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VOLUME XIII

NUMBER 3

BOTANICAL PAPERS

Iowa
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PUBLISHED BY THE UNIVERSITY, IOWA CITY, IOWA

Issued semi-monthly throughout the year. Entered at the post office at Iowa
City, Iowa, as second class matter under the Act of October 3, 1917.

UNIVERSITY OF IOWA STUDIES
IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

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CONTRIBUTION TO THE KNOWLEDGE OF THE
HYDNACEAE AND PHYLACTERIACEAE
OF IOWA

K. CEJP

Department of Cryptogamic Botany, Charles University, Praha, Czechoslovakia

Through the kindness of Professor G. W. Martin of the University of Iowa I have received rich collections of species belonging to the families Hydnaceae and Phylacteriaceae from various localities in the state of Iowa, together with a few specimens from New Jersey and Ohio. Among them are many species not hitherto cited from North America and which are only rarely mentioned in European literature, for example, *Acia denticulata*, *Acia uda*, *Acia setosa*, *Mucronella aggregata*, and *Odontia corrugata*.

GRANDINIA Fr.

Grandinia farinacca (Pers.) B. and G. On branches of various frondose trees, Estherville, Iowa, August 7, 1926; North Liberty, Iowa, July 5, 1924, G. W. M.

ODONTIA Fr.

Odontia stipata (Fr.) Quél. On Quercus, Iowa City, October 25, 1925, July 17, 1924, G. W. M.

Odontia arguta (Fr.) Quél. On coniferous plank, West Okoboji, Iowa, August 16, 1926, G. W. M.

Odontia corrugata Fr. On *Tilia americana*, Dickinson County, Iowa, July 7, 1925; E. side of West Okoboji Lake, Iowa, July 7, 1925, G. W. M. On *Quercus macrocarpa*, West Okoboji, Iowa, June 15, 1926, Lohman, Longnecker and Martin.

ACIA Karst.

Acia setosa (Pers.) Cejp, Monographia, p. 61, 1928. On trunk of dead Crataegus. Iowa City, April 6, 1924, H. Nicholson. In Europe a dangerous parasite on fruit trees, especially apple trees (= *Hydnum Schiedermayeri* Heufl.). Broadly effused, like a sulphur cover, filling hollows under old bark and in fissures. Attacks dead branches at first, later healthy wood. Although the fungus produces a huge quantity of spores, there is no rapid infection from tree to tree. Infection is oftener caused by the transmission of bits of infected wood from tree

to tree. The species seems to form a transition to the genus *Dryodon*, which it resembles in many respects.

Acia denticulata (Pers.) B. and G. Iowa City, November 2, 1923. The American specimens correspond in every detail with the European ones, for example, those which I collected at Letiny in Bohemia, on *Fagus* (Monographia, p. 61). Fairly rare.

Acia uda (Fr.) B. and G. Muscatine County, Iowa, November 10, 1923, G. W. M. In Europe very rare, on various kinds of wood. Characterized by the lemon or sulphur yellow color of the hymenium and spines. The American specimens correspond completely with the European ones.

Acia eriozona (Bres.) Cejp. (= *Odontia eriozona* Bresadola, Mycologia 17:71. 1925.) Estherville, Iowa, August 7, 1926, G. W. M.

Acia stenodon (Pers.) B. and G. Resupinate on dead log. Pine barrens of New Jersey, August 26, 1920, G. W. M.

RADULUM Fr.

Radulum membranaceum (Bull.) Bres. North Liberty, Iowa, July 5, 1924, G. W. M.

Radulum concentricum Cooke and Ellis, Grev. 1885. On *Quercus*, Iowa City, June 25, 1924, G. W. M.

Radulum orbiculare Fr. Iowa City, October 14, 1923, G. W. M.

Radulum pallidum Berkeley and Curtis. Iowa City, August 2, 1923, G. W. M.

MUCRONELLA Fr.

Mucronella agregata Fr. Midriver, Johnson County, Iowa, November 8, 1924, G. W. M. A rare species, easily escaping observation, characterized by very short spines, which are simple, free, and arranged in groups. Affiliated with *M. calva* (A. and S.) Fr.

MYCOLEPTODON Pat.

Mycoleptodon fimbriatum (Pers.) B. and G. Very frequent. West Okoboji, Iowa, August 14, 1926; Estherville, Iowa, August 7, 1926, on *Populus tremuloides*.

Mycoleptodon ochraceum (Pers.) B. and G. North Liberty, Iowa, June 8, 1923; Iowa City, September 2, 1924; on *Betula alba* var. *papyrifera*, New Brunswick, N. J., August 26, 1920, G. W. Martin

and E. West; Iowa City, August 2, 1923. Very abundant, often cited from North America. The American specimens have a rather broadly effused receptacle, they are larger than the European forms, and the spines are longer and darker, otherwise they closely resemble specimens from France and Czechoslovakia. This is the species referred to by Banker (1, p. 125) as *Steccherinum ochraceum* (Pers.) Gray.

STECCHERINUM S. F. Gray

Steccherinum pulcherrimum (Berk. and Curt.) Banker. On *Quercus*, Iowa City, June 25, 1924, F. F. Smith; Iowa City, April 6, 1924, H. Nicholson.

Steccherinum strigosum (Swartz) Banker. On *Quercus*, North Liberty, Iowa, September 27, 1925, G. W. M.

Steccherinum agaricoides (Swartz) Banker. On *Acer*, Preble County, Ohio, August 29, 1925, M. L. Lohman.

DRYODON Quélet

Dryodon septentrionalis (Fr.) Cejp (= *Steccherinum septentrionalis* (Fr.) Banker. On *Carya ovata*, Iowa City, June 25, 1924, G. Newbro.

PHELLODON Karst.

Phellodon Ellisianum Banker. Under pines, Cedar Bridge, N. J., August 22, 1920, G. W. M.

Phellodon delicatus (Schw.) Banker. North Liberty, Iowa, July 5, 1924, G. W. M.

REFERENCES CITED

1. Banker. A contribution to a revision of the North American Hydnaceae. Mem. Torrey Bot. Club 12. 1906.
2. Bourdot & Galzin. Hyménomycètes de France. Bull. Soc. Myc. de France.
3. Cejp. Monografie Hydnaceí republiky československé. Praha 1928-'29.
4. Saccardo. Sylloge fungorum, v. 6. 1888.

PLATE 1

Figs. 1, 2, 3. *Odontia stipata* (Fr.) Quel.

Figs. 4, 5. *Acia denticulata* (Pers.) B. & G.

All figures natural size.

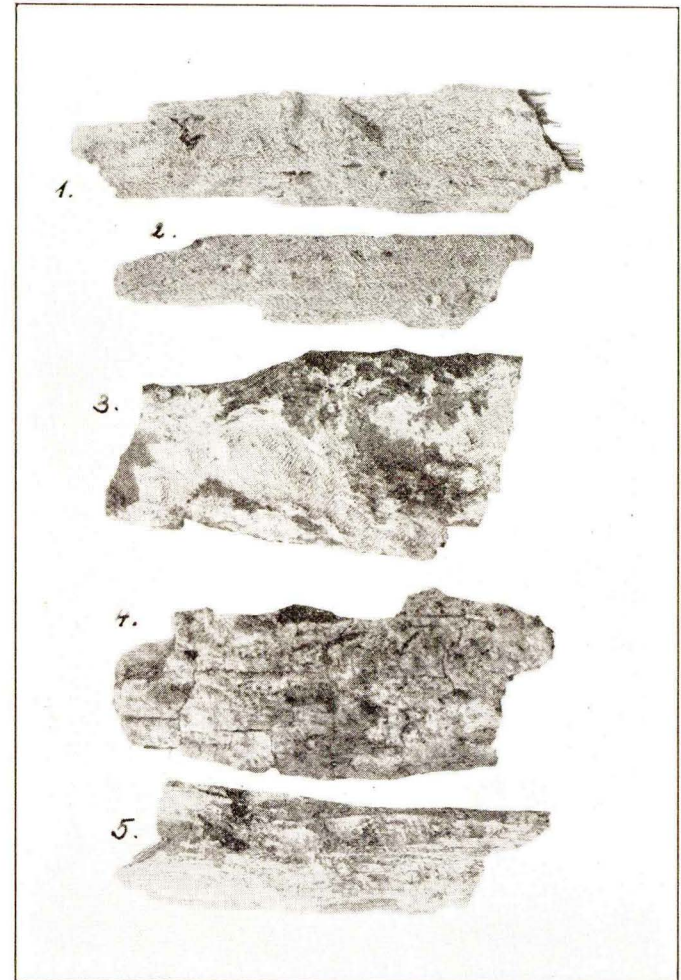
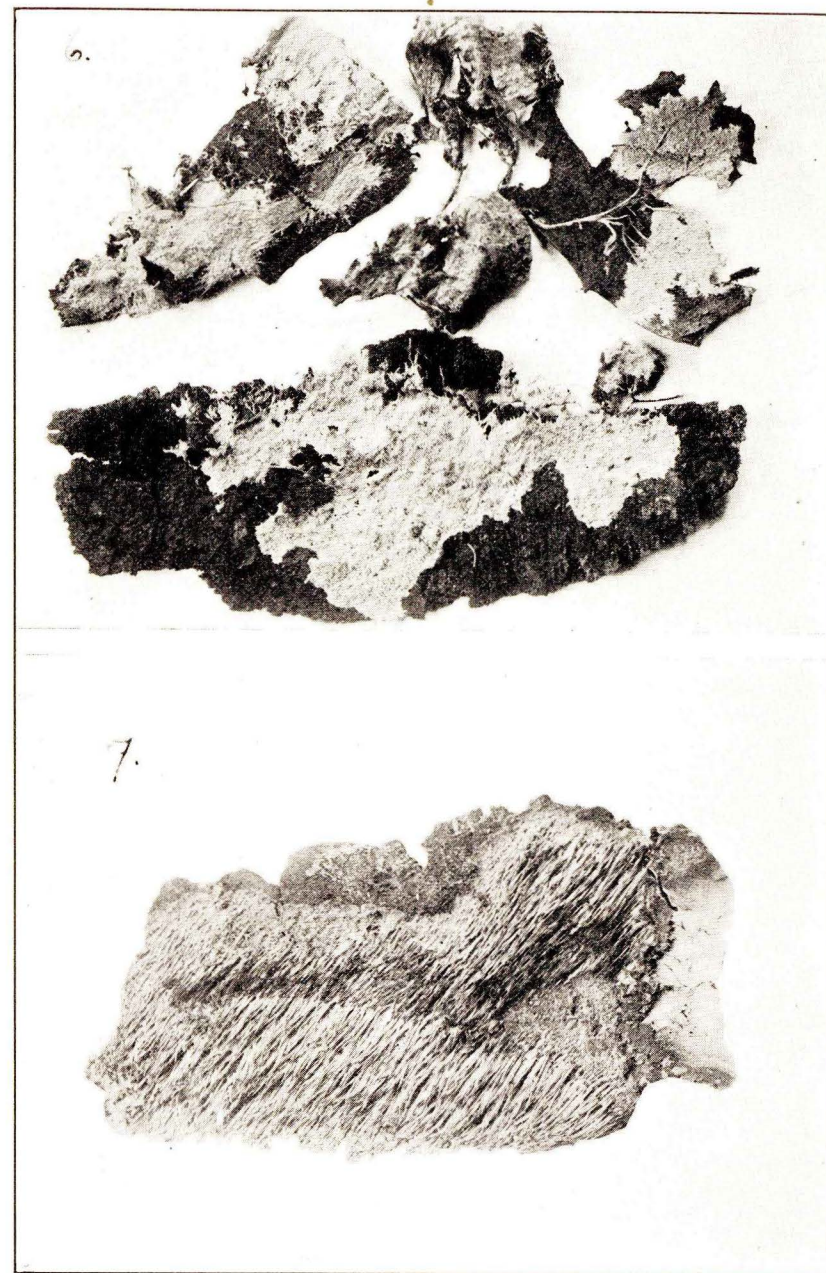


PLATE 2

Fig. 6. *Mycoleptodon fimbriatum* (Pers.) B. & G.

Fig. 7. *Acia setosa* (Pers.) Cejp.

All figures natural size.



THE MORPHOLOGY AND BIOLOGY OF CERATOPHYLLUM DEMERSUM

EDWARD N. JONES

Among the seed plants more completely adapted to an aquatic environment is *Ceratophyllum demersum* L. Its dissected leaves, slender and weak stems, total lack of roots, sub-surface pollination, and complete submergence through all phases of the life cycle give abundant evidence of a long association with water. Arber (1) pays tribute to its achievements by saying, "In the genus *Ceratophyllum* the aquatic habit seems to have reached its ultimate expression."

Ceratophyllum (Plate I, fig. 1), is commonly known as the hornwort, hornweed, morass weed, fish blankets, coontail moss, and coontail. Classification of the species is based chiefly upon the fruit. Its variability in shape, in size, and in the presence, exact location or absence of marginal spines (Plate I, fig. 2), has stimulated the suggestion of many species. The total number to date is thirty-five, according to Hooker and Jackson (9) and (10). The present tendency is to limit the number of species to two. Under this plan *C. demersum* includes all the forms having fruits with spines of any type and *C. submersum* all those without spines. This is a commendable solution of the question, at least until experimental morphology can determine the degree of the modifiability of the fruits. Many of the thirty-five descriptions of species have been based upon immature fruits and other unsound considerations.

In distribution *Ceratophyllum* is world wide. Specimens in the herbarium of the New York Botanical Garden may alone serve as the basis for this statement. These were reviewed by the writer in December, 1924. At that time the localities of collection included all of the continents, the Philippine Islands, and several temperate and subtropical islands of the Atlantic.

PART I. VEGETATIVE MORPHOLOGY

The vegetative organization of *Ceratophyllum* follows a distinct nodal and internodal plan. The nodes bear whorls of seven to twelve

leaves which are two or three times dichotomously forked into nearly cylindrical segments (Plate I, fig. 1). Each leaf segment bears short lateral projections which are quite acute. They serve to make the leaves rough to the touch. A dense growth of *Ceratophyllum* is in appearance somewhat like a "pine forest under water."

The Stem

The stem is slender, from one to three millimeters in diameter, and in length may be from a few centimeters to three and four meters. One large plant, taken from West Okoboji Lake, had a main stem 3.73 m. (12 ft., 2 in.) in length. Lateral branches are numerous. Their total length on this specimen was 14 m. (37 ft., 7 in.).

The internodes increase gradually in length from fractions of a millimeter at the growing tip to eight to ten centimeters in the fully elongated portions of the plant. The short internodes of the apical regions cause the imbrication of the leaves of the first fifteen to twenty nodes so that compact and almost bud-like tips are formed, both on the main axis and on the lateral branches. If stripped of these numerous leaves the stem sinks, which indicates that its specific gravity is greater than one; also that the plant depends upon the leaves for buoyancy.

Ceratophyllum does not develop roots. Modified branches, called "holdfasts," serve as anchorage organs. The basal portion of the main axis, with attached lateral branches, may be buried in the substratum for purposes of attachment. The degree of anchorage seems to be largely dependent on the nature of the bottom. In West Okoboji Lake, where most of the plants are over soft mud, attachment is so efficient that they resist removal as well as do many of the plants possessing root systems. The lack of roots is due to the failure of the radicle to develop beyond the rudimentary stage in the embryo. No further development takes place during or after germination.

Internally the stem of *Ceratophyllum* shows many structural adaptations which have been induced by an aquatic medium. In comparison with stems of terrestrial angiosperms these changes may be regarded as distinct reductions in structural complexity. However the three main tissues of epidermis, cortex, and vascular cylinder are present.

A very definite adaptation to the aquatic habitat is the non-cutini-

zation of the epidermal cells (Plate IV, fig. 21, E). There is little differentiation of the cells of the cortex. The air spaces, which are in the form of canals, are situated in the inner portions of the cortex (Plate IV, fig. 21 AS). The small bodies in the cells of the inner portion of the cortex are starch grains. The substance, which completely fills some of the cells and photographs black, is tannin.

The vascular tissue is so modified as to make difficult the recognition of xylem and phloem. There is an endodermal layer surrounding the vascular cylinder (Plate IV, fig. 21, EN). This is one indication of the rather primitive structure of the stem. The phloem is concentric to the xylem. There are no special mechanical cells in either tissue. Repeated tests of free-hand sections with stains specific for lignin failed to indicate its presence.

Sieve-tubes, companion cells, and phloem parenchyma are the cells found in the phloem. Surrounding each of the tubes are small cells, some of which are companion cells and others are phloem parenchyma. Some of the sieve-tubes show evidences of transformation into air spaces. This degeneration is particularly evident in stems in which the aerenchyma is strongly developed, as in the "pond" type of plant to be described later. In such stems the walls of the cells bordering the sieve-tube-like cells are curved into them and the tubes are very large (Plate IV, fig. 26, AS). This inward convexity is characteristic of the cells surrounding true air spaces as will be noticed in the cortical aerenchyma on the same figure. Stems of the lake type, with less development of aerenchyma, do not have this convexity of cell wall. Hence, it seems that stems in which there is a demand for a large air space system, the erstwhile sieve-tubes are being modified for this purpose. This is an additional indication of the modification of structure related to the aquatic environment.

The xylem is so degenerated that there is in reality very slight evidence of this tissue. There are two kinds of cells composing the xylem. One is larger than the other in diameter and has thicker walls. It is probably a reduced vessel (Plate IV, fig. 23, X). The other is of the xylem parenchyma type.

There is abundant evidence that the reduced vessel-like cells are becoming parenchymatous. Tannin, a storage product, is found in some of them. It appears as black cell content, chiefly in cells of the cortex (Plate IV, figs. 21-26). In fresh material chloroplasts are sometimes observed in this same type of cell, which is a condition

far removed from the true xylem conducting and mechanical elements. Starch grains, another storage product, are also sometimes found in some of the thick walled cells surrounding central canal (Plate IV, fig. 25, C CA). These observations all support the suggestion that the xylem is very degenerate. It is perhaps more appropriate to designate all the tissue inside the phloem as pith since the cells appear to be assuming the function of parenchyma, and in a few cases, even that of chlorenchyma. Furthermore they are quite similar to parenchyma cells in appearance.

Some of the outstanding features of stem structure which show modification by the aquatic medium are non-cutinization of the epidermis; lack of mechanical cells in either xylem or phloem; development of an occasional sieve-tube into aerenchyma; and transformation of some of xylem vessels into parenchyma.

Leaf Development

The meristem develops the usual primary layers, *dermatogen*, from which the epidermis arises; *periblem*, from which the cortex is formed; and *plerome*, which gives rise to the vascular tissue.

The origin of these layers in *Ceratophyllum* has been much disputed. The view which is probably correct is that advanced by Sanio (18) and upheld and further developed by Haberlandt (7) and Klercker (13). According to these observers, the dermatogen always forms by anticlines and may, in the case of young stems, develop from a single initial cell, supplemented by more initials as development proceeds. They believed that the periblem and plerome arise from single initials.

There is scarcely any differentiation in the terminal 125 microns of the vegetative axis. At 150-175 microns from the apex the first suggestions of leaf primordia appear. A slight bulge in the dermatogen and a disrupting of the even cell layering of the periblem are early evidences of leaf formation.

The initial step in leaf development consists of the periclinal division of a cell of the periblem (Plate II, fig. 7, at PB D). The outer of the two cells resulting from this division then divides anticlinally and produces the first two cells of the leaf periblem (Plate II, fig. 7, cells 1 and 2 at P₂). The laying down of these two cells produces the first slight protuberance on the side of the stem axis (Plate II, fig. 6, at P₁ and P₂). Further divisions, both in the same plane and at right and inclined angles to the original, result in the proliferation

of the periblem in three dimensions (Plate II, fig. 9, PB). The development of cells in this manner does not produce a solid periblem tissue, however. The protrusion of the plerome as a central core causes the periblem to develop in the form of a cylinder, as described below.

The dermatogen increases its area by cell division and thus accommodates the tissue developing within. Mitotic figures in the dermatogen (Plate II, fig. 8, at D), have been noted in leaves as far from the apex as the fifteenth node. This indicates that increase in the epidermal layer by cell division continues for a considerable time.

The plerome of the leaf originates by the division of a cell which has become surrounded by the periblem on all sides except toward the center of the axis (Plate II, fig. 11, PL). By continued anticlinal divisions the plerome enlarges and protrudes into the periblem like a finger in a glove (Plate II, fig. 7, PL and fig. 12, PL). This strand is apparent even at the first visible node below the apex where it may be distinguished by the darker staining reaction and by its periclinal divisions (Plate II, fig. 6, PL S). The connection between the vascular cylinder of the stem and the vascular tissue of the leaf is indicated by the dark, heavily nucleated rows of cells seen extending out to some of the leaves (Plate II, fig. 7).

The cell divisions taking place in the leaf primordia of the first three or four nodes are chiefly anticlinal but there is some increase in diameter due to cell enlargement. However, the first real radial thickening comes with the division of the original single layer of the periblem to form two radially arranged layers of the leaf cortex. This thickening is apparent at the fifth or sixth node so that in the leaves of these nodes and those subsequent below, a distinct diametrical increase accompanies the longitudinal. The latter far exceeds the former, however, for the leaves become as much as 20 mm. in length, whereas they are but 0.6 to 0.75 mm. in diameter.

Tanniferous trichomes are formed at the apices of young leaves by the enlargement and protrusion of epidermal tissue into rows of cells which secrete tannin. The leaves show the beginnings of this specialization at the sixth to eighth nodes where they are 150-200 microns in length. The tannin imparts a brown to reddish tinge to the tips. The imbrication of the young leaves in the bud results in these trichomes forming a layer which covers the growing point. Klercker (13) suggests that these may be of value also in protection against parasites.

Air spaces begin to develop when the leaf is 350 to 400 microns long—on 11th to 12th nodes. They originate by the pulling apart of certain cortical cells in the abaxial portion of the leaf near the base. The development of air spaces is thus schizogenous. As the leaf elongates, the development of these spaces progresses toward the apex (Plate III, fig. 13, A S).

The aerenchyma becomes well developed, even in immature leaves (Plate III, fig. 15). In mature foliar organs it constitutes about one-third of the total volume. This accounts for leaf buoyancy. The leaves of the "holdfasts" have less extensive air space development, due to their subterranean surroundings.

As the air spaces enlarge, their borders come to be composed of several cortical cells instead of parts of two, as in the younger stages. Increase in the number of cells along the lateral walls of the lacunae is accompanied by similar divisions in the septa, so that the spaces enlarge in diameter as well as in length (Plate III, fig. 14, C and C₂). The air space system of the leaves is directly responsible for keeping *Ceratophyllum* plants afloat. The stem itself sinks in water, although equipped with small air spaces, as previously described.

The Mature Leaf

The mature leaf differs from the younger stages in slightly changed relations of the parts. The slender vascular strand is central in position in the terminal portion of the mature leaf but stops 50 to 60 microns short of the tip (Plate III, figs. 16 and 17).

The cortical cells are arranged in rows radially. Air spaces occupy the interstices. This general radial plan is continued down the leaf with a gradual change from the nearly radial to a true radial arrangement at 200 to 300 microns from the apex. Here the vascular bundle has enlarged to a group of ten to fifteen elongated cells of small diameter.

Beginning about a millimeter below the apex, the series of air chambers on the abaxial side of the leaf enlarge and push the vascular tissue to one side (Plate III, fig. 19, V). This continued enlargement of the air spaces, with the resultant eccentricity of the vascular tissue, continues in each of the dichotomous segments to the point where junction takes place. Just below the junction of the two forks, the vascular bundles of the two branches coalesce (Plate III, fig. 20,

V). The air spaces from the branches are continued in one series of larger air cavities which extends to the base of the leaf.

Experimental Morphology

Ceratophyllum is easily modified in form by various factors of the environment. The aquatic habitats of the Okoboji region, exclusive of swamps, are classifiable into clear lakes, semi-stagnant lakes, and stagnant ponds. A characteristic vegetative expression of *Ceratophyllum* is found in each of these habitats.

The first is the *lake type*, represented by plants of sturdy habit, found in West Okoboji Lake. This lake is characterized by clear water which in summer reaches a temperature of 25°-26°C. A lake type plant has a stem of large diameter, and leaves which are relatively short, stiff, and rough (Plate IV, fig. 22, C).

A second form, which will be called the *intermediate type*, is found in the shallow Minnesota projection of Spirit Lake, in Upper Gar Lake and in Little Spirit Lake. These habitats vary in depth from 0.3 m. to 1.3 m. The water is of medium clearness and at times reaches a temperature of 32°-33°C. The plants are very bushy in form and have very long tip regions by means of which they are easily recognized.

The third form, called here the *pond type*, is very spindling and is found only in shallow, semi-stagnant water which may be warmed to 32°-33°C. The best examples of this type (Plate IV, fig. 22 A), were found in Gull Point Pond. The marshes to the west of Spirit Lake and the one to the northwest of Swan Lake also produce this form. Both stem and leaves are very fine in texture, and the latter collapse limply when the plants are removed from the water. The leaves of the lake and intermediate types remain rigid when the supporting action of the water is withdrawn.

In order to determine whether or not *Ceratophyllum* can be modified by being changed from one habitat to another, plants were taken from Miller's Bay of West Okoboji Lake and transplanted in Gull Point Pond. The transfer was made on July 4, 1923, and the marked plants were removed from this pond for examination on August 13, following. Modification was considered to have taken place when newly developed portions of the plants were slender and spindling, and when the region of transition from the coarse lake type to the slender pond type was apparent. On this basis 61%, or sixteen out of twenty-six transplanted specimens, showed modification of form.

Typical results are shown on the experimental specimen (Plate IV, fig. 22, B). The old lake type stem is shown below (Plate IV, fig. 22, B at L S) with its whorl of stiff lake type leaves (Plate IV, fig. 22, B at L L). A gradual reduction in size of stem and coarseness of leaves is apparent from the base toward the apices of the newly developed branches, marked P. This transition is due to the beginning of the growth of the branch while still in the lake under conditions fostering coarse growth, and its continuance in the pond under conditions promoting slender growth. A portion of a pond type control plant is pictured at A, and of a lake type control at C. There is evident similarity between the pond type control (Plate IV, fig. 22, A), and the upper portion of the experimental specimen (Plate IV, fig. 22, B), and between the lake type control (Plate IV, fig. 22, C), and the lower portion of the experimental plant.

A comparative study of the structure of stems of the pond, intermediate, and lake types shows that the factors which cause slender growth also bring about the development of a relatively large amount of air space. The stems of the slender pond type (Plate IV, fig. 26, A S) have more air space in proportion to their size than do the larger stems of the lake plants (Plate IV, fig. 23, A S). The intermediate type of stem has also an intermediate amount of air space (Plate IV, fig. 25, A S).

Thus, it is apparent that modification of the vegetative form of the plants is accompanied by a parallel modification in air space development within the stem.

PART II. FLOWERS AND POLLINATION

In floral habit the genus is monoecious and diclinous. The flowers are sessile to subsessile and are borne inconspicuously at the nodes in the axils of the leaves.

Both staminate and pistillate flowers are found only on the younger portions of the main axis and of the larger lateral branches. Doubtless this is due to the absence of meristematic tissue in their older portions. To determine which nodes, if any, bear flowers the most frequently, eighty-nine plants from West Okoboji Lake were examined. The results show that pistillate flowers may be developed to a stage visible to the naked eye on nodes as near the tip as the nineteenth,

which is really the second visible node¹. By far the greater majority are borne on nodes twenty to twenty-six. The staminate flowers range in location from nodes nineteen to forty-two but most of them are grouped from the twenty-second to the twenty-ninth. Thus, on the average, the staminate flowers are located slightly farther away from the tip of the axis than are the pistillate, and, therefore, a little lower in the water. Since the pollen grains of *Ceratophyllum* sink, though slowly, it is probable that the relative position of the two kinds of flowers tends to promote cross-pollination to some degree.

Previous to 1806, it had been accepted as axiomatic that pollination of *all* plants is aerial. Willdenow (21) was the first to suggest the completely hydrophilous pollination of *Ceratophyllum*. All recorded observations state that anther dehiscence occurs only after the stamen has broken loose from the receptacle and risen to the surface. To check these reports staminate flowers were examined while still in their natural position on the plant. In order to facilitate this study a water tight cell was made by sealing together two 50x60 mm. micro slides with a 3 mm. space between them. Sections of the stem with flowers still attached, were placed in this cell which was in turn placed on the stage of a dissecting binocular microscope. The following observations were made with this set-up.

The mature stamens have a mottled appearance under magnification due to the accumulation of gas in the endothelial tissue just under the epidermis. The first visible step of dehiscence is the appearance of a large gas bubble at a median apical point on the surface of one of the two locules of the anther. As the bubble rises in the water a small rupture is apparent in the wall of the anther at the point where it appeared.

From this opening one or two more bubbles of gas escape, followed by the emergence of the pollen grains. The aperture increases in size by the continuance of the slit down the face of the locule. The pollen grains emerge rather slowly at first, and then, as the opening enlarges, tumble out as do apples being poured from a sack (Plate I, fig. 3).

These observations establish the possibility of actual dehiscence of anthers while the stamens are still attached to the plant. Furthermore, stamens have been found with locules open and empty before separation from the receptacle has taken place. This qualifies the view

¹The average "bud-like" tip, see figure 1, has fifteen to twenty nodes within it which are invisible to the naked eye. Hence the seventeenth is taken as an average for the first visible node.

previously advanced by Dutailly (3) and upheld by Rose (17) that dehiscence occurs *only after* ("alors seulement") the stamens have become detached and risen to the surface. It was observed that all stamens do become detached ultimately, irrespective of whether dehiscence takes place before or after leaving the receptacle. This mode of behavior suggested the following experiment on stamen shedding.

During the summer of 1924, *Ceratophyllum* plants which had been received from West Okoboji Lake on June 5, grew luxuriantly in the aquaria of the University of Iowa greenhouses. Flowers were first noted on these plants on June 25th, and records of the rate of stamen shedding were begun on July 15th. Twenty-four staminate flowers were examined three times daily, at 7:00 A.M., 1:30 P.M., and 6:30 P.M., and records made of the number of stamens detached from each flower at each reading.

It was found that most of the stamens detach during daylight hours. The release of gas, presumably oxygen escaping as a by-product of photosynthesis, seems to be the mechanical force which causes the stamens to break loose. It was frequently noted that a vigorous stream of bubbles comes from the point of attachment on the receptacle just after the stamen has been detached and risen to the surface. This, together with the fact that most of the stamens break loose during the daily period of photosynthesis, suggests the theory that gas pressure is the immediate mechanical cause of detachment. Wylie (22) observed the same phenomenon in *Elodea canadensis*. He also reported that the gas aids in bringing the stamens to the surface.

The stamens of *Ceratophyllum* mature in centripetal order. Occasionally some at the edge of the flower are shed before those in the center are recognizable as stamens. The total elapse of time between the shedding of the first and last stamens of a flower averages about seven days.

The number of pollen grains produced is quite large—over 100,000 grains per plant. This estimate is based upon the study of eighty-nine plants collected in Miller's Bay, which revealed the following:

Average number of staminate flowers per plant-----	3
“ “ “ stamens per flower-----	13
“ “ “ pollen grains per stamen-----	2600
“ “ “ “ “ flower-----	33,800
“ “ “ “ “ plant-----	101,400

The number of pollen grains developing at one time on a plant is even larger in the case of specimens growing in smaller and shallower bodies of water, such as Gull Point Pond and Little Spirit Lake, since the number of staminate flowers per plant is greater. Furthermore, the plants in those habitats grow in great profusion and form regular under-water mats. Therefore, the number of pollen grains discharged per day into each cubic centimeter of water must run into the hundreds. Truly it seems that the best assurance of pollination is the prolific production of the pollen grains.

Preparatory to the discussion of the actual process of pollination, consideration is given to the structure of the style and stigma of the pistillate flower. The elongated style is usually more or less flattened and twisted in its apical portion but is cylindrical below (Plate I, fig. 4). The adaxial surface of the stigma is grooved, and this groove terminates at its lower end in a depression which is here called the *stigmatic pocket*. The pollen grains must come to rest in this pocket in order to accomplish pollination. Strasburger (20) reports the presence of a similar stigmatic device in *Ceratophyllum submersum*.

It is possible to approximate the natural conditions under which pollination takes place by the use of the water cell described in connection with stamen dehiscence. Portions of stems with pistillate flowers attached were placed in the water of the mount for microscopic observation.

Stamens in actual dehiscence were seen but rarely. It therefore became necessary to secure pollen grains by artificial dehiscence. Only these stamens were used which gave every indication of being mature. There were no noticeable differences in the appearance of the pollen from naturally and from artificially opened anthers. Exposure of flowers, stamens or pollen grains to the air was not permitted at any phase of the procedure.

Pollen grains of *Ceratophyllum* sink slowly in the water following dehiscence. It requires eight to ten seconds for an unobstructed grain to move across the microscopic field of 1.6 mm. diameter. The rate of movement is thus approximately 0.16 to 0.2 mm. per second. While the tendency of most of the grains is to sink slowly, some have been observed suspended in the water a little more than two hours after dehiscence. Their buoyancy makes them responsive to currents. Transportation of the grains from the vicinity of the plant is thus facilitated and with it the chances for cross-pollination are increased.

Pollen grains were carefully observed as they came in contact with the stigma but there was no evidence of sticky secretions, nor are there stigmatic hairs. The only pollen catching adaptation noticed was a torsion of the style so as to place the stigmatic pocket on the dorsal surface. This was observed in a majority of the flowers examined.

All observations made in this study indicate that in order to reach the stigmatic pocket pollen grains must either fall directly into it or into the groove situated just above. As may be seen in figure 4, this receptive area is relatively small, even in comparison with the style itself, which is seldom over three millimeters in length. The chances of a pollen grain striking this small surface seem rather hazardous, and the best guarantee of successful pollination is through the abundant supply of pollen mentioned above.

Sterility is quite common in *Ceratophyllum*. The plants growing in West Okoboji Lake flower freely but fruits are rarely ever found. Only one record of such fruiting could be obtained. Dr. B. Shimek of the Department of Botany, University of Iowa, reported verbally to the writer the development of fruits on *Ceratophyllum* plants growing in the shallower portions of Miller's Bay during the summer of 1913, when the water level became very low.

In Gull Point Pond and Little Spirit Lake, both of which are shallow and semi-stagnant, fruits were set in large numbers during each of the three summers that these areas were under observation by the writer. A third observed habitat was in the large cement aquaria in the University greenhouses at Iowa City during the summers of 1924 and 1925. No fruits were produced in these although the plants flowered profusely.

Differences in temperature furnish the most promising suggestion as to the factor responsible for fruit production in some habitats and sterility in others. The water in Gull Point Pond averaged 32.5°C. (91°F.) from June 23 to August 13, 1923. The average in Miller's Bay of West Okoboji Lake was 25.6°C. (78.5°F.) during the same period according to unpublished records kept by Dr. G. E. Potter. The average daily temperature in the greenhouse aquaria during the summer of 1924 was 25.7°C. (78.7°F.). The average for the two habitats where fruits were not produced was thus very nearly the same, whereas, in Gull Point Pond, where fruits were produced in abundance, it was nearly seven degrees higher.

Guppy (6) determined that the temperature of the water must

rise daily to over 26.5°C. (80°F.) before the fruits of *Ceratophyllum* will mature. It seems probable, therefore, that the plants in West Okoboji Lake and in the greenhouse aquaria did not produce fruits because of the failure of the water to reach daily, during the flowering season, the critical temperature of 26.5°C. The evidence indicates that light is not a potent factor, since the lake and the pond are both open, unshaded habitats. The plants in the aquaria were shaded in early morning and late afternoon. However, there is no correlation between light and sterility, for the lake plants, exposed to strong light, were also sterile.

Wind could have had little or no effect. In the lake, the dense vegetation at the surface of Little Miller's Bay, where the observations were made, almost entirely prevents wave formation. The aquaria, being in-doors, were protected, and Gull Point Pond is too small and too shallow to permit the formation of more than ripples on its surface. In that portion of Little Spirit Lake where the fruits were formed, the water is also shallow with resulting lack of waves. Absence of marked wave action is thus common to all of the habitats, and wind, therefore, could not have been important. Temperature is the only factor which, as above described, could be correlated with sterility and its alternative of fertility.

Vegetative Propagation

The chief method of reproduction is by vegetative propagation. This is readily accomplished by the breaking up of larger plants and by the shedding of shorter branches and also bud-like tips.

The efficiency of vegetative propagation is illustrated by the following experiment. Following a severe storm on July 5, 1922, three hundred and eighty fragments of *Ceratophyllum* were picked up on twenty meters of the shore of Miller's Bay. The average number of pieces cast up was nineteen fragments to the meter. These had been thrown clear of the water and were partially dried. In order to test the powers of rejuvenation and regeneration, twenty pieces were selected, ranging from a bud-like stem-tip 7 mm. long to a stem 14.8 cm. long, absolutely stripped of leaves. These were placed in an aquarium and records of their growth were kept for forty days. Nineteen of the fragments lived, and at the close of the experiment, each was well on the way toward the formation of a new plant. The average growth of each specimen was 1.78 cm., and nine developed

one or more secondary branches. The only piece which died was the naked stem.

The fact that these fragments were 95 per cent efficient in the propagation of new plants proves that detached pieces of *Ceratophyllum* will continue growth even after temporary or partial drying. Fragments which are stranded of course soon die, but those caught in the tangle of surface vegetation in the bays or carried into quiet waters commonly grow into new plants.

In the fall of the year, the plant stem in many cases becomes quite brittle, which results in fragmentation. The inception of brittleness is accompanied by loss of buoyancy due presumably to decrease in photosynthetic activity with its release of oxygen. The pieces which break from the parent plants settle to the bottom. The fragments thus formed go through a period of winter dormancy and are apparently lifeless as they lie on the bottom where they gradually become covered, either in part or entirely, with silt and other deposits. In the spring these fragments resume vegetative activity and send out one or more new branches from branch buds which have remained dormant in the leaf axils. These fragments are here called winter buds in view of their marked power to develop new branches which subsequently develop into new plants.

In the case of *Ceratophyllum* plants growing in greenhouse aquaria in the latitude of Iowa City, 42°N., the period of dormancy begins during the latter part of October, and continues until the latter part of April. This winter dormancy was broken experimentally by means of increased illumination and higher temperature. On November 15, 1923, four 200-watt electric bulbs were placed, by special insulation of the sockets, near the bottom of the aquarium and allowed to burn day and night. Continuous illumination was thus provided and the water warmed from the usual average of 12-14°C. to 24°C. The plants were completely rejuvenated by November 27, and were kept in almost midsummer luxuriance from then until February 23, 1924, at which time the experiment was discontinued.

While some plants undergo fragmentation in varying degrees, others vegetate during the winter. This fact is reported by Clark (4) and Irmisch (11). Also, the writer took plants from beneath the ice on Miller's Bay of West Okoboji Lake on March 3, 1923, which were very similar in appearance to summer plants except that the chlorophyll was less vivid.

PART III. BIOLOGY

Distribution and Other Biological Aspects

West Okoboji is a typical fresh water lake situated near the northern boundary of Iowa, in Dickinson County. Its exact location is latitude 43°35'N. and longitude 95°15'W. Geologically, it is of glacial origin and is a feature of the Wisconsin drift sheet.

The following figures quoted in condensed form from Birge and Juday (2), give size and depth. Area, 3788 acres (1535 hectares)²; greatest length, 5.45 mi. (8.79 kilometers); greatest breadth, 2.84 mi. (4.57 km.); length of shore line, 18.2 mi. (29.3 km.); mean depth³, 40.4 ft. (12.3 meters); maximum depth, 132 ft. (40.2 m.).

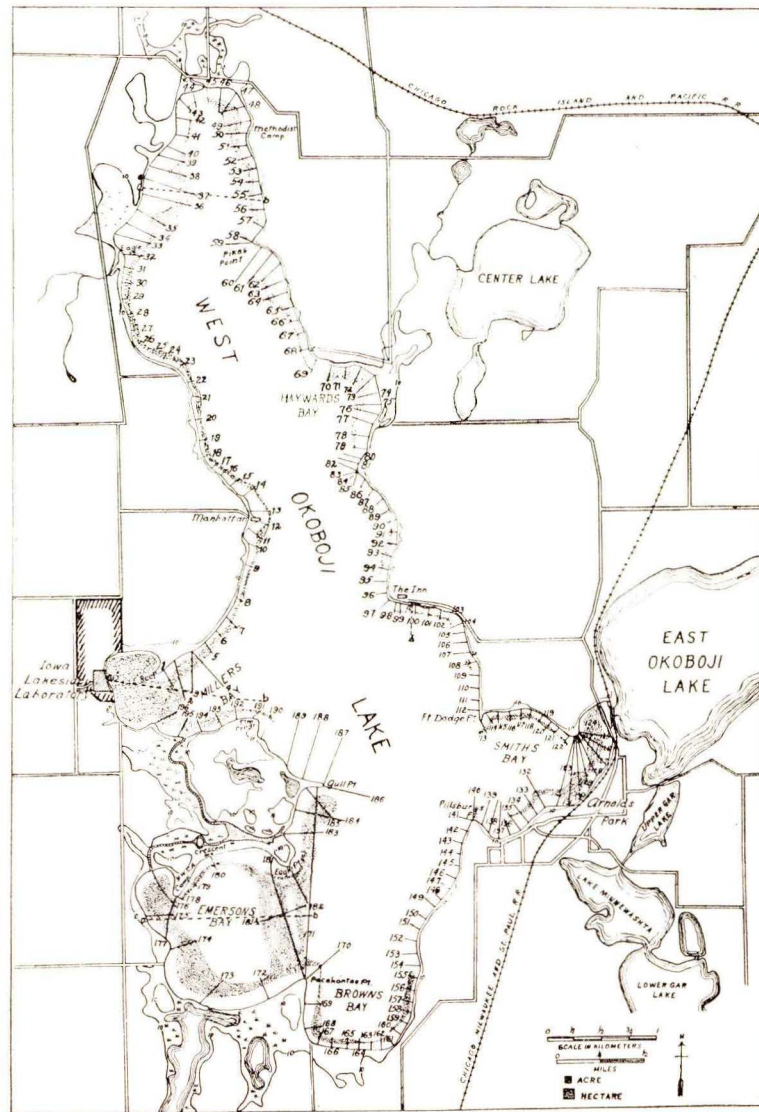
A Survey of the Macrophytic Area—During the summers of 1921, 1922, and 1923, a survey was made by the writer of all portions of the lake which support macrophytes, or those plants visible to the naked eye. One hundred and ninety-six survey stations were established along the 29.3 kilometers (18.2 mi.) of shore line.

The lines numbered from 1 to 196 on text figure 1, show the location of these stations. The average distance between them was 149.5 meters. The distribution of plants at each station was determined by examining the vegetation along a line placed generally at right angle to the shore. The water was usually clear enough to permit the recognition of plants in depths up to two meters, and beyond this limit of visibility a many pronged hook was used for dredging. A calibrated, weighted line was the means of securing depth measurements. The distances out from shore and along shore between stations were determined by use of the Hymans Pocket Range Finder, an instrument rated as giving results with about five per cent error. Notes were taken of the species at each station and of their position, both as to depth and distance from shore. A rowboat equipped with detachable out-board motor was used in making the survey.

It is impracticable, in the scope of this report, to give all of the data secured, but as an example, the report on three typical stations is given in table I. A list of the genera and species of the macrophytes precedes the table.

²For comparative size of an acre and a hectare see scale, text figure 1.

³Mean depth is found by dividing volume by area of surface.



Text Figure 1. Map of West Okoboji Lake showing distribution of *Ceratophyllum* (indicated by stippled areas). Survey stations shown by numbered lines extending out from shore. Lines marked a—b are referred to in Text Fig. 2.

List of Species Noted in Survey of West Okoboji Lake

Abbreviations in Table I are as follows:

- C-----*Ceratophyllum demersum* L.
 B-----*Bidens Beckii* Torr.
 Ch-----*Chara* sp.
 E-----*Elodea ioensis* (Michx.) Wylie
 H-----*Hypnum fluitans* var.
 M-----*Myriophyllum spicatum* L.
 N-----*Najas flexilis* (Willd.) R. and S.
 Ni-----*Nitella* sp.
 P-----*Potamogeton amplifolius* Tuck.
 Pf-----*Potamogeton foliosus* Raf.
 Pn-----*Potamogeton natans* L.
 Pp-----*Potamogeton pectinatus* L.
 Ppr-----*Potamogeton praelongus* Wulf.
 Ppu-----*Potamogeton pusillus* L.
 PR-----*Potamogeton Richardsonii* (Benn.) Ryd.
 Pz-----*Potamogeton zosterifolius* Schumacher.
 R-----*Ranunculus aquatilis* L.
 T-----*Tolypella* sp.
 V-----*Vallisneria spiralis* L.

TABLE I. DATA OF THREE REPRESENTATIVE SURVEY STATIONS.

Sta.	Location	Vegetation*	Depth	Dist. from shore	Substratum at shore
64	592 m. south of Pike's Point	Ch, Pp, PR, Pn, Pa	ns-3.5	ns-125	boulders
		C, Ppr	3.5-4.5	125-231	cobbles
		T	4.5-4.6	231-247	
95	357 m. north of The Inn	Ch, PR	ns-4.1	ns-74	boulders
		Ch	4.1-6	74-111	cobbles
174	In southwest portion Emerson's Bay	Nothing	ns-1.2	ns-30	cobbles
		Ch, Pn	1.2-1.7	30-37	pebbles
		Ch, M	1.7-1.8	37-74	
		C, Ch	1.8-2.1	74-115	
		Ch	2.1-3	115-160	
		C, Pa, B	3-3.3	160-177	
		C	3.3-5.3	177-274	

*For key to abbreviations used in this column see List of Species given just preceding this table.

Sta. 64 has plant distribution typical of low, open-shore habitat; Sta. 95 of precipitous, cliff-like shore; and Sta. 174 of bays (see text fig. 1). Measurements are recorded in meters. Letters "ns" (meaning "near shore") when placed in depth column indicate a depth of 0 to 1 meter, and in distance from shore column, indicate a distance of 0 to 5 meters from shore.

The survey data as a whole indicate that the major vegetation is distributed over three to four zones, depending on the location along the shore line. These zones have been previously discussed by Wylie (23) and by the writer (12), and are, therefore, only mentioned here. Zone I, near shore, is characterized by a lack of vegetation, zone II by Chara, zone III by Ceratophyllum, and zone IV by either Nitella, Tolypella, or Chara. This zonation is quite marked off the shores which are low and slope gradually up from the water. It is not so distinct, however, in the bays. Here the large areas of shallow water over a mud substratum favor dominance by any or all such aquatic Angiosperms as Myriophyllum, Bidens, Ranunculus, Ceratophyllum, and species of Potamogeton.

The distribution of Ceratophyllum in the entire lake is shown on text figure 1. The stippled portions which are seen to be opposite most of the shore line, show the exact locations of the areas occupied by the plant. It is estimated that Ceratophyllum covered a total of

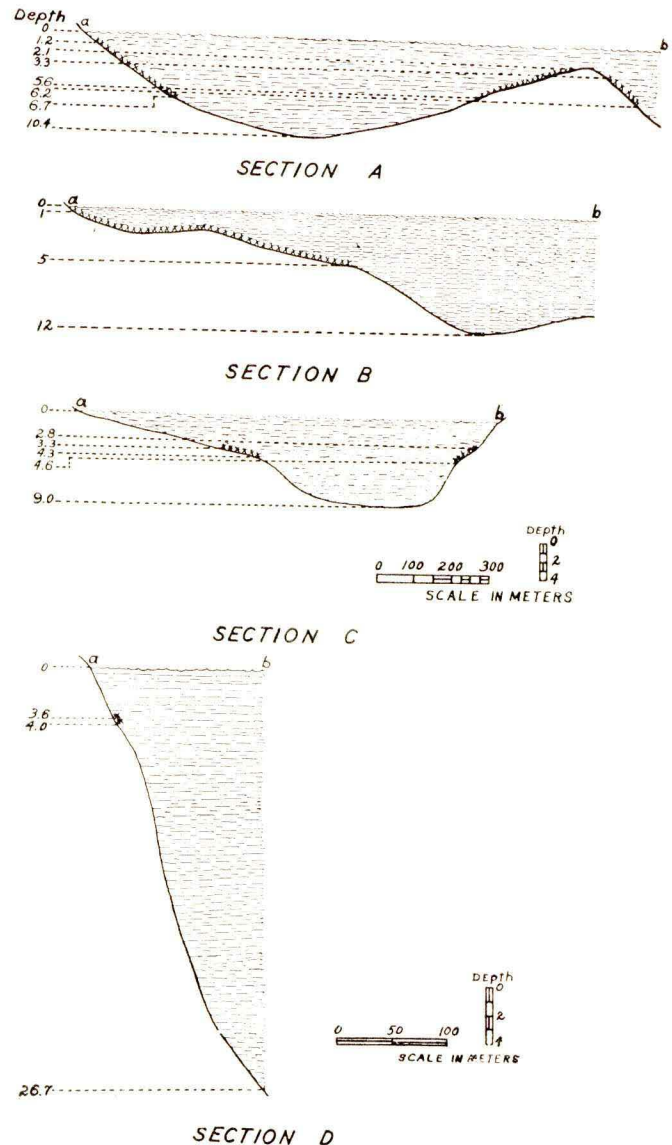
434 acres, or 175.5 hectares, at the time of the survey. As a basis for this estimate the width of the Ceratophyllum zone at each station, and between stations, was plotted on the map. The total map area so covered was determined and converted by scale into acres.

The area of 434 acres covered by the plant is equal to 11.5 per cent of the total surface area of the lake. The effects on distribution of such factors as depth, gradient of bottom slope, and nature of substratum are evident in the fact that 77.9 per cent of the total acreage is found on the west side as compared with the east side of the lake, and 72 per cent in the bays as contrasted with the main body of the lake. A complete summary of these areas and percentages is given in Table II.

TABLE II—GENERAL COMPARISON OF AREAS COVERED BY CERATOPHYLLUM.

Portion of Lake	Total Area		Per Cent of Total Area		Per Cent of Total Area C. demersum		Per Cent of Total Area Lake	
	acre	hectare	Lake	demersum	demersum	demersum	Lake	
Entire Lake	3788	1535	100.0	433.88	175.5	100.0	11.45	
West ½ of Lake	1894	767.5	50.0	338.07	136.8	77.9	9.19	
East ½ of Lake	1894	767.5	50.0	95.81	38.7	22.1	2.26	
Bays only	1226.1	496.2	32.4	312.06	126.36	72.14	8.25	
Entire Lake excluding Bays	2561.9	1038.8	67.6	121.82	48.14	27.86	3.20	

There is a direct correlation between the degree of gradient of substratum slope and the distribution of Ceratophyllum. This correlation is graphically represented by the figures of vertical sections through Emerson's and Miller's Bays which have gradual slopes; across the North End with a medium gradient; and just off The Inn where the slope is very abrupt (text figure 2). It will be noted by comparing the various diagrams that the width of the Ceratophyllum zone is in almost direct proportion to the rate of decline of the slope of the bottom.



Text Figure 2. Vertical sections of West Okoboji Lake at various points to show effect of depth and substratum slope on width of *Ceratophyllum* zone (indicated by x's). Depth recorded in meters. For location of lines a—b see Text Fig. 1.

- Section A—Through Emerson's Bay
 Section B—Through Miller's Bay
 Section C—Through north end of lake
 Section D—Through abrupt slope near The Inn

The nature of the substratum is influenced by the gradient of the slope and is, therefore, correlated with it. Gradual slopes are usually of mud. Abrupt slopes, on the other hand, are usually of gravel and sand, and the waters above are commonly wind and wave swept because of non-protecting shores adjacent. This situation is unfavorable to a rootless plant such as *Ceratophyllum*.

The bays are the favorite habitats of the plant largely because of substratum which is muddy in nature and gradual in slope. A comparison of the bays with respect to their suitability is given in Table III. Miller's Bay has two-thirds of its area covered by *Ceratophyllum*, which is a larger proportion than that of any other bay. Emerson's Bay supports approximately one-fourth of all the *Ceratophyllum* found in the lake, while Miller's has the smaller fraction of one-fifth. The former, however, is nearly three times as large. As a result of the comparison, it is found that Miller's Bay is the most favorable habitat for the plant. In addition, it has in its waters practically every other plant found in the lake. The under-water gardens of this bay are indeed an asset to the Iowa Lakeside Laboratory situated on its western shore.

TABLE III—AREAS OF THE RESPECTIVE BAYS IN ACRES AND IN PER CENT OF TOTAL AREA OF LAKE. ACREAGE OF *CERATOPHYLLUM* AND PER CENT OF TOTAL IN EACH BAY ALSO INDICATED.

Bay	Area (Acres)	Per Cent Total Area of Lake	Acreage of <i>Ceratophyllum</i>	Per Cent Total Area <i>Ceratophyllum</i>
Emerson's	377	9.95	107	24.6
Miller's	131	3.45	87	20.0
North End	267	7.06	53	12.3
Smith's	273	7.20	35	8.1
Hayward's	71	1.9	15	3.4
Brown's	107	2.82	16	3.6
Totals	1226	32.38	313	72.0

It seems probable that light is the factor limiting the downward extent of the *Ceratophyllum* zone. A steep bottom gradient with its rapid increase in depth narrows the substratum area to which light sufficient for plant growth can penetrate. Rickett (16) found that in the two Wisconsin lakes, Mendota and Green, the lower limit of plant growth corresponds quite closely to the depth at which the

amount of light penetrating is one per cent of that striking the surface. The lower depth limit of the *Ceratophyllum* zone in Lake Okoboji is 8.5 m. or 27 ft. 9 in. approximately. Tests of the amount of light penetrating to this depth were not made.

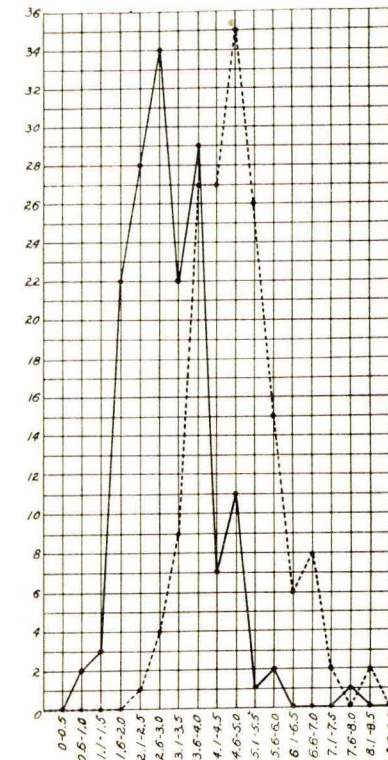
The general distributional aspects indicate that the predominance of *Ceratophyllum* in the bays in general, is due to an average gradual substratum slope, which in turn brings into operation the factors leading to favorable mud substratum and to extensive areas within the limits of efficient light penetration.

Statistical Interpretation of Survey Data

Ceratophyllum was recorded at one hundred and fifty-five of the one hundred and ninety-six survey stations. *Curves of variation* or frequency polygons have been prepared to show the variation in both the depth and distance from shore of the inner and outer margins of the *Ceratophyllum* zone.

Variation in the *depth* of the inner margin is shown by the solid line on text figure 3. The curve is bimodal with the two "popular" depths, being 2.6-3.0 m. and 3.6-4.0 m. This fluctuation of the depth measurement around two modes is due to the two main types of habitat, the bay and the main body of the lake. The substratum configuration and the surface protection found in the bays favor a wide distribution of the plants at shallower depths. On the other hand, the wave action opposite less protected shores prevents their growth in shallower waters. The first mode of 2.6-3.0 m., therefore, is in general that of the bays, and the second of 3.6-4.0 m. is that of the main lake. These latter figures indicate the tendency of the under water conditions opposite the shores exposed to severe wave action to force the plants to grow only in the deeper water.

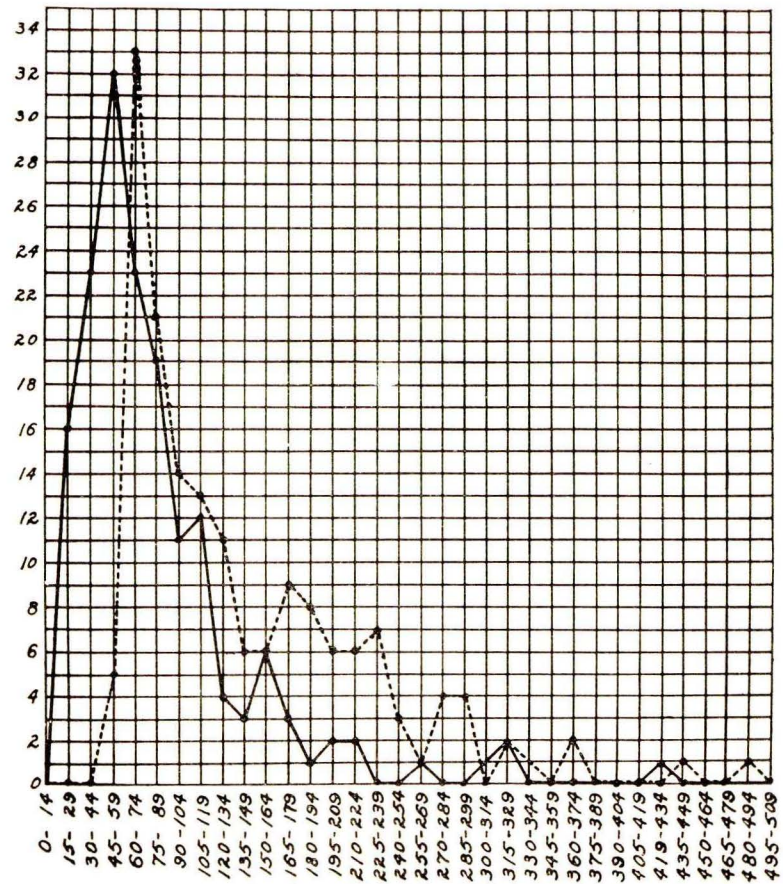
The more nearly symmetrical curve of the variation in the depth of the outer margin, the dotted line on text figure 3, shows that, in this case, the contrast between the bay and the main lake situations is not as marked as in the inner margin. Wave action can have little hindering effect upon the plants at greater depths. Hence, while invasion of the shallows by the *Ceratophyllum* zone is hindered in the main body of the lake by this factor, there is, in the same habitat, no similar prohibition placed upon the outer margin. Furthermore, deep water is found in all of the bays as well as in the main lake.



Text Figure 3. Curves of variation in depth of inner (_____) and outer (.....) margins of *Ceratophyllum* zone. Depth indicated in meters on abscissa.

Also *Ceratophyllum* grows in Emerson's, Miller's, and Smith's bays at a considerable depth. These similarities in the bays and the main body of the lake at many points tend to permit the more uniform invasion of the greater depths in both habitats. Thus, the depth of the outer margin of the *Ceratophyllum* zone is made more uniform around the entire lake than is the depth of the inner or shoreward margin.

The variation in *distance from shore* is shown by the curves on text figure 4. It will be noted that the curves are markedly askew, with the mode in each case nearer the lesser extreme. The skewness indicates that the zone at a majority of the stations is quite near shore but that at some points various factors permit an extension outward to greater distances. Over half of the stations (78 of the



Text Figure 4. Curves of variation in distance from shore of inner (——) and outer (-----) margins of *Ceratophyllum* zone.

155) have the inner margin between 30 and 74 m. out from shore. These are found mostly in the main body of the lake such as stations No. 6, 7, 8, and 9, and in the more exposed portions of the bays such as stations No. 52-56 in the bay-like north end. In the case of the outer margin, the most commonly found distances from shore were between 60 and 104 m.

At a majority of the stations the outer margin is relatively near shore as is also the inner margin. This is due in both cases to the more uniformly rapid slope of the substratum off abrupt shores.

There is the tendency, on the other hand, for the zone to expand outward at certain points. Thus the descent of the curves of variation for both margins is rather gradual so as to comprehend the scatter of the variates over all distances from quite close in to a little more than one-fourth mile out from shore.

The stations with the greater distances from shore are found in the bays. Especially is this true in the bay-like north end of the lake where, at stations 33 to 42, there is a *huge under-water shelf* causing markedly shallow depths. Here the zone, in the form of a narrow band, is found far out from shore as it parallels the outer edge of the shelf. At station 27, the inner and outer margins are 425 and 492 m. respectively, out from shore, or over one-fourth mile. Furthermore, the unfavorable sand substratum south of Pike's Point and in Hayward's Bay pushes the zone quite far out at these points. The wide lateral spread of the curves of variation is due to areas such as these.

To conclude the interpretation of the curves of variation, it may be pointed out that the skewness of those indicating distance from shore shows, in a definite manner, that there is a relatively narrow area or zone opposite a little more than half of the shore line; by the spread of the curves is shown the tendency of the zone to extend to much greater distances from shore where shallower depths permit *Ceratophyllum* growth.

The *average* or *mean depths* for the two margins are 3.14 ± 0.55 m. for the inner, and 4.88 ± 0.58 m. for the outer. The difference between them is 1.74 ± 0.03 m. This figure is significant for it shows that the zone lies "on the average" within a depth range of less than two meters. By taking half of this range of 1.74 m. and adding it to the shallower mean, a theoretical mean of the depth of the *Ceratophyllum* zone as a whole is secured. This figure is 4.01 m. and is the depth most favored by *Ceratophyllum* in West Okoboji Lake. It is slightly more than thirteen feet.

The favored distance from shore of the zone as a whole is 111 m. or slightly more than 121 yards. The inner margin has as its mean the distance of 83 ± 3.35 m. and that of the outer margin is 139.23 ± 4.5 m. The difference between these two means is 56.23 ± 0.15 m. This is the average width of the zone as a whole. The half of this average added to the smaller mean gives 111.11 m. as the average distance from shore.

The amount of the fluctuation of the zone in depth and in distance from shore is, of course, an indication of the effects of environmental factors. The factors, both in kind and degree of potency, are not the same at all stations. Variation from the average or mean is the result. This variation or deviation is discussed in the following paragraphs.

The standard deviation in depth is 1.04 ± 0.39 m. for the inner, and 1.08 ± 0.41 m. for the outer margin. In distance from shore it is 61.5 ± 2.38 m. and 83 ± 3.21 m. for the same two margins respectively.

The *coefficient of variation* provides a very satisfactory expression of the amount of these deviations. It is simply a measure of the amount of deviation in terms of per cent of the mean. The coefficients of variation in depth are 33.1 ± 1.27 per cent for the inner, and 22.1 ± 0.85 per cent for the outer margin. These figures definitely indicate more variation in the inner as compared with the outer margin. The same comparative relationship holds in distance from shore in the large coefficient of 74 ± 2.86 per cent for the inner margin, and the smaller figure of 58.8 ± 2.27 per cent for the outer.

The outlines of the inner and outer margins of the *Ceratophyllum* zone on the map (text figure 1), reveal more irregularity in the former. The coefficients of variation above given, provide a mathematical indication of the amount of this difference in the two margins. The curves of variation, previously noted, also show the same situation. *Thus all the methods and formulae applied to the problem agree on the greater variability of the inner as compared with the outer margin in both depth and distance from shore.*

Fluctuation in the potency of certain environmental factors is the cause of this larger variability in the inner margin. Of these factors *wave action* is probably the most active. It has a tendency to disturb the growth of plants in shallow water, but fails to do so in greater depths. This disturbance is largely mechanical. Shifting of the substratum makes permanent anchorage difficult and the currents set up by action of the waves actually subject the plants and substrata to mechanical abuse.

Analysis of the variation in the inner and outer margins of the *Ceratophyllum* zone is concluded with the simple observation that there is less variation from the mean in the case of the outer margin as compared with the inner, due to the greater uniformity of con-

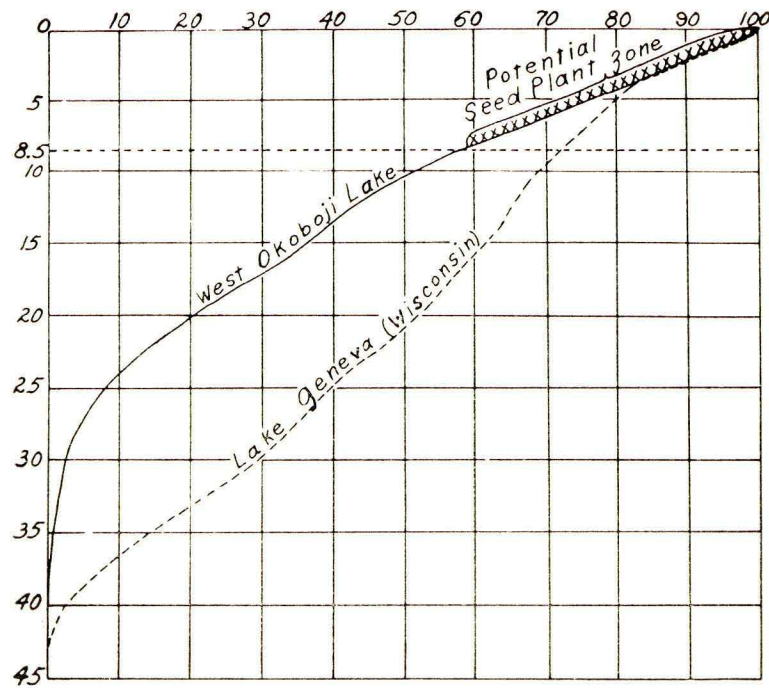
ditions at greater depths. The purpose of this section has not been to minutely analyze all these environmental factors, but rather to indicate what the actual variation is, determined mathematically.

The configuration of a lake basin effects plant distribution. The shape of the basin of Lake Okoboji is favorable to a large area of *Ceratophyllum* and other macrophytes in spite of the fact that it is a deep lake. The survey indicated that depths between one and one-half to two meters and about eight and one-half meters are most favorable to *Ceratophyllum*. It is fortunate that the morphometry of the basin of West Okoboji Lake is such as to provide unusually large areas of substratum within this range. The whole basin is not available for plant growth because of lack of light and oxygen (Stromsten, 20) in the greater depths.

Birge and Juday (2) state that in most lakes there is a "steep slope of the sides to below the level to which the work of the waves extends," and then a gradual slope to a nearly flat bottom, thus producing a saucer-shaped basin. Comparison of the basin of West Okoboji with that of a lake which more nearly approaches this normal condition tends to emphasize the favorability of the Okoboji basin to large plant areas. Lake Geneva in Wisconsin is an example of such a normal basin, and the comparison is made in text figure 5, which is adapted from Birge and Juday (2). It will be noted that, on the average, the slope of the sides of West Okoboji Lake is quite gradual and uniform to a depth of about 14 m., whereas, that of Lake Geneva becomes markedly steeper at the 5 m. level. There is thus provided in West Okoboji an unusually large area between the shoreward margin and the lowermost, and hence, outermost, level at which the aquatic seed plants grow.

The maximum depth noted for the growth of *Ceratophyllum* was 8.5 m. This depth was recorded at two stations, No. 59 off Pike's Point, and No. 168 in Brown's Bay. By taking this depth as a basis for comparison of the two lake basins, West Okoboji is found to have a bottom area between the depths of 0 and 8.5 m. which is equal to 41 per cent of the total surface area, whereas, Lake Geneva has only 28 per cent. Thus Lake Okoboji, because of its unusual basin, has an area of favorable depth for the growth of *Ceratophyllum* which is 13 per cent greater than that of Lake Geneva with its basin typical of the average lake.

Ceratophyllum is not very efficient however, in establishing itself



Text Figure 5. Comparison of morphometry of unusual basin of West Okoboji Lake with that of the usual saucer-shaped basin of Geneva Lake, Wisconsin. Curves show area of lake basin at any depth as a percentage of area of surface. The Potential Seed Plant zone in West Okoboji Lake is equal to 41 per cent (59-100) of surface area, whereas it is but 28 per cent (72-100) at same depth in Lake Geneva. Depth in meters on ordinate; percentage of surface area on abscissa. Adapted from Birge and Juday (2).

in all of the area which is in the depth range of 0.5 m. to 8.5 m. This area is actually 583 hectares (1439 acres) according to the percentile hypsographic curves prepared by Birge and Juday (2). It is termed the *Potential Seed Plant Zone* (text figure 5), since it is the portion of the substratum which is in depth suitable to the macrophytes. The total area covered by *Ceratophyllum* is 434 acres. It is, therefore, only 30.1 per cent efficient in occupying the area potentially open to it. Competition with other plants, *Chara* chiefly, and unfavorableness of slope and texture of substratum as previously referred to, are the factors contributing to this rather low efficiency.

If there were absolute uniformity in the slope of the substratum around the entire lake, there would be perfect correlation between

depth and distance from shore. There is, however, no such uniformity, and, as a result, some method of showing the actual degree of correlation is necessary. The *coefficient of correlation*⁴ provides such a measure. For the inner margin it is 0.36 ± 0.47 , and for the outer margin it is 0.07 ± 0.054 . These figures mean that the greater depths at which *Ceratophyllum* will grow fluctuate more than do the lesser depths in their distance from shore.

It has been stated previously (page 36) in connection with depth and distance from shore that, when each of these is considered separately, there is more variation in the inner as compared with the outer margin. The higher coefficient of correlation of the inner margin is indicative of the fact that, while its depth and shore distance do fluctuate more, they vary together more consistently than in the case of the outer margin. The contour of the substratum may be used to explain this situation, with the minimum and maximum depths of the *Ceratophyllum* zone, 0.5 m. and 8.5 m. respectively, serving as examples. A depth of 8.5 m. may be found quite near the shore line in the case of an abrupt shore, or it may be far out as in the case of the under-water shelf found in the north end of the lake (see page 35). On the other hand, the depth of 0.5 m. is found more uniformly at a given distance from the water's edge, irrespective of whether opposite abrupt or gradual shores. This greater uniformity at shallower depths is, of course, due to the tendency of the waves to level the substratum with which they actually come in contact. Thus, while the inner margin does have more variation than the outer in each of the attributes, depth and distance from shore, they fluctuate together and thus have more correlation between them.

⁴The value of the coefficient of correlation may vary from 0 to 1. 0 indicates no correlation, and 1 indicates perfect correlation.

TABLE IV—SUMMARY OF STATISTICAL ANALYSIS OF SURVEY DATA OF CERATOPHYLLUM ZONE.

All figures are in meters except coefficients of variation and of correlation.

Statistical Terms	Inner Margin		Outer Margin	
	Depth	Dist. from shore	Depth	Dist. from shore
Total Range of Variation	7 (1 to 8)	410 (15 to 425)	6 (2.5 to 8.5)	445 (47 to 492)
Range of Variation for Each Class	0.5	15	0.5	15
Mode	Class of 2.6 to 3	Class of 45 to 59	Class of 4.6 to 5	Class of 60 to 74
Mean*	3.14±	83±3.35	4.88±	139.23±
Average Deviation	0.82	41.9	0.8	64.9
Standard Deviation	1.04±	61.5±	1.08±	
Coefficient of Variation	0.039	2.38	0.041	83±3.21
	33.1±	74±2.86%	22.1±	58.8±
	1.27%		0.85%	2.27%
Coefficient of Correlation	0.36±0.047		0.07±0.054	

*Mean depth of zone considered as a whole is 4.01 m.
 Mean distance from shore 111.11 mm.
 Average width is 56.23 m.
 Average depth range is 1.74 m.

Before passing to the next section, it should be observed that a study such as this biometrical interpretation of the Ceratophyllum distribution in West Okoboji Lake cannot yield its full value until similar studies of other lakes have been made. Comparison is necessary for the fullest interpretation of the values of the curves of variation, standard deviation, coefficient of variation, etc.

The Value of Ceratophyllum as a Physical and Biotic Factor

The abundant growth of the plant and its dominance at depths of two and one-half to five meters where there is mud substratum, undoubtedly make it an important factor in the biology of West Okoboji Lake.

The value of Ceratophyllum as an oxygenating agent is marked, according to Evermann and Clark (4). The vegetative activity of the plant continues throughout the entire year, although in diminished amount during the winter. The release of oxygen into the water

while the lake is closed by ice is especially helpful. During the summer months the activities of phytoplankton in most of the lakes of the Okoboji region undoubtedly add greatly to their oxygen supply, but due to relatively small plankton growth in West Okoboji, its waters receive less from this source. The services of Ceratophyllum as an oxygenator are thus enhanced.

The question of main interest is that of the immediate as well as secondary relations of this plant to the fish. It has been noted that the favorite fishing grounds of the lake are near the edges of the extensive Ceratophyllum beds at Pocahontas Point, near Elm Crest, and in the north end. This would indicate that the beds are good feeding grounds for the fish and it is probable that they are also used for shelter. The plants harbor many small animal forms such as Hyallela. Their chief food value is indirect, for, as a direct source of food, they are known to be eaten only by the carp and the bluegill.

Ceratophyllum rates high in fish culture according to two of the scientists formerly located at the United States Fisheries Biological Station, Fairport, Iowa. R. L. Barney⁵, formerly Director of the Fairport Station, stated to the writer in a letter of January 2, 1923, "I am satisfied that, from the genuinely practical outlook, the plant has no equal." H. Walton Clark⁶, then Scientific Assistant at the same Station, wrote in letters of December 7, and 22, 1922, "I have always been especially enthusiastic about Ceratophyllum as I believe it one of the best pond and lake plants we have. I like it because it supplies food (via Hyallela, etc.), oxygen and shelter, and makes illicit seining difficult. Ceratophyllum would be my first choice in stocking ponds for fish."

The writer is greatly indebted to Dr. R. B. Wylie, Head of the Department of Botany of the State University of Iowa, and former Director of the Iowa Lakeside Laboratory, for the suggestion of the problem which has been herein discussed, and for his consistent inspiration and instruction in its pursuit. The coöperation of Miss Lucille Sawyer in making the survey of West Okoboji Lake is also highly appreciated.

SUMMARY AND CONCLUSIONS

1. There is no adequate justification for the thirty-five species of Ceratophyllum which have been proposed to date. It is suggested

⁵Quoted with permission.

⁶Quoted with permission.

that two species only be recognized,—*C. demersum* to include all forms having fruits with spines of any type, and *C. submersum* all forms with spineless fruits.

Part I. Morphology

2. Long association with water has modified stem structure in several ways, viz., non-cutinization of epidermis, lack of mechanical cells in either xylem or phloem, metamorphosis of sieve-tubes occasionally into air spaces, and transformation of some of vessels of xylem into parenchyma cells.

3. The first leaf primordia appears at 150-175 microns from the apex of the axis.

4. The first step in leaf development is related to a periclinal division of a periblem cell. The outer of the two cells thus formed divides anticlinally to form two cells which by periclinal, anticlinal, and oblique divisions proliferate into the periblem, and, finally, into the cortex of the leaf.

5. The plerome originates by the division of a cell which has become surrounded by the periblem on all sides except toward the center of the axis. By continued anticlinal divisions the plerome is formed along the central axis of the developing leaf.

6. The air space development is schizogenous in method.

7. About one-third of the volume of the mature organ is occupied by air spaces in submerged leaves. Those which are subterranean on the "holdfast" branches have less extensive air space development.

8. There are three main vegetative expressions of *Ceratophyllum* in the Okoboji region—the *lake*, *intermediate*, and *pond* types.

9. The form of the plant may be modified readily by transplanting. New branches which appeared on lake plants transplanted to Gull Point Pond developed the slender, fragile habit of the pond type in 61 per cent of the transplanted specimens.

10. The volume of the air space system in both leaf and stem is responsive to environmental conditions. The same factors which cause slender growth also bring about the development of large air spaces.

Part II. Flowers and Pollination

11. The pistillate flowers are borne most commonly on nodes twenty to twenty-six, and the staminate flowers on nodes twenty-two to

twenty-nine. This relatively lower position of the pollen producing flowers probably has a slight tendency to promote cross-pollination.

12. The stamens may dehisce while *still attached* to the receptacle as well as after separation from it. The latter method has been recorded previously by other observers as the *only* mode of stamen dehiscence.

13. Stamens become detached more commonly during daylight hours than at night.

14. The theory is suggested that the immediate mechanical cause of stamen separation from the receptacle is the pressure of gas, presumably oxygen.

15. The total elapse of time between the shedding of the first and last stamens of a flower averages about seven days.

16. The total number of pollen grains produced per plant averages over 100,000.

17. The rate of sinking of *Ceratophyllum* pollen grains in the water is 0.16 to 0.2 mm. per second.

18. The mechanism of pollination is seemingly very inefficient. The success of the process depends almost entirely upon abundant pollen production.

19. The sterility of *Ceratophyllum* in West Okoboji Lake is due to the failure of the water to reach daily, during the flowering season, the critical temperature of 26.5°C. (80°F.), found by Guppy (6) to be necessary for fruit development.

20. Beached and partially dried fragments of the plant are found to be 95 per cent efficient in regeneration and the beginning of development of new plants.

21. Vegetative propagation by fragmentation is common.

22. *Ceratophyllum* in greenhouse aquaria in latitude 40°N., undergoes a period of winter dormancy which continues approximately from October 15 to May 1. The plants can be rejuvenated in mid-winter and caused to vegetate luxuriantly by means of artificial light and temperature supplied by immersed electric bulbs.

Part III. Biology

23. The total area of *Ceratophyllum* in West Okoboji Lake was 434 acres at the time of the survey in 1922 and 1923.

24. During the survey, nineteen species of macrophytes were found—eighteen Angiosperms and one aquatic moss.

25. There is direct correlation between the gradient of substratum slope and the width of the *Ceratophyllum* zone. The zone is narrow on abruptly sloping substratum and proportionately broader, on the average, on more gradual slopes.

26. The bays contain 72.14 per cent of the total area of *Ceratophyllum* whereas their actual area is but 32.4 per cent of that of the entire lake. This favorability in the bays is due to the predominance of mud substratum with gradual slope.

27. Miller's Bay is the best habitat for *Ceratophyllum* in all of the lake.

28. The *Ceratophyllum* zone lies, on the average, within a depth range of 1.74 m. (5 ft. 5 in.). The depth most favored by the plant is 4.1 m. (13 ft. 4 in.). The maximum depth is 8.5 m. (27 ft. 9 in.), occurring at Stations 59 and 168.

29. The width of the zone, on the average, is 56.23 m. (61.8 yds.). The distance from shore most favored by *Ceratophyllum* is 111.11 m. (121 yds.). The maximum distance from shore of the outer margin is 492 m. (538 yds.) at Station 37.

30. The depth of the *Ceratophyllum* zone averages approximately one meter more in the main lake than in the bays.

31. The inner or shoreward margin of the zone is more variable than the outer margin in both depth and distance from shore. This is due to the greater uniformity and decrease in potency of negative environmental conditions, such as wave action, at the greatest depths.

32. The shape of the basin of West Okoboji Lake—somewhat as a cone with sides curved inward—is especially favorable to a large area of seed plants. It has, for example, 13 per cent more substratum area within depths suitable to macrophytes than does Lake Geneva, Wisconsin, which has the saucer shaped basin typical of the average lake.

33. For mode, mean, average and standard deviation, coefficient of variation, coefficient of correlation, and general summary of biometrical interpretation of survey data of *Ceratophyllum* distribution see Table IV, page 40.

34. *Ceratophyllum* has its chief value as a biotic factor in the lake in its oxygenation of the water and as a shelter and indirect source of food for the fish.

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PLATES

Plate I

- Fig. 1. *Ceratophyllum demersum* L. as seen in water from above. x $\frac{1}{3}$.
- Fig. 2. Fruits of the three species of *Ceratophyllum* found in North America. x $\frac{1}{2}$. a—*C. submersum*; b—*C. echinatum*; c—*C. demersum*. a and b photographed through courtesy of N.Y. Botanical Garden.
- Fig. 3. Staminate flower showing method of dehiscence. x 11. A—anther with pollen grains escaping; a—anthers not yet dehisced; S—stem; L—leaves; B—bracts of involucre.
- Fig. 4. Style of pistillate flower showing nature and position of stigmatic pocket. x 30. s p—stigmatic pocket; o—ovary.
- Fig. 5. Photomicrograph of style showing stage just preliminary to pollination. x 31. Note pollen grain, pg., caught in debris on style. At s p just below pollen grain, is silhouette of the cavity in which the stigmatic pocket is located. The pollen grain will likely fall into it if dislodged.

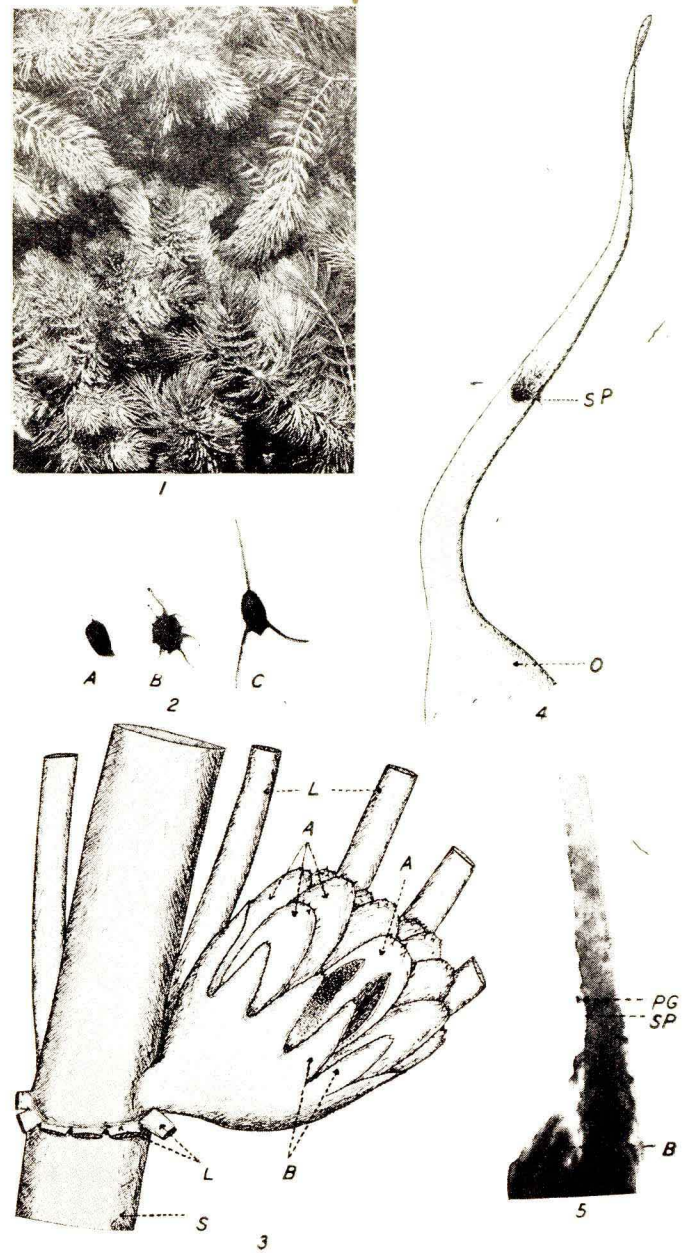


Plate II

Leaf Development and Anatomy

Fig. 6. Median longitudinal section of tip of vegetative axis showing general structure of meristematic region. x 225. P₁ and P₂—leaf primordia in first stages of development. In all figures on this plate, d—dermatogen; pb—periblem; and pl—plerome. Light stippling indicates dermatogen; medium — periblem; and heavy — plerome.

Fig. 7. Transverse section of meristem near apex at a node showing method of origin of leaf primordia. Dermatogen of leaf is continuous with dermatogen of axis. Periblem of leaf arises from a cell in outer layer of periblem of axis. Plerome of leaf arises from outer cell of a strand of plerome cells radiating from stem plerome to leaf primordium. This shown at P₁, P₂, P₃, and P₄, all of which are leaf primordia.

Fig. 8. Photomicrograph of portion of median longitudinal section of meristem showing leaf primordium with cell of dermatogen in mitosis, illustrating how dermatogen increases in size. Section through second primordium below apex. x 433.

Fig. 9. Median longitudinal section through second primordium below apex showing position and nature of periblem. x 433.

Fig. 10. Cross section of leaf primordium showing concentric arrangement of dermatogen, periblem, and plerome. Plerome cell here shown is same in position as that shown in division in Fig. 11. x 303.

Fig. 11. Median longitudinal section of leaf primordium showing plerome initial in mitosis. This cell is same as that marked pl, in Fig. 7 and Fig. 12. x 303.

Fig. 12. Two further steps in plerome development showing increase in length of plerome strand at primordium A and increase in diameter at primordium B.

Note. In leaf development the meristematic layer referred to as the dermatogen gives rise to the epidermis; the periblem to the mesophyll or cortex-like portion; and the plerome to the vascular strand.

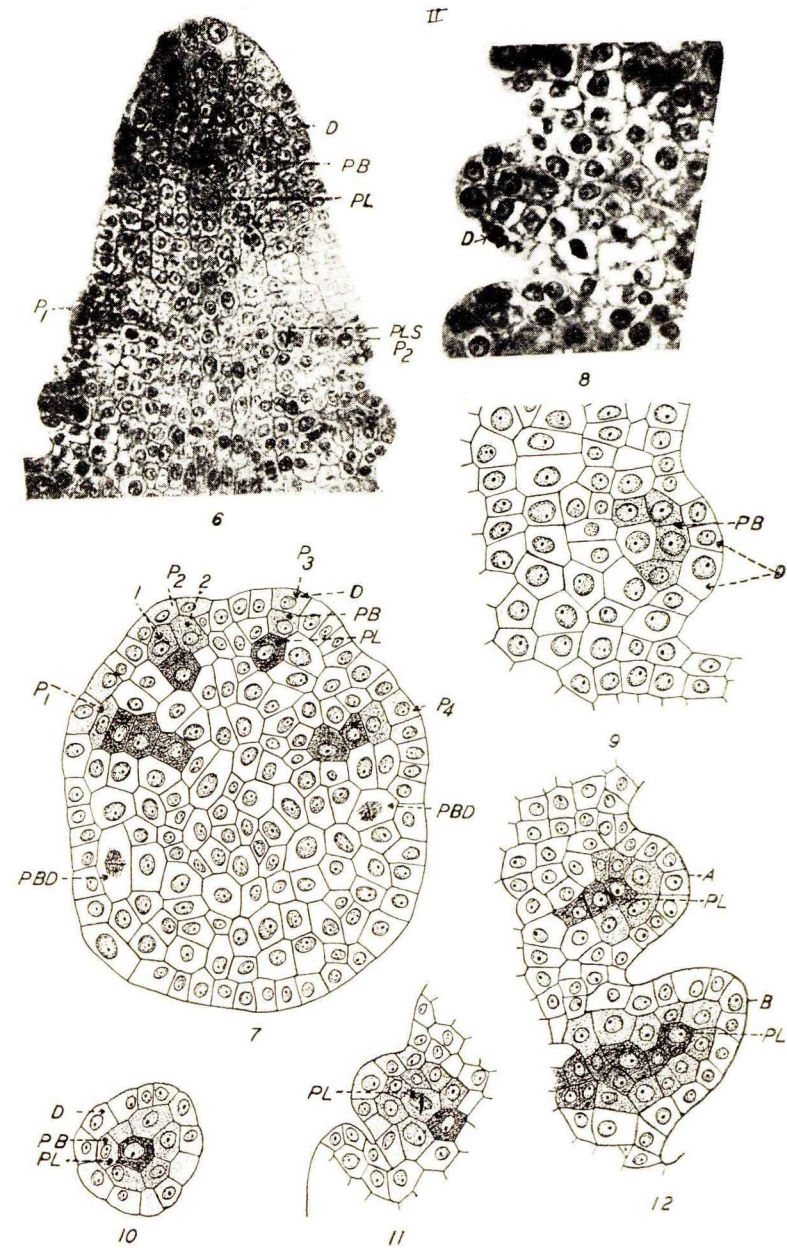


Plate III

In Figures 13-20, e—epidermis; c—cortex; a s—air space; v—vascular strand

- Fig. 13. Longitudinal section of leaf near apex showing schizogenous origin of air spaces in mesophyll. x 308.
- Fig. 14. Longitudinal section of portion of leaf showing method of enlargement of air spaces by division of cells bordering the cavity. x 308. c_1 and c_2 —cells of mesophyll in prophase and anaphase, respectively.
- Fig. 15. Median longitudinal section of nearly mature leaf showing position and relative size of air spaces. x 257.
- Figures 16-20. Series of transverse sections of leaf showing anatomy from apex to base.
- Fig. 16. Section 40 microns from apex. Vascular strand not yet differentiated. x 59.
- Fig. 17. Section 70 microns from apex. Vascular strand apparent. x 58.
- Fig. 18. Section 280 microns from apex showing central position of vascular strand. x 56.
- Fig. 19. Section 1300 microns from apex showing eccentric position of vascular strand due to development of air space. x 58.
- Fig. 20. Section 6030 microns from apex and just below junction of the two forking leaf segments. The vascular strands have just joined but the two air spaces are still separate. x 65.

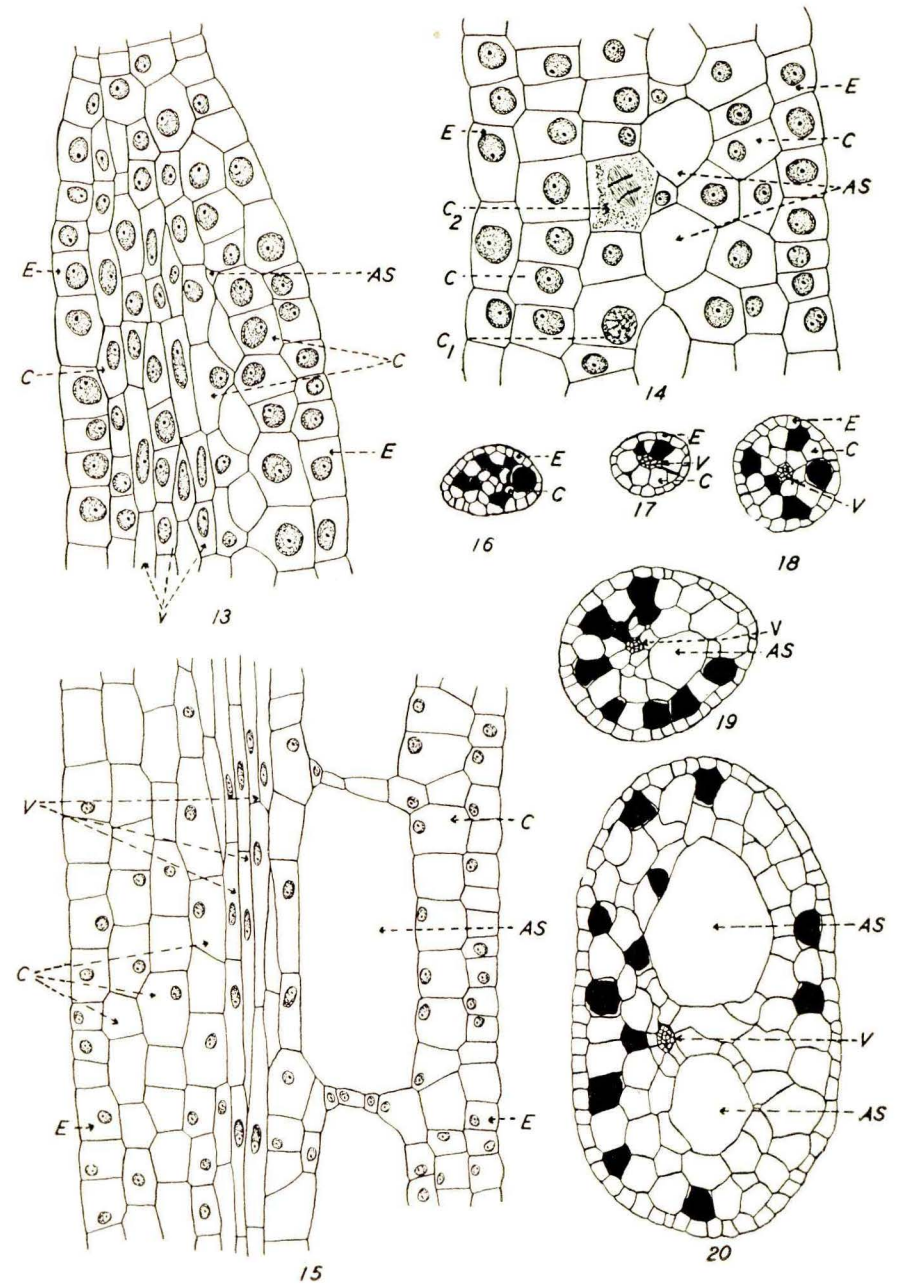
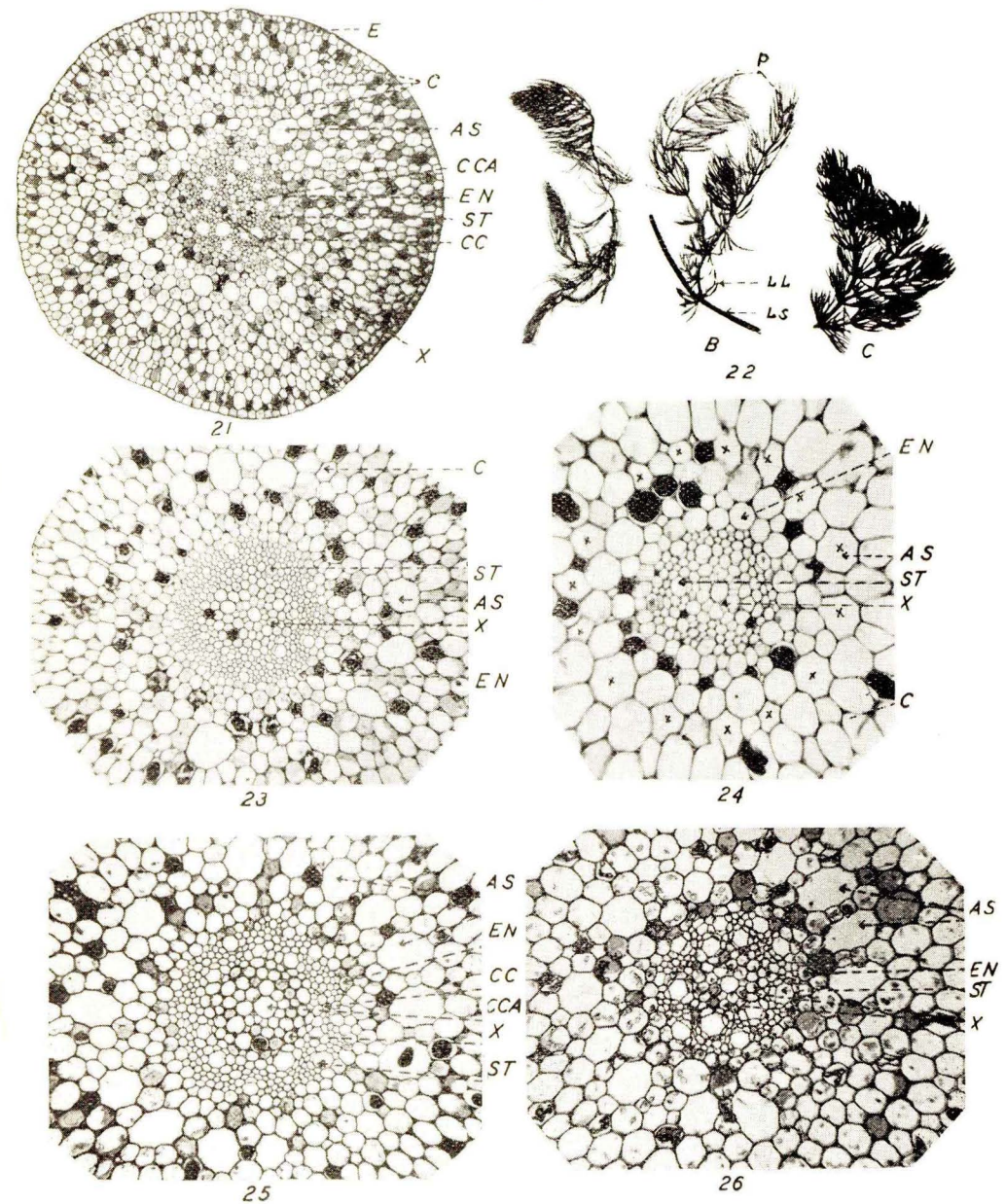


Plate IV

Modification of Form and Structure by Environment

- Fig. 21. Transverse section of mature stem. Arrangement of xylem and phloem is concentric. Phloem is to outside and is composed of cells which resemble a lacework. Xylem is made up of scarcely differentiated cells in center. x 30.
- Fig. 22. Modification of form of plant by transplanting from West Okoboji Lake to Gull Point Pond. Time of exposure to changed environment—40 days. x 2/5. a—pond control; b—transplanted specimen; c—lake control. The lower portion of b developed in the lake—note similarity to lake control; the upper portion developed in the pond—note similarity to pond control. P—pond growth; L L—lake growth leaf; L S—lake growth stem.
- Figures 23-26. A series of photomicrographs designed to show the modification of internal structure, especially the aerenchyma, by conditions of the environment. All are stem cross sections. In all figures: e—epidermis; c—cortex; a s—air space. Dark content in some of cortical and xylem cells is tannin. Small objects in some cells are starch grains.
- Fig. 23. Lake plant stem. Water clear, relatively cool, and not stagnant. Air spaces mediumly developed. x 39.
- Fig. 24. Subterranean stem from "holdfast." Exposure to mud. Air spaces very poorly developed, indicated by x's. x 104.
- Fig. 25. Intermediate type of stem from Little Spirit Lake. Water moderately clear, warm, and slightly stagnant. Air spaces well developed. x 69.
- Fig. 26. Pond type from Gull Point Pond. Water turbid, very warm, and stagnant. Air spaces well developed. x 68.



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