, inflated type; parts of leaves, x 20. Fig. 90. Holland (GH). Fig. 91. Chile, Meyer 2203 (GH).

Figures 92-94. C. demersum from Europe: parts of leaves, x 20. Fig. 92. Ireland, Prae ger (GH). Fig. 93. France, Jeanport 730 (GH). Fig. 94. Germany, Braun (GH).

Figures 95-100. C. echinatum: parts of leaves, x 20. Fig. 95. Tamaulipas, LeSueur(MO).

Fig. 96. Florida, Simpson (MO). Fig. 97. Connecticut, Harger (GH). Fig. 98. Minnesota, Cooper 263 (GH). Fig. 99. New York, Burnham (GH). Fig. 100. Florida, Chapman (GH).

Figures 101-102. C. Llerenae: parts of leaves, x 20. El Salvador, Fassett 28553 (WIS).

Figure 103. C. floridanum: part of leaf, x 20. Florida, A.W.C [hapman] (NY).

Figures 104-107. Fruits of Ceratophyllum, x about 4. Fig. 104. C. demersum, Illinois, Eggert (MO). Fig. 105. New York, LeRoy (NY). Fig. 106. C. Llerenae, El Salvador, Fassett 28553 (WIS). Fig. 107. C. floridanum, Florida, C [hapman] (NY).

SINOPSIS DEL GENERO CERATOPHYLLUM EN EL NUEVO MUNDO AL NORTE DEL ECUADOR

Hierbas siempre acuáticas, sumergidas, sin raíces; tallo débil, flexible, con la base dentro del fango; hojas verticiladas, 1-4 veces bilaciniadas, rara vez enteras; aquenios en las axilas de las hojas, con rostro largo y en algunas especies armados con espinas frágiles.

- a. Hojas 2-4 veces bilaciniadas (Figs. 76-80); dientes marginales de las lacinias pequeños y sin base verde (Figs. 95-103); fruto con ala o espinas marginales
 - b. Cuerpo del fruto de 3 mm o más de ancho, con espinas marginales

 - c. Margen del fruto con 16-18 espinas